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Improving the Use of Migration Counts for Wildlife Population Monitoring

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Graduate Program in Biology
A thesis submitted in partial fulfillment of the requirements for the degree in Doctor of Philosophy
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MONITORING

(Thesis Format: Integrated Article)

by

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Abstract

Counts of migrating animals are used to monitor populations, particularly for species that are not well sampled by breeding and wintering surveys. The use of migration counts for population monitoring relies on the assumptions that new individuals are detected each day, and that probability of detecting those individuals remains constant over time. The impact of violating these assumptions on our ability to estimate reliable population trends is not well understood. Further, on a broad spatial scale, our ability to combine data across sites to estimate regional or national trends has been limited by the possibility that trends vary regionally in an unknown way. Using simulated migration count data with known trend, I tested whether sampling effort (daily vs. non-daily sampling) and a temporal change in stopover duration (and thus detection probability) influenced our ability to estimate the known trend. I also tested whether analyzing data as hourly, daily or annual counts, or accounting for random error using analytical techniques, could improve accuracy and precision of estimated trends by reducing or better modeling variation in counts, respectively. Further, using model selection analytical techniques, I tested whether we could detect when trends vary regionally using current or increased number of sampling sites in a region. My findings show that trends can be improved for species with highly variable daily counts by sampling less frequently than daily or by aggregating hourly counts to annual totals. Commonly and rarely detected species were better analyzed as daily counts, collected daily throughout the migration. A linear increase in stopover duration over time biased trends and lead to a high probability of detecting an incorrect trend, which is only improved by both reducing sampling effort and including a covariate for stopover duration in regression analyses. Regional variation in trends can be detected, and increasing the length of the time series was more efficient for improving accuracy and precision of regional trends than increasing the number of sites sampled. Continued advancement of our knowledge of breeding origins and stopover duration of migrants are priorities for the further refinement of trends estimated using migration counts.

Keywords

Co-Authorship Statement

Chapters 2-4 are not yet published, but were co-authored with Philip D. Taylor and Denis Lepage. Dr. Taylor and Dr. Lepage contributed to the design of the simulation experiment and provided editorial comments to the draft manuscripts. Chapter 3 has been submitted for consideration for publication at The Condor: Ornithological Applications.

A modified, peer-reviewed version of Chapter 5, 'Crewe, T.L., P.D. Taylor, and D. Lepage. 2015. Modeling systematic change in stopover duration does not improve bias in trends estimated from migration counts' has been accepted for publication in PLoS One, and is co-authored with Philip D. Taylor and Denis Lepage. Dr. Taylor and Dr. Lepage provided guidance on the design of the simulation experiment and provided editorial comments on a draft of the manuscript.

A version of Chapter 6 has been submitted for consideration for publication by the Journal of Wildlife Management. This paper is co-authored with Philip D. Taylor, Denis Lepage, Adam Smith and Charles M. Francis, and was submitted as a technical report to Environment Canada – Canadian Wildlife Service as a contribution to their Avian Monitoring Review. All co-authors contributed to the design of the experiment and to the choice of analytical methods used. Dr. Taylor, Dr. Lepage and Dr. Smith also contributed editorial comments on a draft manuscript.

Chapter 7 is a pre-copy-editing, author-produced version of an article accepted for publication in the Annals of the Entomological Society of North America following peer review. The definitive publisher-authenticated version, 'Crewe, T.L., and J.D. McCracken. 2015. Long-term trends in the number of monarch butterflies (Lepidoptera:Nymphalidae) counted on fall migration at Long Point, Ontario, Canada (1995-2014), in press doi: 10.1093/aesa/sav041' will be made available online by the journal as part of an invited series on long-term trends in monarch butterfly populations, which is due out late 2015. This paper is co-authored by Jon D. McCracken, who contributed to the development of the monarch sampling protocol used at Long Point, and provided editorial comments on a draft manuscript.

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There is nothing like a child to motivate a person to be and do better. My little B came into this world half-way through this endeavor and since then has been an endless source of joy and wonder. She has motivated me to be a stronger person, and, perhaps most importantly at this point, to get this PhD done, get it done now, and get it done right. While this began before she was a thought, I dedicate its completion to the sweet little soul who grew mine (at least) five times larger.

I'm not sure where to begin with thanking my family. Growing up, I never had any doubt that I could do or be anything I put my mind to. There was never any doubt that I would attend University - an assumption that was not violated. Their confidence in me and in my independence has been priceless, and has played a large role in getting me to where I am today. Since having Brooke, my mom and stepdad have also provided an un-measurable amount of emotional and child-care support. Without them, this surely would have taken a much longer time to complete. I will forever be in their debt.

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List of Abbreviations

AIC - Akaike's Information Criterion

AR1 - 1st order auto-regressive

B - rate of population change (log-linear)

B - Bayes factor

BBS - Breeding Bird Survey

CI - credible intervals (Bayesian)

CL - confidence limits (frequentist)

CMMN - Canadian Migration Monitoring Network

CV- coefficient of variation

DIC - Deviance Information Criterion

ENSO - El Nino Southern Oscillation

EV - east vector (wind speed/direction)

GAM - Generalized Additive Model

GAMM - Generalized Additive Mixed Model

GLM - Generalized Linear Model

GLMM - Generalized Linear Mixed Model

HMANA - Hawk Migration Association of North America

INLA - Integrated Nested Laplace Approximation

IUCN - International Union for Conservation of Nature

LnPois - log-Normal Poisson

LPBO - Long Point Bird Observatory

MCMC - Markov chain Monte Carlo

n - count population size

NB - negative binomial

OD - over-dispersed

OMNRF - Ontario Ministry of Natural Resources and Forestry

p - detection probability

P - p-value

phi - survival probability

Pois - Poisson

Q-Q - quantile-quantile (plots or scores)

Rho - autocorrelation coefficient

RPI - Raptor Population Index

SE - standard error

SHARCNET - Shared Hierarchical Research Computing Network

SV - south vector (wind speed/direction)

ZINB - zero-inflated negative binomial

Chapter 1 - Introduction

1 General Introduction

1.1 Monitoring wildlife populations

Wildlife population monitoring provides a foundation to assess population status and the success of management efforts by quantifying temporal and spatial variation in species richness (Studeny et al. 2013), abundance (Bildstein et al. 2008, Crewe et al. 2008, Kéry et al. 2010) and demographics (Pleasants and Oberhauser 2013), and how patterns of change relate to environmental processes including landscape and climate change (Parmesan 2007, Paprocki et al. 2014). Sampling protocols, including the location and spatial extent of sampling, are often chosen to balance data quantity and quality with logistical constraints, including site accessibility, detectability of the target organism(s), availability of observers to collect data, and financial constraints. In order to collect data at the broad spatial scales required to assess range-wide population variability, citizen scientists are often engaged in the collection of monitoring data (Greenwood 2007). Engaging citizens in science has many advantages beyond expanding the geographic scope of data collection, including educating the public on our role in ecosystems, engaging the public in ecosystem planning and management efforts, and promoting public involvement in policy development (Conrad and Hilchey 2011).

Population trends of wildlife are most commonly estimated using counts collected on breeding or wintering grounds (Kéry and Royle 2010, Sauer and Link 2011, Bled et al. 2013). However, because geographic coverage of broad-scale breeding and wintering surveys is typically restricted to accessible and human populated regions (Bart et al. 1995) where volunteer engagement is more likely, these surveys may not provide a representative sample for taxa that breed in remote or inaccessible locations. Population trends for northern and boreal breeding birds, for example, are often derived from breeding bird survey (BBS) data collected in the southern portion of their breeding range, where breeding densities are often low and may not be characteristic of change occurring in the northern forests, where the bulk of the populations breed (e.g., northern

waterthrush; Bird Studies Canada et al. 2006). Further, raptors tend to be secretive breeders and are not well captured by breeding bird surveys. Counts of individuals migrating to or from their breeding grounds (hereafter 'migration counts') are used as an alternative source of data to estimate trends for these and other migrant taxa (Francis and Hussell 1998, Gibbs et al. 2006, Farmer et al. 2007, Bildstein et al. 2008, Crewe et al. 2008, Findlay et al. 2011). Trends derived from songbird migration counts have shown correspondence with breeding surveys (Francis and Hussell 1998).

Currently in North America, over 200 sites collect raptor migration counts (Hawk Migration Association of North America 2015), over 20 sites collect migration counts for nocturnally migrating songbirds (Canadian Migration Monitoring Network, CMMN; Crewe et al. 2008) and at least four sites collect counts of migrating monarch butterflies each year. The majority of CMMN sites are located in populated regions along the southern border of Canada. The placement of count sites south, or in the southern portion, of a species' breeding range allows a single site to capture individuals from a broad geographic range (Dunn et al. 2006). The entire breeding range can therefore be sampled with relatively few sites (Dunn et al. 2006), providing financial and logistical benefits over conducting labour- and financially-intensive surveys in unpopulated, roadless regions. Raptor and monarch butterfly count sites are also typically located in human populated regions and along known migration corridors, where the ability to recruit and maintain volunteers and the probability of detecting migrants are maximized.

Migration counts are typically collected as hourly (e.g., raptors; Bildstein et al. 2008) or daily (e.g., songbirds: Crewe et al. 2008; monarch butterflies: Gibbs et al. 2006; shorebirds: Drever et al. 2014; whales: Findlay et al. 2011) counts of the number of individuals detected actively migrating past a count site (Bildstein et al. 2008, Findlay et al. 2011) or as of the number of individuals captured or detected at a count site while on migratory stopover (Gibbs et al. 2006, Crewe et al. 2008, Robinson 2012). The number of individuals detected on each sampling occasion is assumed independent and proportional to the size of the hourly or daily migratory population, and the sum of individuals observed over an entire migration is assumed representative of the size of the monitored population each year (Dunn 2005). In other words, migration counts provide

an index of population abundance, where any fluctuation or trend in annual indices over time is assumed to be proportional and representative of any fluctuation or trend in the size of the monitored population. The effect that violation of the assumptions of independence and proportionality could have on precision and accuracy of population trends derived from migration count data is not well understood.

Further, the breeding origin of migrants detected at each count site is not known or known only broadly. Analysis of stable hydrogen isotopes in feathers of several songbird species detected across the CMMN network suggests that breeding origin can vary among sites and among species at a site (Dunn et al. 2006). Therefore, factors that influence breeding success, overwinter survival, and detection of monitored populations can also vary regionally among sub-populations, which could result in region-specific rates of population trend. Because specific breeding origin and the potential for variation in trends among sub-populations and sites is unknown, migration count data have not been combined across sites to estimate regional or national rates of population trend, which limits their use for broad-scale population monitoring. The ability to model regional variation in trends has not been tested, and would provide a first assessment of the use of migration counts to estimate regional and national trends.

1.2 Factors influencing the relationship between counts and population size

Only in rare circumstances and at small spatial scales can true abundance of animals, N, be quantified. Rather, monitoring programs derive estimates of N from counts, C, of the number of target organisms detected, where probability of detection = p (Nichols et al. 2009). For migration counts, then, the sum of counts across n days in a migration provides an index of annual abundance that relies on the assumption that the relationship between C and N does not change over time, i.e., $\sum_{i=1}^{i=n} C = N \times p$. Because counts are conditional on detection, long-term trends in population counts are proportional to trends in population size only if probability of detection remains consistent over time (assumption of proportionality).

In most circumstances, however, the relationship between counts and population size is not well understood, nor is the potential for variation in probability of detection to introduce bias and error to the relationship (Dickinson et al. 2010). Probability of detection can be broken down into several components, including the probability that individuals are present at the count site during sampling (p_p); given presence, the probability that individuals are 'available' to be detected during sampling (p_a), i.e. vocalizing or otherwise visible to the observer; and given presence and availability, the probability that an individual will be detected by an observer (p_d), where $p = p_p \times p_a \times p_d$ (Nichols et al. 2009). Neglecting to account for sources of temporal change in any component of detection probability during analysis can lead to poor inference from results (Hochachka and Fiedler 2008, Kéry et al. 2009, Nichols et al. 2009).

Migration counts tend to be highly variable among days and years. The probability that individuals will migrate past a count site can vary annually with individual variation in migration route (Vardanis et al. 2011). Further, weather fronts can result in large migratory movements, when a higher than average proportion of the migratory population is detected at a site (Allen et al. 1996). For species counted on stopover, the probability of stopping and duration of stopover can also vary among days and years with weather (Meitner et al. 2004, Schaub et al. 2004, Calvert et al. 2009), physiological condition (Schaub et al. 2008) or with habitat structure and quality. Migratory stopovers regularly extend greater than 24 hours (Schaub et al. 2001), violating the assumption of independence. Because stopovers typically occur at a much larger scale than the count area (Buler et al. 2007, Taylor et al. 2011), probability of presence and thus counts will also vary as a result of temporary emigration from the count site.

Given presence at a site, frequency of bird vocalization (availability) and detection of migrants by an observer will vary with weather conditions, distance and orientation from the observer, as well as with habitat structure (Schieck 1997, Lengagne and Slater 2002). Variation in observer experience, age, hearing ability or sight can also increase variability in counts (Link and Sauer 2002, Dickinson et al. 2010). Further, a reliance on citizen scientists for data collection has the potential for inconsistent use of sampling protocols, inconsistent or sporadic sampling effort and high rates of volunteer turnover (Dickinson

et al. 2010), all of which can increase variability in probability of detection, and therefore in the relationship between counts and population size.

Variability in migration counts will result in less precise trends and lower statistical power, but it is often assumed that variation in probability of detection alone will not bias trends if detection probability varies randomly and not systematically over time (Farmer et al. 2007). However, systematic variation in detection probability can be introduced in many ways. Climate or landscape change and its influence on breeding distribution (Parmesan 2007, Paprocki et al. 2014), for example, can result in a directional change in the proportion of the migratory population that migrates past a site, which at the scale of a single site, could be misinterpreted as a change in population size. Long-term trends in daily survival probability, trapability and stop-over duration of migrating songbirds and shorebirds have also been reported (Ydenberg et al. 2004, Hochachka and Fiedler 2008, Calvert et al. 2009), which if left unaccounted for can bias trends (Hochachka and Fiedler 2008). Because recaptures cannot be excluded from counts of unmarked migrants, a change in stopover duration can result in a corresponding change in the proportion of the migratory population detected by counts, as well as in the proportion recounted on one or more subsequent sampling occasions. The effect of a systematic change in stopover duration on the precision and accuracy of trends in counts of unmarked migrants has not been explored.

1.3   Methods to reduce or model variability in counts

Many of the sources of variability in counts that are commonly attributed to the collection of data by citizen scientists, including variable effort and skill, can be minimized with appropriate sampling design, and by standardizing sampling protocols and observer training (Dickinson et al. 2010). For taxa counted on migratory stopover, sampling migrants at exposed coastal sites with poor stopover habitat quality can minimize violation of the assumption of independence by lowering the probability that individuals will remain on site for more than 24 hours (Hussell and Ralph 1998, 2005). Placing count sites at exposed coastal sites with relatively stable habitat structure will also minimize the probability that habitat succession will alter stopover behaviour and bias trends. Habitat management is encouraged at sites experiencing habitat succession

(Hussell and Ralph 1998, 2005), however this is rarely achieved in practice, in part because the scale at which stopover decisions are made is unknown, will vary among sites and species, and is likely much larger than a given sampling area (Taylor et al. 2011).

Filtering data prior to analysis can also reduce variability in counts and improve the precision and accuracy of estimated trends. Data can be filtered to remove or flag for verification any inconsistent data or individuals that regularly submit unusual or unlikely observations (Dickinson et al. 2010). In order to better meet the assumptions of linear regression (normality, heteroscedascity), previous analyses of landbird migration counts also excluded rare species and dropped observation days for remaining species that were predicted to have fewer than zero birds (Francis and Hussell 1998, Farmer et al. 2007). Further, these previous analyses excluded species that were not sampled during 75 % or more of their migration (Francis and Hussell 1998, Farmer et al. 2007). Despite efforts to standardize sampling protocols, it is often the case that the entire migration is not sampled for every species detected at a site. The effect of sampling less than 75 % of the migration or less frequently than daily on accuracy and precision of trends has not been formally examined using migration counts with known rate of change.

Hourly and daily counts of unmarked migrants do not meet the assumptions of statistical models that allow the direct estimation of detection probability from the data (e.g., mark-recapture: Hochachka and Fiedler 2008; N-mixture models: Royle et al. 2004). Double observer approaches have been used to estimate and account for probability of observer detection (p_d) in trend analyses (Berthiaume et al. 2009), but in practice, a double-observer approach is unlikely to be maintained over the long term at most migration count sites that rely on volunteers for data collection. As an alternative to explicitly estimating probability of detection, relevant correlates of detection, including local weather, climate, effort and observer skill, can be collected and used as covariates in the estimation of trends using migration counts (Francis and Hussell 1998), though the effect of covariates on abundance and detection probability is confounded, and could be acting on N, p, or both.

Choice of analytical technique can also influence precision and accuracy of trends. The development of new methods to model and evaluate the use of large monitoring datasets for population monitoring has been an increasingly published topic in recent years (e.g., Sauer and Link 2011, Dennis et al. 2013), and is an important aspect for improving the utility of monitoring data (Dickinson et al. 2010). Previous analyses of songbird, raptor and monarch butterfly migration counts in North America have used linear regression to estimate annual indices, and either linear regression or re-parameterized polynomial regression to estimate trends (Francis and Hussell 1998, Farmer et al. 2007, Davis 2012). Generalized linear or additive models are now standard in the analysis of count data because some of the assumptions of linear models (normality, heterogeneity) are relaxed (O'Hara and Kotze 2010). Hierarchical models can extend generalized linear or additive models by allowing variation in annual counts, for example, to be partitioned between trend and random error, which can improve precision and inference drawn from monitoring data (Kéry 2010). A recent comparison of hierarchical models with generalized linear and additive models using simulated BBS data with known trend showed that hierarchical models resulted in more accurate and precise estimates of trend (Amano et al. 2012). Further, temporal auto-correlation of counts among days and years can be accommodated using hierarchical models, which should result in more conservative (and realistic) estimates of precision (Ross et al. 2012). For species that vary widely in abundance among days and years, aggregating hourly counts to annual totals has also been shown to improve precision of trend (Miller et al. 2002). A comparison of various modeling techniques in terms of their ability to recover accurate and precise trends has not been completed.

1.4 Goals and objectives

The overall goal of my thesis was to assess the use of migration counts for broad-scale population monitoring. I used simulated migration count data with known underlying rate of change and realistic levels of random variation (error) in counts, to assess how well trends could be recovered under ideal conditions, and when the assumptions of proportionality and count independence were violated. I also examined how precision and accuracy of trends varied with analytical technique, sampling frequency (e.g.,

number of days per year), number of sites in a region, and length of the time series, in order to make recommendations to optimize both the recovery of trends and sampling effort. My intention is that results from this work will provide a better understanding of how sampling protocols and analytical techniques can be used to optimize the use of migration counts for broad-scale population monitoring, and lead to the development of further refinements.

1.4.1 Effect of modeling random effects on estimated trends

In the Chapter 2, I simulated 10- and 20-year datasets of hourly raptor migration counts with realistic levels of low and high variation in annual, daily and hourly counts, to compare the precision and accuracy of population trends estimated using generalized linear models and generalized linear mixed (hierarchical) models that assumed counts were distributed with variance equal to the mean or greater than the mean (over-dispersed). Models were compared for three species that represented a commonly detected species, a rarely detected species with zero-inflated counts, and a super-flocking species with highly over-dispersed counts. Results from this study clearly show that partitioning variation among fixed and random effects improved power and resulted in a lower probability of detecting a false trend than did generalized linear models.

1.4.2 Effect of incomplete sampling of a migration on estimated trends

Even when data collection protocols are standardized, it is often the case that insufficient volunteer capacity can result in incomplete coverage of the migration window, or infrequent or sporadic sampling of days within a migration. In Chapter 3, I tested how the timing and frequency of sampling during a migration can influence our ability to recover population trend by sub-setting the hourly count datasets simulated in Chapter 2 in multiple ways: weekends only, first 25 %, 50 % and 75 % of the migration window, and by randomly sampling 40 %, 60 % or 80 % of observation days throughout the migration. My results show that while power typically declines with a decline in sampling coverage, probability of detecting a false trend does not increase. Further, for

highly over-dispersed species, our ability to recover a precise and accurate trend can improve by randomly sub-sampling data.

1.4.3   Effect of aggregating counts on estimated trends

Some evidence has shown that aggregating migration counts of highly over-dispersed species can improve precision of estimated trends (Miller et al. 2002). However, aggregating counts also results in a loss of information about the daily and seasonal distribution of counts, which may improve estimates for some species (Dennis et al. 2013). In Chapter 4, I use simulated hourly raptor migration counts for a common, rare and over-dispersed species to test whether aggregating hourly counts to daily or annual totals influenced the accuracy and precision of trends. In this chapter, I also assess whether estimating a zero-inflation parameter using hierarchical models improved the accuracy and precision of trends for data with a high proportion of zero-observation counts. My findings suggest there is little benefit of analyzing hourly as opposed to daily counts for common and rare species, and support previous work that suggests power could be improved for highly over-dispersed species by aggregating counts to annual totals. Modeling a zero-inflation parameter did not improve the precision or accuracy of estimated trends for these data.

1.4.4   Effect of a systematic change in probability of detection on estimated trends

A change in the stopover duration of migrants will be more likely to occur in response to climate and habitat change. In Chapter 5, I use simulated white-throated sparrow (*Zonotrichia albicollis*) daily migration count data to test how variation in stopover duration influenced the precision and accuracy of estimated trends. I simulated data with constant stopover duration, and compared trend estimates with data where stopover duration was allowed to vary randomly, cyclically (e.g., in response to climatic cycles) or linearly over time. Results from this study clearly show that a linear change in stopover duration will bias trends and lead to a high probability of misinterpreting trends as population change. Importantly, this analysis also shows that collecting additional data on stopover duration is imperative to test whether a change in stopover duration has

occurred, and if so, that sampling modifications to reduce the incidence of recounting individuals on subsequent days must be made in addition to modeling the underlying change in stopover duration when estimating trends.

1.4.5   Use of model selection to model regional variation in trends

Combining migration count data across sites represents an important step toward their use in regional and national population assessments. As a first step toward this goal, in Chapter 6 I used simulated migration counts for a commonly and rarely detected songbird to test whether model selection could be used to model regional variation in trends with current (based on CMMN network) or increased number of sites, when underlying pattern of change among regions is not known. My results show that model selection shows promise for modeling regional variation in trends. Even when a model that assumes regional differences in trend was selected for datasets with no underlying variation in trend, results show that there is little impact on bias or on probability of drawing false inference from the data, particularly using longer (40 year) time series. Results also suggest that investing in the current selection of CMMN sites over the long term would be more efficient at improving trend estimates than investing in the collection at more sites for fewer years. In fact, increasing the number of sites can result in overly precise trends and higher probability of error than when fewer sites are analyzed in each region.

1.4.6   Application to real data: Monarch butterfly trends

In Chapter 7, I apply hierarchical models and model selection to real migration counts collected for monarch butterflies at two sites at Long Point, Ontario, Canada over the past 20 years. Both sites vary in habitat structure, which may influence stopover probability and duration of monarchs, but are assumed to be detecting the same migratory population, and should therefore show similar rates of change if site-specific changes in detection probability (e.g., in response to change in stopover duration) are not occurring. I used model selection to test whether a difference in trend between sites was supported. Results show that a difference in trend among sites was not supported, and suggest that

monarch counts have declined by approximately 5 %year^{-1}, a trend that is supported primarily by declines in the last several years.

1.5   References

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<div align="center">Chapter 2</div>

2   Hierarchical models lower the probability of drawing false inference about trends in the number of animals counted on migration

2.1   Introduction

Conservation efforts rely on precise and accurate estimates of population trends to assess species status and inform management efforts (COSEWIC 2012). Choice of analysis method can influence precision and accuracy, and therefore inference drawn about long-term trends derived from population counts (Amano et al. 2012). The development of new modeling techniques to maximize the utility of data collected by large-scale monitoring programs is therefore an active field of study (Thomas 1996, Sauer and Link 2011, Amano et al. 2012, Bled et al. 2013).

Hourly counts of raptors actively migrating overhead during migration are currently collected at over 200 raptor watch sites across Central and North America (Hawk Migration Association of North America 2015), and are often used to assess raptor population trends (Farmer et al. 2007, Bildstein et al. 2008). Previous published analyses estimated trends using log-transformed linear regression (Farmer et al. 2007, Bildstein et al. 2008). However, generalized linear and additive models (GLMs/GAMs) are currently standard in the analysis of count data (Fewster et al. 2000, O'Hara and Kotze 2010, Fedy and Aldridge 2011, Dennis et al. 2013) because the assumptions of the linear model (e.g., heterogeneity) are relaxed and a non-normal distribution of errors can be specified (O'Hara & Kotze 2010). Thus, it should no longer be necessary to filter migration count data to better meet the assumptions of linear regression, for example by excluding rare species with many zero-observation counts or by dropping days predicted to have fewer than zero birds (Francis and Hussell 1998, Farmer et al. 2007, Bildstein et al. 2008).

Further, hierarchical models, including generalized linear mixed models (GLMMs) and generalized additive mixed models (GAMMs) extend GLMs/GAMs to allow variation in counts to be partitioned among fixed and random effects (Gelman et al. 2014), where the

population means of random effects are assumed to be drawn from a specified distribution, and are thus no longer assumed independent as are fixed effects (Kéry and Schaub 2011).   Because the dependency among sample means is acknowledged by the specification of a random effect, random effects can result in more realistic estimates of precision around population estimates (Kéry and Schaub 2011), and therefore lower probability of drawing false inference from the data (i.e., detecting a false positive result). Using simulated Breeding Bird Survey data, hierarchical models also resulted in more accurate estimates of population trend than did GLMs and GAMs (Amano et al. 2012).

Most common breeding or wintering bird surveys estimate annual indices of abundance and long-term trends using a single observation count per site per year, where the count might represent the total abundance across assumed independent stops along a route (Link et al. 2008) or the maximum abundance across repeated visits of an assumed closed population (Fedy and Aldridge 2011). Because migration counts are typically analyzed as hourly or daily counts of the number of individuals migrating past a given geographic location during the annual spring or fall migration(s) (Farmer et al. 2007, Bildstein et al. 2008, Crewe et al. 2013), we assume that a new cohort of migrants is detected during each sampling occasion. Across days in a migration, the total number of individuals counted is assumed proportional to the size of the monitored population (Dunn 2005). Migration counts tend to be highly variable, due in part to the influence of climate and local weather conditions on variation in annual migration route (Vardanis et al. 2011), probability of migrating on a given day (Allen et al. 1996, Miller et al. 2002), and probability of observer detection (Berthiaume et al. 2009). Thus, a large number of often highly variable observation counts are used to estimate a long-term trend. The specification of random effects in the analysis of migration counts can account for the dependence among annual, daily and hourly counts, and partition variation in counts among fixed (e.g., trend) and random (e.g., random error around underlying trend) effects, which should result in more appropriate estimates of trend precision.

The goal of this chapter was to use simulated hourly migration counts with a known long-term trend to provide a first formal comparison of GLMs and GLMMs in terms of the accuracy and precision with which the simulated trend was recovered. Because the

simulated trend was linear on a log scale, I did not compare additive models. Count data typically follow a Poisson distribution, or, when variance is greater than the mean (over-dispersion), a negative binomial distribution (Kéry 2010). I therefore compared the precision, accuracy, power and probability of error (false positive) for trends estimated using a GLM with Poisson or negative binomial distribution of errors, with a GLMM with Poisson or log-normal Poisson distribution of errors. A log-normal Poisson distribution models over-dispersed count data similar to the negative binomial, by fitting an observation-level random effect (Elston et al. 2001); over-dispersed Poisson models have been used previously to estimate bird population trends using BBS data (Link and Sauer 2002; Sauer and Link 2011; Bled et al. 2013; Sauer and Link 2002). Counts were simulated to represent species with three types of count distributions, to test whether zero-inflation and over-dispersion of counts influenced the performance of each model: sharp-shinned hawk (*Accipiter striatus*) is a commonly detected species with relatively low dispersion of counts; broad-winged hawk (*Buteo platypterus*) is a super-flocking species with highly over-dispersed counts; and merlin (*Falco columbarius*) is typically detected in low numbers, with a high proportion of 0-observation counts, i.e., counts are highly zero-inflated. Further, to test how length of the time series and magnitude of random error influenced trend recovery under the different model structures, I simulated 10- and 20-year time series with realistic low and high levels of annual and daily random error in counts for each species.

2.2   Methods

2.2.1   Real Data Summary

I accessed raptor migration counts online through the Hawk Migration Association of North America (Hawk Migration Association of North America 2015) for sharp-shinned hawk, broad-winged hawk and merlin collected at eight eastern North American hawk watch sites: 1) Beamer conservation area (Ontario, Canada: 1995-2009); 2) Cape May (New Jersey, USA: 1974-2004); 3) Hawk Mountain (Pennsylvania, USA: 1966-2009); 4) Hawk Ridge (Minnesota, USA: 1974-2009); 5) Holiday Beach (Ontario, Canada: 1979-2009); 6) Militia Hill (Pennsylvania, USA: 1992-2009); 7) Montclair (New Jersey, USA: 1977-2009); and 8) Waggoner's Gap (Pennsylvania, USA: 1987-2009). These sites

collect hourly counts of the number of individuals of each species actively migrating overhead during daylight hours throughout spring and/or fall migration. Detailed count methodology for each site is described elsewhere (Hawk Migration Association of North America 2015). For each species and site, I filtered data to exclude days of the year at the tail ends of the migration window that were not included in the middle 95 %ile of observations. I then estimated the mean and coefficient of variation (CV) in hourly, daily and annual counts, and in the proportion of 0-observation hours and days, and used those values as a guide to simulate data with realistic low and high levels of variation in counts for each species (Table B1). I used data from eight separate sites to estimate a realistic range in expected counts for each species because counts can vary among sites due, for example, to variation in the size of the source population among sites, variation in the proportion of the source population that migrates past a given site, and variation in the probability that individuals migrating past a site will be detected (Dunn 2005).

2.2.2 Migration Count Simulation

Hourly raptor migration counts were simulated in R (R version 2.14.2, R Core Team 2013; see Appendix A for simulation code and parameterization). The simulation model assumed that the count population at a migration monitoring site was a consistent and representative sample of the size of the monitored population. Total simulated number of birds (n) migrating in the first year, $n_{i=1}$, was defined by the simulation, and chosen to approximate the observed mean total count (across years and sites) observed with real migration count data (Table B1). Total number of birds available to be counted in all subsequent years, $n_{i>1}$, was then a function of starting population size, a defined constant rate of population change, β, random normal error on the log scale (i.e., stochastic variation in annual counts), and Poisson error on the response scale (i.e., process variation in annual counts):

$$n_i = Pois(\lambda_i) = Pois\left((n_{i-1} \times (1 + \beta)) + \varepsilon_i\right), \ \varepsilon_i \sim N(0, \sigma^2),$$

where random error in the size of the annual count population was assumed to incorporate annual variation in migratory behaviour, including variation in migration route (Alerstam et al. 2006, Vardanis et al. 2011), and variation in detection probability

due to extrinsic factors including habitat and climate (e.g., ENSO cycles; Calvert et al. 2009).

I then distributed the annual count population across days in a migration season, where length of the migration season varied among years with normal error. The daily migratory population in year i on day j, n_{ij}, was a function of the size of the annual count population, n_i, and a seasonal probability that birds migrated on a given day, P_{ij}, where the seasonal probability assumed a normal density to allow peak migration to occur mid-season (Miller et al. 2002), and with added random error on the log scale and negative binomial error on the response scale to simulate stochastic and process variability in the seasonal distribution of counts:

$$n_{ij} = NegBin(\lambda_{ij}, k.\,day) = NegBin((n_i \times P_{ij} + \varepsilon_i), k.\,day),$$

where *k.day* was the size of the negative binomial observations (clumping parameter) and was defined by the simulation (Appendix A), $\varepsilon_i \sim N(0, \sigma^2)$ and $P_{ij} \sim N(\mu_i, \sigma_i^2)$, and where μ_i and σ_i varied with year to simulate annual variation in the seasonal distribution of the annual count population. Birds then had a binomial probability of being recruited to, or arriving at, the count site each day:

$$nrecruit_{ij} \sim binom(n_{ij}, Pr_{ij}),$$

where probability of recruitment, Pr_{ij}, was generated as a uniformly distributed random variable between 0 and 1 to simulate random variation in the recruitment process due to weather, habitat, or any combination of factors, with added Poisson variability to simulate the temporal autocorrelation among days in a season that can result from weather fronts, for example, where adjacent days have more similar weather conditions, and therefore more similar probabilities of recruitment, than days further apart. Below a specified threshold, $Pr_{ij} = 0$ and no birds were recruited from the available migratory population. All birds that were not recruited from the migratory population on day j were carried forward to the following day's migratory population, $n_{i,j+1}$, which allowed the

number of available birds to build up and add the extra variability typically observed with migration counts.

Each day, the number of birds recruited in hour k, $nrecruit_{ijk}$, was a function of the number recruited each day, $nrecruit_{ij}$, and a daily probability that birds migrated on a given hour, P_{ijk}, where the daily probability assumed a normal density distribution to allow peak migration to occur mid-day, with added random error on the log scale and negative binomial error on the response scale to simulate stochastic and process variability in the daily distribution of counts:

$$nrecruit_{ijk} = NegBin(\lambda_{ijk}, k.hr) = NegBin((nrecruit_{ij} \times P_{ijk} + \varepsilon_{ij}), k.hr)$$

where *k.hr* was defined by the simulation (Appendix A), $\varepsilon_{ij} \sim N(0, \sigma^2)$ and $P_{ijk} \sim N(\mu_{ij}, \sigma_{ij}^2)$, and where μ_{ij} and σ_{ij} varied among days to simulate variation in the hourly distribution of the daily migratory population. The simulation model assumed that all birds departed the count site prior to the following count, i.e. hourly and daily counts were independent observations. Because probability of detection was confounded with probability of recruitment and population size, these could not be estimated independently.

Simulation parameter values (Table A1) were chosen to maximize the concordance of real and simulated counts in terms of mean and coefficient of variation of hourly, daily and annual counts, and of the proportion of 0-observation hours (Tables B1-B4). I ensured the distribution of real and simulated counts represented similar distributions of counts using quantile-quantile plots (qqplot, stats package, R version 2.14.2).

2.2.3   Simulated Factor Levels

I simulated data for three representative species: 1) broad-winged hawk, which migrates in large flocks, and typically shows high over-dispersion in counts among days and years (hereafter 'over-dispersed'; 2) sharp-shinned hawk, which is a commonly detected species that does not vary as widely in abundance from day to day (hereafter 'common'); and 3) merlin, which is detected less frequently and in low numbers, i.e. is considered a

rarely detected species with a high proportion of 0-observation counts (hereafter 'zero-inflated'). I simulated 10- and 20-year datasets, with an annual rate of population change of -3.9 %year^{-1}, which is approximately a 30 % decline in 10 years or 50 % decline in 20 years. A decline of 30 % in 10 years is often used as an assessment criterion for species at risk (COSEWIC 2012).

For each species and time series length, I simulated 1000 datasets under each of four variance scenarios: 1) low annual and low 'daily and hourly' variation in counts (hereafter 'daily' variation), 2) low annual and high daily variation, 3) high annual and low daily variation, and 4) high annual and high daily variation. Thus, in total 8000 datasets were simulated for each species (2 time periods × 1 trend × 4 variance scenarios).

2.2.4   Data Analysis

I analyzed all simulated datasets in R (v. 2.14.2, R Core Team 2013) using 1) GLM with Poisson distribution ('GLM Pois'; MASS Package: Venables and Ripley 2002), 2) GLM with negative binomial distribution ('GLM NB'; MASS Package), 3) GLMM with Poisson distribution ('GLMM Pois'; lme4 Package, Bates et al. 2013), and 4) GLMM with log-normal Poisson distribution ('GLMM LnPois'; lme4 Package) using a high performance computing network (Shared Hierarchical Academic Research Computing Network 2015). A continuous year effect was fit to estimate log-linear trend in counts over time. I fit first and second-order polynomials for day and hour to model the seasonal and daily distribution of counts. For all mixed models, I also estimated random effects for year, day nested within year, and hour, and for the log-normal Poisson GLMM, I included an additional random observation level effect to account for over-dispersion of counts (Elston et al. 2001). The random day effect was nested within year to allow random error in the seasonal movement of birds to vary among years. For each simulated dataset, I extracted the estimate, standard error, 95 % confidence limits (CL) and p-value of the fixed year coefficient, and year coefficients were transformed into a rate (%year^{-1}) using $100 \times \left(\exp\left(yearcoefficient \right) - 1 \right)$.

For each species, I tested whether bias (estimated – simulated trend) or standard error of estimated trends (n = 1000 simulated datasets × 4 model structures × 4 variation levels × 2 time series lengths = 32,000 bias or standard error estimates) varied among model structures, with level of annual and daily variation, and with length of time series using a generalized linear model with Gaussian distribution (identity link; MASS package, R version 2.14.2; Venables and Ripley 2002), where bias or standard error was the response variable, and model structure, variation level, length of time series and the interaction between model structure and variation level were explanatory factors. I log-transformed standard errors to better meet the assumption of normality. I used backward model selection using stepAIC in R (MASS Package, R version 2.14.2; Venables and Ripley 2002) to determine the model parameters with greatest support.

I also examined how bias and precision of the estimated trend influenced the probability of drawing false inference from the data by plotting 1) coverage, i.e. the proportion of simulated datasets where the simulated trend fell within the CL of the estimated trend, 2) power, i.e. the proportion of simulated datasets with good coverage and a significant year effect (p <0.1), and 3) rate of error, i.e. the proportion of simulated datasets with a significant trend despite poor coverage of CL. A α-value of 0.1 was used because it better balances the probabilities of detecting false positive (type I error) and false negative (type II error) trends using bird monitoring data (Bart et al. 2004).

2.3   Results

For over-dispersed counts with low annual and high daily variation, and zero-inflated counts with high annual and high daily variation, log-normal Poisson GLMMs often resulted in singular or false convergence (over-dispersed: 5.5 % and 4.8 % of simulations did not converge for 10 and 20 year datasets, respectively; zero-inflated: 4.3 % did not converge for 10 and 20 year datasets), signs that the model specification was too complex for the data. Datasets with convergence errors were dropped from all comparisons.

Using backward model selection on data for the commonly detected species, effects of model structure, variance type and years on bias of population trends, and effects of model structure, variance type, years and an interaction between model and variance type

on standard error of trend estimates were supported by the data (Table 2-1). Trends were more positively biased and less precise (larger standard errors) for GLMMs than for GLMs (Figure 2-1, Table 2-2). Trends were most biased when annual and daily variation in counts were high, and standard errors were largest when daily variation was high (Table 2-). Mean bias and standard error of trend estimates were also smaller using 20- than 10-year datasets. Using 20-year simulated datasets, bias was below the recommended maximum allowable bias for landbird monitoring of ±0.5 %year^{-1} (Bart et al. 2004) for all model structures.

For over-dispersed counts, a difference in bias among model structures or among variation levels was not supported, with the exception that trends estimated for datasets with low annual and high daily variation using GLMM LnPois were on average strongly negatively biased using 10-year datasets, and strongly positively biased using 20-year datasets (Table 2-22, Figure 2-2). Standard errors of trends estimated using GLMM LnPois for over-dispersed counts with high variation in daily counts were particularly large, and trends were in general more precise for GLMs than GLMMs (Table 2-, Figure 2-2). Trends were less biased and more precise using longer time series.

With the exception of datasets with high variation in daily counts, trends estimated for zero-inflated data were less biased using GLMMs than for GLMs for 10-year datasets, but more negatively biased using GLMMs than GLMs for 20-year datasets (Table 2-2, Figure 2-3). However, when variation among daily counts was high, trends estimated using GLMM LnPois were strongly positively biased with large standard deviation (Table 2-, Figure 2-3). As with the other two species, trends were more precise using longer time series and for GLMs compared to GLMMs.

The higher precision of trends estimated using GLMs, and particularly GLM Pois, resulted in an overall lower probability that confidence limits included the simulated trend, and a higher rate of error, compared with trends estimated using GLMMs (Figure 2-4). For over-dispersed or zero-inflated datasets with low variation among annual counts and high variation among daily counts, coverage and error rates for the negative binomial GLM showed little variation from rates observed using the Pois GLMM, and

also had increased power to correctly detect a significant trend. This was not observed for the other levels of annual and daily variation examined, nor for the commonly detected sharp-shinned hawk. When annual variation among counts was high and counts were over-dispersed or zero-inflated, power was essentially 0 for the log-normal Poisson model, due to the strong positive bias in trends which resulted in few (over-dispersed broad-winged hawk) to no (zero-inflated merlin) confidence limits that included the simulated trend.

Table 2- 1. Map of backward model selection using AIC for models that tested the effect of model structure ('Model'; generalized linear model with Poisson or negative binomial distribution, or generalized linear mixed model with Poisson or log-Normal Poisson distribution), variation level ('Var'; high or low annual and daily variation in counts) and length of the time series ('years'; 10 or 20) on mean bias or (log) standard error of the estimated trend in migration for a commonly detected species (Sharp-shinned Hawk; SSHA), a super-flocking. species with highly overdispersed counts (Broad-winged Hawk; BWHA), and a more rarely detected species (Merlin; MERL).

Dependent Variable	Species	Step	Initial Model	- Param	-DF	Deviance	AIC		Resid. DF
Bias	SSHA	1	Model + Var + Years + Model:Var	Model:Var	9	48.7	-116235	*	
						48.6	-116222		31869
				Years	1	48.7	-116208		
		2	Model + Variation + Years			48.7	-116235	*	31860
				Type	3	48.7	-116222		
				Years	1	48.7	-116222		
				Model	4	48.8	-116169		
	BWHA	1	Model + Var + Years + Model:Var			253.1	-58782	*	30221
				Model:Var	9	253.3	-58779		
				Years	1	253.2	-58776		
	MERL	1	Model + Var + Years + Model:Var			88.4	-93425	*	30929
				Years	1	88.5	-93406		
				Model:Var	9	88.9	-93271		
Std Error	BWHA	1	Model + Var + Years + Model:Var			1038.9	-16082	*	30221
				Model:Var	9	1974.9	3322		
				Years	1	8574.1	47735		
	SSHA	1	Model + Var + Years + Model:Var			769.3	-28214	*	31860
				Model:Var	9	1704.4	-2877		
				Years	1	9599.1	52238		
	MERL	1	Model + Var + Years + Model:Var			681	-30246	*	30929
				Model:Var	9	2537.4	10440		
				Years	1	8403.1	47512		

* Depicts model selected using backwards model selection using AIC
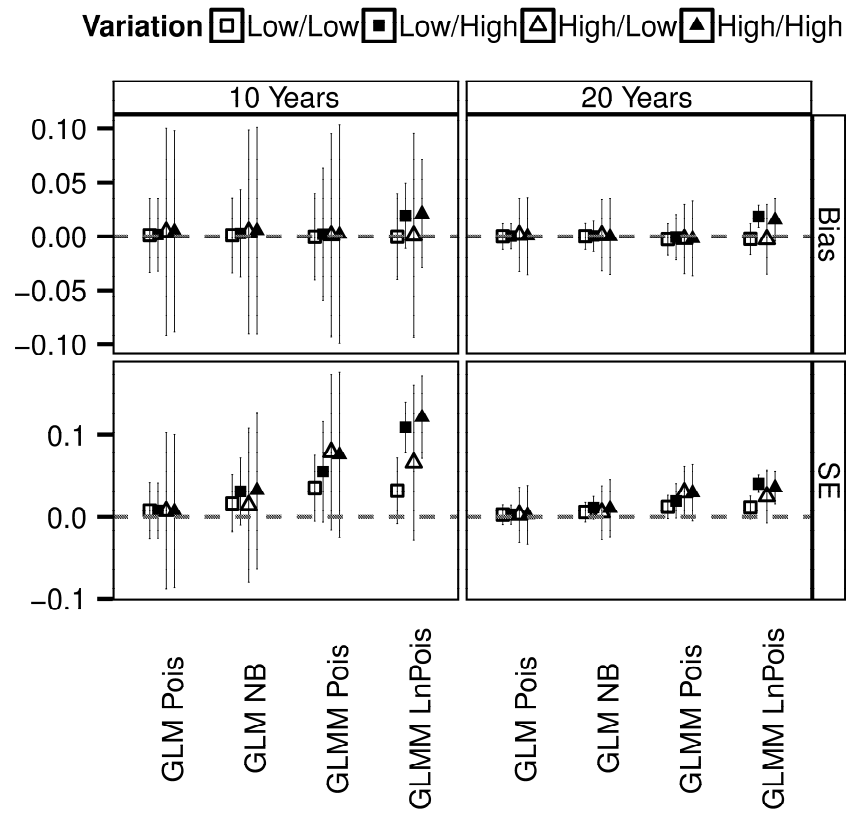
Figure 2-1. Mean bias (simulated – estimated trend; ± standard deviation) and standard error (± standard deviation) of trend in migration counts estimated across 1000 10- or 20-year datasets simulated to represent a commonly detected species (sharp-shinned hawk). Data were simulated to have low (triangles) or high (squares) variation in annual counts, and low (no fill) or high (black) variation in daily counts ('annual/daily'), and were analyzed using generalized linear models (GLMs) with Poisson or negative binomial (NB) distribution, or generalized linear mixed models (GLMM) with Poisson or log-normal Poisson distribution.

Table 2-2. Coefficients for the terms explaining variation in bias among trends in migration counts estimated using datasets simulated to represent a commonly detected species (sharp-shinned hawk), an over-dispersed species (broad-winged hawk) and a rarely detected species with zero-inflated counts (merlin), after backward model selection using AIC was applied to a model that included model structure, variation level, number of years, and an interaction between model and variation level as explanatory factors.

Parameter	Sharp-shinned Hawk			Broad-winged Hawk			Merlin		
	Coeff	SE	P	Coeff	SE	P	Coeff	SE	P
GLM Pois	0.0018	0.0006	0.004	0.0020	0.0021	0.343	0.0021	0.0012	0.095
GLM NB	0.0016	0.0006	0.010	0.0021	0.0021	0.310	0.0021	0.0012	0.091
GLMM Pois	0.0043	0.0006	<0.001	0.0032	0.0021	0.135	0.0001	0.0012	0.954
GLMM LnPois	0.0043	0.0006	<0.001	0.0028	0.0021	0.181	0.0002	0.0012	0.842
Low/High	-0.0012	0.0006	0.062	-0.0010	0.0030	0.728	0.0004	0.0017	0.803
High/Low	-0.0006	0.0006	0.364	0.0018	0.0029	0.530	0.0022	0.0017	0.187
High/High	0.0014	0.0006	0.020	0.0022	0.0030	0.469	0.0025	0.0017	0.145
20-Year	-0.0017	0.0004	<0.001	-0.0028	0.0011	0.007	-0.0028	0.0006	<0.001
GLM NB: Low/High				0.0003	0.0041	0.939	0.0005	0.0024	0.828
GLMM Pois:Low/High				0.0047	0.0042	0.263	0.0017	0.0024	0.466
GLMM LnPois:Low/High				0.0180	0.0047	0.000	0.0198	0.0024	<0.001
GLM NB: High/Low				0.0004	0.0041	0.924	-0.0002	0.0024	0.940
GLMM Pois:High/Low				0.0018	0.0041	0.661	-0.0016	0.0024	0.495
GLMM LnPois:High/Low				0.0018	0.0041	0.664	-0.0019	0.0024	0.420
GLM NB:High/High				0.0001	0.0042	0.973	-0.0002	0.0024	0.940
GLMM Pois:High/High				0.0025	0.0042	0.549	-0.0010	0.0024	0.667
GLMM LnPois:High/High				0.0039	0.0042	0.346	0.0171	0.0026	<0.001

Table 2-3. Coefficients for the terms explaining variation in standard error among trends in migration counts estimated using datasets simulated to represent a commonly detected species (sharp-shinned hawk), an over-dispersed species (broad-winged hawk) and a rarely detected and zero-inflated species (merlin), after backward model selection using AIC was applied to a model that included model structure, variation level, number of years, and an interaction between model and variation level as explanatory factors.

Parameter	Sharp-shinned Hawk			Broad-winged Hawk			Merlin		
	Coef	SE	P	Coef	SE	P	Coef	SE	P
GLM Pois	-6.60	0.004	<0.001	-7.00	0.004	<0.001	-4.82	0.003	<0.001
GLM NB	-5.06	0.004	<0.001	-4.23	0.004	<0.001	-4.11	0.003	<0.001
GLMM Pois	-3.55	0.004	<0.001	-2.67	0.004	<0.001	-3.37	0.003	<0.001
GLMM LnPois	-3.57	0.004	<0.001	-2.86	0.004	<0.001	-3.45	0.003	<0.001
Low/High	0.00	0.005	0.572	0.01	0.006	0.099	-0.01	0.005	0.226
High/Low	-0.06	0.005	<0.001	-0.16	0.006	<0.001	-0.11	0.005	<0.001
High/High	-0.05	0.005	<0.001	-0.15	0.006	<0.001	-0.12	0.005	<0.001
20-Year	-1.05	0.002	<0.001	-1.00	0.002	<0.001	-1.00	0.002	<0.001
GLM NB:Low/High	0.38	0.007	<0.001	0.88	0.008	<0.001	0.64	0.007	<0.001
GLMM Pois:Low/High	0.15	0.007	<0.001	0.31	0.008	<0.001	0.46	0.007	<0.001
GLMM LnPois:Low/High	0.02	0.007	0.008	0.87	0.009	<0.001	1.24	0.007	<0.001
GLM NB:High/Low	0.12	0.007	<0.001	0.05	0.008	<0.001	-0.01	0.007	0.290
GLMM Pois:High/Low	0.69	0.007	<0.001	0.45	0.008	<0.001	0.94	0.007	<0.001
GLMM LnPois:High/Low	0.70	0.007	<0.001	0.50	0.008	<0.001	0.80	0.007	<0.001
GLM NB:High/High	0.51	0.007	<0.001	0.61	0.008	<0.001	0.73	0.007	<0.001
GLMM Pois:High/High	0.77	0.007	<0.001	0.54	0.008	<0.001	0.92	0.007	<0.001
GLMM LnPois:High/High	0.66	0.007	<0.001	0.51	0.008	<0.001	1.35	0.007	<0.001
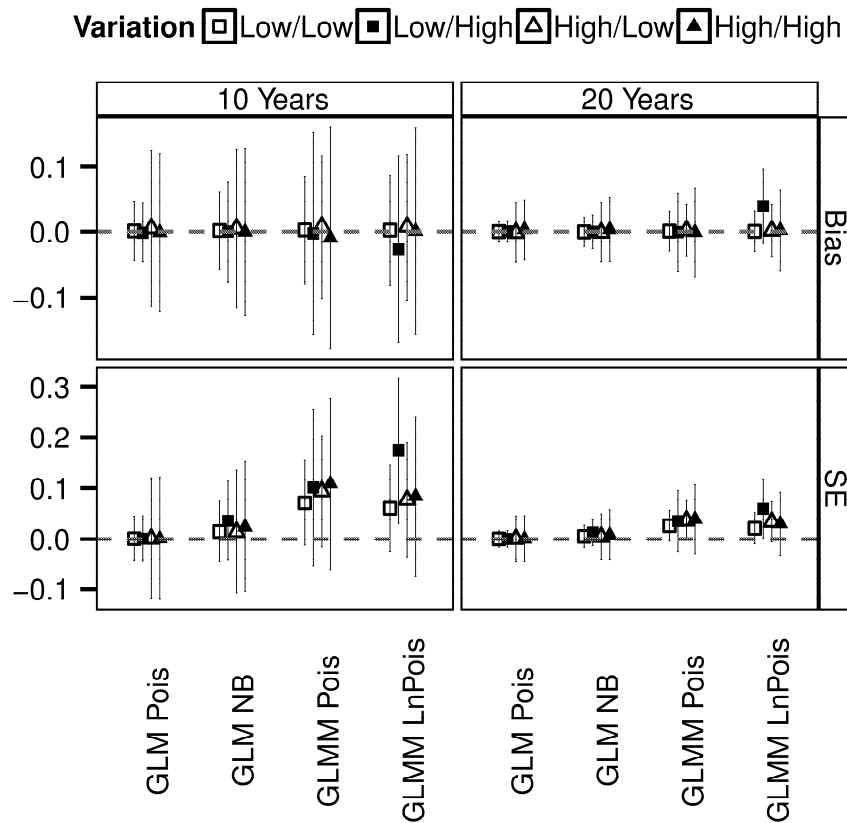
Figure 2-2. Mean bias (simulated – estimated trend; ± standard deviation) and standard error (± standard deviation) of trend in migration counts, estimated across 1000 10- and 20-year datasets simulated to represent a species (broad-winged hawk) with highly over-dispersed counts. Data were simulated to have low (triangles) or high (squares) variation in annual counts, and low (no fill) or high (black) variation in daily counts ('annual/daily'), and were analyzed using generalized linear models (GLMs) with Poisson or negative binomial (NB) distribution, or generalized linear mixed models (GLMM) with Poisson or log-normal Poisson distribution.
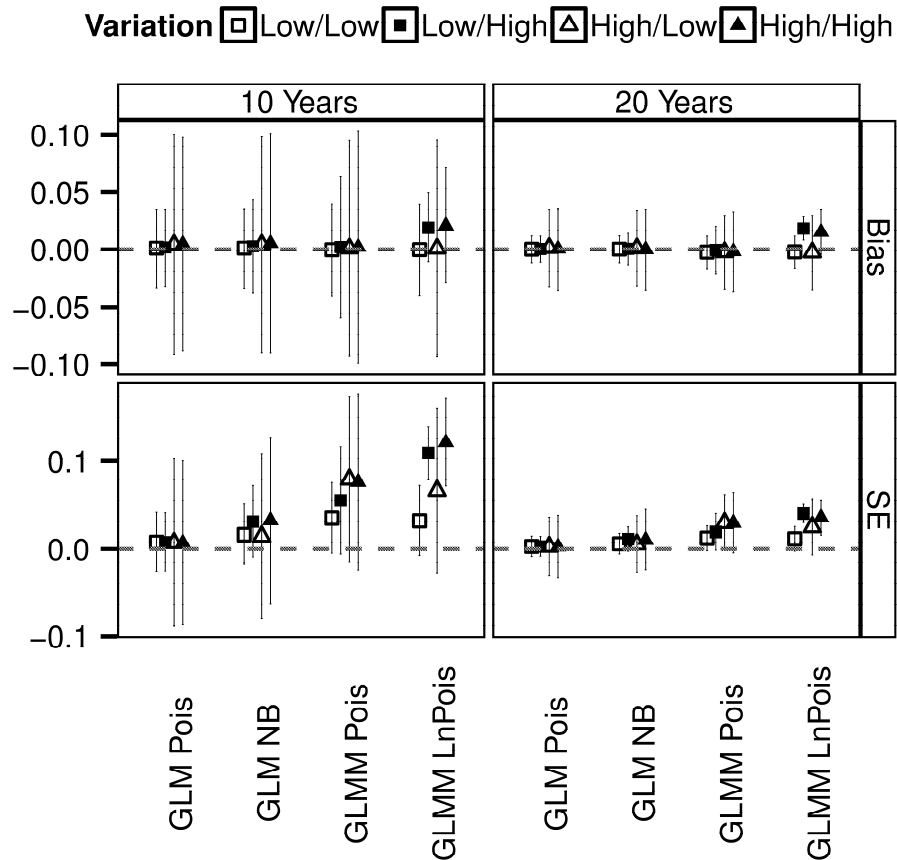
Figure 2-3. Mean bias (simulated – estimated trend; ± standard deviation) and standard error (± standard deviation) of trend in migration counts estimated across 1000 10- and 20-year datasets simulated to represent a rarely detected species (merlin) with zero-inflated counts. Data were simulated to have low (triangles) or high (squares) variation in annual counts, and low (no fill) or high (black) variation in daily counts ('annual/daily'), and were analyzed using generalized linear models (GLMs) with Poisson or negative binomial (NB) distribution, or generalized linear mixed models (GLMM) with Poisson or log-normal Poisson distribution.
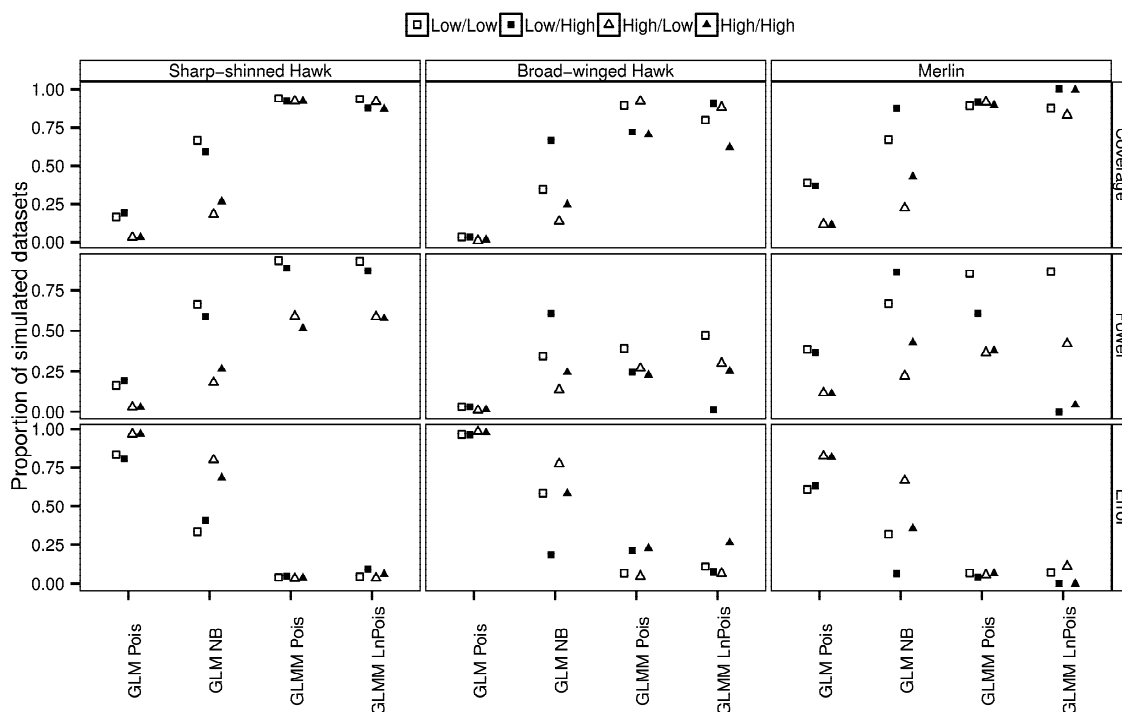
Figure 2-4. Proportion of 1000 20-year simulated datasets where the estimated trend in counts had 1) good coverage of confidence limits, 2) good coverage and statistical significance (p≤0.1; 'Power'), and 3) poor coverage and statistical significance ('Error'). Results are shown for three species simulated to represent 1) a commonly detected species (sharp-shinned hawk), 2) a species with highly over-dispersed counts (broad-winged hawk) and 3) a rarely detected species with zero-inflated counts (merlin), analyzed using generalized linear models (GLM) with Poisson (Pois) or negative binomial (NB) distribution, or generalized linear mixed models (GLMM) with Poisson or log-normal Poisson (LnPois) distribution. Data were simulated to have low (triangles) or high (squares) variation in annual counts, and low (no fill) or high (black) variation in daily counts ('annual/daily').

2.4 Discussion

Although trends estimated using GLMMs tended to be more biased than GLMs, the lack of appropriate accounting of the hierarchical structure of errors among years, days and hours using GLMs resulted in overly precise trend estimates, and as a result, lower coverage of confidence limits, lower power to detect a significant trend, and higher probability of drawing false inference from the data.   Using simulated annual Breeding Bird Survey counts at many sites, and assuming a Poisson distribution of errors, Amano et al. (2012) also found hierarchical models resulted in lower rates of error in estimated trend compared to GLMs and GAMs.

For over-dispersed and zero-inflated counts with high daily variation, the GLMM LnPois model often resulted in strongly biased trends with low power. Combined with the poor model fit (false or singular convergence) of a small proportion of over-dispersed and zero-inflated datasets using the over-dispersed model, results suggests that an observation-level random effect to account for over-dispersion and zero-inflation was too complex for the data. Hierarchical models that explicitly account for both zero-inflation and over-dispersion (e.g., zero-inflated negative binomial; Ross et al. 2012) might be more appropriate for these data, but were not explored here (but see Chapter 4).

Further, although in most cases the GLMM Poisson model outperformed the GLMs, specifying a GLM that assumed a negative binomial distribution of counts for over-dispersed or zero-inflated counts with low annual and high daily variation did not affect coverage and error rates, and resulted in slightly higher power to detect a significant trend than did the Poisson GLMM. When annual variation is low and data are collected at a single site, there is limited information available to partition variation among fixed and random year effects. Analyzing data from several sites that monitor the same population should improve estimates by allowing site-specific random error to be estimated independently from random error in annual counts. In addition, smoothed hierarchical models (Amano et al. 2012, Ross et al. 2012) that account for correlation of counts among days and years should be explored, particularly for real migration count data which are unlikely to be linear over the long term. Smoothed hierarchical models are less sensitive to large outlying observation counts than non-smoothed hierarchical models

(Amano et al. 2012), and may provide some benefit over the Poisson GLMM in the analysis of highly over-dispersed species.

Using simple linear regression on annual means, Lewis and Gould (2000) found that for 20-year raptor migration counts and alpha of 0.1, a decline of 3 % could be detected with 80 % power when the coefficient of variation of annual counts was less than 0.22. While not directly comparable, when annual coefficient of variation was 0.3 or less (low annual/high daily variation; Table B2), a decline of 3.9 %year^{-1} was detected with a minimum 89 % power using hierarchical models fit to 20-year simulated datasets of a commonly detected species. For 20-year datasets for the rare species, 85 % power was achieved when annual and daily coefficients of variation were both low (0.4 and 1.6, respectively; Table B4). Typically, statistical power describes the probability of detecting a trend that differs significantly from zero (Lewis and Gould 2000). In this study, power is defined as the probability of detecting a significant trend that also includes the known simulated trend within the confidence limits of the estimated trend. Thus, power is not only greater using the analytical methods described here, but the definition of power used in this is a more conservative estimate of power because it excludes significant trends that do not include the real trend within the confidence limits of the estimated trend. These results suggest that using hierarchical models to model hourly counts resulted in similar or potentially improved power to detect a significant trend compared with linear regression on annual means. For over-dispersed species like the broad-winged hawk, aggregating data from hourly to daily or annual totals could improve precision and power of population trend analyses (Miller et al. 2002, Chapter 4)

Because hierarchical models resulted in a lower probability of error overall compared with GLMs, and bias for all models tended to be within the suggested allowable limit of 0.5 %year^{-1} for landbird monitoring programs (Bart et al. 2004), hierarchical models should be preferred over GLMs when estimating trends in migration counts. An observation-level random effect is not recommended for zero-inflated and highly over-dispersed species. However, the effect of aggregating counts to daily or annual totals, as well as alternative analysis methods to account for over-dispersion, zero-inflation, and

correlation of counts among days and years (Amano et al. 2012, Ross et al. 2012) should be explored (see also Chapter 4).

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Chapter 3

3 Effect of incomplete sampling of migration on estimates of long-term trend in migration counts

3.1 Introduction

Accurate and precise estimates of long-term population trends are imperative for providing reliable assessments of population status, particularly for the assessment of species at risk (COSEWIC 2012). For bird populations, the Breeding Bird Survey (BBS) is the most commonly used large-scale monitoring program to assess bird population trends in North America (Blancher et al. 2009, Sauer and Link 2011). However, due to insufficient BBS coverage in northern Canada and the secretive nature of many raptor species, many species of raptors and northern-breeding songbirds are not well monitored by BBS or other large-scale bird surveys (Dunn 2005). Counts of birds migrating between wintering and breeding grounds can be used as an additional source of information on population trend for these species (Downes et al. 2000, Bildstein et al. 2008, Blancher et al. 2009), and have shown general correspondence with BBS (Francis and Hussell 1998, Farmer et al. 2007)

At present, counts of migrating birds are collected daily at over 200 sites across North America during spring and/or fall migration by sites associated with the Hawk Migration Association of North America (2015) and the Canadian Migration Monitoring Network (CMMN, Crewe et al. 2008). Many of these sites rely on volunteer observers for data collection. Data collection protocols are typically standardized at each site to minimize the impact of volunteer turnover and random environmental variation on counts (Hussell and Ralph 1998). However, a reliance on unpaid staff can sometimes result in sporadic or incomplete sampling coverage both within and among years. Further, if the full migration season is not sampled at a site, the tail ends of the migration of early or late migrating species might be missed.

Previous analyses of trends in migration counts typically dropped species that were not sampled during an arbitrary portion of their migration window, i.e. days of the year when

a species typically passed through a site (Francis and Hussell 1998, Farmer et al. 2007). The effect of incomplete sampling coverage during peak migration on power to detect trends in annual counts of migrating raptors was previously explored (Lewis and Gould 2000). However, the impact of sampling a smaller portion of the migration window and missing part or all of peak migration on our ability to detect trends in migration counts has not been previously examined.

Further, variation in observer skill (Link and Sauer 2002) and the effect of environmental variation on the number of birds migrating, migratory behaviour (Schaub et al. 2004, Calvert et al. 2009), migratory route (Hall et al. 1992, Allen et al. 1996, Leshem and Yom-Tov 1998, Vardanis et al. 2011), and on observer detection (Berthiaume et al. 2009) can contribute an unknown magnitude of random error to migration counts. Combined with migration strategy (e.g., super-flocking vs. individual migration) and abundance (common vs. rare), the result is often over-dispersed and/or zero-inflated count data where a large proportion of variation in counts is unrelated to underlying changes in population size. The influence of count distribution and magnitude of random error on our ability to detect trends in migration counts with sufficient accuracy and precision to confidently inform conservation efforts has not been rigorously examined.

In this chapter, I used simulated hourly raptor migration counts with known constant rate of change to test whether sampling frequency influenced our ability to recover known trend in counts. Data were subset in several ways: weekends only, or by taking a random sample of 40, 60 or 80 % of observation counts across the entire migration season, or by sampling the first 25 %, 50 % or 75 % of the migration window. The later was used to test whether excluding a complete section of the migration window and part or all of peak migration influenced our ability to recover simulated trend. I simulated hourly migration counts for a commonly detected species (sharp-shinned hawk, *Accipiter striatus*; hereafter 'common'), a super-flocking species with over-dispersed counts (broad-winged hawk, *Buteo platypterus*; hereafter 'over-dispersed') and a less commonly detected species with zero-inflated counts (merlin, *Falco columbarius*; hereafter 'zero-inflated'), each with high and low levels of random error in annual and daily counts, to test whether count distribution and extent of random error influenced accuracy and precision of

estimated trend under the various levels of sampling frequency tested. Results are discussed in terms of how sampling protocols might be used to optimize volunteer effort without compromising inference drawn about trends.

3.2   Methods

3.2.1   Migration Count Simulation

Data were simulated to represent counts of a common, over-dispersed or zero-inflated species, as described in sections 2.2.1-2.2.3 (see Appendix A for simulation code, R Core Team 2013), with two time periods (10 or 20 years) and four levels of annual and daily variation (Low/Low, Low/High, High/Low, High/High). For each species and factor level, 1000 datasets were simulated, resulting in a total of 8000 simulated datasets for each species, and each of those datasets was then subset in seven ways (n = 8000 × 7 = 56,000 subset datasets for each species) to test whether and how accuracy and precision of trends varied with sampling effort: including only the first 25 %, 50 % or 75 % of the migration window; including only data collected on weekends (2 consecutive days out of every 7); and including a random sample of 40 %, 60 %, or 80 % of observation days within the migration window of each species. Simulated counts were assumed to be proportional to underlying population size.

3.2.2   Data Analysis

Trend in migration counts was estimated for each simulated dataset using a generalized linear mixed model (GLMM) which assumed a Poisson distribution of counts, and where a continuous year effect was used to estimate log-linear rate of change (trend) in counts and second-order polynomials for day and hour were included to model the seasonal and daily movement of birds (lme4 package, R version 2.14.2; Bates et al. 2013). Hierarchical terms to account for random variation among years, among days nested within year, and among hours were also included. A previous comparison of generalized linear models (Poisson and negative binomial distribution) with GLMMs (Poisson and log-normal Poisson distribution for over-dispersed data) suggested that this model structure provided the best fit among those tested for hourly migration counts (see Chapter 2). For each simulated dataset, I extracted the estimate, standard error, 95 %

confidence limits (CL) and p-value of the fixed year coefficient. Year coefficients were transformed into a rate (%year^{-1}) of change using $100 \times \left(\exp\left(yearcoefficient \right) - 1 \right)$.

For each species, I tested whether bias (estimated – simulated trend) of estimated trend (n = 1000 simulated datasets × 4 variation levels × 2 time series × 8 sampling efforts [including full dataset] = 64,000 bias estimates) varied among levels of annual and daily variation, with length of dataset and with sampling frequency using a generalized linear model with Gaussian distribution (identity link; MASS package, R version 2.14.2; Venables and Ripley 2002), where bias was the response variable, and length of dataset (10/20 years), variation level (high or low annual/daily variation), subset type (weekends only, etc.), and interactions between subset type and year and subset type and variation level were explanatory factors. I used backward model selection using stepAIC in R (MASS Package, R version 2.14.2; Venables and Ripley 2002) to determine the model parameters with greatest support. I used a similar regression to test whether precision (standard error) of the trend estimate varied with dataset length, variation level and subset type, and again used backward model selection to determine the model with lowest AIC score, and therefore model parameters with greatest support. I log-transformed standard errors to better meet the assumption of normality.

I also examined how bias and precision of estimated trend influenced the probability of drawing false inference from the data by plotting 1) coverage, i.e. the proportion of simulated datasets where the simulated trend fell within the CL of the estimated trend, 2) power, i.e. the proportion of simulated datasets with good coverage and a significant year effect (p <0.1), and 3) rate of error, i.e. the proportion of simulated datasets with a significant trend despite poor coverage of CL. A p-value of 0.1 was used because it better balances the occurrence of type I and II errors in the estimation of bird population trends (Bart et al. 2004).

3.3 Results

Using backward model selection, a difference in bias among sampling frequencies was not supported for the common and zero-inflated species (Table 3- 1;

Species	Step	Initial Model	- Param	- DF	Dev	AIC	Resid

								DF
Bias								
BWHA	1	Subset+Var+Years			1344.9	-61785	*	62114
			Var	3	1345.9	-61746		
			Subset	7	1347.3	-61692		
			Years	1	1347.8	-61654		
SSHA	1	Subset+Var+Years	Subset	7	137.7	-207988	*	
					137.7	-207976		63193
			Var	3	137.8	-207949		
			Years	1	137.9	-207921		
	2	Type+Years			137.7	-207988	*	63200
			Var	3	137.8	-207961		
			Years	1	137.9	-207933		
MERL	1	Subset+Var+Years	Subset	7	319.3	-156294	*	
					319.3	-156284		63612
			Var	3	319.4	-156272		
			Years	1	319.6	-156233		
	2	Type+Years			319.3	-156294	*	63619
			Var	3	319.4	-156283		
			Years	1	319.6	-156244		
Standard Error								
BWHA	1	Subset+Var+Years			4833.9	17692	*	62114
			Var	3	7731.4	46863		
			Subset	7	8740.2	54474		
			Years	1	20453.1	107306		
SSHA	1	Subset+Var+Years			2807.0	-17443	*	63193
			Subset	7	4139.4	7093		
			Var	3	6054.8	31139		
			Years	1	21595.2	111515		
MERL	1	Subset+Var+Years			3153.2	-10581	*	63612
			Subset	7	5136.8	20456		
			Var	3	7093.6	40999		
			Years	1	19029.1	103786		

* Model selected using backwards model selection using Akaike's Information Criterion

Table 3-). In other words, bias in estimated trend did not vary regardless of whether the

entire migration was sampled, or collected as infrequently as weekends (Figure 3-1,

Figure 3-2). This was also true for over-dispersed migration counts, with the exception

that when daily variation in counts was high and data were subset to the first 25 % of the

migration window, trends were strongly positively biased (

Species	Step	Initial Model	- Param	- DF	Dev	AIC		Resid DF
Bias								
BWHA	1	Subset+Var+Years			1344.9	-61785	*	62114
			Var	3	1345.9	-61746		
			Subset	7	1347.3	-61692		
			Years	1	1347.8	-61654		
SSHA	1	Subset+Var+Years	Subset	7	137.7	-207988	*	
					137.7	-207976		63193
			Var	3	137.8	-207949		
			Years	1	137.9	-207921		
	2	Type+Years			137.7	-207988	*	63200
			Var	3	137.8	-207961		
			Years	1	137.9	-207933		
MERL	1	Subset+Var+Years	Subset	7	319.3	-156294	*	
					319.3	-156284		63612
			Var	3	319.4	-156272		
			Years	1	319.6	-156233		
	2	Type+Years			319.3	-156294	*	63619
			Var	3	319.4	-156283		
			Years	1	319.6	-156244		
Standard Error								
BWHA	1	Subset+Var+Years			4833.9	17692	*	62114
			Var	3	7731.4	46863		
			Subset	7	8740.2	54474		
			Years	1	20453.1	107306		
SSHA	1	Subset+Var+Years			2807.0	-17443	*	63193
			Subset	7	4139.4	7093		
			Var	3	6054.8	31139		
			Years	1	21595.2	111515		
MERL	1	Subset+Var+Years			3153.2	-10581	*	63612
			Subset	7	5136.8	20456		
			Var	3	7093.6	40999		
			Years	1	19029.1	103786		

* Model selected using backwards model selection using Akaike's Information Criterion

Table 3-), with mean bias exceeding 6 %year^{-1} using 10-year datasets and exceeding 1 % year^{-1} using 20-year datasets (Figure 3-3). Sub-setting data to weekends or by drawing a random sample of observation days from across the migration season did not have the same biasing effect on trends estimated using over-dispersed counts.

Population trends estimated for a commonly detected species were less biased when annual variation was low and daily variation high, or vice versa (annual high, daily low). Zero-inflated datasets with low annual and high daily variation in counts resulted in a higher positive bias than the other levels of variation in counts using 10-year datasets, but less biased trends overall using 20-year datasets. In general, increasing the length of the time series resulted in less-biased trends for the common and over-dispersed species, and in more negatively biased trends when counts were zero-inflated, i.e. for rarely detected species, the simulated declining trend was estimated to be more extreme than reality as the time series increased from 10 to 20 years.

Effects of subset type, variation level and length of time series on standard error of trend estimates were supported by the data for each species (Table 3- 1). Precision of trend estimates also increased, and standard errors became smaller, with length of the time series and with sampling frequency (Table 3-; bottom panels Figure 3-1 - Figure 3-3), as is expected as the number of observations in a dataset increases. For the common and zero-inflated species, precision was higher for simulated datasets with low annual variation in counts, and standard errors did not vary among similar sized data subsets, regardless of whether data were a random sample or a continuous period of time (e.g., 80 % random sample vs. 75 % of the migration window; Table 3-). For the over-dispersed and highly variable broad-winged hawk, trend estimates were more precise when daily variation in counts was low, and when data were collected as a random sample of observation days, as opposed to a continuous but incomplete sample of the migration window (Table 3-, Figure 3-3).

Confidence limits of the estimated trend were more likely to include the simulated trend, and rate of error was therefore less, for low compared with high annual variation in counts for the common and zero-inflated species, and for low compared with high daily

variation in counts for the over-dispersed species (Figure 3-4). For over-dispersed counts with high daily variation, coverage of confidence limits declined and error increased with an increase in sampling frequency. This is likely the result of smaller standard errors with increased sampling frequency, despite similar levels of bias across sampling frequencies. Thus, as sampling frequency increased, confidence limits became tighter and were less likely to include the simulated trend.

Power to detect a significant trend increased with the number of years in the dataset (not shown) and with an increase in sampling frequency (Figure 3-4). For the common and zero-inflated species, the increase in power with sampling frequency was more extreme when annual variation in counts was low. Overall, however, power to detect a significant trend only exceeded 80 % for 20-year datasets for a commonly detected species with low annual variation in counts. Power to detect a significant trend was particularly low when counts were highly over-dispersed, and did not reach 50 % regardless of length of time series and sampling intensity.

Table 3- 1. Map of backward model selection using AIC for models that tested the effect of subset type, variation level ('Var'; high or low annual and daily variation in counts) and length of the time series ('years'; 10 or 20) on mean bias or (log) standard error of the estimated trend in migration for a commonly detected species (Sharp-shinned Hawk; SSHA), a super-flocking. species with highly overdispersed counts (Broad-winged Hawk; BWHA), and a more rarely detected species (Merlin; MERL).

Species	Step	Initial Model	- Param	- DF	Dev	AIC		Resid DF
Bias								
BWHA	1	Subset+Var+Years			1344.9	-61785	*	62114
			Var	3	1345.9	-61746		
			Subset	7	1347.3	-61692		
			Years	1	1347.8	-61654		
SSHA	1	Subset+Var+Years	Subset	7	137.7	-207988	*	
					137.7	-207976		63193
			Var	3	137.8	-207949		
			Years	1	137.9	-207921		
	2	Type+Years			137.7	-207988	*	63200
			Var	3	137.8	-207961		
			Years	1	137.9	-207933		
MERL	1	Subset+Var+Years	Subset	7	319.3	-156294	*	
					319.3	-156284		63612
			Var	3	319.4	-156272		
			Years	1	319.6	-156233		
	2	Type+Years			319.3	-156294	*	63619
			Var	3	319.4	-156283		
			Years	1	319.6	-156244		
Standard Error								
BWHA	1	Subset+Var+Years			4833.9	17692	*	62114
			Var	3	7731.4	46863		
			Subset	7	8740.2	54474		
			Years	1	20453.1	107306		
SSHA	1	Subset+Var+Years			2807.0	-17443	*	63193
			Subset	7	4139.4	7093		
			Var	3	6054.8	31139		
			Years	1	21595.2	111515		
MERL	1	Subset+Var+Years			3153.2	-10581	*	63612
			Subset	7	5136.8	20456		
			Var	3	7093.6	40999		

	Years	1	19029.1	103786

* Model selected using backwards model selection using Akaike's Information Criterion

Table 3-2. Coefficients for the terms explaining variation in bias of estimated trend in hourly migration counts for datasets simulated to represent a commonly detected species (sharp-shinned hawk), a super-flocking species with highly over-dispersed counts (broad-winged hawk) and a less commonly detected species with zero-inflated counts (merlin), after backward model selection using AIC was applied to a model that included sampling frequency, variation level, number of years, and interactions between sampling frequency and variation level and sampling frequency and years as explanatory factors.

Parameter	Sharp-shinned hawk			Broad-winged hawk			Merlin		
	Coeff	SE	P	Coeff	SE	P	Coeff	SE	P
Intercept	0.0061	0.0005	<0.001	0.0038	0.0035	0.280	0.0011	0.0006	0.079
Weekend				0.0011	0.0047	0.814			
Random 0.4				0.0013	0.0047	0.777			
Random 0.6				0.0002	0.0047	0.958			
Random 0.8				-0.0003	0.0047	0.945			
Window 25				0.0040	0.0047	0.393			
Window 50				0.0013	0.0047	0.786			
Window 75				0.0007	0.0047	0.881			
Low/High	-0.0028	0.0007	<0.001	0.0113	0.0050	0.023	0.0030	0.0008	<0.001
High/Low	-0.0028	0.0007	<0.001	0.0061	0.0049	0.216	0.0003	0.0008	0.716
High/High	0.0019	0.0008	0.011	0.0138	0.0050	0.006	0.0011	0.0008	0.156
20-Year	-0.0033	0.0007	<0.001	-0.0041	0.0023	0.082	-0.0041	0.0006	<0.001
Weekend:Low/High				0.0045	0.0066	0.498			
Random 0.4:Low/High				0.0033	0.0067	0.615			
Random 0.6:Low/High				-0.0001	0.0066	0.988			
Random 0.8:Low/High				-0.0002	0.0066	0.972			
Window 25:Low/High				0.0268	0.0068	<0.001			
Window 50:Low/High				0.0113	0.0067	0.090			
Window 75:Low/High				-0.0016	0.0066	0.812			

Weekend:High/Low				0.0029	0.0066	0.663
Random 0.4:High/Low				-0.0002	0.0066	0.977
Random 0.6:High/Low				-0.0006	0.0066	0.930
Random 0.8:High/Low				0.0012	0.0066	0.853
Window 25:High/Low				0.0009	0.0067	0.895
Window 50:High/Low				-0.0008	0.0066	0.902
Window 75:High/Low				0.0000	0.0066	0.996
Weekend:High/High				-0.0021	0.0066	0.748
Random 0.4:High/High				-0.0021	0.0066	0.749
Random 0.6:High/High				0.0014	0.0066	0.834
Random 0.8:High/High				-0.0005	0.0066	0.939
Window 25:High/High				0.0360	0.0068	<0.001
Window 50:High/High				0.0091	0.0067	0.173
Window 75:High/High				0.0027	0.0066	0.679
Low/High:20-Year	0.0017	0.0010	0.113	-0.0155	0.0033	<0.001
High/Low:20-Year	0.0027	0.0010	0.009	-0.0050	0.0033	0.131
High/High:20-Year	-0.0024	0.0011	0.023	-0.0183	0.0033	<0.001
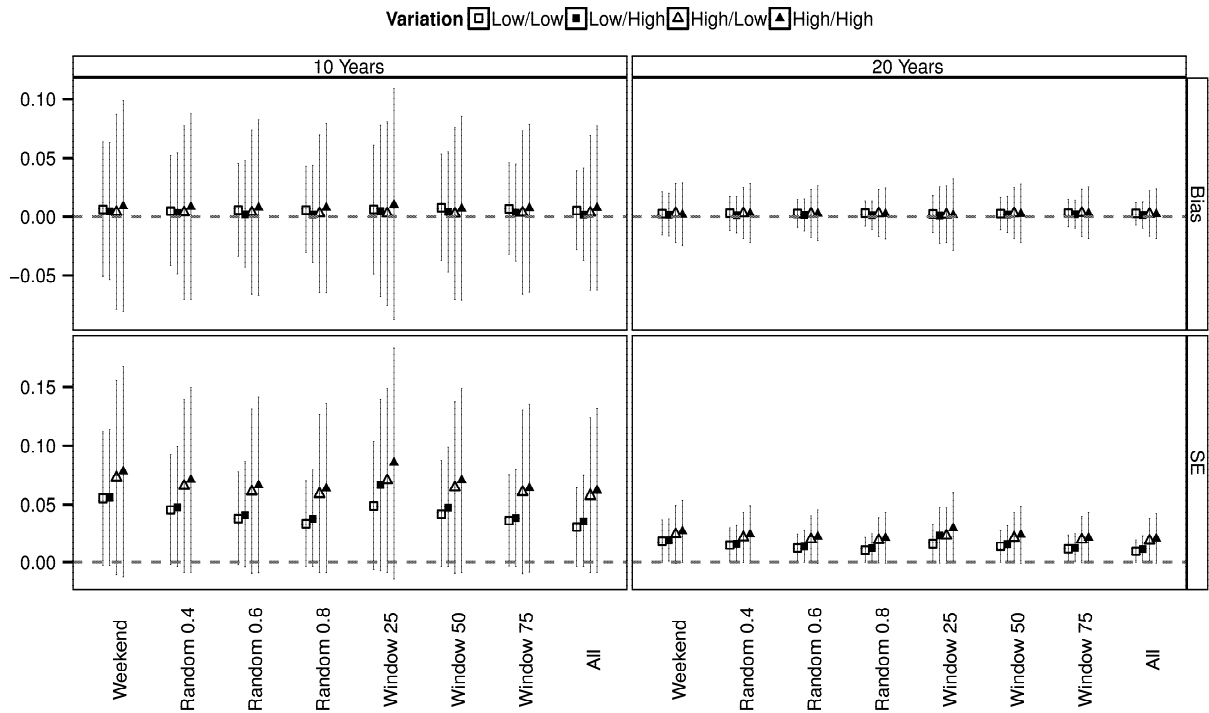
Figure 3-1. Mean bias (simulated – estimated trend; ± standard deviation) and standard error (± standard deviation) of estimated trend in hourly migration counts, across 1000 10- or 20-year datasets simulated to represent a commonly detected species (sharp-shinned hawk). Counts were simulated to have low (triangles) or high (squares) annual variation, and low (no fill) or high (black) daily variation ('annual/daily'), and were subset by sampling weekends, sampling a random sample of 40 %, 60 %, or 80 % of the migration, or by sampling the first 25 %, 50 %, or 75 % of the migration.
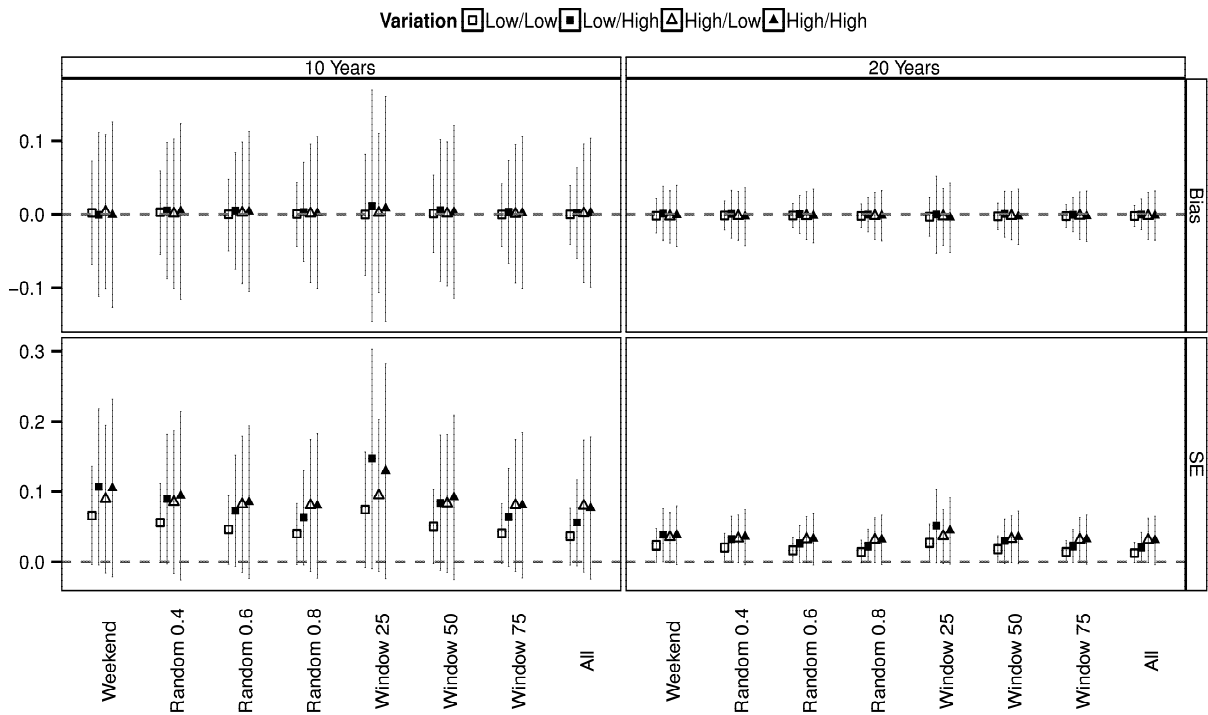
Figure 3-2. Mean bias (simulated – estimated trend; ± standard deviation) and standard error (± standard deviation; n = 1000) of estimated trend in hourly migration counts, across 10- or 20-year datasets simulated to represent a rarely detected species with zero-inflated counts (merlin). Counts were simulated to have low (triangles) or high (squares) annual variation, and low (no fill) or high (black) daily variation ('annual/daily'), and were subset by sampling weekends, sampling a random sample of 40 %, 60 %, or 80 % of the migration, or by sampling the first 25 %, 50 %, or 75 % of the migration.
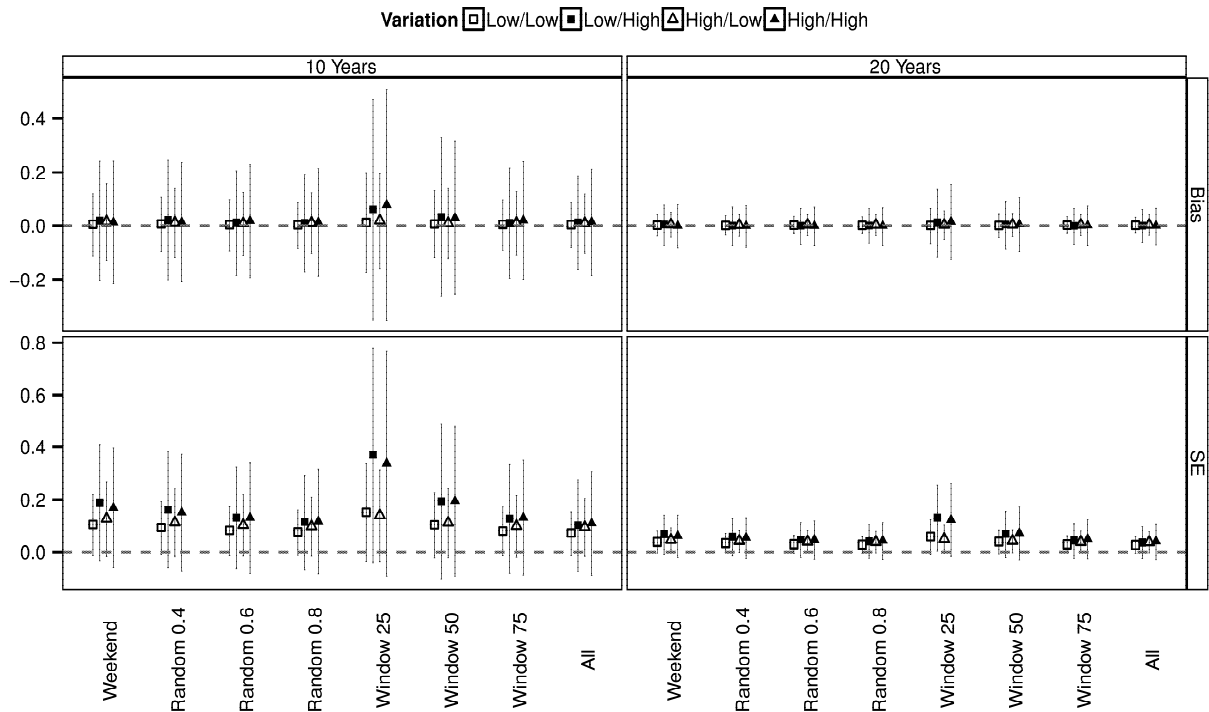
Figure 3-3. Mean bias (simulated – estimated trend; ± standard deviation) and standard error (± standard deviation; n = 1000) of estimated trend in hourly migration counts, across 10- or 20-year datasets simulated to represent a super-flocking species with highly over-dispersed counts (broad-winged hawk). Counts were simulated to have low (triangles) or high (squares) annual variation, and low (no fill) or high (black) daily variation ('annual/daily'), and were subset by sampling weekends, sampling a random sample of 40 %, 60 %, or 80 % of the migration, or by sampling the first 25 %, 50 %, or 75 % of the migration.

Table 3-3. Coefficients for the terms explaining variation in standard errors of trends in hourly migration counts, estimated using data simulated to represent a commonly detected species (sharp-shinned hawk), a super-flocking species with highly over-dispersed counts (broad-winged hawk) and a rarely detected species with zero-inflated counts (merlin), after backward model selection using AIC was applied to a model that included sampling frequency, variation level, number of years, and interactions between sampling frequency and variation level and sampling frequency and years as explanatory factors.

| Parameter | Sharp-shinned hawk | | | Broad-winged hawk | | | Merlin | | |
	Coef	SE	P	Coef	SE	P	Coef	SE	P
Intercept	-3.44	0.003	<0.001	-2.70	0.004	<0.001	-3.27	0.003	<0.001
Weekend	0.40	0.003	<0.001	0.42	0.004	<0.001	0.42	0.004	<0.001
Random 0.4	0.26	0.003	<0.001	0.29	0.004	<0.001	0.29	0.004	<0.001
Random 0.6	0.13	0.003	<0.001	0.15	0.004	<0.001	0.16	0.004	<0.001
Random 0.8	0.05	0.003	<0.001	0.06	0.004	<0.001	0.07	0.004	<0.001
Window 25	0.42	0.003	<0.001	0.84	0.005	<0.001	0.55	0.004	<0.001
Window 50	0.22	0.003	<0.001	0.41	0.004	<0.001	0.23	0.004	<0.001
Window 75	0.09	0.003	<0.001	0.12	0.004	<0.001	0.07	0.004	<0.001
Low/High	0.12	0.002	<0.001	0.50	0.003	<0.001	0.49	0.002	<0.001
High/Low	0.45	0.002	<0.001	0.17	0.003	<0.001	0.56	0.002	<0.001
High/High	0.55	0.002	<0.001	0.50	0.003	<0.001	0.63	0.002	<0.001
20-Year	-1.09	0.002	<0.001	-1.00	0.002	<0.001	-1.00	0.002	<0.001
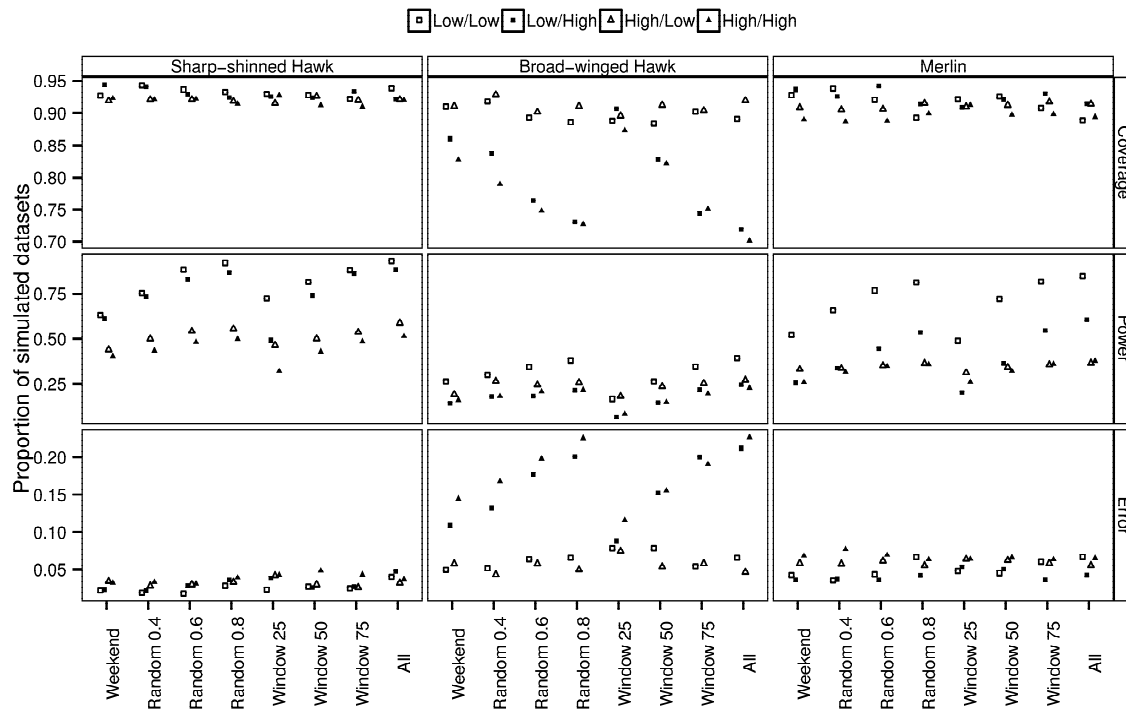
Figure 3-4. Proportion of 1000 simulated datasets where the estimated trend in hourly migration counts had 1) good coverage of confidence limits, 2) good coverage and statistical significance (p≤0.1; 'Power'), and 3) poor coverage and statistical significance ('Error') for 20-year datasets simulated to represent a commonly detected species (sharp-shinned hawk), a super-flocking species with highly over-dispersed counts (broad-winged hawk) and a rarely detected species with zero-inflated counts (merlin). Counts were simulated to have low (triangles) or high (squares) annual variation, and low (no fill) or high (black) daily variation ('annual/daily'), and were subset by sampling weekends, sampling a random sample of 40 %, 60 %, or 80 % of the migration, or by sampling the first 25 %, 50 %, or 75 % of the migration.

3.4   Discussion

With few exceptions, mean bias in the estimated trend was within the suggested acceptable limit of 0.5 %year^{-1} suggested for landbird population monitoring (Bart et al. 2004). Further, bias, coverage of confidence limits and rate of error did not vary greatly among sampling frequencies. Together, this suggests that, with the exception of super-flocking species with highly over-dispersed daily counts, sampling as infrequently as weekends or missing peak migration will not result in a higher probability of drawing false inference from the data than would sampling the entire migration. In contrast, coverage of confidence limits declined and probability of error increased with sampling frequency when counts were over-dispersed with high daily variation. For species with over-dispersed daily counts, randomly sampling 40 % of the migration can minimize bias and the probability of drawing false inference from the data compared with sampling the entire migration, but at the expense of a 22-25 % decline in power using 20-year datasets.

Power to detect a significant trend was in general poor. Power to detect a 3.9 %year^{-1} decline over 20 years was 82-93 % for a commonly detected species with an annual coefficient of variation ≤0.3 and when a minimum of 60 % of the entire migration or 50 % of the migration window were sampled. For a rarely detected and zero-inflated species, power of 81-85 % was detected for 20-year datasets with an annual coefficient of variation of 0.4 when at least 80 % of the entire migration or 75 % of the migration window were sampled. These results suggest that probability of detecting a significant trend was similar or higher than the 80 % power to detect a 3 % decline previously reported using annual raptor counts with coefficient of less than 0.22 (Lewis and Gould 2000). Power would be higher for more extreme rates of change and for longer time series, and in this study power improved with sampling frequency, particularly for the commonly and rarely detected species when annual variation in counts was low.

Given the high variability in hourly and daily migration counts observed when counts were over-dispersed, and the high proportion of 0-observation counts for rarely detected species, aggregating hourly counts into daily or annual totals could improve model fit, and thus improve power and reduce the probability of drawing false inference from the data (Miller et al. 2002, Chapter 4). Incorporating weather or habitat covariates into data analysis can also improve the

precision of annual population indices (Francis and Hussell 1998, Farmer et al. 2007), and in the case that a systematic change in environmental covariates has occurred, their inclusion could model any associated bias in trend. Further, the precision of trends might be more heavily influenced by weather and other environmental covariates when estimated using hourly as opposed to daily counts, particularly when sampling frequency is low (Farmer et al. 2007). The influence of weather covariates on bias and precision of trends should be examined for both hourly and daily migration count data.

Migration counts are assumed to be proportional to the size of the monitored population. However, the specific breeding origin of migrants detected at a site is currently known only broadly. For several songbird species detected across CMMN sites, broad catchment areas were defined using stable hydrogen isotopes in feather samples (Dunn et al. 2006). As data from weather radar (migration volume and direction; Laughlin et al. 2013) and large-scale telemetry studies (stop-over behaviour, migration orientation; Taylor et al. 2011) become more readily available, the breeding origin of migrants can be refined, and trends could then be correlated with underlying changes in habitat or land-use on the breeding grounds. Further, estimation of daily and annual variation in migration route and/or migration volume through a site might be possible, and could be used as covariates to improve precision of trend analyses. Enhancing spatial coverage of the migration corridor by combining data from multiple sites that sample the same larger population could also improve the accuracy and precision of estimated trends by allowing site-specific variation in counts to be estimated independently of underlying change in the count population (Amano et al. 2012, see also Chapters 6,7).

Overall, my results suggest that while sampling the complete migration of a species is preferred to maximize power to detect a trend, probability of false inference is not compromised by sampling less frequently. For species with highly over-dispersed daily counts, the probability of drawing false inference can be minimized by sampling a smaller proportion of the migration window, with little influence on bias if counts are collected randomly throughout the migration. Thus, sites that do not have the volunteer capacity to sample daily throughout the entire migration of each monitored species should not be excluded from trend analyses on this basis alone. Rather, standardization of the timing of sampling within and among migration seasons should be the primary factor influencing whether data are used to estimate trends at each site.

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Chapter 4

4 Temporal aggregation of hourly or daily migration counts can improve accuracy and precision of trends

4.1 Introduction

Population monitoring programs often use temporally or spatially repeated counts of animals to estimate long-term population trends (Link and Sauer 2002, Farmer et al. 2007, Kéry et al. 2009, Fedy and Aldridge 2011). During analysis, counts are often aggregated, for example, by taking the maximum abundance across repeated visits of an assumed closed population (Fedy and Aldridge 2011), or total abundance across assumed independent stops along a survey route (Link et al. 2008). Similarly, hourly or daily counts of the number of individuals migrating past or stopped at a specific geographic location (migration counts), which are assumed to detect a new cohort of migrants during each sampling occasion (Dunn 2005), are also often aggregated to daily or annual total counts in the estimation of long-term trends (Francis and Hussell 1998, Farmer et al. 2007, Knudsen et al. 2007). The temporal aggregation of counts represents a loss of potentially useful information which may impact the accuracy and precision of estimated trends.

Analytical methods to estimate population trends from count data are in a constant state of development (Hochachka and Fiedler 2008, Kéry and Royle 2010, Dail and Madsen 2011, Ross et al. 2012). Methods are now available that can garner information from non-aggregated count data that were lost using previous analysis techniques, including detection probability from repeated counts (Kéry et al. 2009, Kéry and Royle 2010) and home range centers from spatial mark-recapture data (Royle et al. 2013). In the case of hourly or daily migration counts, detection and abundance are confounded and cannot be estimated independently. Thus, the primary information lost by aggregating hourly or daily migration counts to a higher level is information about the hourly and seasonal patterns of migration. Previous work has shown that modeling the seasonal distribution of counts can account for missing observations and improve the precision of long-term trends (Dennis et al. 2013). However, hourly migration counts can result in poor model convergence for rare species with zero-inflated counts, and for super-flocking species, which typically have highly variable and over-dispersed counts (see Chapter

17).   Aggregating counts to a higher level (hourly to daily or annual) can reduce zero-inflation and count variability, and allows one to ignore or 'assume away' temporal auto-correlation (non-independence) of hourly and/or daily counts. Indeed, annual broad-winged hawk counts resulted in more precise (and statistically significant) estimates of trend compared to when data were analyzed as daily counts (Miller et al. 2002).

In the past decade, however, regression techniques that accommodate over-dispersed, zero-inflated and auto-correlated data have become more common and accessible (e.g., Ross et al. 2012). A negative binomial distribution of counts is often assumed when variance is larger than the mean and a zero-inflation parameter can model excess 0-observation counts which arise from true absence or non-detection given presence (Zipkin et al. 2010, Ross et al. 2012). Further, the ability to account for the hierarchical structure of errors among hourly, daily and annual counts and to acknowledge and model temporal autocorrelation of counts can result in more realistic estimates of precision which better reflect the true variability in the data (Ross et al. 2012), benefits which may be lost when counts are aggregated. The effect of aggregating hourly migration counts to daily or annual totals on the precision and accuracy of estimated trends, and whether aggregation is necessary given the more recent development of analytical tools that accommodate over-dispersion and zero-inflation, have not been validated using data with known underlying trend.

In this chapter, I use simulated hourly raptor migration counts with known constant rate of change to test whether and how aggregating hourly counts to daily or annual totals for analysis influenced bias and precision of estimated trends and inference drawn from results. I simulated data for three species, to test whether the effect of aggregating data varied with count distribution: northern harrier (*Circus cyaneus*) was representative of a commonly detected species (hereafter 'common'), broad-winged hawk (*Buteo platypterus*) was representative of a super-flocking species with highly over-dispersed counts (hereafter 'over-dispersed'), and peregrine falcon (*Falco peregrines*) was representative of a rarely detected species with highly zero-inflated counts (hereafter 'zero-inflated'). I assumed a negative binomial distribution of counts, included hierarchical terms to model the temporal autocorrelation of hourly and daily counts, and compared the recovery of simulated trend between models with and without a zero-inflation parameter.

Analyses of raptor population trends for over 50 raptor watch sites by the Raptor Population Index (2015) currently restricts trend analyses to sites that submit hourly migration counts. A large number of sites that historically submitted only daily totals are therefore excluded from trend updates. Results from this Chapter will help inform whether aggregation of migration counts is necessary or recommended to estimate raptor trends given the tools currently available to data analysts, and whether the current restriction of sites based on submission of hourly data is warranted.

4.2 Methods

4.2.1 Real Data

I acquired hourly migration count data online through Nature Counts (2015) for three species detected at Hawk Mountain Sanctuary, Pennsylvania (1966-2010), which represented 1) a commonly detected species with low variation in counts among hours, days and years (northern harrier), 2) a rarely detected species with low magnitude of counts, but intermediate levels of variation in counts among hours and days (peregrine falcon), and 3) a commonly detected, super-flocking species with high over-dispersion of hourly and daily counts (i.e., counts vary widely in magnitude among hours and days; broad-winged hawk). Raptor migration counts were collected as the total number of individuals of each species detected flying overhead on an hourly basis during daylight hours (Barber et al. 2001). I included only the inner 95 %ile of observation days for each species, to exclude outlying observations at the tail-ends of the migration window, where the migration window represents the days of the year when a species typically moves through a site. I then summarized counts to calculate the mean, median and coefficient of variation (CV) of annual, daily and hourly counts, and of the proportion of 0-observation hours and days (Table C 1).

4.2.2 Migration Count Simulation

I simulated 1000 20-year migration count datasets for each of the three species described above in R (R Core Team 2013) using the simulation model described in section 2.2.2 (see Appendix A for simulation code), and chose simulation parameter values (Table A 4) such that simulated data approximated the distribution of real migration count data. All simulated datasets had complete hourly and daily coverage at a site across days and years. However, because sampling coverage

is never complete, particularly at sites dependent on the availability of volunteers for data collection, I dropped a random selection of days and a random selection of hours from the start or end of remaining observation days. I included counts collected on day i and year j (n_{ij}) with binomial probability 0.8 ($n_{ij} = binom(1, 0.8)$), which resulted in approximately 20 % of observation days being excluded from each simulated dataset. For the remaining days, I dropped zero to six hours from the beginning or end of each day according to a Poisson distribution ($nHoursDropped_{ij} = Pois(\lambda_{ij} = 1)$), which allowed a higher proportion of days having no hours dropped, and a decreasing proportion of days having one to six hours dropped from a given day. Hours were dropped from the beginning of the day with binomial probability 0.5, which allowed an approximately equal distribution of days with hours being dropped from the beginning or end of the day. I did not drop hours mid-day, because it is more likely that surveys would either start late or end early on a given day depending on observer availability. I ensured simulated counts approximated the distribution of real counts using quantile-quantile plots (qqplot function, R version 3.0.3).

For each of the 1000 simulated hourly migration count datasets for each species, I aggregated the simulated hourly migration counts into daily and annual totals by summing all counts across days and years, respectively. I corrected daily and annual counts for sampling effort by multiplying the total daily or annual count by the ratio of standardized count hours to observed count hours (Farmer et al. 2007, Bildstein et al. 2008). Thus, the corrected count for year i, day j (C_{ij}) was a product of the observed count, n_{ij}, and the ratio of standardized hours (in this case 8 hours) to the number of hours sampled on a given day ($nhours_{ij}$):

$$C_{ij} = round(n_{ij} \times \frac{8}{nhours_{ij}})$$

For annual counts, the corrected count (C_i), was the product of the observed count, n_i, and the ratio of the total number of standardized hours each year (8 hours×number of days sampled in year i, $ndays_i$) to the total number of observation hours each year ($nhours_i$):

$$C_i = round(n_i \times \frac{8 \times ndays_i}{nhours_i})$$

4.2.3   Data Analysis

I analyzed all simulated datasets in a Bayesian framework using Integrated Nested Laplace Approximation (R-INLA; Rue et al. 2014). Models that assumed a negative binomial count distribution ($y_{ijt} \sim NegBinom(\mu_{jt}, \varphi)$), were compared to models that assumed a zero-inflated negative binomial distribution, where

$$y_{ijt} \sim \begin{cases} 0, & \text{with probability } \rho \\ NegBinom(\mu_{jt}, \varphi), & \text{with probability } (1-\rho) \end{cases}$$

I assumed a negative binomial distribution because migration counts typically have larger variance than the mean, though the negative binomial approximates a Poisson distribution as the variance approaches the mean (Bolker 2008). I fit both data models using log-linear regression, with a fixed year effect to estimate the overall linear trend in counts (Ross et al. 2012). For analyses of hourly and daily counts, the seasonal distribution of counts was also modelled using fixed first and second-order polynomial day and hour terms. Finally, hierarchical terms were included to account for random variation in counts among years, and to account for temporal auto-correlation structure (1st-order auto-regressive, or AR1; Havard et al., 2014) in counts across days nested within years (hourly and daily counts) and across hours in a day (hourly counts). I did not include an AR1 structure on the random year effect because estimated correlation (Rho) of the AR1 effect on year was 1 % or less across all simulated datasets for each species. I back-transformed the year coefficient estimate into a rate of change using $100 \times (\exp(year\ coefficient) - 1)$.

For each species, I tested whether bias (estimated – simulated trend) of the trend estimate varied with count type (hourly, daily or annual) and model structure (negative binomial or zero-inflated negative binomial) using a linear model (lm function; R version 3.0.3) where bias was the response variable (n = 1000 datasets × 3 count types × 2 model structures = 6000 bias estimates), and data type (hourly, daily, annual), model structure (zero-inflated or not) and their interaction were explanatory factors. To determine whether data type and model structure influenced inference drawn from estimated trends, I also assessed for each species, data type and model structure 1) coverage of credible intervals (hereafter 'coverage'), or proportion of simulated

datasets where 95 % credible intervals (CI) included the simulated trend, 2) power, or proportion of simulated datasets with good coverage and CI that did not include zero (i.e. considered 'significantly' different from zero), and 3) type I error rate (hereafter 'error'), or proportion of simulated datasets with poor coverage and CI that did not overlap zero, i.e., probability of a false positive result.

Finally, I used Bayes factor (B = exp(marginal loglikelihood(model 1) – marginal loglikelihood(model 2))) to compare the negative binomial and zero-inflated negative binomial data models and test which was better supported by the data for each species, and whether model selection varied depending on whether data were analyzed as hourly, daily, or annual counts. A Bayes factor greater than three suggests substantial to strong support for the first model in the set, while a value < 1/3 suggests substantial or strong support for the second model in the set. Values between 1 and 3 suggest weak support for the first model, and values between 1/3 and 1 suggest weak support for the second model (Raftery 1996).

4.3 Results

Trends estimated for the common and zero-inflated simulated datasets were least biased using daily counts, with the exception that trends for the common northern harrier estimated using a zero-inflated model on daily counts were positively biased (Table 4-1, Figure 4-1). Hourly counts for the over-dispersed simulated datasets resulted in negatively biased trend estimates (Table 4-1, Figure 4-1). While mean bias of trends did not vary significantly between daily and hourly counts using over-dispersed simulated datasets (Table 4-1), the range in bias values, and therefore the probability of detecting a biased trend, was less using annual counts (Figure 4-1).

For all species and count types, coverage of credible intervals was 89 % or more using the zero-inflated negative binomial model, and 94 % or more using the negative binomial model (Figure 4-2). Error rate was less than 10 % using the zero-inflated negative binomial model, and less than 6 % using the negative binomial model. Across all species, power exceeded 85 % only when datasets of the commonly detected northern harrier were analyzed using hourly or daily counts. Power was also greatest when data for the rare species were analyzed as hourly (50-51 % for the zero-inflated and non-zero-inflated models, respectively) or daily counts (54-55 % for the zero-inflated and non-zero-inflated models, respectively). Compared to daily counts,

analysis of annual counts resulted in a 99 % and 71 % reduction in power to detect a significant trend for common and zero-inflated counts analyzed using a negative binomial model, respectively (Figure 4-2). On the other hand, when over-dispersed counts were fit with a negative binomial model, power increased to 34% when counts were aggregated to annual totals, compared with 25% observed using daily totals.

Table 4-1. Coefficients for the terms explaining variation in bias among estimated trends for datasets simulated to represent a commonly detected species (northern harrier), a rarely detected species with zero-inflated counts (peregrine falcon) and a super-flocking species with highly over-dispersed counts (broad-winged hawk). Trends were estimated using a model that assumed bias varied as a function of count type (hourly, daily or annual), model structure (zero-inflated or not) and their interaction (n = 6000).

	Common (northern harrier)			Rare (peregrine falcon)			Over-dispersed (broad-winged hawk)		
	Est	SE	P	Est	SE	P	Est	SE	P
Hourly	-0.0023	0.0003	<0.001	-0.0036	0.0011	0.001	0.0026	0.0011	0.022
Daily	0.0000	0.0003	0.965	-0.0013	0.0011	0.215	0.0009	0.0011	0.430
Annual	0.0003	0.0003	0.324	-0.0589	0.0011	<0.001	-0.0006	0.0011	0.576
ZINB	0.0002	0.0004	0.598	0.0002	0.0015	0.882	0.0007	0.0016	0.643
Daily:ZINB	0.0027	0.0006	<0.001	0.0024	0.0022	0.262	0.0006	0.0022	0.783
Annual:ZINB	-0.0002	0.0006	0.708	0.0036	0.0022	0.099	-0.0007	0.0022	0.743
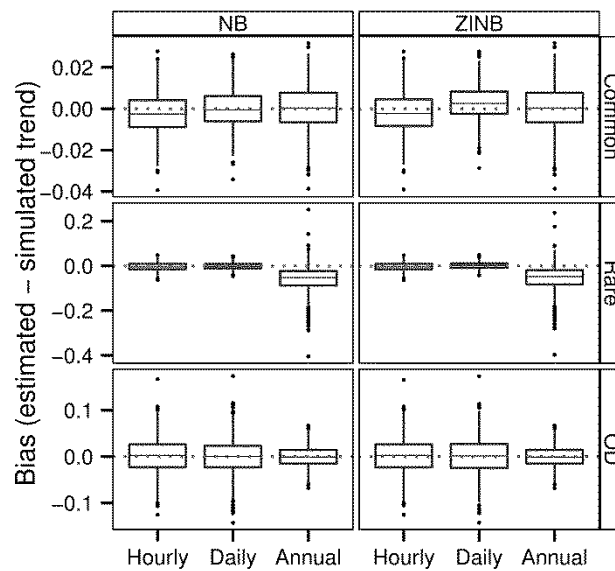
Figure 4-1. Box and whisker plots (n = 1000 each) of bias of estimated trend across datasets simulated to represent a commonly detected species (northern harrier), a rarely detected species with zero-inflated counts (peregrine falcon) and a super-flocking and highly over-dispersed (OD) species (broad-winged hawk), when hourly migration counts were analyzed using raw counts, or aggregated to daily or annual totals. Models that assumed a negative binomial distribution (NB) of counts were compared to models that assumed a zero-inflated negative binomial (ZINB) distribution.
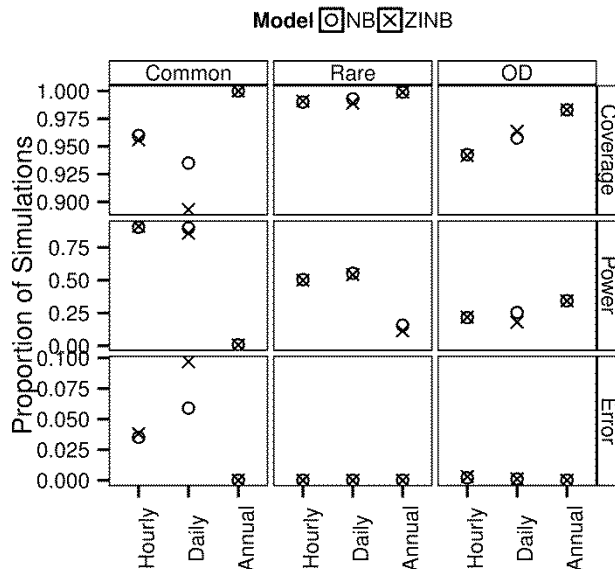
Figure 4-2. Proportion of 1000 simulated datasets where 1) simulated trend fell within the 95 % confidence intervals (CI) of the estimated trend (Coverage); 2) simulated trend fell within the CI of the estimated trend and CI did not include zero (Power); 3) simulated trend fell outside the CI, and CI did not include zero (Error). Results are shown for data simulated to represent a commonly detected species (northern harrier), a rarely detected species with zero-inflated counts (peregrine falcon), and a super-flocking species with highly over-dispersed (OD) counts (broad-winged hawk), analyzed as hourly, daily and annual counts, fit with either a negative binomial (NB) or zero-inflated negative binomial (ZINB) model.

Using Bayes factor as a model selection tool, the zero-inflated negative binomial model had better support than the negative binomial model only when datasets for the commonly detected northern harrier and rare peregrine falcon with zero-inflated counts were analyzed as daily totals (Figure 4-3). However, compared to the negative binomial model, population trends estimated using the zero-inflated model were more positively biased for the commonly detected species when data were analyzed as daily totals, and also had lower coverage of credible intervals and a higher rate of error, which suggests some discrepancy between model selection and model inference.
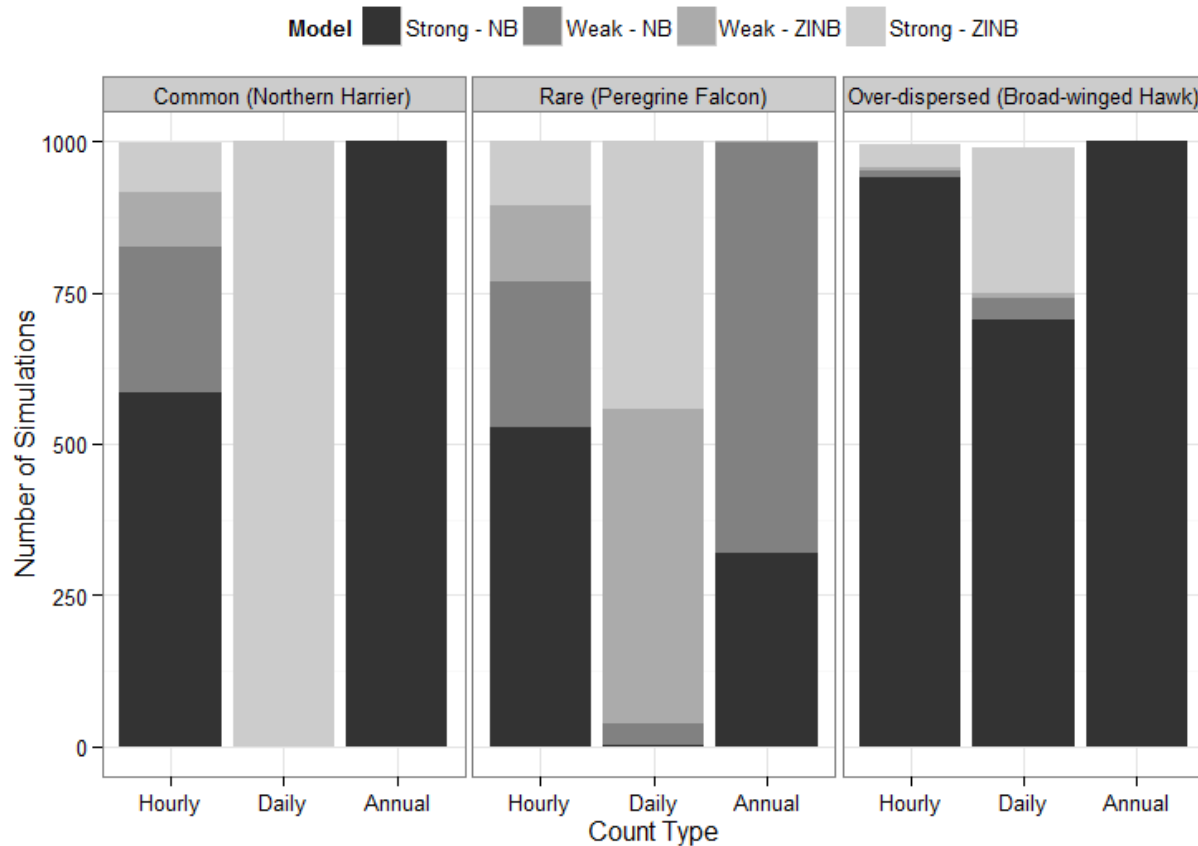
Figure 4-3. Number of simulations where the Bayes factor suggested strong or weak support for the negative binomial and zero-inflated negative binomial models as the best model for analyses of hourly, daily or annual migration counts for Northern Harrier, Peregrine Falcon and Broad-winged Hawk simulations.

4.4 Discussion

Overall, there appears to be little benefit of estimating trends in migration counts using raw hourly totals as opposed to daily totals corrected for effort. While analysis of hourly counts resulted in slightly better coverage of credible intervals and lower rates of error compared to daily counts for the commonly detected northern harrier, differences between hourly and daily counts were minimal. Additionally, probability that the estimated trend will be biased was less when counts for the common and rare (zero-inflated) species were aggregated to daily totals, and when over-dispersed counts were aggregated to annual totals.

Miller et al (2002) found that population trend was more precise when broad-winged hawk data were analyzed as annual as opposed to daily totals, and suggested that large over-dispersion of counts among days was a likely factor. My results support this suggestion, and further support that bias, power and inference drawn from population trend estimates can also be improved by aggregating data to annual totals when counts vary widely in magnitude from day to day. Aggregating counts to annual totals did not have the same benefit for the zero-inflated and commonly-detected species I examined. Peregrine falcon and northern harrier counts did not vary as widely in magnitude and were much less over-dispersed than broad-winged hawk counts. For such common and rare species, including information on the seasonal distribution of counts resulted in higher power and lower probability of drawing false inference from the data than did annual totals.

Power to detect a significant decline of -3.6 %year^{-1} (a 50 % decline in 20 years) was greater than 80 % only for the commonly detected species when data were analyzed as hourly counts or daily totals. The rate of decline simulated was fairly extreme, and is a rate often used to assess population status for species at risk (COSEWIC 2012). Because rare species are typically the ones being assessed for conservation status, these results suggest that raptor migration counts collected over a 20-year period would detect this magnitude of decline only about 50 % of the time for rare species with a mean annual abundance of less than 30 individuals per year (Table C1). Power to detect a significant trend was even less for the highly-over-dispersed broad-winged hawk, despite being counted in large numbers. Despite a low probability to detect a significant trend, rate of error and therefore the probability of drawing false inference from the data was low for all three count distributions.

Power to detect a significant trend would be better for longer time-series and for more extreme rates of population change. Precision of population trends, and therefore power, can also be improved by incorporating environmental or other relevant covariates to account for some of the observed variation in counts (Francis and Hussell 1998). For example, large movements of raptors are often associated with the passage of cold fronts (Hall et al. 1992, Allen et al. 1996), and probability of detecting raptors migrating overhead can also vary with weather conditions (Berthiaume et al. 2009). The effect of including covariates on model fit using hourly or daily counts should be explored, particularly for over-dispersed species like broad-winged hawk,

which may then benefit from being analyzed as daily totals. Combining data across sites assumed to monitor the same source population can also improve power to detect a significant change (Chapter 6).

The use of migration counts to estimate population trends relies on the assumption that the relationship between migration counts and the population they are monitoring has not changed directionally over time. In other words, we assume factors that influence the proportion of the monitored population that is detected each year vary randomly and not systematically over time (see Chapter 5). Annual variability in migration route (Vardanis et al. 2011) or breeding and wintering distribution (Paprocki et al. 2014) in response to climate change or other factors have the potential to bias population trends and can lead to poor inference from results. The analysis of real migration count data needs to take potential sources of bias into consideration, either through the collection of ancillary data (e.g., weather, effort, habitat) to be included as covariates, or, at a minimum, by explicitly stating how potential sources of bias might impact the results reported. Combining various sources of data, including data on the breeding or wintering distribution or abundance, into an integrated population model (Link et al. 2008, Paprocki et al. 2014) also has the potential to improve inference drawn about population trends using migration counts.

There was some discrepancy between results of model selection using the Bayes factor and inference drawn about population trends in terms of bias, rate of error, and power to detect a significant trend. Trends estimated for a commonly detected species using daily totals were positively biased using the zero-inflated model, despite the zero-inflated model having greater support according to the Bayes factor. The zero-inflated negative binomial model resulted in large estimated of precision for the random year effect for these data, which suggests issues with model fit. Accounting for zero-inflation in addition to assuming over-dispersed counts by assuming a negative binomial distribution was likely over-parameterized for the analysis of daily totals for commonly detected species. Indeed, using the simulated datasets for the commonly detected species used here, unpublished data suggests that a Poisson model would result in less biased population trends, a 3 % increase in coverage of CI to 97 %, a 2 % increase in power to 92 %, and a 67 % reduction in the rate of error to 2 % when compared with the negative binomial model fit to daily totals (Crewe, unpubl. data). A Poisson model might also provide a

better fit than the negative binomial when counts are aggregated to annual totals, particularly for commonly detected species that do not vary widely in abundance from year to year. These results highlight the importance of taking model fit characteristics into consideration when interpreting model selection results.

The RPI currently estimates population trends using hourly migration counts, and therefore restricts analysis to sites that submit hourly counts (Crewe et al. 2013). Results, here, suggest that while submission of hourly counts might be preferred and recommended in order to keep track of hourly effort and the specific hours sampled each day, bias, power and error rates can be improved for the majority of species by analyzing daily totals corrected for effort. The inclusion of sites that submit daily totals has the potential to greatly expand the geographic coverage of RPI analyses. However, this suggestion relies on the assumption that daily effort is provided, and that the count period, including the number of hours and which hours were sampled each day, were standardized and did not changed systematically over time. Therefore, while daily totals can be analyzed without consequence to the precision and accuracy of population trends, it is recommended that raptor watch sites continue to submit migration counts in an hourly format to ensure effort can be properly accounted for during analysis.

4.5 References

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Chapter 5

5 Modeling bias in detection probability due to systematic change in stopover duration does not improve trend estimates from migration counts

5.1 Introduction

Daily counts of unmarked animals migrating past or stopped at a specific geographic location (migration counts) have been used as an index of abundance to monitor long term population change, particularly for taxa that breed or winter in inaccessible, unpopulated, or otherwise unmonitored geographic regions (e.g., whales: Findlay et al. 2011; songbirds: Crewe et al. 2008, Blancher et al. 2009; raptors: Bildstein et al. 2008; shorebirds: Drever et al. 2014; insects: Gibbs et al. 2006).   The use of daily migration counts to estimate long-term population trends relies on several assumptions, including that a new cohort of individuals is detected each day, and that the proportion of the monitored population detected remains consistent over time (assumptions of count independence and proportionality, respectively; Dunn 2005, Findlay et al. 2011). The assumption of count independence is likely reasonable for populations counted while actively migrating past a count site, but is more likely to be violated for populations that are counted while on migratory stopover, which for songbirds and shorebirds, can last several days or even weeks (Schaub et al. 2001, Ydenberg et al. 2004, Calvert et al. 2009). Regardless, violation of the assumptions of independence and proportionality are often ignored in analyses of population trends using migration counts (Francis and Hussell 1998, Farmer et al. 2007), because, it is argued, if stopover duration and its influence on probability of detection remains consistent over time, annual indices of population size should provide an unbiased index of population trend.

Many factors contribute variability to the proportion of a population detected by migration counts each day and year. Annual variation in migration route (Alerstam et al. 2006, Vardanis et al. 2011) will influence the proportion of the monitored population present to be detected at a site each year. Stopover behaviour, including daily probabilities of arrival (immigration) and departure (emigration; 1-probability that an individual will 'survive' or remain on site), and therefore stopover duration (Schaub et al. 2001, 2004), can also vary with climate (Calvert et al. 2009), weather (Schaub et al. 2004, Brattström et al. 2008), physiological condition (Schaub et

al. 2008), and presence of predators (Ydenberg et al. 2004). Further, individuals present at a site might be unavailable to be perceived by an observer if they are not visible or vocalizing during the sampling period (Kéry and Schmidt 2008, Kéry et al. 2009, Nichols et al. 2009). In his review of the factors influencing the availability and perceptibility of birds, Johnson (Johnson 2008) suggests season, weather, observer skill, sampling effort and habitat structure are potentially confounding variables.

Unexplained variability in the various components of detection probability can reduce precision of monitoring programs (Nichols et al. 2009), and a systematic bias in probability of detection can violate the assumption of proportionality and lead to false inference of population trends (Ydenberg et al. 2004, Hochachka and Fiedler 2008, Kéry et al. 2009). Counts of unmarked migrants reflect the proportion of the population detected by the sampling protocol (Dunn 2005), and detection probability is not directly estimable from the data. As a result, derivatives of detection probability, including observer skill (Link and Sauer 2002), date or local weather conditions (Francis and Hussell 1998), are often used as covariates in trend analyses to account for their potential influence on the proportion of the migrating population detected during a count. Importantly, a temporal change in stopover duration (Ydenberg et al. 2004, Hochachka and Fiedler 2008, Calvert et al. 2009) in particular has the potential to influence the proportion of migrants that are detected not only once, but also the proportion of migrants that are detected on more than one count occasion, thus violating both the assumptions of proportionality and count independence. Western sandpipers (*Calidris mauri*) stopping over at Sydney Island, British Columbia, Canada, for example, experienced a decline in stopover duration from 8.4 days in 1992 to 2.7 days in 2001 in response to increasing predation risk (Ydenberg et al. 2004). Early migrating warblers captured at a migration monitoring site in Nova Scotia, Canada, also experienced an increase in departure probability from a minimum of less than 0.2 in 1996/1997, to a maximum of approximately 0.8 in 2007 (Calvert et al. 2009), which resulted in a corresponding decline in stopover duration. The effectiveness of using a covariate for probability of detection to improve inference drawn from trends in counts of unmarked migrants when a temporal bias in stopover duration has occurred has not been fully explored.

Using simulated migration count data with known constant rate of change in count population size, I tested whether systematic variation in stopover duration influenced the accuracy and

precision of the estimated trend. I simulated data with previously observed low to high daily probabilities of departure (Calvert et al. 2009) that either remained constant or varied randomly over a 20 year period. I compared results across simulated datasets with a cyclic (e.g. in response to climatic cycles like NOA and ENSO; Calvert et al. 2009) or linear change in departure probability over the same time period. Further, I tested whether any bias in population trend that resulted from a linear change in departure could be modelled by incorporating a covariate for annual departure probability (assuming an independent estimate was available) or by sampling less frequently to reduce the probability of counting the same individual on more than one sampling occasion.

Conservation efforts often rely on broad-scale monitoring programs to provide assessments of population status and trend to guide management efforts (e.g., Rich et al. 2004). In order to use counts of unmarked migrants as a reliable index of population trend, it is important to understand how systematic changes in probability of detection, and in this case stopover duration, influence trend estimates, so that appropriate measures can be taken to model, or provide caution about, these sources of error. Although my simulation is modelled on the biology of a nocturnally migrating songbird, the results are applicable to any species counted on migratory stopover, where counts represent the total number of individuals detected at a count site each day during a migration season over multiple years, and where individuals are unmarked and not individually identifiable (e.g. monarch butterflies: Gibbs et al. 2006; shorebirds: Drever et al. 2014).

5.2 Methods

5.2.1 Migration Count Simulation

Counts of migrating individuals are typically collected daily during a migration. Sampling methods include visual counts of individuals actively migrating past a count site (e.g., raptors: Farmer et al. 2007; whales: Findlay et al. 2011), census or transect counts of individuals on migratory stopover (e.g., monarchs: Gibbs et al. 2006; bees: Robinson 2012; shorebirds: Drever et al. 2014), or as an 'estimated total' derived from a combination of census, visual counts, and daily banding totals from mist-netting, also on migratory stopover (e.g., songbirds; Francis and Hussell 1998, Hussell and Ralph 2005, Crewe et al. 2008). I simulated data for white-throated sparrows (*Zonotrichia albicollis*) counted on migratory stopover using program R (R Core Team

2013; see Appendix D for simulation and parameterization). The total number of individuals migrating and available to be counted in the first year, $n_{i=1}$, was defined such that simulated data approximated the observed mean total count (across years) observed for the species in spring at the tip station of the Long Point Bird Observatory (LPBO), Ontario, Canada, between 1961-2011 (Table E1). Daily estimated total data from LPBO were accessed online (Long Point Bird Observatory 2011), and were collected at that site with the permission of the Ontario Ministry of Natural Resources and Forestry (OMNRF), Bird Studies Canada, and Long Point Bird Observatory, with additional permitting provided by Environment Canada - Canadian Wildlife Service (Permit Number: 10169). All of LPBO field and sampling procedures were approved by the OMNRF Animal Care and Use Committee (Protocol Number: 07-36).

Given the defined size of the count population in the first year, the total number of birds available to be counted in all subsequent years, $n_{i>1}$, was then a function of $n_{i=1}$, a defined constant rate of change (trend), β, random normal error on the log scale (i.e., stochastic variation in annual counts), and Poisson error on the response scale (i.e., process variation in annual counts):

$$n_i = Pois(\lambda_i) = Pois\left(\left(n_{i-1} \times (1 + \beta)\right) + \varepsilon_i\right), \varepsilon_i \sim N(0, \sigma^2).$$

Each year, n_i was distributed across days in a migration season using a Jolly-Seber (JS) simulation model, which required specification of annual population size (n_i), daily probability of arrival into the count site (b_{ij}), daily probability of survival (phi_{ij}) and daily probability of capture (p_{ij}; details of JS simulation in Kéry and Schaub 2011). Daily probability of arrival at the count site was assumed to be highest mid-season during peak migration, and was modelled using a normal density distribution (s) with temporal autocorrelation among days, and Poisson and random error to simulate added variability due to the influence of factors such as local weather conditions on migratory behaviour (Schaub et al. 2004) and arrival probability. The outcome was a Poisson mean 'count', which was transformed into a daily probability of arrival, b_{ij}, by scaling values to add to one. Specifically, the Poisson mean 'count' used to derive b_{ij} was

the product of annual population size (n_i) and a seasonal probability of movement, s, with temporal autocorrelation among days:

$$n_{ij} \sim Pois(\lambda_{ij}) \sim Pois\left(n_i \times s_{ij} \times exp\left(c \times \left(x_{ij} - \frac{j-1}{ndays_i-1}\right) \times npred_{i(j=ndays_i)}\right)\right),$$

where c was a constant, *ndays* was the number of days in the migration season in year i, and *npred* was a function of an autocorrelation coefficient, a, and the previous day's count, i.e.,

$$npred_{i(j+1)} = a \times x_{ij};$$

x_{ij} was derived from the addition of random normal error on *npred*, i.e.,

$$x_{ij} \sim N(npred_{ij}, \sigma^2),$$

and s_{ij} was the product of a normal density distribution and binomial probability of moving:

$$s_{ij} \sim binom(ndays_i, Pm) \times \left((2 \times pi \times sigma)^{-0.5} \times exp\left(-0.5 \times (j-\mu)^{\frac{2}{sigma}}\right)\right),$$

where *Pm* was the probability of migrating on a given day, which remained constant at 0.85.

Daily probability of survival represented the binomial probability that birds 'survived' and remained at the count site until the following day, and is therefore directly related to probability of departure ($1 - phi$), and to stopover duration (Schaub et al. 2001). Survival was simulated to remain constant (0, 0.2, 0.5, 0.7), or to vary 1) randomly, 2) cyclically (5 year cycle), or 3) linearly among years between 0.4-0.5, 0.35-0.55, 0.3-0.6, 0.25-0.65 and 0.2-0.7 (Figure 5-1), but was assumed constant across days in a year. A range in probability of survival between 0.2-0.7 corresponds to the approximate range in mean probability of departure observed for warblers at a migratory stopover site in Atlantic Canada (Calvert et al. 2009), and a linear increase in survival probability from 0.2 to 0.7 over a 20 year period resulted in a range of mean stopover duration from 1.2 to 3.4 days in my simulated datasets (Figure 5-2). A constant survival probability of zero was used as a control to simulate all birds departing after the current day's count, which

ensured independence of daily counts and no detection bias. Daily probability of observer detection, p_{ij}, was assumed constant at 0.30 across days and years.
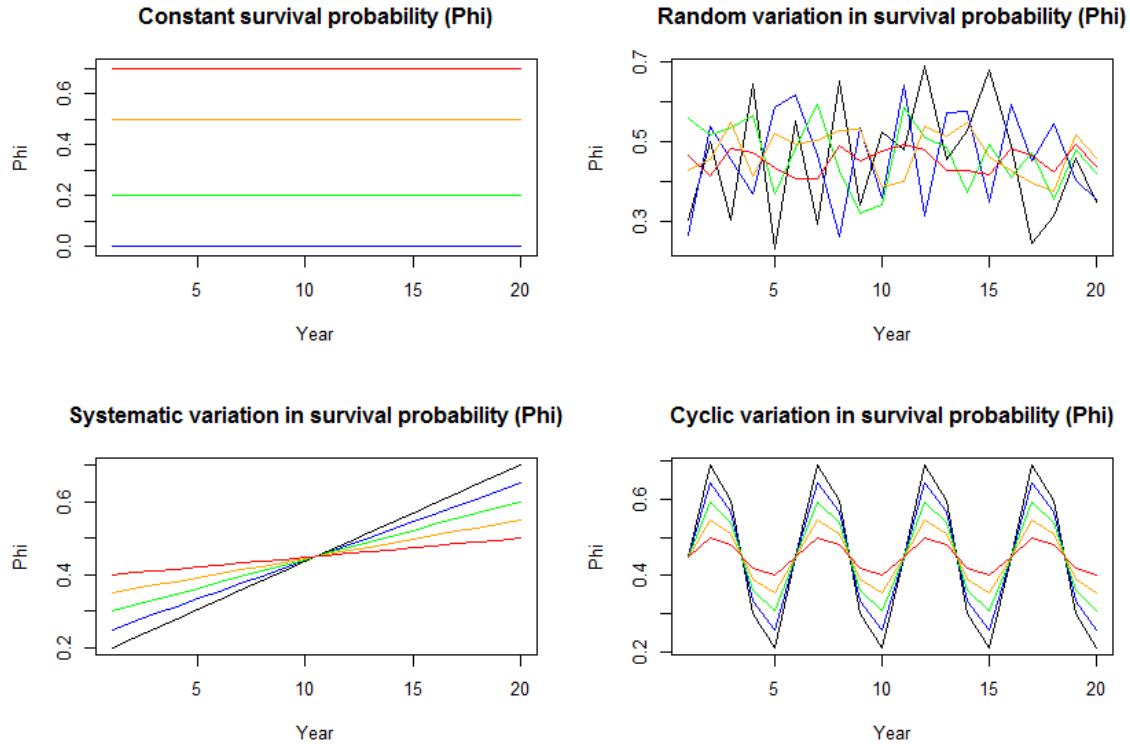
Figure 5-1. Simulated levels and pattern of change in daily probability of survival (*phi*), where *phi* was simulated to remain constant or vary randomly, systematically (linearly) or cyclically over time, but remained constant within a year. Values shown for random variation in *phi* depict one draw from a random uniform distribution. For random, systematic and cyclic variation, *phi* varied between 0.2–0.7, 0.25–0.65, 0.3–0.6, 0.35–0.55, and 0.4–0.5.
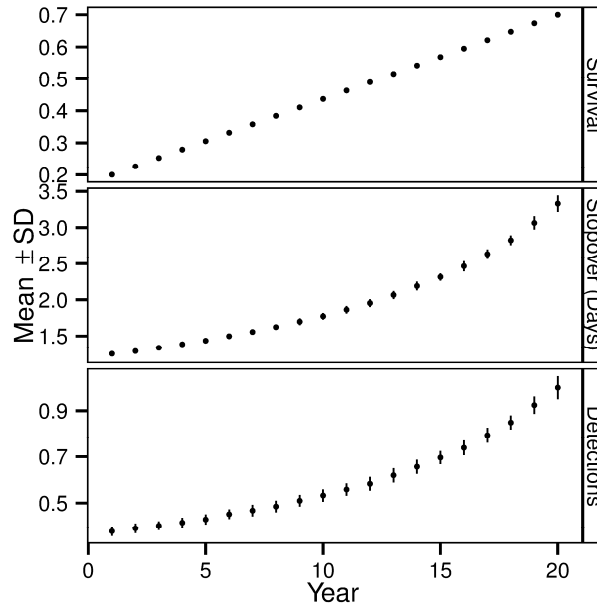
Figure 5-2. Simulated increase in daily survival, and associated increase in mean (SD) stopover duration and number of sampling occasions during which an individual was detected, across 100 datasets simulated to have a linear increase in survival probability from 0.2 to 0.7 over a 20-year period, a constant probability of observer detection ($p = 0.3$), and no underlying trend in population size (0 %year^{-1}).

The realized count on a given year and day (Y_{ij}) was derived using the JS simulation model (Kéry and Schaub 2011), using n_i, b_{ij}, phi_{ij}, and p_{ij} as input, and was the product of the sum of newly arriving individuals and individuals that survived and remained on site following the previous day's count, and the binomial probability of observer detection, given presence. For each level of survival probability examined (4 constant and 5 levels each of random, cyclic or linear change), I simulated 100 datasets for each of three rates of population change: a decline of 20 % in 20 years (-1.2 %year^{-1}), no change (0 %year^{-1}), and an increase of 20 % in 20 years (+0.96 %year^{-1}). Thus, in total, 5,700 white-throated sparrow datasets were simulated and analyzed to estimate population trend.

Simulation parameter values (Table D1) were chosen such that simulated datasets approximated the distribution of real migration count data collected for white-throated sparrow at the tip station of LPBO, Ontario, Canada (1961-2011), in terms of mean and coefficient of variation (CV) of

annual and daily counts, proportion of 0-observation days, and length of the migration season (Tables E2-E7). The distribution of real and simulated count data were compared using quantile-quantile (Q-Q) plots. Correspondence of simulated and real datasets was assessed by visual inspection of Q-Q plots and by testing the Pearson correlation of Q-Q scores. A correlation coefficient near one suggests quantiles of the two datasets originate from a similar distribution of counts, even if one dataset has a higher mean count than the other (Table E8).

5.2.2   Statistical Analysis

Trend in migration counts was estimated for each simulated dataset in a Bayesian framework using integrated nested Laplace approximation using the R package R-INLA (Rue et al. 2014). Counts on day i, year j (Y_{ij}) were assumed to result from a negative binomial distribution, and were fit using a log-linear regression model with a fixed year effect to estimate population trend, and first and second order polynomial terms for day to account for the seasonal pattern of migration. I included hierarchical terms to account for 1) 1st order autoregressive correlation (AR1) of errors among days in a season, and 2) random year effects.   An AR1 model for the random year effect resulted in low autocorrelation (rho) estimates, and was deemed unnecessary for these simulations. The estimated year coefficient was back-transformed into a trend or rate of change (%year^{-1}) using 100×(exp (year coefficient) – 1). Bias in the estimated trend was then the difference between estimated and simulated trends. For simulations with constant probability of survival, I tested whether bias in estimated trend varied among simulated factor levels by fitting a linear regression model that assumed bias (n = 1200) was a function of direction of simulated trend (declining: -1.2 % year^{-1}; no change: 0 % year^{-1}, or increasing: 0.96 % year^{-1}) and survival probability (phi = 0, 0.2, 0.5, 0.7). For simulations where survival was allowed to vary, I fit a linear regression model which assumed bias (n = 4500) was a function of the direction of simulated trend, and an interaction between pattern of change in survival (random, cyclic, or linear) and magnitude of change in survival (phi = 0.4–0.5, ..., 0.2–0.7). All linear regression models were fit using the *lm* function in R (R Core Team 2013).

I tested whether bias in estimated trend could be modeled using a covariate for probability of detection by running the above described log-linear regression model with simulated survival probability as an annual covariate. Regressions were run on datasets simulated to have a linear

increase in survival probability and a declining trend in counts (- 1.2 %year^{-1}) over the 20-year period. Because any bias in estimated trend would result at least partially from an increased probability of counting the same individuals on successive days, I ran the regression on the full simulated dataset (n = 500), as well as on those same datasets subset to every third or fifth observation day, to test whether sub-sampling can reduce bias in trend by lowering the probability that an individual will be detected on more than one count occasion. Using the estimated trends, I then tested whether the addition of a covariate and/or sub-sampling influenced bias in trend by fitting a linear regression model which assumed that bias (n = 1500) was a function of a three-way interaction between magnitude of change in survival (0.4–0.5, ..., 0.2–0.7), whether a covariate for detection probability was included or not, and whether data were subset (no subset, every three days, or every five days).

In addition to bias, I also examined how simulated variation in survival, simulated rate of population change, the use of a covariate for probability of detection, and sub-sampling influenced precision of trend estimates by examining 1) 'coverage' of credible intervals, or the proportion of simulations where the simulated trend fell within the 95 % credible interval of the estimated trend, 2) 'power' to detect a 'significant' trend, or the proportion of simulations with good coverage and credible intervals that did not include zero, and 3) rate of 'error', or the proportion of simulations with poor coverage (simulated trend fell outside the credible interval of the estimated trend) and credible intervals that did not include zero. Rate of error describes the probability that false inference will be drawn from the data.

5.3 Results

When survival was constant, mean bias in estimated trend did not differ among simulated rates of trend or among simulated survival probabilities (Figure 5-3a,

Table 5-1). Coverage of confidence limits was greater than 86 %, rate of error was less than 12 %, but power to detect a significant trend was also low, at less than 6 % (Figure 5-4a).
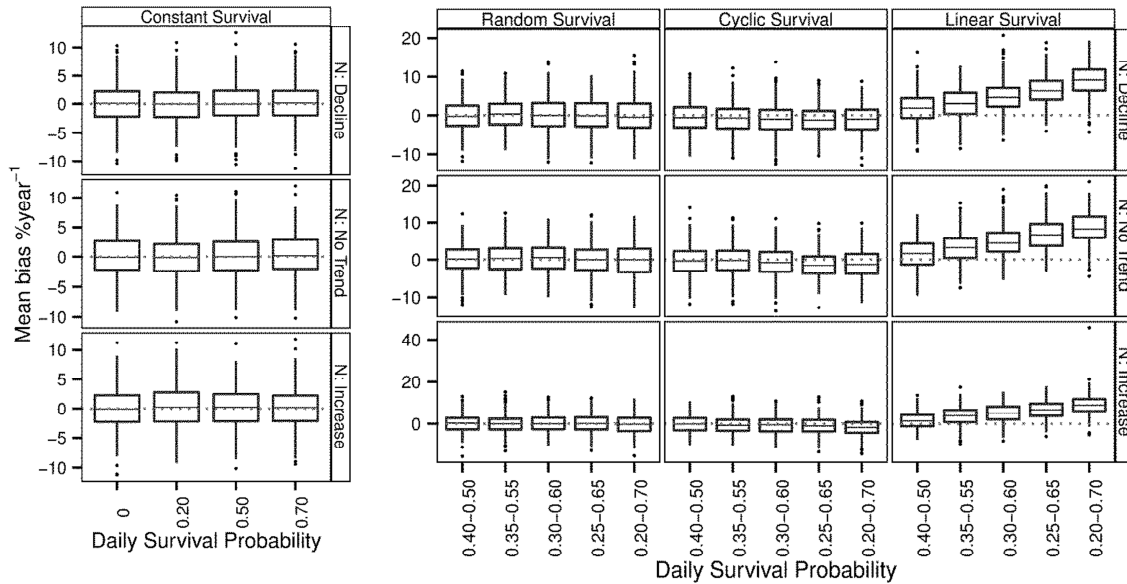
Figure 5-3. Box and whisker plots (n = 100 each) of bias (% year^{-1}) in estimated trend (estimated – simulated trend) in migration counts, when trend was estimated using datasets simulated to have either an increasing trend (0.96 % year^{-1}), no long term trend (0 % year^{-1}) or a declining trend (-1.2 % year^{-1}) in the count population, and where daily probability of survival a) remained constant across years at 0, 0.20, 0.50, or 0.70, or b) varied randomly, cyclically or increased linearly over time between 0.40–0.50, 0.35–0.55, 0.30–0.60, 0.25–0.65 or 0.20–0.70. Lines of the boxplots represent the 25th percentile, median and 75th percentile of bias estimates across 100 simulated datasets. The horizontal dashed line depicts no bias in trend.

Table 5-1. Parameter estimates for a linear model that examined the influence of direction of simulated trend and survival probability on bias of estimated trend, when bias was simulated to remain constant over time.

Parameter	Coeff	SE	t-value	P
Trend: -1.2 %year^{-1}	0.00004	0.0011	0.04	0.97
Trend: 0 %year^{-1}	0.00065	0.0011	0.58	0.56
Trend: .96 %year^{-1}	0.00059	0.0011	0.53	0.60
phi: 0.20	0.00012	0.0013	0.10	0.92
phi: 0.50	0.00110	0.0013	0.83	0.41
phi: 0.70	0.00169	0.0013	1.32	0.19
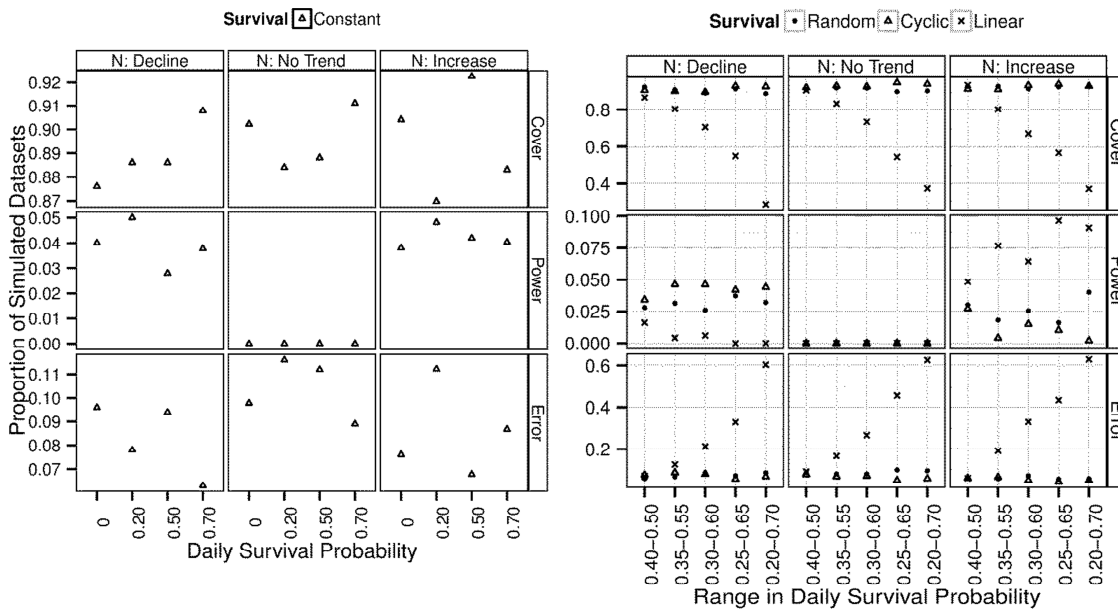
Figure 5-4. Proportion of 100 simulated datasets with good coverage of credible intervals (simulated trend fell within credible intervals of estimated trend), power to correctly detect a 'significant' trend (good coverage; credible intervals did not include zero), and rate of error, or rate of falsely detecting a trend (poor coverage; credible intervals did not include zero). Results are shown for datasets simulated to have a declining trend (-1.2 %year^{-1}), no trend (0 %year^{-1}), or increasing trend (0.96 %year^{-1}) in the count population, and a) a constant survival probability of 0, 0.20, 0.50 or 0.70, or b) random, cyclical or linear variation in survival among years between 0.40–0.50 and up to 0.20–0.70.

When survival was simulated to vary randomly, cyclically or linearly, mean bias in estimated trend also did not differ among simulated rates of trend (Figure 5-3b, Table 5-2). However, compared to when survival varied randomly, trends became increasingly positively biased as the linear bias in survival probability became more extreme, and to a lesser extent, increasingly negatively biased as the amplitude of cyclical change in survival increased (Figure 5-3b,

Table 5-2), due in part to the simulated cycle ending at a lower probability of survival than it began (Figure 5-2). Credible intervals of estimated trends had greater than 85 % coverage and probability of error was less than 10 % when survival varied randomly or cyclically, and when the linear bias in survival probability was low (Figure 5-4b). However, coverage declined to less than 40 % and error increased to over 60 % as the linear bias in survival increased in magnitude (Figure 5-4b) and estimated trends became more positively biased (Figure 5-3b). Power to detect a significant trend was typically less than 5 %, but for datasets simulated to have an increasing population trend, a positive linear bias is survival probability resulted in an increase in power to almost 10 % (Figure 5-4b) due to fewer credible intervals that included zero as estimated trends became increasingly positively biased.

Compared to datasets analyzed without a covariate or sub-sampling, bias in estimated trend was not influenced by sub-sampling data to every third or fifth observation day (Figure 5-5,

Table 5-3). Trends became less biased with the inclusion of a covariate for probability of detection (Figure 5-5), and with both sub-sampling and a covariate. The observed reduction in bias was greater as the positive linear bias in survival increased, most notably when data were subset, and particularly when data were subset to every fifth observation day. Including both a covariate and sub-sampling in the estimation of trends largely compensated for the effect that a positive linear bias in survival probability had on coverage of credible intervals, power and error (Figure 5-6). For all levels of bias in survival probability, coverage was over 85 %, probability of error was less than 20 %, but power to detect a significant trend remained below 5 %.

Table 5-2. Parameter estimates for a linear model that examined the influence of simulated direction of trend, type of variation in survival (random, linear or cyclic) and range in survival probability on bias of estimated trend in migration counts (n = 4500).

Parameter	Coeff	SE	t value	P
Trend: -1.2 %year^{-1}	0.0005	0.0011	0.41	0.68
Trend: 0 %year^{-1}	0.0007	0.0011	0.60	0.55
Trend: 0.96 %year^{-1}	0.0012	0.0011	1.08	0.28
Cyclic Survival	-0.0041	0.0015	-2.83	0.005
Linear Survival	0.0161	0.0015	11.03	<0.001
Phi: 0.35-0.55	0.0016	0.0015	1.11	0.27
Phi: 0.30-0.60	0.0018	0.0015	1.21	0.23
Phi: 0.25-0.65	-0.0006	0.0015	-0.43	0.67
Phi: 0.20-0.70	-0.0019	0.0015	-1.31	0.19
Cyclic Survival: 0.35-0.55	-0.0038	0.0021	-1.84	0.07
Linear Survival: 0.35-0.55	0.0147	0.0021	7.12	<0.001
Cyclic Survival: 0.30-0.60	-0.0054	0.0021	-2.57	0.01
Linear Survival: 0.30-0.60	0.0298	0.0021	14.43	<0.001
Cyclic Survival: 0.25-0.65	-0.0070	0.0021	-3.37	<0.001
Linear Survival: 0.25-0.65	0.0506	0.0021	24.48	<0.001
Cyclic Survival: 0.20-0.70	-0.0082	0.0021	-3.97	<0.001
Linear Survival: 0.20-0.70	0.0737	0.0021	35.54	<0.001
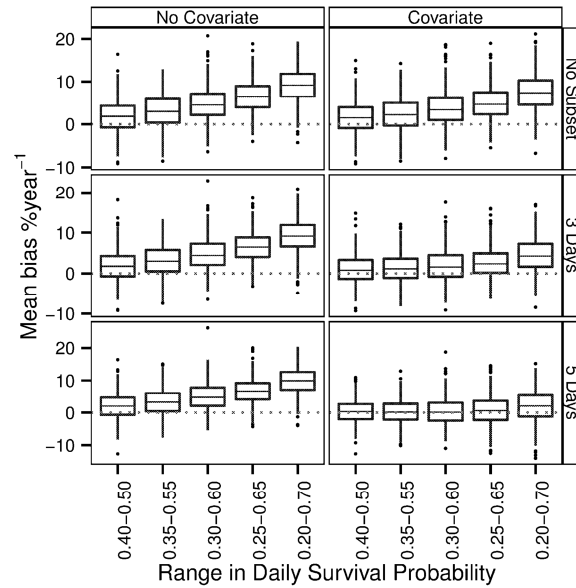
Figure 5-5. Bias (%year^{-1}) in estimated trend (estimated – simulated trend) in migration counts, when trend was estimated with and without a covariate for detection probability, and with and without sub-sampling to every third or fifth observation day. All datasets were simulated to have a declining population trend of 1.2 %year^{-1} and a linear increase in probability of survival between 0.40–0.50, 0.35–0.55, 0.30–0.60, 0.25–0.65 or 0.20–0.70 over a 20-year time series. Lines of the box-plots represent the 25th percentile, median and 75th percentile of bias estimates across 100 simulated datasets. The horizontal dashed line depicts no bias in estimated trend.

Table 5-3. Parameter estimates for a linear model that examined the influence of 1) including a covariate for bias in survival, 2) sub-sampling to every third or fifth observation day, 3) magnitude of change in survival, and 4) their interactions on bias of estimated trend for 20-year white-throated sparrow datasets with a simulated decline in the count population of 1.2 %year^{-1} (n = 1500).

Parameter	Coeff	SE	t value	P
0.40-0.50	0.0188	0.0018	10.565	<0.001
0.35-0.55	0.0310	0.0018	16.997	<0.001
0.30-0.60	0.0477	0.0018	26.772	<0.001
0.25-0.65	0.0648	0.0018	36.377	<0.001
0.20-0.70	0.0906	0.0018	49.852	<0.001
Every 3 Days	-2.2E-05	0.0025	-0.009	0.99
Every 5 Days	0.0012	0.0025	0.493	0.62
Covariate	-0.0033	0.0025	-1.308	0.19
0.35-0.55:Every 3 Days	0.0007	0.0036	0.207	0.84
0.30-0.60:Every 3 Days	0.0006	0.0036	0.166	0.87
0.25-0.65:Every 3 Days	0.0009	0.0036	0.247	0.80
0.20-0.70:Every 3 Days	0.0013	0.0036	0.357	0.72
0.35-0.55:Every 5 Days	0.0006	0.0036	0.156	0.88
0.30-0.60:Every 5 Days	0.0012	0.0036	0.326	0.74
0.25-0.65:Every 5 Days	0.0024	0.0036	0.665	0.51
0.20-0.70:Every 5 Days	0.0061	0.0036	1.711	0.09
0.35-0.55:Covariate	-0.0034	0.0036	-0.95	0.34
0.30-0.60:Covariate	-0.0076	0.0036	-2.131	0.03
0.25-0.65:Covariate	-0.0108	0.0036	-3.039	0.002
0.20-0.70:Covariate	-0.0138	0.0036	-3.851	<0.001
Every 3 Days:Covariate	-0.0057	0.0036	-1.609	0.11
Every 5 Days:Covariate	-0.0124	0.0036	-3.474	<0.001
0.35-0.55:Every 3 Days:Covariate	-0.0059	0.0051	-1.175	0.24
0.30-0.60:Every 3 Days:Covariate	-0.0121	0.0050	-2.401	0.02
0.25-0.65:Every 3 Days:Covariate	-0.0184	0.0050	-3.645	<0.001
0.20-0.70:Every 3 Days:Covariate	-0.0256	0.0050	-5.081	<0.001
0.35-0.55:Every 5 Days:Covariate	-0.0102	0.0051	-2.013	0.04
0.30-0.60:Every 5 Days:Covariate	-0.0237	0.0050	-4.704	<0.001
0.25-0.65:Every 5 Days:Covariate	-0.0346	0.0050	-6.881	<0.001
0.20-0.70:Every 5 Days:Covariate	-0.0489	0.0050	-9.681	<0.001
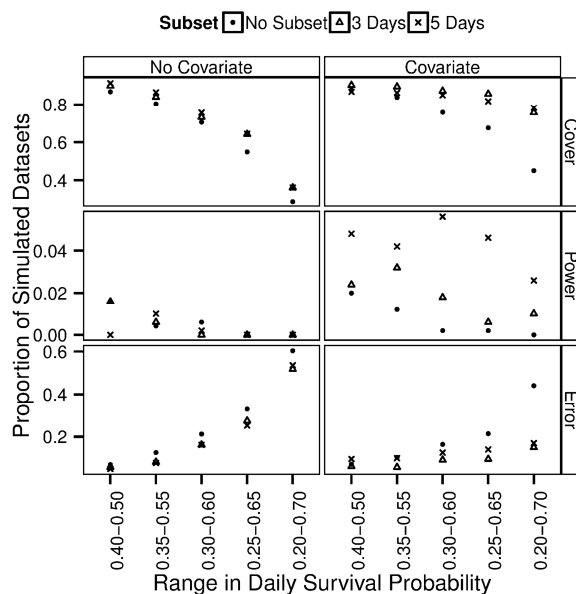
Figure 5-6. Proportion of 100 simulated 20-year white-throated sparrow datasets with 1) good coverage of credible intervals (simulated trend fell within credible intervals of estimated trend), 2) power to correctly detect a 'significant' trend (good coverage; credible intervals do not include zero), and 3) error, or false detection of a trend (poor coverage; credible intervals do not include zero). Results are shown for datasets that were not sub-sampled or sub-sampled to every third or fifth observation day, and when a covariate for probability of detection was or was not included in analysis. Datasets were simulated to have a declining trend in the count population of 1.2 %year^{-1} and a linear increase in daily probability of survival from 0.40–0.50, 0.35–0.55, 0.30–0.60, 0.25–0.65 or 0.20–0.70.

5.4 Discussion

Conservation efforts rely on monitoring programs to guide management priorities through accurate and precise assessments of population status and long-term trend (Rich et al. 2004). However, ecological systems are inherently complex and variable, and in the analysis of time series data, the potential exists for any number of factors to generate a bias in the proportion of a population detected (Kéry and Schmidt 2008, Kéry et al. 2009). If left unaccounted for, a bias in probability of detection can lead to the estimation of false population trends (Hochachka and Fiedler 2008, Kéry and Schmidt 2008, Kéry et al. 2009). My results support the assertion that a violation of the assumption of proportionality through a linear bias in probability of detection, and specifically in daily probability of survival and stopover duration, will bias trends and lead to

a higher probability of drawing false inference from migration count data. As survival probability increased linearly from 0.25 to 0.65 or from 0.20 to 0.70 in 20 years, probability of error, and therefore probability of drawing false inference from the data, exceeded 60 %. Compared to previously observed rates of change in departure probability for early migrating warblers (0.2-0.8 in 11 years; Calvert et al. 2009) and in stopover duration for shorebirds (8.4-2.7 days in 10 years; Ydenberg et al. 2004), the probability of falsely detecting a trend observed here should be considered conservative. To a lesser extent, cyclical variation in survival probability also has the potential to bias estimated trends when the amplitude of fluctuations is large and cycles are not completed during the time span analyzed, which in real situations cannot be known. Random variation in survival did not bias trends, but as expected, the resulting unexplained variation in migration counts did result in lower power compared to when survival remained constant.

In order to improve inference of population trends derived from counts of unmarked animals, monitoring programs often use data on derivatives of detection probability, including weather (Francis and Hussell 1998) and observer (Link and Sauer 2002), as covariates in population trend analyses. However, when the assumption of count independence is violated by a systematic linear change in the length of migratory stopover, my results suggest that a reliance on covariates to model detection probability is not sufficient to improve inference of population trends estimated using daily counts of unmarked migrants. This is true even though the covariate I tested represented the known bias in detection probability without estimation error. As survival probability increased linearly over time, individuals became more likely to stay on site and be detected on an increasing number of sampling occasions. Lacking the ability to exclude recaptures, the resulting inflation or compounding effect on daily counts was not accounted for by a covariate for probability of detection alone. Rather, my results suggest that in order to minimize the probability of drawing false inference from counts of unmarked migrants, analyses of population trends must model the underlying bias in probability of detection, as well as incorporate modifications to the sampling protocol to either exclude 'recaptures' (e.g. only count birds newly arriving at a site) or minimize the probability that individuals will be counted on more than one sampling occasion.

Ideally, monitoring programs would be designed to allow for the direct estimation of probability of detection and recapture. Temporally or spatially replicated counts of territorial animals collected annually, for example, can be used to estimate population trend while explicitly modeling components of detection probability (Kéry and Schmidt 2008, Kéry et al. 2009, Schmidt et al. 2013). This would likely be considered the ideal sampling protocol to monitor population abundance and distribution of commonly detected species with accessible breeding grounds (Kéry and Schmid 2004, Schmidt et al. 2013). However, migration monitoring typically targets species that are either secretive breeders not commonly detected by breeding surveys (e.g., raptors; Farmer et al. 2007), or species that breed in inaccessible, remote locations, where breeding surveys can be logistically or financially unrealistic (Francis and Hussell 1998, Findlay et al. 2011). This is the case for many long-distance landbird migrants that breed in the northern and boreal forests of Canada. A large proportion of the breeding population of many of these species lies north of human populated regions (Bird Studies Canada et al. 2006), and therefore beyond the range of other large-scale monitoring programs (e.g., Breeding Bird Survey; Environment Canada 2014). Migration monitoring has been identified as an important source of data for these northern-breeding populations (Rich et al. 2004).

The use of daily capture-recapture sampling protocols to monitor migrating populations would allow recaptures to be excluded and variability in stopover parameters that influence probability of detection (e.g., trapability, survival) to be modeled and accounted for when estimating population trends (Hochachka and Fiedler 2008). Currently, a majority of member sites of the Canadian Migration Monitoring Network (CMMN), which focuses primarily on monitoring populations of long-distance landbird migrants, do collect banding data in addition to daily estimated totals (Crewe et al. 2008). For species that are detected in sufficient numbers, the use of banding data to estimate population trends using mark-recapture analyses that account for probability of detection (Hochachka and Fiedler 2008) should be considered a preferred alternative to estimating trends using counts of unmarked animals. However, a majority of species that pass through migration count sites are not captured in sufficient numbers to be analyzed in a mark-recapture framework (Hochachka and Fiedler 2008, Calvert et al. 2009). Indeed, this is a primary reason why Hussell and Ralph (1998, 2005) recommend combining multiple count methods into a daily estimated total for migratory landbird monitoring. The use of two or more count methods to derive a daily estimated total allows a greater number of

species to be detected in numbers sufficient for analysis, and allows counts to be estimated during poor weather conditions when nets used for banding are typically closed (Hussell and Ralph 1998, 2005).

In order to improve estimates of population trend using counts of unmarked migrants, I recommend the collection of independent data on all of the components of probability of detection to be included either as covariates in population trend analyses, or as components of the underlying models themselves. For example, incorporating radar and acoustic monitoring data into estimates of daily migration volume (Buler and Dawson 2014, Sanders and Mennill 2014) could be profitable. In addition, stopover parameters (e.g. stopover duration) could also be estimated for a given species or species group using local band recoveries (Hochachka and Fiedler 2008, Calvert et al. 2009), large-scale automated telemetry arrays (Taylor et al. 2011), or other mark-recapture techniques. Finally, the probability of observer detection given presence at a count site could be modeled either through the collection of independent data on sampling effort or observer skill (Link and Sauer 2002), or through the use of double observer or other repeated sampling approaches (Johnson 2008, Berthiaume et al. 2009, Drever et al. 2014). Where independent data on probability of detection are not available, correlates (e.g., weather) should be used as covariates in trend analyses (Francis and Hussell 1998).

When individuals are known to stop at a count site for extended periods of time and recaptures cannot be excluded from daily counts, the incidence of multiple-counting should be addressed through sub-sampling or other modifications to the sampling protocol. Hussell and Ralph (1998, 2005) suggest recording and subtracting the number of probable or known stopovers from daily counts of migrating landbirds, which can be calculated directly from band recoveries (where available) or estimated based on observer knowledge of the count site and individuals present. At sites where stopover duration is typically short and independent data on stopover parameters are collected, the omission of days with a low estimated probability of departure should also be tested for its effectiveness in reducing both the incidence of multiple counting and bias of estimated population trends. Compared to sub-sampling, the latter method has the potential to minimize a reduction in sample size and therefore power. Count sites should also be placed in locations with a high turnover of migrants, such as exposed coastal sites that funnel migrants but are considered poor quality stopover habitat, to reduce the probability that extended migratory

stopovers will occur (Hussell and Ralph 1998, 2005). Alternatively, modifications to analytical methods can also address a bias in stopover duration. Population trends for migrating shorebirds, for example, are often calculated using an estimate of annual abundance derived from the total number of individuals observed (or estimated) from daily counts, corrected by average length of stay (Bishop et al. 2000, Drever et al. 2014). This method assumes an annual estimate of stopover duration is available, and that all individuals present are observed (Bishop et al. 2000). Thus, as opposed to an index of abundance, this method provides an estimate of the total number of individuals using a site each year, and is highly sensitive to estimated length of stay (Bishop et al. 2000).

Overall, statistical power of my analyses was low, at approximately 10 % or less to detect a 20 % change in 20 years. Typical of migration counts, white-throated sparrow counts collected at Long Point, and simulated here, were highly variable both within and among years (Tables E1-E4). A similar analysis of population trends using counts of western sandpipers on migratory stopover in British Columbia, Canada, resulted in power to detect a minimum rate of change of 3.2 %year^{-1}, or approximately 55 % in 20 years (Drever et al. 2014), which is over double the rate of population change in my simulated data. A power of 80 % to detect a 50 % decline in 20 years with a significance of 0.1 was suggested as a goal for landbird population monitoring (Bart et al. 2004). The low rate of population change simulated here highlights the impact that a bias in probability of detection can have on the interpretation of time series data when populations are stable or changing at a low rate relative to the bias in detection probability. The relative impact of a given bias in probability of detection on inference drawn about population trends will decline as rate of population change increases. Future work should assess the minimum rate of population change required to achieve a pre-determined level of power given the magnitude of detection bias and count variability simulated here or observed elsewhere (Hochachka and Fiedler 2008, Calvert et al. 2009). Further, the sensitivity of various rates of population change to the different magnitudes of detection bias should also be explored. In general, power can be improved and probability of error will decline with the use of covariates, by increasing the length of the time series, and by combining data across migration count sites that are assumed to monitor the same population. The latter would allow site-specific variation in counts, including variation in probability of detection, to be estimated independently from underlying population change. Because different sampling protocols will be subject to different sources of detection

bias (Johnson 2008), the use of standardized sampling protocols across sites is recommended. In addition, the assumption of proportionality is more likely to be violated as the length of a time series increases, which further emphasizes the importance of accounting for annual and daily variability in probability of detection through the use of covariates or other method.

All sampling methods are susceptible to various potentially interacting sources of detection bias (Hochachka and Fiedler 2008, Johnson 2008). While standardization of sampling protocols is important to minimize the probability that a bias in probability of detection will occur, not all sources of variability in probability of detection can be controlled or effectively measured. The recommendation for stable habitat structure at a migration count site (Hussell and Ralph 2005), for example, is rarely achieved, and can have important implications on bird behaviour and detection probability (Harrison et al. 2000). Mark-recapture sampling protocols provide an ideal means to monitor migrating populations while accounting for variation in detection probability (Hochachka and Fiedler 2008), but unless analyzed in a guild context, sample-size requirements exclude rare species that are often the primary focus of conservation efforts. Further, even though migration counts provide only an index of population abundance that is confounded by detection probability, correspondence between bird population trends derived from migration counts and the North American Breeding Bird Survey supports their use (Francis and Hussell 1998, Farmer et al. 2007). Thus, while I recommend the collection of additional data to model detection probability, the absence of relevant covariates for probability of detection should not preclude the use of migration counts for population trend analyses. Rather, in the absence of additional information on detection probability, population trends estimated using migration counts should simply state clearly and openly whether and how variation in factors known to influence stopover behaviour and detection might influence inference drawn about long-term population change.

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Chapter 6

6   Application of model selection to quantify regional population trends using migration counts

6.1   Introduction

Broad-scale population monitoring provides information on whether and how populations are changing over time (Bildstein et al. 2008, Bled et al. 2013). For government and other organizations that are mandated or otherwise engaged in the conservation of biodiversity or species at risk, population monitoring plays an integral role in determining whether management decisions and species recovery efforts are having their anticipated effect (Conrad and Hilchey 2011). However, for many broad-scale monitoring programs, data collection is biased towards accessible and human-populated regions (Dunn and van Strien 1995, Bled et al. 2013). An example is the more northern regions of Canada's boreal forests, which are not well sampled by the North American Breeding Bird Survey (BBS) and other broad-scale bird monitoring programs (Peterjohn et al. 1995, Dunn 2005). A large proportion of the breeding population of many migratory bird species inhabits these unmonitored regions of the boreal forest (Blancher and Wells 2005), and at least 40 species are considered inadequately sampled by the BBS (Rich et al. 2004). Northern waterthrush, for example, was detected with highest probability in the northern boreal forests of Ontario (Bird Studies Canada et al. 2006), but long-term BBS trends for Ontario were derived from the southern portion of their breeding range (Environment Canada 2014), where probability of detection was low, and potentially not representative of the entire breeding range.

An alternative approach to the more costly prospect of conducting breeding bird surveys in those largely unpopulated and remote regions, migration monitoring typically comprises a standardized daily count of individuals migrating past or stopping over at a particular geographic location while individuals move to or from their breeding grounds (Francis and Hussell 1998, Farmer et al. 2007, Drever et al. 2014). The Canadian Migration Monitoring Network (CMMN; Crewe et al 2008) is a network of approximately 25 independent sites situated primarily across southern Canada that collect counts of migrating landbirds. Feather isotope analysis and band recoveries suggest that the current composition of sites is sufficient to sample the entire

Canadian breeding range of many species (Dunn et al. 2006), and at site-specific scales, correspondence of songbird and raptor population trends with BBS (Francis and Hussell 1998, Farmer et al. 2007, Crewe et al. 2008) supports their use for population monitoring.

However, migration counts can be highly variable within and among sites due to the influence of extrinsic factors such as local weather, climate and habitat quality on annual migration route (Vardanis et al. 2011), stopover behaviour (Schaub et al. 2004, Calvert et al. 2009), and probability of detection (Berthiaume et al. 2009). Further, because the exact geographic breeding and wintering origin of migrants is unknown and varies among sites and among species at each site (Dunn *et al.* 2006), extrinsic factors influencing sub-populations, and thus underlying rates of sub-population change, are also likely to vary among regions, resulting in the potential for species- and region-specific patterns of population change. Partially as a result of these uncertainties, population trends estimated using migration counts in North America have been site-specific to date (Bildstein et al. 2008, Crewe et al. 2008).

In this paper, I assess whether, in the absence of prior information on whether and how population trends vary among regions, model selection using Akaike's Information Criterion (AIC; Burnham and Anderson 2002) can be used to select among a set of competing models, the model that best describes underlying regional patterns of population trend when data are pooled across a network of migration monitoring sites such as the CMMN. Specifically, I used simulated migration count data with known constant rate(s) of population trend, which may or may not vary among regional sub-populations, to determine whether I can rely on model selection procedures to select the correct model structure for the data, given current or increased numbers of stations in each geographic region or given current or increased number of years surveyed. I also examine whether and how increasing the number of sites in a region and number of years surveyed influences precision and accuracy of population trends, power to detect a significant trend, and rate of error (probability of detecting a significant but incorrect trend) when: 1) model assumptions match simulated data, and 2) model assumptions do not match simulated data (e.g., population trend does not vary regionally, but the model assumes it does). I simulate data for both a rare and a more abundant and commonly detected species to test whether results vary with count size and proportion of 0-observation counts in the data.

6.2 Methods

6.2.1   Migration Count Simulation

I simulated migration count data using a probability-based simulation (R version 3.0.2, R Core Team 2013); see Appendix F for simulation code and parameterization). The simulation model assumed that migration counting sites within a region monitored the same sub-population, and that the count population at a migration monitoring site was a consistent and representative sample of regional population size. I either fixed the properties of sub-populations (population size and trend) to be the same, or to vary among sub-populations/regions.

The total simulated number of birds (n) available to be counted in each region (j) in the first year (i), $n_{i=1, j=1...nregions}$, was defined by the simulation function. Because I assumed that regions sampled discrete sub-populations, regional abundance in all subsequent years, $n_{i>1,j}$, was a function of starting regional population size and a region-specific constant rate of population change, β_j:

$$n_{i=2...nyears,j} = n_{i-1,j} \times (1 + \beta_j)$$

Site specific annual population size was then a function of a multinomial distribution with size equal to regional abundance each year, n_{ij}, and with probability P_{ijk} that birds would move through site k in region j in year i. Site-specific random normal error was added on the log scale (i.e., site-specific stochastic variation in counts):

$$\log(\hat{n}_{ijk}) = \log(multinom(n_{ij}, P_{ijk}) + \varepsilon_{ijk}), \ \varepsilon_{ij} \sim N(0, \sigma^2).$$

Annual variability in site-specific population size can result from annual variation in migration route, stopover probability, probability of detection, or other factor (Alerstam et al. 2006, Hochachka and Fiedler 2008, Calvert et al. 2009, Vardanis et al. 2011), for example in response to climatic cycles (e.g., ENSO cycles; Calvert et al. 2009).

Because migration counts are collected daily across a migration season, I simulated site-specific daily migration counts, n_{ijkl}, to be a function of $\hat{n}_{ijk}$ and a probability that birds were available to migrate through a site on a given day, P_{ijkl}, where P_{ijkl} assumed a normal density distribution

to allow peak migration to occur mid-season. Of those individuals available to migrate each day, the number that actually migrated depended on a binomial probability of migrating (given available), Pm_{ijkl}, which was generated as a uniformly distributed random variable with added Poisson variability to simulate the temporal autocorrelation among days in a season which often results from weather fronts:

$$n_{ijkl} \sim binom\left((\hat{n}_{ijk} \times P_{ijkl}), Pm_{ijkl}\right), \quad P_{ijkl} \sim N\left(\mu_{ijk}, \sigma^2_{ijk}\right),$$

where μ_{ijk} and σ_{ijk} varied with site, region and year to simulate site-specific annual variation in the timing and distribution of available birds across days in a migration season. Below a given 'bad migratory weather' threshold, I forced $Pm_{ijkl} = 0$, and no birds migrated. All birds available to migrate were then carried forward to the following day's total number of birds available to migrate, which allowed the number of available birds to build up and add the extra variability typically observed with migration counts.

Finally, the expected daily count at a site each year was a function of n_{ijkl}, random normal error (stochastic variation) on the log scale, and Poisson error (process variation) on the response scale:

$$\hat{n}_{ijkl} = Pois\left(\lambda_{ijkl}\right) = Pois(n_{ijkl} + \varepsilon_{ijkl}), \quad \varepsilon_{ijkl} \sim N(0, \sigma^2)$$

Random error in daily migration counts represented variability in the observed count due to factors such as local weather conditions, which can influence both daily stopover behaviour (Schaub et al. 2004, Calvert et al. 2009) and daily probability of observer detection ((Berthiaume et al. 2009). Because stopover and detection probabilities are confounded, they cannot be estimated independently.

The simulation model also assumed the following: 1) daily counts were an independent sample of the migrating population, or in other words, all birds departed the count site within 24 hours; 2) birds moved through all sites at the same time each year, with site- and year-specific random error around mean start date; and 3) all sites had consistent and complete seasonal coverage of a species' migration window, i.e., the time of year when a species typically migrates through a site. While in practice these assumptions may not be met (particularly that daily counts are

independent), in the absence of systematic change, violation of these assumptions will not bias long-term population trends (Chapter 5).

6.2.2   Simulated Factor Levels

I simulated migration count data for two boreal-breeding songbirds: Canada warbler (*Cardellina Canadensis*) and white-throated sparrow (*Zonotrichia albicollis*). White-throated sparrow is commonly detected in large numbers across most of the CMMN network (Table 6-1), whereas Canada warbler was chosen as representative of a rare species, detected in low numbers across most of the network (Table 6-2). For each of the two species, I simulated data from four regions (sub-populations), and varied the 'true trends' for each region under the following three trend-scenarios: 1) '1-trend', sub-population trends did not vary among regions (-1.2 %year^{-1}, or 20 % decline in 20 years in all regions); 2) '2-trends', sub-populations in two regions declined by 1.2 %year^{-1}, and in the other two regions sub-populations increased by 0.96 %year^{-1} (or 20 % increase in 20 years); or 3) '4-trends', sub-population trends varied among all regions (-3.6 %year^{-1}, or 50 % decline in 20 years in region 1; -1.2 %year^{-1} in region 2; +0.96 %year^{-1} in region 3; and +2.1 %year^{-1}, or 50 % increase in 20 years, in region 4). Under each trend-scenario, I varied the number of sites per region (3, 5, or 10 sites) to test the sensitivity of model selection and trend precision and accuracy to the number of sites sampled in a region. Finally, for each of the nine combinations of trend-scenarios and numbers of sites per region, I also varied the distribution of the starting population among regions and sites by modifying the starting regional population size $n_{i=1,j}$, and the multinomial probability P_{ijk} that birds in region j moved through site k. The starting population size in the first year was distributed in one of two ways: 1) equal distribution, i.e., equally among regions and equally within regions, among sites, or 2) unequal distribution, i.e., unequally among regions and unequally within regions, among sites. For simulated datasets with unequal abundance, I distributed abundance among regions and sites such that simulated data approximated mean regional and site abundance observed using real CMMN data (Table 6-1Table 6-2). Abundance varied widely among sites, particularly for white-throated sparrow, with an average annual abundance of less than 50 individuals in the western region, and over 6000 individuals in the central region (Table G2). Such high variability in counts among sites might reflect variation in the proportion of the overall population moving through a site and/or variation in the proportion of the population that is detected at each site,

including the probability that birds will migrate over and stop at a site, and given presence at a site, the probability that birds are available and perceived by an observer during the sampling period (Kéry and Schmidt 2008, Nichols et al. 2009). Because abundance and probability of detection are confounded using daily migration counts, I assumed that probability of detection was constant among sites and over time. For each of the 36 combinations of factors (3 trend types × 3 levels of sites per region × 2 abundance distributions × 2 species = 36 factor levels), I simulated 100 iterations of a 40-year time-series (i.e., I simulated 3600 40-year datasets), which I analyzed using the first 20 or all 40 years, in order to test how well model selection procedures could detect the appropriate model structure under these two time frames.

Table 6-1. Mean (coefficient of variation) of annual regional population size, annual site-specific population size, daily count, proportion of 0-observation counts, length of migration window, and estimated standard deviation of random year and day nested within year effects for White-throated Sparrow data collected at member sites of the Canadian Migration Monitoring Network. Regional summaries were calculated using data collected during fall migration from 2008-2010, and site-specific summaries were calculated using the last 6 years of data collected at each site. Site Codes are defined in Table 10.

Region	Site	Annual Population Size (Region)	Annual Population Size (Site)	Mean Daily Count (Site)	Proportion 0-Obs Days	Ndays/ year	SD Random Year Effect	SD. Random Day/Year Effect
Eastern	ATBP	2234 (0.36)	265 (0.72)	3.84 (2.84)	0.58 (0.11)	74	0.18	3.10
Eastern	ATSI		174 (1.12)	3.93 (2.35)	0.56 (0.4)	59	1.00	2.40
Eastern	MGBO		1753 (0.39)	19.25 (1.2)	0.16 (0.53)	90	0.13	0.75
Eastern	OOT		109 (0.53)	1.44 (1.9)	0.48 (0.4)	86	0.22	1.10
Central	BPBO	6461 (0.55)	496 (0.7)	7.45 (2.09)	0.44 (0.39)	67	0.65	1.90
Central	LPBO-1		1401 (0.27)	21.81 (1.83)	0.22 (0.49)	66	0.26	2.30
Central	PEPBO		656 (0.17)	11.19 (1.37)	0.28 (0.27)	60	0.02	1.40
Central	PIBO		756 (0.46)	11.23 (1.53)	0.25 (0.4)	67	0.27	1.10
Central	TTPBRS		2160 (1.07)	25.23 (1.42)	0.39 (0.81)	69	6.40	1.30
Prairies	BBO	909 (0.31)	45 (0.81)	1.46 (2.42)	0.67 (0.3)	37	0.66	1.80
Prairies	DMBO		832 (0.58)	15.03 (2.15)	0.52 (0.22)	58	0.60	2.00
Prairies	LMBO		120 (0.62)	2.28 (2.25)	0.6 (0.22)	52	0.25	1.50
Prairies	LSLBO		208 (0.31)	2.72 (1.04)	0.25 (0.37)	80	0.07	0.49
Prairies	TCBO		207 (0.79)	3.51 (1.18)	0.34 (0.61)	61	0.51	0.81
Western	MNO	32 (0.23)	57 (0.76)	1.5 (1.48)	0.46 (0.42)	37	0.19	0.84
Western	RPBO		7 (0.54)	0.25 (2.32)	0.79 (0.13)	37	0.00	0.00
Western	VLMMS		4 (1.49)	0.12 (3.47)	0.92 (0.12)	34	0.00	0.00
	Mean	2409 (0.36)	544 (0.67)	7.78 (1.91)	0.47 (0.37)	61	0.67	1.34

Table 6-2. Mean (coefficient of variation) of annual regional population size, annual site-specific population size, daily count, proportion of 0-observation counts, length of migration window, and estimated standard deviation of random year and day nested within year effects for Canada Warbler data collected at member sites of the Canadian Migration Monitoring Network. Regional summaries were calculated using data collected during fall migration from 2008-2010, and site-specific summaries were calculated using the last 6 years of data collected at each site. Site Codes are defined in Table 10.

Region	Site	Annual Count Population (Region)	Annual Count Population (Site)	Mean Daily Count (Site)	Proportion 0-Obs Days	Migration Window (n days)	Std. Dev. Random Year Effect	Std. Dev. Random Day/Year Effect
Eastern	ATBP	34 (0.45)	7 (0.56)	0.16 (3.25)	0.89 (0.06)	45	0.12	0.00
Eastern	MGBO		28 (0.5)	0.41 (2.58)	0.79 (0.13)	68	0.00	0.79
Central	BPBO	145 (0.23)	4 (0.35)	0.12 (3.06)	0.89 (0.03)	34	0.00	0.00
Central	LPBO-1		49 (0.34)	0.96 (1.98)	0.65 (0.09)	58	0.19	1.60
Central	PEPBO		37 (0.62)	1.14 (1.65)	0.54 (0.18)	32	0.00	1.00
Central	PIBO		34 (0.22)	0.63 (2.03)	0.69 (0.11)	53	0.00	0.63
Central	TTPBRS		25 (0.95)	0.77 (1.78)	0.76 (0.29)	32	0.57	2.00
Prairies	BBO	263 (0.11)	2 (0.72)	0.08 (4.05)	0.92 (0.06)	27	0.68	0.00
Prairies	DMBO		28 (0.4)	0.72 (1.77)	0.65 (0.1)	40	0.13	1.80
Prairies	LMBO		38 (0.56)	1.11 (2.02)	0.64 (0.14)	33	0.07	1.00
Prairies	LSLBO		173 (0.2)	3.19 (1.25)	0.32 (0.21)	54	0.06	0.56
Prairies	TCBO		78 (0.49)	1.58 (2.15)	0.61 (0.08)	49	0.21	1.20
	Mean	148 (0.26)	42 (0.49)	0.91 (2.3)	0.69 (0.12)	44	0.17	0.88

6.2.3   Real Data Summary

I accessed daily estimated total counts for Canada warbler and white-throated sparrow collected at 17 member sites of the CMMN online through Nature Counts, a node of the Avian Knowledge Network (Nature Counts 2015; Table 6-3). Details of data collection methods at each site are described elsewhere (Canadian Migration Monitoring Network 2014). I restricted data to site-specific 95 % migration windows, which limited data to those days of the year that contained the inner 95th percentile of observation counts across all years, with the purpose to omit excess 0-observation counts at the tail-ends of the migration window. I also restricted data to fall migration in order to maximize the number of sites included in my analyses, and because fall migration counts have been shown elsewhere to be a more reliable index of annual population size (Knape et al. 2011).

Table 6-3. Number (n) and span of years that migration counts were collected during spring and fall migration by member sites of the Canadian Migration Monitoring Network. Only sites that submit Daily Estimated Totals in one or both seasons are shown.

Site Name	Site Code	Province	Region	Spring			Fall		
				n	Min	Max	n	Min	Max
Atlantic Bird Observatory - Bon Portage	ATBP	Nova Scotia	Eastern	11	1997	2007	11	1997	2007
Atlantic Bird Observatory - Seal Island	ATSI	Nova Scotia	Eastern	5	1997	2001	11	1997	2007
McGill Bird Observatory	MGBO	Quebec	Eastern	6	2006	2011	6	2006	2011
Observatoire d'Oiseaux Tadoussac	OOT	Quebec	Eastern				17	1996	2012
Bruce Peninsula Bird Observatory	BPBO	Ontario	Central	13	2000	2012	13	2000	2012
Innis Point Bird Observatory	IPBO	Ontario	Central	15	1997	2011			
Long Point Bird Observatory - Tip	LPBO1	Ontario	Central	50	1961	2012	52	1961	2012
Long Point Bird Observatory - Breakwater	LPBO2	Ontario	Central	49	1961	2012	50	1961	2012
Long Point Bird Observatory - Old Cut	LPBO3	Ontario	Central	32	1980	2012	33	1980	2012
Prince Edward Point Bird Observatory	PEPBO	Ontario	Central	17	1995	2011	11	2001	2011
Pelee Island Bird Observatory	PIBO	Ontario	Central	9	2003	2011	9	2003	2011
Tommy Thompson Park Bird Research Station	TTPBRS	Ontario	Central	9	2004	2012	9	2004	2012
Beaverhill Bird Observatory	BBO	Alberta	Prairies	20	1992	2011	20	1992	2011
Delta Marsh Bird Observatory	DMBO	Manitoba	Prairies	5	2006	2010	18	1993	2010
Last Mountain Bird Observatory	LMBO	Saskatchewan	Prairies	19	1994	2012	20	1993	2012
Lesser Slave Lake Bird Observatory	LSLBO	Alberta	Prairies	18	1994	2011	18	1994	2011
Thunder Cape Bird Observatory	TCBO	Ontario	Prairies	18	1995	2012	18	1995	2012
Mackenzie Nature Observatory	MNO	BC	Western				17	1996	2012
Rocky Point Bird Observatory	RPBO	BC	Western				14	1998	2012
Vaseux Lake Migration Monitoring Site	VLMMS	BC	Western				12	2001	2012

I categorized CMMN sites into four geographic regions, which were meant to represent groups of sites monitoring the same sub-population of each species: western, prairies, central, or eastern (Table 6-3). Because the exact breeding or catchment area of species migrating through each CMMN site is at present known only broadly through the use of feather-isotope analyses (Dunn et al. 2006), I recognize that classification of sites into regions was somewhat coarse. I estimated mean and coefficient of variation (CV) of region-specific total counts using a limited number of years (2008-2010) when a maximum number of sites (11, Table 6-1, Table 6-3) collected data. I estimated mean and CV of site-specific daily counts using the last six years of data collected at each site (Table 6-1, Table 6-2). In order to estimate realistic levels of standard deviation of random year and day effects, I used the complete fall dataset at each site to fit a log-linear regression model (INLA, R-package version 0.0-1399439934, Rue et al. 2014) for each species, which assumed a log-normal Poisson distribution of counts (Elston et al. 2001), constant rate of change, and which included hierarchical terms to account for stochastic year and day by year effects. I also included fixed first and second-order day effects to model the seasonal movement of birds. I used the resulting estimates of standard error for the random annual and day effects as approximate inputs for the standard error of the normal distributions of simulated random year and day effects. I chose all other simulation parameters (Table F1) to maximize the concordance of real and simulated count distributions using quantile-quantile plots (qqnorm, stats package, R version 3.0.2), and the similarity between real and simulated data of: mean and CV of daily counts, mean and CV of 0-observation days, and length of the migration window.

6.2.4   Statistical Analysis

I estimated a population trend for each simulated dataset using log-linear regression models (lme4, R package version 1.1-6, Bates et al. 2013) that assumed counts on day i, year j, at site k in region l (Y_{ijkl}) resulted from an overdispersed or log-normal Poisson distribution by including a hierarchical term to account for over-dispersion at the observation level (Elston et al. 2001). I also included a hierarchical term to account for stochastic variation in annual counts nested within site, and fixed first and second order polynomial terms for day to account for the seasonal pattern of migration. For each dataset (n = 2 species × 3 trend scenarios × 3 site levels × 2 abundance distributions × 2 year lengths × 100 simulated replicates = 7200 datasets), I used AIC (lme4, R package version 1.1-6) to compare three models with increasing complexity: 1) a model

with a national population trend, that assumed abundance did not vary among regions, i.e., a single slope and intercept ('national - 1 int' model); 2) a model with a national population trend that allowed abundance to vary with region, i.e., region-specific intercepts and a single slope ('national - 4 int.' model); and 3) a model that assumed region-specific abundance and population trend, i.e., region-specific intercepts and slopes ('regional' model; Table 6-4). Neither of the above models matched the assumptions of 2-Trend simulated datasets exactly (Table 6-4), but the regional model was considered most appropriate because it allowed population trend to vary among the four regions. Including '2-trend' datasets allowed us to test how inference drawn about population trends was influenced when the ideal model was not included in the set of competing models.

Table 6-4. Structure (intercept and slope) of 'correct' model structure for each trends type (1, 2, or 4) and abundance distribution (equal, unequal) simulated. Note that datasets with two simulated rates of population change ('2 Trend') were nevertheless simulated to have four regions, and so were best fit by the varying slope and intercept model.

Trend	Model Name	Abundance Distribution	Linear model for Year and Region	# Regions (Intercepts) Assumed	# Trends (Slopes) Assumed
1 Trend	National – 1 Int	Equal	Year	1	1
	National – 4 Int	Unequal	Year + Region	4	1
2 Trend	Regional – 4 Int	Equal	Year*Region	4	4
		Unequal	Year*Region	4	4
4 Trend		Equal	Year*Region	4	4
		Unequal	Year*Region	4	4

I assessed the use of model selection to detect the underlying pattern of regional population change by calculating the proportion of simulated datasets where the correct model was ranked as the top or a competing model (ΔAIC $\leq$2; Burnham & Anderson 2002) for each species and factor level. I then fit a separate generalized linear model for each species to test whether the binomial probability that the correct model was ranked as either the top or a competing model varied as a result of number of sites in a region (3, 5, or 10), number of years (20 or 40), trend type (1-, 2-, or 4-Trends), abundance distribution (equal or unequal), species, and the interaction

between trend type and number of sites, and number of years and number of sites (n = 7200 simulations × 3 model structures = 21,600; glm, stats package, R version 3.0.2).

Using trends estimated for 1-, 2-, and 4-trend simulated datasets using the model that best matched the assumptions of the data, I tested the effect of increasing the number of sites and years surveyed on accuracy and precision of population trends by fitting linear regression models (lm, stats package, R version 3.0.2) which assumed a Gaussian distribution, with either bias (estimated – simulated trend) or the log of standard error of the trend estimate as a response variable (n = 7200 each), and where number of years, number of sites, abundance distribution, trend type, species and the interaction between number of years and sites were predictor variables. Standard errors were log-transformed to better approach normality. I also fit linear regression models (Gaussian distribution) to estimated bias and the log standard errors of 1-trend simulated datasets estimated using the correct and incorrect model structures, to test whether bias and precision of population trends (n = 7200) varied depending on whether data were fit with the correct model (correct national, incorrect national, or incorrect regional model), and with number of sites in a region, number of years surveyed, abundance distribution and interactions between whether model was correct and abundance distribution, and between number of years and sites.

Finally, for the above two scenarios (1-, 2- and 4-trend datasets fit with the correct model, and 1-trend datasets fit with the correct and incorrect models), I calculated and compared among simulated factor levels a) power, i.e., proportion of 100 simulated datasets where the simulated trend fell within the confidence limits of the estimated trend, and was statistically significant at p < 0.1, and b) type I error rate, i.e., proportion of 100 simulated datasets where the simulated trend fell outside the confidence limits of the estimated trend, when the estimated trend was statistically significant at p < 0.1. I used p < 0.1 following the recommendation of Bart et al. (2004) for estimating trends in landbird abundance.

6.3 Results

6.3.1 Model Selection

The probability that the correct model was ranked as a top or competing model did not vary with number of sites in a region or with length of the time series (Figure 6-1a,b,

Table 6-5), with the exception of 2-trend datasets, where the probability that the correct and more highly parameterized regional model was ranked as a top or competing model increased with the number of sites in a region, particularly for 20-year white-throated sparrow simulated datasets (Figure 6-1b). This effect was apparent for 20-year but not 40-year 2-trend simulated datasets. The correct (regional) model was ranked as a top or competing model 100 % of the time for 40-year 2-trend datasets and 100 % of the time for 20-year (unequal abundance) and 40-year (equal and unequal abundance) 4-trend datasets, regardless of the number of sites in a region (Figure 6-1a,b).
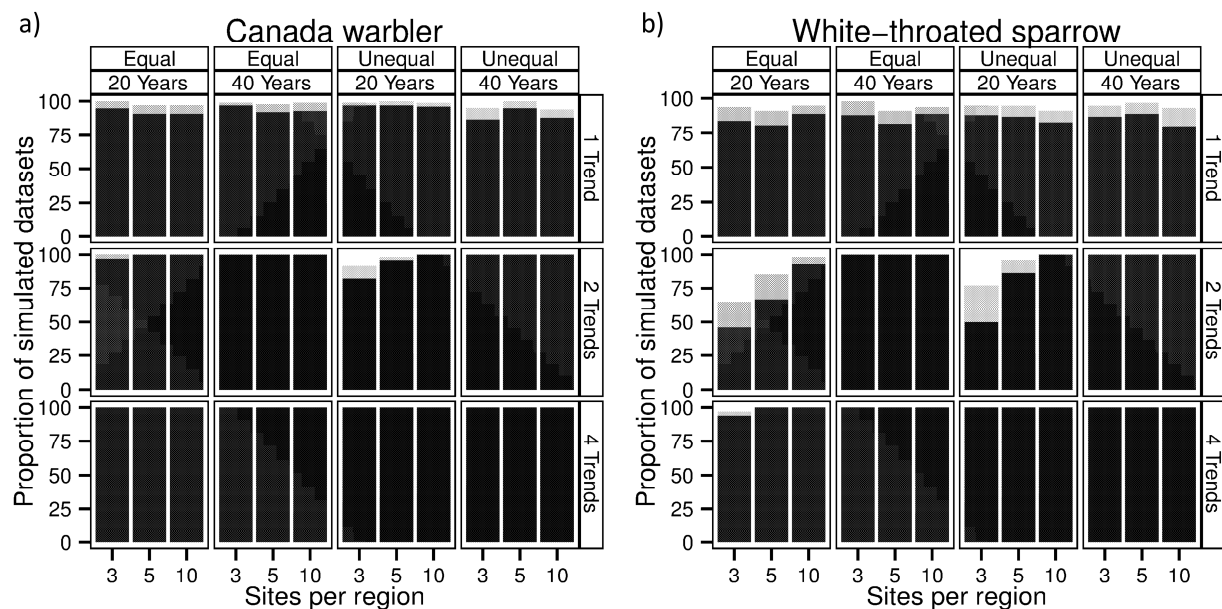
Figure 6-1. Proportion of 100 a) Canada warbler and b) white-throated sparrow simulated datasets where the model that most closely matched the assumptions of simulated data was ranked as the top (black) or a competing (grey) model using Akaike's Information Criterion (AIC). Models were considered competing if ∆AIC ≤2. Plots compare 20- and 40-year simulated datasets with either a similar rate of population change across all regions ('1-trend'), two regions experiencing the same rate of decline, and two regions experiencing the same rate of increase ('2-trends'), or all regions experiencing a different simulated rate of population change ('4-trends'). Abundance was distributed equally or unequally among regions and sites.

Table 6-5. Coefficient estimates for a model that tested whether the binomial probability that the correct model was ranked as a top or competing model (ΔAIC ≤2) by AIC varied with species, number of trends simulated (1, 2, or 4), number of sites in a region, length of time series, and with interactions between number of sites and number of trends and number of sites and length of time series (n = 21,600).

Parameter	Est	SE	z value	P
1 Trend	4.18	0.30	14.15	<0.001
2 Trend	7.19	0.75	9.59	<0.001
4 Trend	21.71	607.40	0.04	0.971
N Sites = 3	-0.15	0.32	-0.47	0.636
N Sites = 5	-0.19	0.31	-0.60	0.547
Abundance: equal	-0.20	0.15	-1.31	0.190
White-throated sparrow	-1.61	0.19	-8.27	<0.001
N Years = 40	0.00	0.33	0.00	1.000
2 Trend:N Sites = 3	-4.13	0.77	-5.37	<0.001
4 Trend:N Sites = 3	-15.34	607.40	-0.03	0.980
2 Trend:N Sites = 5	-2.60	0.78	-3.32	0.001
4 Trend:N Sites = 5	-0.23	852.70	0.00	1.000
N Sites = 3:N Years = 40	2.00	0.45	4.46	<0.001
N Sites = 5:N Years = 40	1.05	0.46	2.29	0.022

The correct model was more likely to be ranked as the top or a competing model for 4-trend datasets than for 1- and 2-trend datasets. For 1-trend datasets, the correct national model was ranked as the top model 87-97 % of the time for Canada warbler and 81-89 % of the time for white-throated sparrow, regardless of the length of time series, number of sites in a region, or distribution of abundance (Figure 6-1). Thus, for 1-trend datasets, the more highly parameterized and incorrect regional model was consistently ranked as the top model a small proportion of the time for both species, regardless of the number of sites in a region or length of

the time series (Figure 6-1).   The probability that the correct model was ranked as a top or competing model did not vary with abundance distribution.

6.3.2   Model Assumptions Match Simulated Data

Using the model that best matched the assumptions of the simulated data (Table 6-4), mean bias in population trends was significantly less for longer time series, when abundance was distributed equally as opposed to unequally, for 2-Trend compared with 1- and 4-Trend datasets, and for white-throated sparrow compared to the rare Canada warbler (Figure 6-2, Table 6-6), though effect sizes were all less than ±0.1 %/year.   Mean bias did not vary with the number of sites in a region. Despite little difference in mean bias among simulated factor levels, the tighter distribution of bias estimates using 40-year datasets, and to a lesser extent with an increase in the number of sites in a regions (Figure 6-2), suggests that the probability of estimating a strongly biased trend was lower using longer time series and when more sites were sampled in each region.

Standard errors of the trend coefficients were significantly less, and precision of the trend estimates greater, for longer time series, when a greater number of sites were sampled in each region, when abundance was distributed equally as opposed to unequally among regions and sites, for Canada warbler compared with white-throated sparrow and for 1-trend compared to 2- and 4-trend datasets (Figure 6-3, Table 6-7). The higher precision of 1-trend datasets is owed at least partly to the greater degrees of freedom available to estimate a single trend versus four regional trends using a similar sized dataset.

For 1-trend 20- and 40-year Canada warbler simulated datasets, a slight positive bias in population trends combined with an increase in precision of trends with number of sites sampled, resulted in a corresponding decline in power and increase in error rate with number of sites sampled in each region (Figure 6-4). Otherwise, power tended to increase with the number of sites sampled in a region for 20-year datasets of both species. Increasing the time series to 40 years was more effective at achieving >80 % power for both species than was increasing the number of sites in each region. Error rates were typically less than 10 %, with the exception of 20-year 1-trend Canada warbler simulations, where error increased with the number of sites in a region to >25 % when 10 sites were simulated in each region (Figure 6-4).
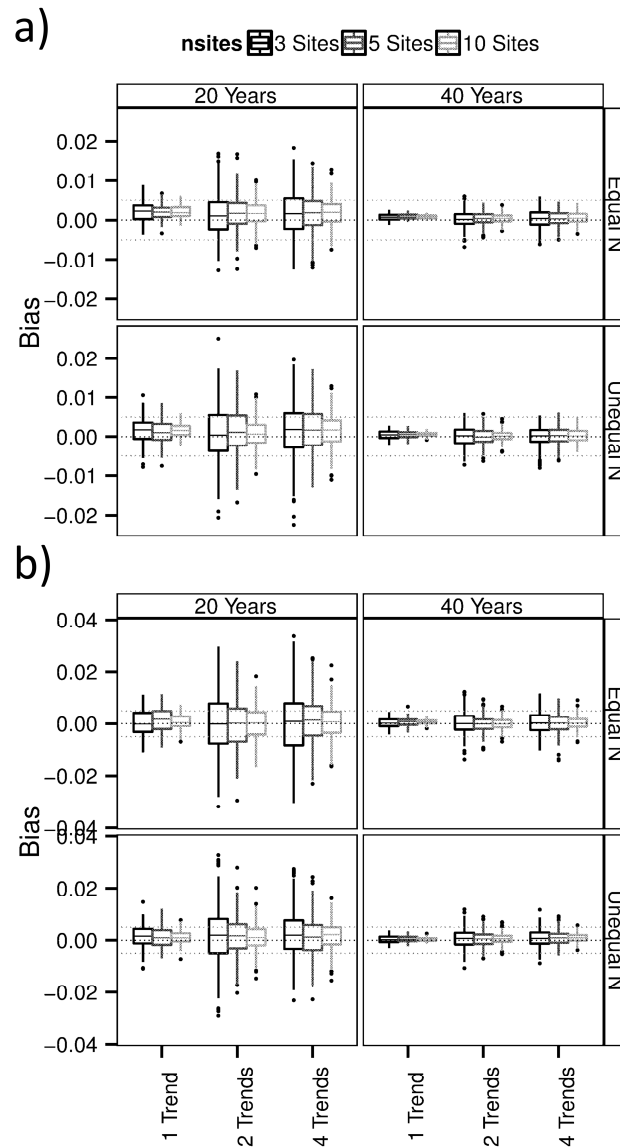
Figure 6-2. Box and whisker plots (n = 100 each) showing bias (estimated – simulated trend) of population trends for 20- and 40-year a) Canada warbler and b) white-throated sparrow simulated datasets, when data were fit with a model that most closely matched the assumptions of simulated data. Plots compare datasets simulated to have a similar rate of population change across all regions ('1-trend'); two regions experiencing the same rate of decline, and two regions experiencing the same rate of increase ('2-trends'); and all regions experiencing a different simulated rate of population change ('4-trends'). Abundance was distributed equally or unequally among regions and sites.

Table 6-6. Coefficient estimates for a model that tested whether bias in population trend varied with length of time series, number of sites in a region, species, abundance distribution, number of trends simulated, and an interaction between number of years and number of sites, for simulated datasets that were fit with the model that best matched the assumptions of the data (n = 7200).

Parameter	Est	SE	t value	P
Intercept	0.0013	0.0001	10.00	<0.001
N Years = 40 Years	-0.0008	0.0001	-7.16	<0.001
N Sites = 5	0.0001	0.0001	1.22	0.22
N Sites = 10	0.0000	0.0001	0.10	0.93
White-throated sparrow	-0.0002	0.0001	-2.82	0.005
Unequal N	0.0002	0.0001	3.52	<0.001
2 Trends	-0.0003	0.0001	-2.80	0.005
4 Trends	0.0000	0.0001	-0.25	0.78
N Years = 40 Years:N Sites = 5	-0.0002	0.0002	-1.05	0.29
N Years = 40 Years:N Sites = 10	0.0000	0.0002	0.23	0.82
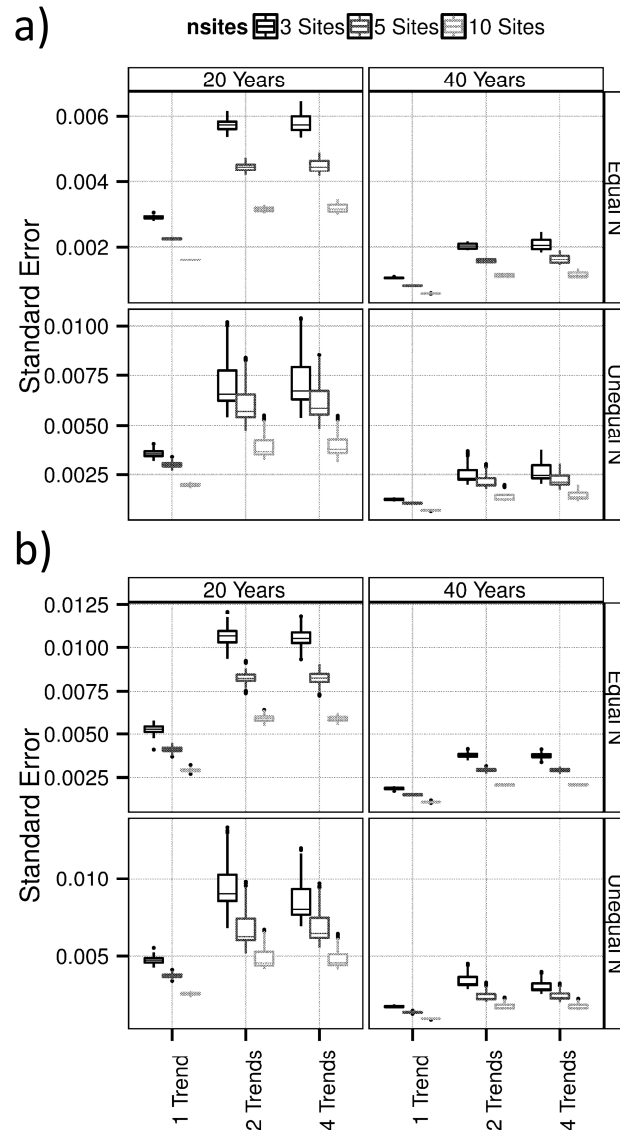
Figure 6-3. Box and whisker plots (n = 100 each) showing variation in standard error of population trends estimated for 20- and 40-year a) Canada warbler and b) white-throated sparrow simulated datasets, when data were fit with a model that most closely matched the assumptions of simulated data. Plots compare datasets simulated to have a similar rate of population change across all regions ('1-trend'); two regions experiencing the same rate of decline, and two regions experiencing the same rate of increase ('2-trends'); and all regions experiencing a different simulated rate of population change ('4-trends'). Abundance was distributed equally or unequally among regions and sites.

Table 6-7. Coefficient estimates for a model that tested whether standard error in population trend varied with length of time series, number of sites in a region, species, abundance distribution, number of trends simulated, and an interaction between number of years and number of sites, for simulated datasets that were fit with the model that best matched the assumptions of the data (n = 7200).

Parameter	Est	SE	t value	P
Intercept	-5.74	0.004	-1333.94	<0.001
40 Years	-1.03	0.004	-276.74	<0.001
5 Sites	-0.23	0.004	-62.19	<0.001
10 Sites	-0.60	0.004	-159.74	<0.001
White-throated Sparrow	0.39	0.002	182.63	<0.001
Unequal N	0.04	0.002	16.74	<0.001
2 Trends	0.68	0.004	189.13	<0.001
4 Trends	0.68	0.004	189.52	<0.001
40 Years :5 Sites	0.005	0.005	-0.87	0.38
40 Years:5 Sites	-0.01	0.005	-1.10	0.27
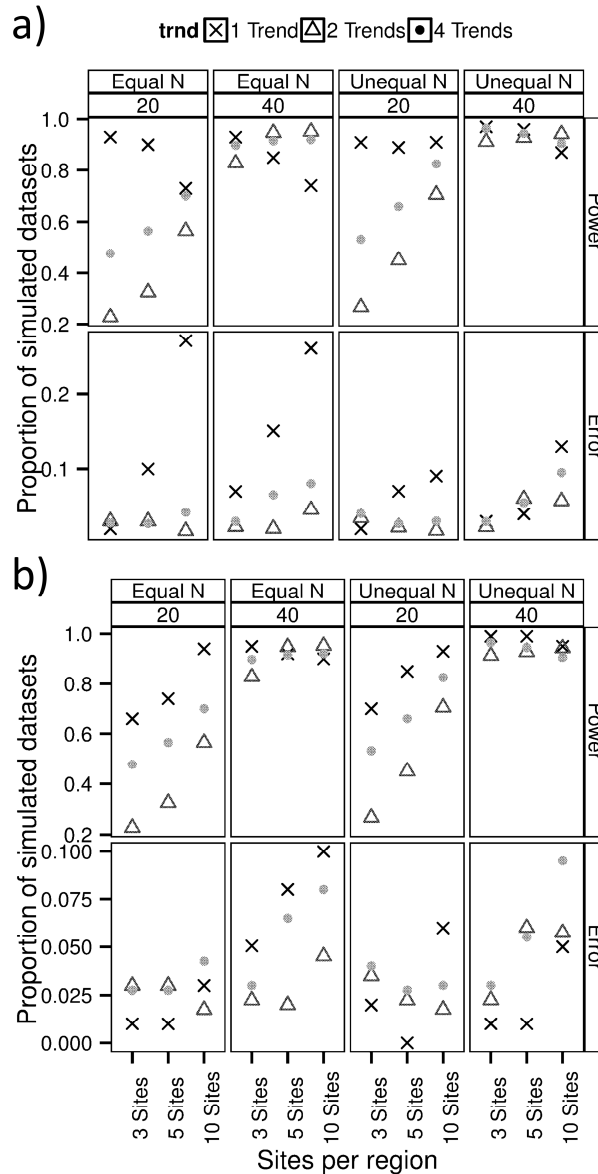
Figure 6-4. Proportion of 100 a) Canada warbler and b) white-throated sparrow datasets, fit with a model that most closely matched the assumptions of the data, where 1) simulated population trend fell within the 95 % confidence limits of the simulated trend (P < 0.1; 'Power'), and 2) estimated population trend was significant (P < 0.1), but confidence limits did not include the simulated trend ('Error'). Plots compare datasets simulated to have a similar rate of population change across all regions ('1-trend'); two regions experiencing the same rate of decline, and two regions experiencing the same rate of increase ('2-trends'); and all regions experiencing a different simulated rate of population change ('4-trends'). Abundance was distributed equally or unequally among regions and sites.

6.3.3   Model Assumptions do not Match Simulated Data

Mean bias and precision of population trends did not differ among 1-trend datasets analyzed using the correct or incorrect national model structure, for example, 1-trend datasets with equal abundance analyzed using the 'national - 4 int' model instead of the correct 'national - 1 int' model (Tables 6-8, 6-9, Figures 6-5, 6-6). Mean bias of population trends estimated for 1-trend datasets using the incorrect and more highly parameterized regional model also did not differ from mean bias estimated using the two national model structures. However, both the probability of estimating a biased trend (broader range in estimated bias values [Figure 6-5]), and the standard error of trend estimates (Figure 6-6), were both greater when data were analyzed using the more highly parameterized model structure.

Bias in population trends also tended to decline with an increase in the length of the time series but effect sizes for the effect of number of years, number of sites, abundance distribution and species on bias were small ($<\pm0.1$ %year^{-1}). However, the probability of estimating a biased trend was greater for shorter time series and, to a lesser extent, with fewer sites in a region (Figure 6-5). Further, trend estimates were more precise for longer time series, with more sites in a region, for datasets with equal as opposed to unequal distribution of abundance, and for Canada warbler compared with white-throated sparrow simulated datasets (Table 6-9; Figure 6-6).

The lower precision and higher probability of estimating a biased population trend using the incorrect regional model structure resulted in lower power to detect a significant trend for 20-year datasets of both species, and a lower rate of error for 20-year Canada warbler simulated datasets (Figure 6-7). However, using 40-year datasets, differences in power and error between the incorrect regional model and the correct and incorrect national models were negligible, and particularly when only 3 sites were sampled in each region, power was higher and error rate lower when data were fit with the incorrect regional model (Figure 6-7).

Table 6-8. Coefficient estimates for a model that tested whether bias in population trend varied depending on whether 1-trend simulated datasets were fit with the model that best matched the assumptions of the data or not, and with abundance distribution (equal/unequal), length of time series, number of sites in a region, species. Interactions between model and abundance distribution and number of years and sites were also tested (n = 7200).

Parameter	Est	SE	t value	P
Intercept	0.00169	0.00016	10.81	<0.001
Incorrect-Nat Model	0.000003	0.00018	-0.02	0.986
Incorrect-Reg Model	0.000004	0.00014	0.03	0.978
Unequal N	-0.00016	0.00018	-0.87	0.387
40 Years	-0.00093	0.00013	-7.31	<0.001
5 Sites	0.00021	0.00013	1.65	0.100
10 Sites	-0.00008	0.00013	-0.60	0.549
WTSP	-0.00052	0.00007	-7.01	<0.001
Incorrect-Nat Model:Unequal N	0.000002	0.00026	0.01	0.994
Incorrect-Reg Model:Unequal N	-0.00023	0.00020	-1.15	0.250
40 Years:5 Sites	-0.00003	0.00018	-0.15	0.879
40 Years:10 Sites	0.00027	0.00018	1.49	0.136

Table 6-9. Coefficient estimates for a model that tested whether standard error of population trend estimates varied depending on whether 1-trend simulated datasets were fit with the model that best matched the assumptions of the data or not, and with abundance distribution (equal/unequal), length of time series, number of sites in a region, species. Interactions between model and abundance distribution and number of years and sites were also tested (n = 7200).

Parameter	Est	SE	t value	P
Intercept	-5.758	0.005	-1216.59	<0.001
Incorrect-Nat Model	-0.002	0.005	-0.29	0.78
Incorrect-Reg Model	0.690	0.004	159.68	<0.001
Unequal N	0.050	0.005	9.21	<0.001
40 Years	-1.034	0.004	-267.49	<0.001
5 Sites	-0.230	0.004	-59.44	<0.001
10 Sites	-0.600	0.004	-155.19	<0.001
White-throated Sparrow	0.418	0.002	187.29	<0.001
Incorrect-Nat Model:Unequal N	0.0005	0.008	0.06	0.95
Incorrect-Reg Model:Unequal N	0.024	0.006	3.97	<0.001
40 Years:5 Sites	-0.001	0.005	-0.20	0.84
40 Years:10 Sites	-0.0004	0.005	-0.08	0.94
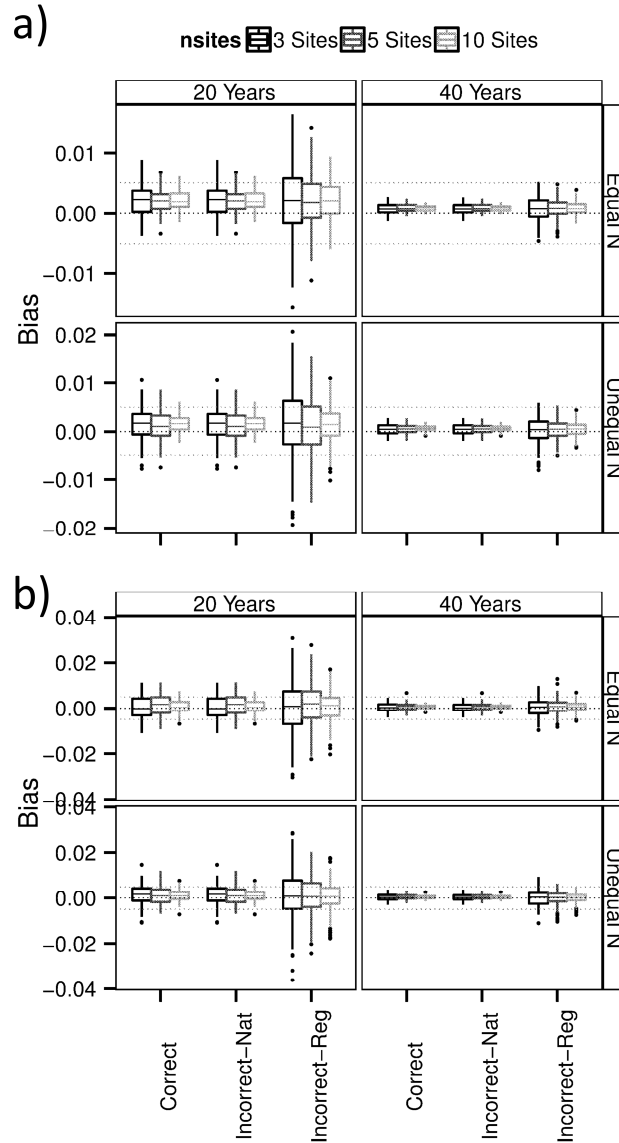
Figure 6-5. Box and whisker plots (n = 100 each) showing variation in bias (estimated – simulated trend) of population trends for 20- and 40-year a) Canada warbler and b) white-throated sparrow simulated datasets, for 1-trend datasets (similar rate of population change across all regions) fit with either the correct national model (1 intercept for equal abundance; 4 intercepts for unequal abundance) or the incorrect regional model (regionally varying slope and intercept).
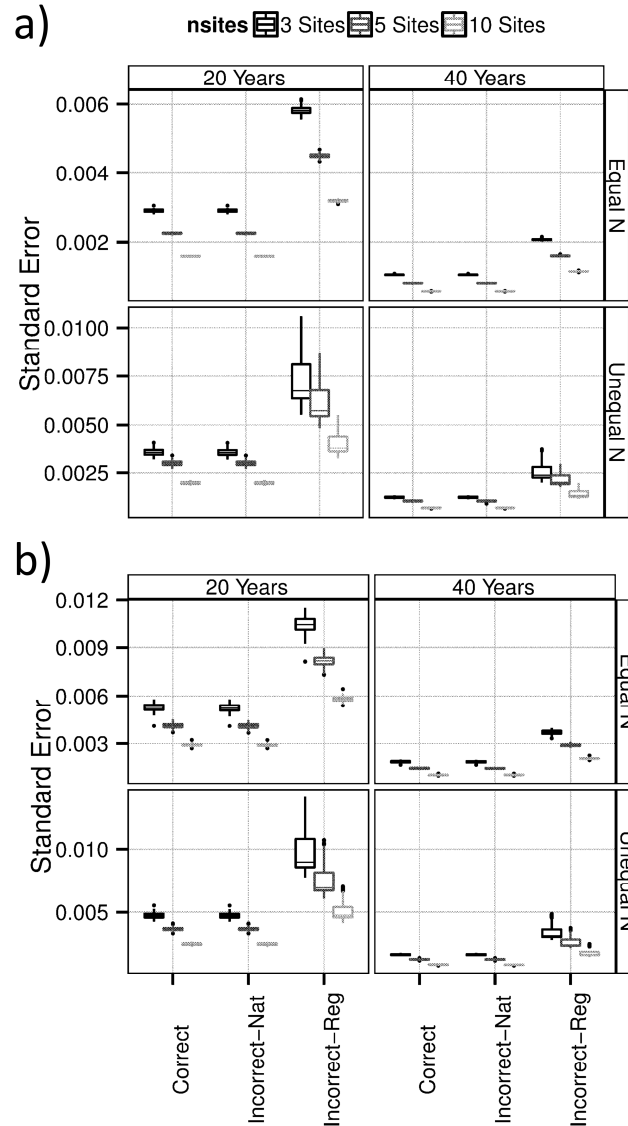
Figure 6-6. Box and whisker plots (n = 100 each) showing variation in standard error of estimated population trends for 20- and 40-year a) Canada warbler and b) white-throated sparrow simulated datasets, for 1-trend datasets (similar rate of population change across all regions) fit with either the correct national model (1 intercept for equal abundance; 4 intercepts for unequal abundance) or the incorrect regional model (regionally varying slope and intercept).
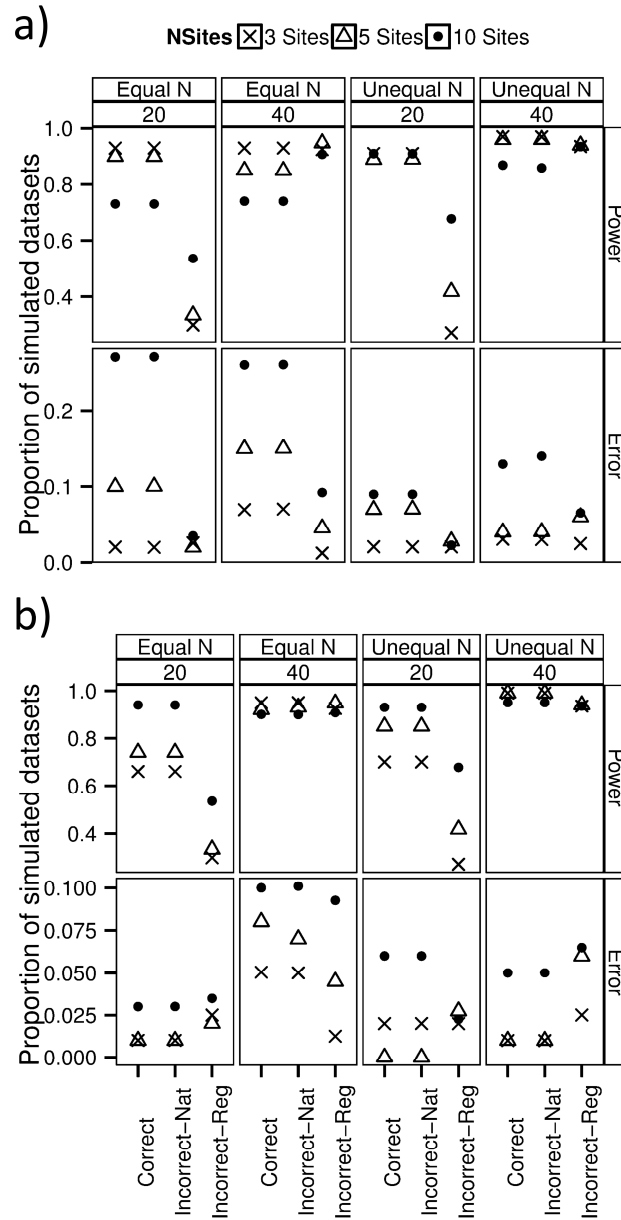
Figure 6-7. Proportion of 100 a) Canada warbler and b) white-throated sparrow 1-trend datasets (all regions simulated to have the same rate of population change), fit with either the correct national model (1 intercept for equal abundance; 4 intercepts for unequal abundance) or the incorrect regional model (regionally varying slope and intercept), where 1) simulated population trend fell within the 95 % confidence limits of the simulated trend (P < 0.1; 'Power'), and 2) estimated population trend was significant (P < 0.1), but confidence limits did not include the simulated trend ('Error').

6.4 Discussion

With sufficient time and effort, AIC model selection has the potential to model unknown regional variation in population trends using migration count data for both rare and commonly detected species. Using 40-year datasets, the appropriate model was ranked as the top or a competing model over 80 % of the time for 1-trend simulated datasets, and 100 % of the time for 2- and 4-trend datasets. The consistent ranking of the incorrect and more highly parameterized regional model as that best model for 1-trend datasets a small proportion of the time is consistent with previous results that suggest AIC does not sufficiently penalize additional parameters (see Kass and Raftery 1995).

However, my results suggest that with a sufficiently long time series (in this case 40 years), fitting the incorrect fully parameterized regional model to data with a single rate of national population change did not influence mean bias of estimated population trends and actually improved power and error rates, possibly negating the need for model selection. As the number of years or sites in a region increased, the larger degrees of freedom available to estimate a single rate of population change using the national models resulted in highly precise estimates of population trend, which combined with a small bias in population trend, resulted in a higher probability of drawing false inference from the data. This effect was most obvious for Canada warbler datasets, which tended to result in more positively biased population trends than did white-throated sparrow datasets.

In my simulated datasets, false negatives were imposed on the data by forcing the probability of migrating to zero on days with simulated poor weather conditions.   Not accounting for detectability, and therefore for the presence of 'false' negatives in the dataset (i.e., non-detection, or 0-observation counts when an individual is present), can result in underestimated or undetected population trends compared to analyses that account for detection error (Tyre et al. 2003, Kéry et al. 2009). A zero-inflated distribution can account for excess 'false' zeros in the dataset that arise from observation error (Tyre et al. 2003, Ross et al. 2012), and its effect on trend bias, precision and error rate should be assessed for trend analyses using migration count data. Accounting for temporal auto-correlation of year effects in a non-linear time series can also lead to more appropriate estimates of precision around trend estimates (Amano et al. 2012, Ross et al. 2012). Although I simulated a constant rate of change, population change in real

populations is rarely constant, and accounting for temporally correlated errors in daily and annual counts should be tested for their effect on trend accuracy, precision and error rate, particularly in the analysis of real migration count data.

In my simulation model, sites were assigned to discrete regions, and sites therefore detected individuals from a single sub-population. In reality, the catchment area of migration count sites is not known, or known only very broadly (Wassenaar and Hobson 2001, Dunn et al. 2006), and some sites are likely to detect individuals from more than one sub-population, particularly sites situated further south in the breeding range, or along geographic 'funnels'. The Long Point Bird Observatory in the Great Lakes region, for example, detects birds from both northeastern and northwestern Canada in fall (Dunn et al. 2006). While my simulated datasets are a simplification of the real system, they provided a means to determine whether, under ideal scenarios, regional and national population trends could be detected with sufficient accuracy and precision to inform conservation efforts, given the amount of variation observed in real migration count data. A next step in this assessment might incorporate simulations where birds counted can originate from more than one sub-population, and allow the contribution from each sub-population to vary randomly over time.

The use of migration counts to monitor long-term population change also assumes that any change in the number of birds counted at a site reflects fluctuations in the monitored population. In other words, I assume there are no systematic changes in effort, habitat cover, or other factors that might influence the relationship between the numbers of birds counted at a site and the population they are meant to index. While detection probability might be modelled with the inclusion of covariates for sampling effort and weather (Berthiaume et al. 2009), estimating and accounting for habitat change at a site would be more difficult, particularly without information on the scale at which birds are making stopover decisions at each site (Taylor et al. 2011). Currently, it is recommended that migration monitoring sites are situated in areas where the potential for successional habitat changes are minimized (Hussell and Ralph 2005), and that any habitat change that does occur is quantified. However in practice, such recommendations can rarely, if ever, be achieved. The sensitivity of regional and national population trends to various rates or patterns (e.g., linear vs. cyclical) of systematic change in effort, habitat, weather, or other variables of interest at one or more sites should be assessed for migration counts.

The relationship between population counts at a site and regional population size might also vary among sites, due to among-site variation in the proportion of the regional population migrating over a site, and in the probability that individuals migrating overhead will stop and be detected. When abundance was distributed unequally among sites, estimating a model with a single slope (national models), assumed that all sites were detecting a similar proportion of the monitored population. Weighting a national population trend by mean abundance at a site might be misleading if higher weight is assigned to a region with high counts due to high detection probability, than a region with similar population size but lower counts due to lower detection probability. Population trend analyses should therefore incorporate information on overall migration volume and/or probability of detection at a site into estimates of regional or national population change when data are pooled across multiple sites. Within a Bayesian analytical framework, this type of information (both the estimates and the uncertainty around the estimates) could be included in the form of informative priors (e.g., pg 480,Gelman et al. 2014).

With the exception of Long Point Bird Observatory, which has been collecting data since 1963, most CMMN sites have been in operation for 20 or fewer years, and with the exception of Ontario, data are currently collected at three or fewer sites in most provinces (Table 10). My results suggest that over the long term, continuing to invest in the current suite of migration monitoring sites for a longer period of time would be more effective to minimize the probability of drawing false inference from population trends than would investing in the expansion of the network to include more sites. While many analytical challenges remain, recent technological advances in the use of weather radar, feather isotope analysis, geolocators and broad-scale telemetry (Dunn et al. 2006, Taylor et al. 2011, Laughlin et al. 2013) have the potential to improve our understanding of the relationship between regional population size and site-specific counts, and of the breeding origin(s) of the count population at a site. As our knowledge is improved, I will be better able to assign sites to regions and better account for variation in counts at and among sites.

6.5   References

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Chapter 7

7 Application: Long-term trends in the number of monarch butterflies (Lepidoptera:Nymphalidae) counted on fall migration at Long Point, Ontario, Canada (1995-2014)

7.1 Introduction

Each spring, monarch butterflies, *Danaus plexippus* (Linnaeus) depart their overwintering grounds in the high-altitude oyamel fir (*Abies religiosa*) forests of central Mexico and begin a multi-generational migration north to breed throughout eastern North America. In fall, the final generation of the year ceases reproduction and begins an approximately 4000-km (2485-mile) migration southward back to Mexico, where they over-winter in large congregations until the following spring (Brower 1995). Survival of the monarch butterfly in the small 800-km^2 (309-miles^2) over-wintering habitat in Mexico is considered by many to be the key limiting factor for monarch survival (Brower 1995, Crolla and Lafontaine 1996, Brower et al. 2012). Threats on the wintering grounds were the primary reason behind its listing as a species of Special Concern under Canada's Species at Risk Act (COSEWIC 2010), and contributed to the filing of a petition in 2014 to seek legal protection for the monarch under the United States Endangered Species Act.

Broad-scale population monitoring programs provide an important contribution towards assessing species conservation status (Rich et al. 2004, Commission for Environmental Cooperation 2008). Counts of migrating individuals are one method to assess broad-scale population trends for migratory animals (Francis and Hussell 1998, Walton et al. 2005, Dunn et al. 2006, Gibbs et al. 2006, Farmer et al. 2007, Findlay et al. 2011, Davis 2012). Standardized daily counts of migrating monarchs collected since 1995 at two sites at Long Point, Ontario provide the only long-term dataset available to assess monarch status in Canada. In late August to mid-October each year, tens of thousands of monarchs funnel through Long Point as they migrate south. The number of individuals detected each year by migration counts are assumed to be a reflection of fluctuations in the underlying catchment population (i.e., of the breeding population for the geographic region from which detected individuals originated).

In Ontario, the distribution and successful breeding of monarchs is determined largely by the distribution of the various species of its larval host plant, milkweed (*Asclepia sp.*; Schappert 1996). Although the historical amount of milkweed, and therefore the distribution of monarchs, increased across Ontario with the development of the road network and an increase in abandoned agricultural fields, the current amount of monarch host and nectaring plants has the potential to be reduced or lost through continued urban development, the regeneration of trees and shrubs in abandoned fields (Crolla and Lafontaine 1996), as well as by the use of herbicides and (at least until 2014) the control of milkweed as a noxious weed under Ontario's Weed Control Act. On a broader spatial scale, low numbers of migrating monarchs are thought to be the result of high storm-caused mortality at the over-wintering sites in Mexico, wet and cold weather during the spring and summer breeding seasons in the United States and Canada, and the loss of milkweed host plants in intensive agricultural systems (Brower 1995, Brower et al. 2012, Pleasants and Oberhauser 2013).

Migration counts provide an index of annual abundance, and therefore rely on the assumption that probability of detection remains consistent over time (Dunn 2005, Crewe et al. 2015). A systematic change in any factor that influences probability of detection has the potential to bias population trends (Hochachka and Fiedler 2008, Kéry et al. 2009, Crewe et al. 2015). At the scale of a migration count site, directional changes in sampling effort, observer skill, habitat, or local weather conditions, and the influence of weather and habitat on stopover behaviour of migrating animals (Link and Sauer 2002, Meitner et al. 2004, Schaub et al. 2004, Calvert et al. 2009), can lead to a bias in detection probability and false inference from population trends (Crewe et al. 2015).

Because of their geographic proximity, both study sites at Long Point are assumed to monitor the same population of migrating monarch butterflies, and should therefore detect similar rates of long-term population change. However, differences in habitat and geographic orientation between the two monitoring sites results in higher counts and a higher stopover probability at the Tip site compared to Breakwater. A site-specific temporal bias in probability of detection, for example due to a systematic change in stopover duration (Hochachka and Fiedler 2008, Calvert et al. 2009) at the Tip site, could lead to between-site differences in detected rate of population change. Correspondence of population trends from nearby sites that monitor the same breeding

population can provide support that such site-specific biases in detection probability are not confounding estimates of the long-term population trend.

In this paper, I use 20 consecutive years (1995-2014) of standardized daily migration counts collected at the two sites on Long Point, Ontario, to estimate trends in the number of migrating monarch butterflies across three time periods: an over-all 20-year trend, the first 10 years, and the most recent 10 years. Further, I use model selection to determine whether a difference in the detected population trend between sites is supported. This analysis provides the first published analysis of monarch population trends for Canada.

7.2 Methods

7.2.1 Study Sites

Long Point, Ontario is a narrow sand peninsula that extends 32 km (20 miles) eastward from the Canadian north shore of Lake Erie (42°35'N, 80°25'W). Including wetlands, Long Point is approximately 16,000 ha (39,500 acres) and is composed of sandy beaches, dunes, expansive wetlands, meadows, savannahs, and forests (Gartshore et al. 1987). Because of the large numbers of monarchs passing through the area each year, Long Point was designated an International Monarch Butterfly Reserve by the Canadian government in 1995 (Anon 1995). The area is also recognized as a World Biosphere Reserve, a Ramsar wetlands site of international significance, and an Important Bird Area of global significance.

Fall migration of monarch butterflies was monitored at two sites on Long Point from 1995-2014: the Tip, at the eastern end of Long Point, and Breakwater, about 15 km west of the Tip and closer to the base of the peninsula. The habitat at both sites has remained relatively stable over the past half-century. However, the two sites differ in habitat structure. The Tip site is dominated by early-successional, dry, open eastern cottonwood-red cedar savannahs, separated by wet interdunal swales, meadows, and dry (sparsely vegetated) sand dunes. Important monarch butterfly food plants, such as milkweed and cylindrical blazing star (*Liatris cylindracea*), are common in the meadows at this site. Conversely, the Breakwater study site is dominated by a mid-successional, open, oak-maple savannah that has a well-developed ground cover dominated by various grasses. Important nectaring plants are less abundant at this site, and blazing star is absent (Table 7- 1) .

Table 7- 1. Mean number of flowering plant stems detected at the Breakwater and Tip sites on the Long Point peninsula, Ontario, Canada. Stems were counted once per week over a five week period between August 25 and September 24, 2009, at 76 and 80 1-m^2 quadrats at the Breakwater and Tip sites, respectively. Mean number of stems was calculated as the mean across quadrats of the maximum number of stems detected across visits.

Common Name	Scientific Name	Breakwater	Tip
Blazing star	*Liatris spicata*	0	15.5
Goldenrod sp.	*Solidago sp.*	7.8	6.7
St. John's wort	*Hypericum perforatum* L.	0	1.2
White aster	*Symphyotrichum sp.*	0	6.8
Milkweed	*Asclepias sp.*	0.07	0.05
Other		7.1	8.8

7.2.2　Data Collection and Statistical Analysis

Every fall since 1995, a standardized daily count (census) of migrating monarchs has been carried out at the Tip and Breakwater sites by volunteer surveyors. Standardized counts consisted of a 1-hour afternoon walking census conducted between 1300-1700 hrs along a delineated path, during which the surveyor counted the number of monarchs seen foraging or passing through the count area. The census was not carried out during rain or extreme weather (storm) events. Surveys began at the beginning of August and continued until the end of September at Breakwater and until late October at the Tip. Access to Breakwater beyond about 22 September each year was restricted, and as a result, the entire fall migration was not monitored at that site. Weather variables, including estimated percent cloud cover (0-100 % in 10 % intervals), wind direction (16-point scale), wind speed (Beaufort scale) and temperature (ºC), were also collected daily at each site.

I restricted my analyses to data collected during August and September, to ensure both sites had the same seasonal coverage. Long-term, constant rate of population trend was estimated in a Bayesian framework using integrated nested Laplace approximation (R-INLA, Rue et al. 2014, Crewe et al. 2015). Counts on day i, year j (Y_{ij}) were assumed to result from a negative binomial distribution, and were fit using a log-linear regression model with a fixed year effect to estimate a constant rate of population change (trend), and first and second order polynomial day terms to model the seasonal pattern of migration. I included hierarchical terms to account for 1) 1st order autoregressive (AR1) correlation of errors among days in a season, nested within year and site, and 2) an AR1 random year effect, nested within site. Fixed effects for cloud cover class (0-20 %, 30-50 %, 60-80 %, and 90-100 %), temperature (1st and 2nd order effects), and wind direction and speed were also included in the regressions to model variation in the number of monarchs migrating and counted due to local weather conditions (Gibo and Pallett 1979, Brower 1995, Davis and Garland 2002, Meitner et al. 2004). For these analyses, I combined wind speed and wind direction into east and south wind vectors (EV/SV) by first transforming wind speed into km/hr using the midpoint along the range of values for each Beaufort wind score. Wind speed was then combined with wind direction to create the EV and SV such that wind speed increased from 0 along each vector in two directions, with negative values representing wind speed in one direction (e.g., east on the EV vector), and positive values representing wind speed in the opposite direction (e.g., west on the EV vector). For wind directions that did not fall directly on either vector (e.g., ENE), I used vector addition to assign a wind speed to both the EV and SV. For the purposes of this analysis, east and north winds received a negative vector value, while west and south winds received a positive vector value. In order to estimate annual indices of population for both sites combined (Fig. 1), I fit the above model with year as a categorical variable.

I used the Deviance Information Criterion (DIC; Rue et al. 2009) to compare the fit of two regression models: 1) a model with a single slope to estimate an overall population trend across sites, and 2) a model which allowed slope to vary with site, to test whether the detected trend in population size varied between the Tip and Breakwater sites. Using the best supported model of the two, I also estimated 10-year population trends using the first and last 11-years of data collected, to test whether more recent population trends (2004-2014) vary from the entire time

series (1995-2014) and from the first 11 years of data collection (1995-2005). Such 10-year population trends are often used to assess the conservation status of species (e.g., IUCN Standards and Petitions Subcommittee 2013). In all cases, the year coefficient was transformed into a constant rate of population change using $100 \times (\exp(yearcoefficient) - 1)$.

7.3 Results

Using DIC, the model that assumed a single population trend across sites (DIC = 11341.97) had comparable support to the model that assumed trend varied between sites (DIC = 11341.35), with a DIC difference of less than 1. However, the 95 % credible interval (CI) for the interaction between site and population trend was not strongly supported (0.05, CI = -0.04, 0.05). Combined, these results suggest that a difference in population trend between the two sites was not strongly supported.

Using the single-slope model, which assumed a single rate of population change for both sites combined, the estimated rate of population change was -5.12 %year^{-1} (CI = -9.81 %year^{-1}, -0.06 %year^{-1}) over the 20-year sampling period, with a posterior probability of 0.98 that the trend was negative (Table 7-, Figure 7-1). This model supported an increase in monarch counts with temperature, lower counts during high (>90 %) cloud cover, and lower counts during east compared to west winds (Table 7-).

Table 7-2. Mean, standard deviation (SD) and lower (LCI) and upper (UCI) credible intervals of fixed and random effects for a model that assumed population trend did not vary between the Tip and Breakwater stations of the Long Point Bird Observatory. Data were analyzed in a Bayesian framework and assumed random 1st order autoregressive effects for year (nested within site) and day (nested within year and site).

Effect Type	Effect	Mean	SD	LCI	UCI
Fixed	Year	-0.0526	0.0259	-0.1032	-0.0006
	Area: Breakwater	3.54	0.51	2.53	4.55
	Area: Tip	2.50	0.46	1.59	3.42
	Day	1.44	0.94	-0.42	3.28
	Day^2	-0.19	0.74	-1.65	1.27
	Temp	-0.45	0.21	-0.88	-0.04

	Temp^2	-0.28	0.22	-0.71	0.16
	Cloud (30-50 %)	0.07	0.09	-0.10	0.24
	Cloud (60-80 %)	0.05	0.10	-0.14	0.23
	Cloud (>90 %)	-0.28	0.08	-0.45	-0.12
	EV	-0.13	0.02	-0.16	-0.10
	SV	-0.02	0.02	-0.05	0.02
	Area: Tip * Day	-5.80	0.87	-7.52	-4.09
	Area: Tip * Day^2	-3.36	0.71	-4.75	-1.98
	EV*SV	0.01	0.01	0.00	0.02
Random	Size for NB Observations	1.57	0.09	1.41	1.75
	Year: Precision	1.55	0.48	0.81	2.67
	Year: Rho	-0.25	0.22	-0.65	0.20
	Day: Precision	1.07	0.19	0.74	1.49
	Day: Rho	0.87	0.03	0.81	0.92
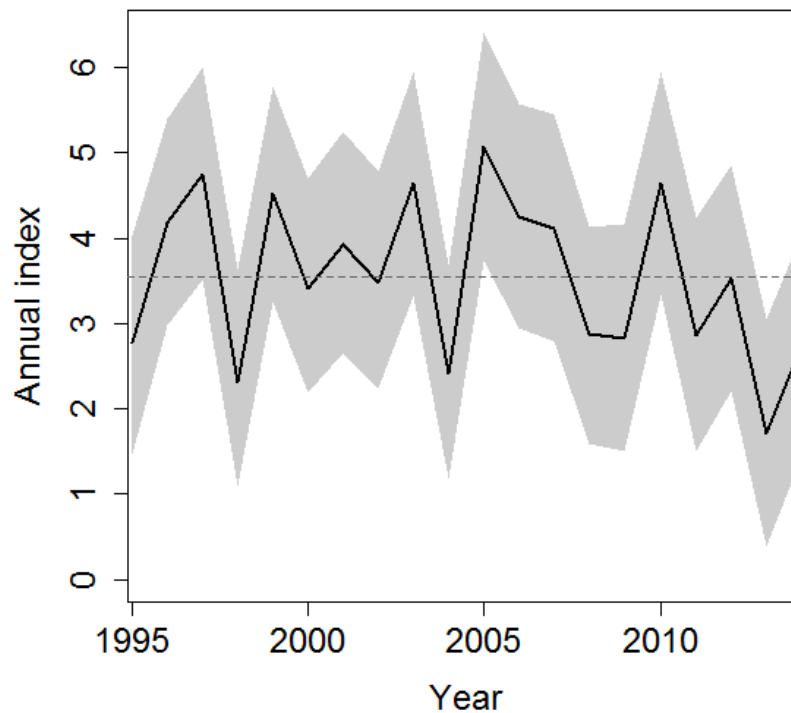
Figure 7-1. Estimated annual indices (± 95 % credible intervals) of the number of monarch butterflies detected on migration at two sites on the Long Point peninsula in Ontario,

Canada between 1995-2014. A decline in annual indices of 5.12 %year^{-1} (CI = -9.81 %year^{-1}, -0.06 %year^{-1}) was detected.

Using the first 11 years of data (1995-2005), the initial 10-year trend was positive (2.02 %year^{-1}), but not strongly supported (CI = -8.61 %year^{-1}, 16.18 %year^{-1}), and with a posterior probability of only 0.64 that the trend was indeed positive. Using the last 11 years of data (2004-2014), the most recent 10-year trend was negative (-6.06 %year^{-1}), but again was not strongly supported (CI = -12.37 %year^{-1}, 0.78 %year^{-1}). Nevertheless, the posterior probability that this most recent 10-year trend was negative was 0.96, suggesting that a real decline has occurred during this time period.

7.4 Discussion

In recent years, there has been an increasing amount of interest and concern surrounding the susceptibility of the eastern North American monarch butterfly population's migratory phenomenon to the loss and degradation of the Mexican overwintering and North American breeding habitats. Evidence to support a decline in the monarch population, however, has varied among datasets, with a reported decline in the number of monarchs overwintering in Mexico from 1994 through 2011 (Brower et al. 2012), but no significant change in the number of monarchs migrating through Cape May, New Jersey (1992-2010) or Peninsula Point, Michigan (1996-2010) during similar time periods (Davis 2012). Using counts of monarchs migrating through two sites on the Long Point peninsula in Ontario, Canada, my results suggest that the number of monarchs counted on migration has likely declined during the 20-year monitoring period ending in 2014.

Typical of insect populations (e.g., Zipkin et al. 2012), the number of monarchs detected migrating through Long Point was highly variable over time. Similar to the results of Davis (2012), monarch counts at Long Point varied substantially up to and including 2010, with troughs in the population trajectory (annual index below the long-term mean) being consistently followed by population peaks within one or two years (Figure 7-1). However since 2010, the annual index has remained below the long-term mean. Indeed, the below-average population indices during this most recent time period are driving the apparent long-term population decline. The estimated size of the overwintering population also declined to a 20-year low of 1.3 acres of

habitat occupied in 2013 compared to a 20-year high of 45 acres in 1996 (World Wildlife Fund 2014).

At Long Point, monarch butterfly counts were typically much larger at the Tip than at the Breakwater study site. Because there is a greater concentration of host and nectaring plants at the Tip compared to Breakwater, individuals counted at Breakwater were more likely to involve migrants actively moving through the site, whereas individuals counted at the Tip likely included a larger proportion of individuals stopping-over to feed for one or more days. Nevertheless, support for the model that assumed a single rate of population change across the two study sites suggests that site-specific sources of bias in probability of detection due, for example, to site-specific biases in stopover behaviour (Hochachka and Fiedler 2008, Crewe et al. 2015), were either not present or were negligible compared to the overall rate of population change detected across sites.

My results cannot exclude the possibility that broad-scale temporal shifts in the breeding distribution or migration route are biasing my estimates of long-term population trend. Correlation of estimated annual indices from Long Point with alternative sources of monitoring data collected in Ontario and across the broader breeding range, such as the distribution or use of milkweed by monarchs collected by the Monarch Larva Monitoring Project (Pleasants and Oberhauser 2013), would lend further credibility to my results. Correspondence of annual indices with other migration count sites in eastern North America (Davis 2012) would also help clarify whether the trend reported here is representative of regional or more broad-scale population dynamics. Such comparisons could be improved with the use of isotope analysis (Flockhart et al. 2013) to determine the breeding origin of monarchs detected at each site. Additional years of data should also be collected to determine whether the apparent decline will continue, or whether the monarch population will recover from recent low levels.

Local weather conditions also influenced the number of monarchs counted at Long Point, and support the results of Meitner *et al.* (2004) from a Great Lakes shoreline site in Michigan, which showed that wind directions from the west resulted in higher monarch counts than winds from the east during fall migration. However, higher counts during west winds might partially reflect an increase in the number of monarchs blown off their overall southwesterly fall migratory

course to the Mexican overwintering sites (Gibo and Pallett 1979, Brower 1995), as opposed to a reflection of the number of monarchs actively migrating. During west winds, the west to east orientation of Long Point in Lake Erie could act as a funnel or bottleneck for individuals migrating or blown off-course, leading to large accumulations of monarchs during headwinds observed here and elsewhere (Davis and Garland 2002). This bottleneck effect is supported by the larger counts at the Tip compared to the Breakwater study site at Long Point.

The monarch butterfly population has the potential to expand exponentially through the production of several successive generations in a single breeding season under ideal conditions. As a result, monarchs are likely resilient to occasional declines in the overwintering or breeding populations, and this resilience could contribute to the lack of a detected decline in the size of fall migratory populations reported elsewhere (Davis 2012), despite a decline in the overwintering population (Brower et al. 2012). In any case, the monarch's resilience and ability to recover from population lows has the potential to be compromised by the combination of a sustained decline in the overwintering population, an increased likelihood of weather extremes with climate change (IPCC 2012), and the continued degradation and loss of breeding and overwintering habitats. An integrated population analysis that combines data collected by monitoring programs during overwintering, breeding and migration would be a logical next step in the assessment of monarch population status, in order to link estimates of population change to demographic parameters, and determine where population limitation is likely occurring (Schaub and Abadi 2011).

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Chapter 8

8 General Discussion

8.1 Monitoring wildlife populations using migration counts

Migration monitoring fills an important gap in species coverage of monitoring programs by capturing species that are inaccessible or not well detected on their breeding and wintering grounds (Dunn 2005). However, the reliability of migration counts for population monitoring is often questioned, in part because many potential sources of variability can lead to the violation of the assumptions of count independence and proportionality, and the effect of assumption violation on precision and accuracy of estimated trends is not well understood. My work shows that when data are analyzed using hierarchical models and the assumption of proportionality is upheld, bias of population trends derived from migration counts largely remained within the 0.5 %year^{-1} bias limit suggested for landbird population monitoring (Bart et al. 2004), regardless of count distribution, length of time series, sampling frequency, or whether the assumption of independence was violated or not. Further, although statistical power to correctly detect a significant trend was typically low, particularly for rare and highly over-dispersed species, the rate of error was also low. Since the probability of detecting a false trend is low, there does not appear to be a need to exclude species *a priori* from analysis based on low detection probability or incomplete sampling of the migration. Rather, data for such species could still provide useful insights about underlying population change that could either be compared to other sources of information on trends, or lead to more concerted monitoring efforts for species that are of management concern.

Violating the assumption of proportionality due to a systematic linear trend in stopover duration did bias estimated population trends and led to a high rate of error, particularly when both stopover duration and simulated trend changed in the same direction (in this case, both increasing). A systematic change in stopover duration is arguably the most problematic source of bias for trends derived from counts of unmarked migrants, and is likely to occur at many sites in response to climate change (Calvert et al. 2009), habitat succession (Harrison et al. 2000) or with the degradation of stopover sites, for example in response to increased risk of predation

with the recovery of many raptor populations (Ydenberg et al. 2004). In order to ensure that a bias in stopover duration is not occurring, or to account for a bias that is occurring, independent data on stopover duration must be collected. At a minimum, stopover duration could be estimated using mark-recapture data from banding for species guilds or groups to improve sample size and model fit (Calvert et al. 2009). Mark-recapture of butterflies on stopover can be conducted using individualized tags (Meitner et al. 2004). Alternatively, stopover duration of shorebirds is often estimated using radio-marked birds (see Drever et al. 2014). With recent technological advancements in automated radio-telemetry arrays (Motus Wildlife Tracking System 2015, Taylor et al. 2011) and tracking devices that allow smaller animals to be tracked for longer periods, the opportunity exists to radio-tag songbirds captured at each migration count site, and gather information on stopover duration and timing of departure for species of interest (Taylor et al. 2011). Also, because time of arrival relative to time of first capture is typically unknown, the spatial scale of the Motus Wildlife Tracking System, which includes an array in Ontario which extends across the south-western portion of the province, could allow measurement of true total stopover if birds stop at additional sites, other than the site of first capture, while within the array space. Direction of departure could also be estimated for songbirds and raptors, and assuming birds depart in the direction of the breeding grounds, could be used to narrow down the catchment areas or breeding origin of species detected at each site (see below).

Shifts in the breeding or wintering distribution of migrating populations in response to climate or habitat change (Parmesan et al. 1999, Paprocki et al. 2014) can also lead to false inference from population trends if the proportion of the migratory population that passes a count site also changes. Population trends derived from migration counts should be interpreted in relation to alternative sources of data on breeding or wintering distribution when available (Paprocki et al. 2014). Combining data across sites to estimate regional population trends may lessen the probability that such a bias will occur if the entire distribution in captured by all sites combined. In this case, site-specific sources of annual variation in counts could be estimated independently from annual variation in the monitored population by the specification of random site-specific year effects (Chapters 6,7). Integrated population models that combine demographic data (where available) and migration counts might also prove useful to improve precision and power of trend estimates, and determine when population limitation occurs during the annual life cycle (Schaub

and Abadi 2011). Monarch butterflies would provide an ideal test of the integrated population model approach because data are collected during all stages of this species' annual life cycle, including estimates of larval density on breeding grounds (Pleasants and Oberhauser 2013), migration counts (Davis 2012, Chapter 7) and estimates of over-wintering population size (Brower et al. 2012).

My research suggests that model selection techniques can be used to model variation in trend among regions, and that increasing the length of the time series would be more efficient at improving power and model selection than would increasing the number of sites in a region. In Chapter 7, I applied the method to monarch migration counts that are assumed to monitor the same population, and so should detect the same rate of change. However, there remains a large amount of uncertainty about the breeding origin of most species detected at migration count sites, which remains a major limitation in the use of migration counts for broad-scale population monitoring. Stable hydrogen isotopes in feathers were recently used to derive broad estimates of breeding origin for several songbird species detected across the CMMN network, and showed that catchment areas can vary among sites and among early and late migrants at a site for a given species (Dunn et al. 2006). The estimated catchment areas could be further refined using information on migration routes and orientation of birds departing each count site in fall. Geo-locators (Stutchbury et al. 2009) and broad-scale automated radio-telemetry arrays (Taylor et al. 2011) could prove useful for this purpose. Geo-locators would provide the added advantage of determining wintering grounds of migrants, and provide the opportunity to improve the interpretation of trends in migration counts by taking into consideration factors influencing populations during all stages of their annual life cycle. Genetic sampling also has the potential to improve our understanding of which sites are detecting the same or different sub-populations of a species (Fedy et al. 2008), and combined with isotope signatures, will provide a more complete picture of how (sub-)populations detected at and among migration count sites are structured, and whether different sites, or early and late migrants at a single site, should be analyzed and interpreted independently. In addition to improving our understanding of how sites should be combined to estimate regional trends, refinement of catchment areas estimated using stable hydrogen isotopes in feathers will allow, for the first time, the opportunity to test whether covariates collected on the inferred breeding grounds, including change in land use or structure, are correlated with annual indices of population size estimated using migration counts.

In my thesis, I simulated data with a constant rate of change, and used linear regression to estimate trend as the slope of a continuous year term. Population trends are often estimated this way, even for non-linear data (Amano et al. 2012, Ross et al. 2012). However, the assumption of constant rate of change is increasingly likely to be violated as the length of a time series increases. Many analytical tools are now available to ecologists to account for non-linearity and auto-correlation among annual counts. For example, hierarchical models that assume a constant rate of population change, as I did here, but that models the temporal autocorrelation of annual counts using a first-order auto-regressive parameter would be more appropriate for real migration counts (Ross et al. 2012; Chapter 6). Alternatively, additive models allow trend to be modeled as a smoothed non-linear function of time (Fewster et al. 2000, Fedy and Doherty 2011, Amano et al. 2012) and trend is then estimated as percentage change between any two annual indices (Fewster et al. 2000). Using simulated Breeding Bird Survey data with known non-linear trend, annual indices estimated using smoothed hierarchical models led to more accurate and precise trends than did annual indices from non-smoothed hierarchical models (Amano et al. 2012). Additive models have the additional benefit of moderating large outlying counts, and may be particularly useful for estimating trends for super-flocking species with highly over-dispersed counts. The above methods should be assessed for the analysis of migration counts using simulated data with known non-linear change.

8.2   Concluding Remarks

As with any wildlife monitoring program, managers and data analysts need to be aware of the limitations of their data (Johnson 2008). In the case of migration counts, a primary limitation is a reliance on annual indices of abundance to provide a proportional representation of the monitored population, and therefore a reliance on the assumption that probability of detection remains consistent over time. Further, because population abundance and probability of detection are confounded and cannot be estimated independently using annual indices of abundance, covariates for weather, habitat or other factor used to model variability in counts may be acting on abundance, probability of detection, or both. All monitoring programs are subject to various sources of bias, even those that are able to estimate probability of detection explicitly from the data (Johnson 2008). A primary concern should therefore be to minimize all controllable sources of variability in counts through the use of specific, detailed and standardized

sampling protocols, appropriate observer training, and appropriate placement of count sites (Hussell and Ralph 2005), for example in poor stopover habitat to reduce the probability of assumption violation, or along geographic funnels or migratory corridors to maximize the relevance of detections to a broader area. Clear acknowledgement of the limitations of migration counts and the factors that may be influencing observed changes in annual indices will improve the interpretation of migration counts for population monitoring, and may lead to the development of novel innovations to overcome those limitations.

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Appendices

Appendix A – Hourly Migration Count Simulation and Parameterization

Simulation Code

Code to generate hourly raptor migration counts, using R (v. 2.14.2, R Development Core Team 2011). Note that R uses as a default the "Mersenne-Twister" random number generator, from Matsumoto and Nishimura (1998). A twisted GFSR with period 2^19937-1 and equidistribution in 623 consecutive dimensions (over the whole period). The 'seed' is a 624-dimensional set of 32-bit integers plus a current position in that set (see ?Random in R).

Definition of simulation parameters (values are shown for parameters that did not differ with species or levels of annual and daily variation; see Tables A1-A3 for parameter values that varied among simulations):

Y.1: starting population size (year = 1).

nyears: number of years to simulate (10 or 20).

sday: start day, determines number of days in season.

sday.err: standard deviation of random normal error on start day.

shr = -3; start hour, determines number of hours in day.

shr.err = 0.5; standard deviation of normal random error on start hour.

prob.move: binomial probability that birds move on a given day.

trend = -0.03885; log-linear decline required to achieve approximately 30 % decline in 10 years.

trend.err: standard deviation of random normal error added to trend on log scale.

day.err/hr.err: standard deviation of random normal error added to daily and hourly counts on log scale.

m.spread = 0/m.spread.err = 0.8; mean and standard deviation of random normal error on the mean of the normal density curve describing distribution of daily counts.

m.peak/m.peak.err: mean and standard deviation of random normal error on the standard deviation of the normal density curve describing distribution of daily counts.

k.day/k.hr = clumping parameter for negative binomial error added to daily and hourly counts.

m.spread.hr = 0/m.spread.err.hr = 0.2; mean and standard deviation of random normal error on the mean of the normal density curve describing distribution of hourly counts.

m.peak.hr/m.peak.err = mean and standard deviation of random normal error on the standard deviation of the normal density curve describing distribution of hourly counts.

weath.pois = 1.2; lambda for Poisson error added to 'weather' vector.

```
######## Beginning of R code

# Packages required:

  require(lattice) # Deepayan, S. 2008. Lattice: Multivariate Data
Visualization with R. Springer, New York. ISBN 978-0-387-75968-5

  require(reshape) # Wickham, H. 2007. Reshaping data with the reshape
package. Journal of Statistical Software 21:12.

###############################################################

# define the "sim.raptors" function to generate hourly raptor counts

# values shown do not vary with simulation, see Table A1 for values of
other parameters

sim.raptors <- function(Y.1, trend = -0.03885, trend.err, nyears,
sday, sday.err, m.spread = 0, m.spread.err = 0.8, m.peak, m.peak.err,
day.err, weath.pois = 1.2, k.day, k.hr, prob.move, shr = -3, shr.err =
0.5, m.spread.hr = 0, m.spread.err.hr = 0.2, m.peak.hr, m.peak.err.hr,
hr.err) {
```

```
## First generate annual population size

years <- 1:nyears

## vector of N, on log (link) scale, of length nyears, changing by
given trend

Log.Y.i <- log(Y.1 * (1 + trend)^(0:(nyears - 1)))

## Add random error to annual totals on log scale

## i.e., generating extra residuals in addition to the implicit
Poisson residuals

Log.Y.i <- log.Y.i + rnorm(n = nyears, mean = trend, sd = trend.err)

## Back-transform to response scale

Y.i <- exp(log.Y.i)

## Generate second level of noise: add Poisson noise around expected
mean

Y.i <- rpois(n = nyears, lambda = Y.i)

####################################################################

## Distribute annual total (Y.i) through days in a year

## set up null dataframe for years, and loop through

hourly.data <- as.data.frame(matrix(nrow = 1, ncol = 6))

names(hourly.data) <- c("day", "hour", "count", "N.1", "doy", "year")

## Loop through years

for(i in 1:nyears) {

## Determine number of days in season
```

```
## allow normal variation around start day (sday), so length of
migration window varies among years

s.day <- round(sday + rnorm(n = 1, mean = 0, sd = sday.err))

e.day <- abs(s.day)   # creates first and last day, centered on 0

ndays <- e.day - s.day + 1   # number days in migration window

days <- seq(from = s.day, to = e.day) # vector of days

## Distribute birds across days in a year.  Assumes bell-shape
(normal) distribution, with peak number birds moving through mid-
season

## adding normal error to mean and sd of curve allows spread to vary
among years

spread <- dnorm(seq(from = s.day, to = e.day), mean = rnorm(n = 1,
mean = m.spread, sd = m.spread.err), sd = rnorm(n = 1, mean = m.peak,
sd = m.peak.err))

spread <- spread/sum(spread)   # so values add to 1

## Add first level of noise to daily counts: random error on log scale

## Gives the number of birds available to migrate each day

Y.ij_avail <- Y.i[i] * spread

log.Y.ij_avail <- log(Y.ij_avail)

log.Y.ij_avail <- log.Y.ij_avail + rnorm(n = length(log.Y.ij_avail),
mean = 0, sd = day.err)

Y.ij_avail <- exp(log.Y.ij_avail) # back-transform to response scale =
number birds available to migrate
```

Second level of noise on daily counts: add negative binomial error to number of birds that want to move each day. Setting k to higher value (10 or so) approaches Poisson distribution

```
Y.ij_avail <- rnbinom(n = ndays, size = k.day, mu = Y.ij_avail)
```

This following ensures the sum of daily counts adds up to annual counts.

```
if(sum(Y.ij_avail) > 0) {

    Y.ij_avail <- round(Y.ij_avail /sum(Y.ij_avail) * Y.i[i], digits
= 0)}
```

Set up a weather variable, based on uniform distribution

```
 weather <- runif(n = ndays, min = 0, max = 1)
```

add Poisson variability to weather, so adjacent days have more similar weather conditions.

```
weather.pois <- rpois(n = 20*ndays, lambda = weath.pois)
```

get rid of zeros in vector (need at least one day with certain weather condition)

```
weather.pois <- subset(weather.pois, weather.pois > 0)
```

limit to two adjacent days with exact same weather, then subset vector to length of days in year

```
weather.pois[which(weather.pois > 2)] <- 2
```

```
weather.pois <- weather.pois[1:ndays]
```

repeat the weather value the number of times specified in weather.pois

```
weather <- rep(weather, times = weather.pois)
```

```
## subset, so vector is same length as number of days in year

weather <- weather[1:ndays]

## Set up a probability that birds will move through a site on a given
day, given they are available to move (= Y.ij_avail).  Base this
probability of moving on weather conditions, so that probability of
moving is 0 during bad weather, and linear relationship with weather
above particular bad-weather threshold

## linear relationship between prob moving and weather

pm <- weather

## adds threshold: below certain weather condition, no birds move

pm[which(pm < (1 - prob.move))] <- 0

## set up blank vector for number of birds that actually migrate

Y.ij <- rep(0, times = length(Y.ij_avail))

## Loop though days, calculate the number that move (nm) based on
binomial distribution. Number actually want to move (nawm) needs to be
the same as number want to move (nwm) in first time step

Y.ij_wantmove <- Y.ij_avail

ndays <- length(Y.ij_avail)

## set up NULL hourly databases to append generated data

hr.count <- NULL

hrly.data <- NULL

for(j in 1:ndays) {

## each individual has a binomial probability of moving
```

```
Y.ij[j] <- rbinom(n = 1, size = Y.ij_wantmove[j], prob = round(pm[j],
digits =3))
```

################# now generate hourly data within the day loop

probability distribution based on normal; 'spread' placed within
the day loop, so spread can differ among days in season

Determine number of hours in a day

allow normal variation around shr, so number hours birds move each
day can vary among days

```
s.hr <- round(shr + rnorm(n = 1, mean = 0, sd = shr.err))
```

```
e.hr <- abs(s.hr)   # creates first and last hour, centered on 0
```

```
nhours <- e.hr - s.hr + 1 # number hours
```

```
hours <- seq(from = s.hr, to = e.hr) # vector of hours
```

```
spread.hr <- dnorm(seq(s.hr, e.hr), rnorm(1, m.spread.hr,
m.spread.err.hr), sd = abs(rnorm(1, m.peak.hr, m.peak.err.hr)))
```

```
spread.hr <- spread.hr/sum(spread.hr) # so values of spread add to 1
```

add first type of error to hourly counts - random normal error on
log scale

```
Y.ijk <- Y.ij[j] * spread.hr
```

```
log.Y.ijk <- log(Y.ijk)
```

```
log.Y.ijk <- log.Y.ijk + rnorm(n = length(log.Y.ijk), mean = 0, sd =
hr.err)
```

```
Y.ijk <- exp(log.Y.ijk) # backtransform to response scale
```

add second type of error: each individual has neg binomial
probability of moving each hour

```
Y.ijk <- rnbinom(n = nhours, size = k.hr, mu = Y.ijk)
```

recalculates, so total number moving across hours in day adds up to that days' total, or close to it (some rounding error does occur)

```
if(sum(Y.ijk) > 0) {

    Y.ijk <- round(Y.ijk/sum(Y.ijk) * Y.ij[j], digits = 0)

    }
```

end of hourly data manipulation, continue with daily data manip

update nm, so pushes birds that did not move to following day

```
Y.ij[j] <- sum(Y.ijk)
```

```
if(Y.ij[j] > Y.ij_wantmove[j]) {Y.ij[j] <- Y.ij_wantmove[j] } #
otherwise can get neg count next step Y.ij_wantmove[j + 1] <-
Y.ij_avail[k + 1] + Y.ij_wantmove[j] - Y.ij[j]
```

populate dataframe with hourly counts, and rbind to create dataframe with all days. Daily counts are no longer of interest.

```
out.df <- data.frame(day = j, hour = 1:nhours, count = Y.ijk)
```

```
out.df$doy <- days[j]
```

```
hr.count <- rbind(hr.count, out.df)
```

```
} # end of day loop
```

```
# Add starting population size and year to hourly database
```

```
hr.count$Y.i <- Y.i[i]
```

```
hr.count$year <- i
```

```
# Append hourly counts from each day
```

```
hourly.data <- rbind(hourly.data, hr.count)
```

```
}  # end of year loop

return(hourly.data)

} # end of sim.raptors function
```

Simulation Parameterization

Table A 1. Parameter values used to simulate sharp-shinned hawk hourly migration count datasets used in Chapters 2-3.

Parameter	10-Year Datasets				20-Year Datasets			
Annual CV	Low	Low	High	High	Low	Low	High	High
Daily CV	Low	High	Low	High	Low	High	Low	High
Y.1	9,000	9,000	9,000	9,000	9,000	9,000	9,000	9,000
trend.err	0.2	0.2	0.6	0.6	0.1	0.1	0.5	0.5
sday	-60	-60	-60	-60	-60	-60	-60	-60
sday.err	7	7	7	7	7	7	7	7
m.peak	11	11	11	11	11	11	11	11
m.peak.err	0.2	0.5	0.2	0.2	0.2	0.5	0.2	0.2
day.err	0.1	1.4	0.1	1.4	0.1	1.4	0.1	1.4
k.day	13	5	15	7	13	7	15	7
prob.move	0.85	0.9	0.85	0.85	0.85	0.9	0.85	0.85
m.peak.hr	9	9	11	11	9	11	11	11
m.peak.err.hr	0.2	0.5	0.2	0.2	0.2	0.2	0.2	0.2
hr.err	0.1	1.1	0.1	1.1	0.1	1.1	0.1	1.1
k.hr	8	13	15	15	8	15	15	15

Table A 2. Parameter values used to simulate broad-winged hawk hourly migration count datasets used in Chapters 2-3. Beginning population size (Y.1) is in thousands.

Parameter	10-Year Datasets				20-Year Datasets			
Annual CV	Low	Low	High	High	Low	Low	High	High
Daily CV	Low	High	Low	High	Low	High	Low	High
Y.1	18	18	18	18	18	18	18	18
trend.err	0.4	0.4	1	1	0.4	0.4	1	1
sday	-40	-40	-40	-40	-40	-40	-40	-40
sday.err	7	7	7	7	7	7	7	7
m.peak	8	9	10	10	8	9	10	9
m.peak.err	0.4	0.5	0.5	0.5	0.4	0.5	0.5	0.3
day.err	0.7	1.2	0.7	1.2	0.7	1.2	0.7	1.2
k.day	0.09	0.02	0.2	0.02	0.09	0.02	0.3	0.02
prob.move	0.9	0.9	0.75	0.9	0.9	0.9	0.8	0.9
m.peak.hr	8	10	10	10	8	10	10	9
m.peak.err.hr	0.4	0.4	0.5	0.5	0.4	0.4	0.5	0.3
hr.err	0.5	0.5	0.5	1.2	0.5	0.5	0.5	1.2
k.hr	0.9	0.09	0.9	0.5	0.9	0.09	1.2	1

Table A 3. Parameter values used to simulate merlin hourly migration count datasets used in Chapters 2-3.

Parameter	10-Year Datasets				20-Year Datasets			
Annual CV	Low	Low	High	High	Low	Low	High	High
Daily CV	Low	High	Low	High	Low	High	Low	High
Y.1	250	250	250	250	250	250	250	250
trend.err	0.3	0.3	0.8	0.8	0.3	0.3	0.8	0.8
sday	-50	-50	-50	-50	-50	-50	-50	-50
sday.err	4	4	4	4	4	4	4	4
m.peak	9	8	10	9	9	8	10	9
m.peak.err	0.5	0.5	0.2	0.2	0.5	0.5	0.2	0.2
day.err	0.2	1.2	0.2	1.2	0.2	1.2	0.2	1.2
k.day	0.7	0.2	1	0.4	0.7	0.2	1	0.6
prob.move	0.8	0.75	0.9	0.9	0.8	0.75	0.9	0.9
m.peak.hr	7	8	10	6	7	8	10	7
m.peak.err.hr	0.2	0.4	0.2	0.4	0.2	0.4	0.2	0.4
hr.err	0.2	1.2	0.2	1.2	0.2	1.2	0.2	1.2
k.hr	0.9	0.2	1.5	0.1	0.95	0.2	1.5	0.15

Table A 4. Parameter values used to simulate the hourly raptor migration count datasets used in Chapter 4, which represented a commonly detected species (northern harrier), a rarely detected species with zero-inflated counts (peregrine falcon), and a super-flocking species with highly over-dispersed counts (broad-winged hawk).

Simulation Parameter	Northern harrier	Peregrine falcon	Broad-winged hawk
nyears	20	20	20
Y.1	350	50	12500
trend	-0.036	-0.036	-0.036
trend.err	0.2	0.2	0.5
sday	-65	-35	-35
sday.err	10	8	7
prob.move	0.95	0.9	0.95
weath.pois	1.2	1.2	1.2
m.peak	32	32	32
m.peak.err	5	5	5
m.spread	0	0	0
m.spread.err	0.8	0.8	0.8
day.err	0.05	0.1	0.3
k.day	13	0.09	0.07
shr	-3	-3	-3
shr.err	0.5	0.5	0.5
m.peak.hr	8	8	11
m.peak.err.hr	0.2	0.2	0.4
m.spread.hr	0	0	0
m.spread.err.hr	0.2	0.2	0.2
hr.err	0.1	0.1	0.3
k.hr	5	1	0.4

Appendix B. Comparison of Real and Simulated Hourly Migration Count Data (Chapters 2-3)

Table B 1. Mean and coefficient of variation (min-max; in parentheses) of annual, daily and hourly counts and proportion of 0-observation days and hours for Sharp-shinned Hawk (SSHA), Broad-winged Hawk (BWHA), and Merlin (MERL) data across eight sites in eastern North America: 1) Beamer conservation area (Ontario, Canada: 1995-2009), 2) Hawk Mountain (Pennsylvania, USA: 1966-2009), 3) Holiday Beach (Ontario, Canada: 1979-2009), 4) Montclair (New Jersey, USA: 1977-2009), 5) Cape May (New Jersey, USA: 1974-2004), 6) Militia Hill (Pennsylvania, USA: 1992-2009), 7) Waggoner's Gap (Pennsylvania, USA: 1987-2009), and 8) Hawk Ridge (Minnesota, USA: 1974-2009).

	Annual	Daily	Hourly	0-Obs Hours	0-Obs Days
SSHA	8,717 (0.2-0.5)	113 (1.1-2.3)	14 (1.6-2.6)	0.34 (0.1-0.4)	0.12 (0.3-0.6)
BWHA	14,104 (0.4-1.2)	291 (3.1-6.2)	37 (4.4-12.3)	0.64 (0.1-0.2)	0.33 (0.2-0.4)
MERL	251 (0.3-0.8)	4 (1.8-2.5)	0 (2.4-6.3)	0.86 (0-0.2)	0.59 (0.1-0.4)

Table B 2. Mean and coefficient of variation (in parentheses) of annual, daily and hourly counts, and proportion of 0-observation days and hours across 1000 simulated Sharp-shinned Hawk datasets. Data were simulated to have low or high variation in annual and daily counts, and to have 10- or 20-years of data.

Annual/Daily Variation	Years	Annual	Daily	Hourly	0-Obs Hours	0-Obs Days
Low/Low	10	7,391 (0.2)	124 (1.3)	18 (1.5)	0.15 (0.4)	0.2 (0.3)
	20	6,078 (0.3)	104 (1.3)	15 (1.5)	0.21 (0.3)	0.16 (0.4)
Low/High	10	7,333 (0.2)	125 (2.0)	18 (3.0)	0.12 (0.4)	0.27 (0.2)
	20	6,053 (0.3)	105 (2.0)	15 (3.0)	0.28 (0.2)	0.13 (0.4)
High/Low	10	8,716 (0.6)	144 (1.6)	21 (1.7)	0.16 (0.4)	0.21 (0.3)
	20	6,847 (0.6)	116 (1.5)	17 (1.6)	0.22 (0.3)	0.16 (0.4)
High/High	10	8,616 (0.6)	145 (2.3)	21 (3.4)	0.17 (0.4)	0.31 (0.3)
	20	6,833 (0.6)	117 (2.3)	17 (3.4)	0.32 (0.3)	0.17 (0.4)

Table B 3. Mean and coefficient of variation (in parentheses) of annual, daily and hourly counts, and proportion of 0-observation days and hours across 1000 simulated Broad-winged Hawk datasets. Data were simulated to have low or high variation in annual and daily counts, and to have 10- or 20-years of data.

Annual/Daily Variation	Years	Annual	Daily	Hourly	0-Obs Hours	0-Obs Days
Low/Low	10	15,702 (0.4)	337 (2.9)	48 (4.2)	0.22 (0.4)	0.4 (0.2)
	20	13,130 (0.5)	284 (2.9)	41 (4.3)	0.42 (0.2)	0.23 (0.4)
Low/High	10	15,550 (0.4)	292 (4.2)	42 (9.3)	0.51 (0.2)	0.83 (0.1)
	20	12,878 (0.5)	241 (4.3)	34 (9.5)	0.84 (0.1)	0.53 (0.2)
High/Low	10	23,983 (1.0)	424 (3.4)	61 (5.0)	0.3 (0.3)	0.43 (0.2)
	20	20,020 (1.1)	358 (3.3)	51 (4.6)	0.36 (0.3)	0.24 (0.3)
High/High	10	23,773 (1.0)	422 (5.5)	60 (9.6)	0.48 (0.3)	0.69 (0.2)
	20	19,630 (1.1)	370 (5.7)	53 (9.3)	0.67 (0.2)	0.49 (0.3)

Table B 4. Mean and coefficient of variation (in parentheses) of annual, daily and hourly counts, and proportion of 0-observation days and hours across 1000 simulated Merlin datasets. Data were simulated to have low or high variation in annual and daily counts, and to have 10- or 20-years of data.

Annual/Daily Variation	Years	Annual	Daily	Hourly	0-Obs Hours	0-Obs Days
Low/Low	10	202 (0.3)	5 (1.6)	1 (2.6)	0.38 (0.2)	0.73 (0.1)
	20	169 (0.4)	5 (1.6)	1 (2.7)	0.75 (0.1)	0.41 (0.2)
Low/High	10	204 (0.3)	5 (2.5)	1 (5.5)	0.55 (0.2)	0.87 (0.0)
	20	171 (0.4)	5 (2.6)	1 (5.6)	0.88 (0.0)	0.57 (0.2)
High/Low	10	268 (0.8)	7 (1.8)	1 (2.6)	0.35 (0.4)	0.69 (0.2)
	20	222 (0.9)	6 (1.9)	1 (2.7)	0.72 (0.2)	0.38 (0.4)
High/High	10	269 (0.8)	6 (2.8)	1 (6.5)	0.52 (0.2)	0.89 (0.0)
	20	229 (0.9)	6 (2.7)	1 (6.0)	0.87 (0.1)	0.49 (0.3)

Appendix C. Comparison of Real and Simulated Hourly Migration Count Data (Chapter 4)

Table C 1. Mean, median, range and coefficient of variation (CV) for annual, daily and hourly counts, proportion of 0-observation days and hours, and number of days between first and last detection for three raptor species detected at Hawk Mountain Sanctuary, Pennsylvania (1966-2010). Mean, median and CV of those same variables are also presented for simulated data, where values are mean (of mean, median, cv) across 1000 simulated datasets for each species.

Variable	Species	Real Data				Simulated Data		
		Mean	Median	Range	CV	Mean	Median	CV
Annual Count	Northern harrier	236	244	(119-466)	0.33	239	230	0.30
	Peregrine falcon	29	24	(6-67)	0.66	34	32	0.35
	Broad-winged hawk	8382	7999	(1773-29515)	0.52	9405	8166	0.57
Daily Count	Northern harrier	3	2	(0-36)	1.24	2	1	1.33
	Peregrine falcon	0	0	(0-31)	2.65	0.5	0	3.13
	Broad-winged hawk	169	13	(0-10066)	3.11	128	11	3.15
Hourly Count	Northern harrier	0	0	(0-13)	2.30	0	0	2.60
	Peregrine falcon	0	0	(0-9)	5.40	0	0	6.12
	Broad-winged hawk	19	0	(0-4927)	5.50	16	0	5.76
0-Obs Days	Northern harrier	0.27	0.27	(0.09-0.49)	0.30	0.44	0.44	0.19
	Peregrine falcon	0.77	0.76	(0.62-0.94)	0.12	0.83	0.83	0.06
	Broad-winged hawk	0.17	0.17	(0.05-0.28)	0.35	0.30	0.31	0.37
0-Obs Hours	Northern harrier	0.78	0.77	(0.64-0.88)	0.08	0.83	0.83	0.05
	Peregrine falcon	0.96	0.96	(0.92-0.99)	0.02	0.96	0.96	0.01
	Broad-winged hawk	0.52	0.51	(0.29-0.67)	0.18	0.64	0.64	0.11
N Days Detect	Northern harrier	107	110	(78-123)	0.10	104	107	0.05
	Peregrine falcon	50	42	(15-103)	0.47	51	52	0.24
	Broad-winged hawk	61	59	(44-94)	0.16	64	67	0.15

Appendix D. Stopover Duration Simulation and Parameterization

Simulation Code

Function to simulate data using a modification of the Jolly-Seber capture-recapture simulation model described in Kery and Schaub (2011) – Bayesian Population Analysis using WinBUGS.

Note that R uses as a default the "Mersenne-Twister" random number generator, from Matsumoto and Nishimura (1998). A twisted GFSR with period 2^19937-1 and equidistribution in 623 consecutive dimensions (over the whole period). The 'seed' is a 624-dimensional set of 32-bit integers plus a current position in that set (see ?Random in R).

Definition of Model Parameters

nyears = number of years of data to simulate

Y1 = starting population size in year 1

trend = log-linear change in population size

trend.err = standard deviation of random normal error added to trend on log scale

nb.annual.size = size of the negative binomial obs on annual counts

ndays = number of capture occasions (days in season)

mean.sigma2 = mean of variance of observation process

sd.sigma2 = sd of variance of observation process

a = autocorrelation parameter

phi.in/phi.in.1/phi.in.2 = start and end values for survival; constant within a year, but can vary among years.

p.in = probability of observer detection, assumed constant

prob.move = binomial probability that birds move on a given day

sim = number of datasets to simulate

phi.type = random, cyclical, linear or constant

out.dir = output directory

```
## Beginning of R code
```

```
simul.js <- function(nyears, Y1, trend, trend.err, nb.annual.size,
ndays, mean.sigma2, sd.sigma2, sd.mu, c, a, phi.in, phi.in.1,
phi.in.2, p.in, prob.move, xpred.err, sim, phi.type, out.dir) {

## set up NULL files for output
  out.data <- NULL
  years <- 1:nyears

## Log-linear population change:
  log.Yi <- log(Y1 * (1 + trend)^(0:(nyears - 1)))

## Add random year effects on log scale
  Yi <- exp(log.Yi + rnorm(nyears, trend, trend.err))

## add Negative Binomial noise around expected mean
  Yi <- rnbinom(n = nyears, size = nb.annual.size, mu = Yi)

## Define the parameter values for the daily distribution of counts
  for(i in 1:nyears) {
  n.occasions <- ndays
  date <- c(1:n.occasions)
  sigma2 <- rnorm(1, mean = mean.sigma2, sd = sd.sigma2)     # allows
variation to vary among years
  mu <- rnorm(1, mean = n.occasions/2, sd = sd.mu)     # allows mean of
distribution to vary among years

## NULL files for output
  s <- rep(NA, times = n.occasions)         # probability of birds
entering each day
  xpred <- rep(0, times = n.occasions)
  x <- rep(NA, times = n.occasions)
  b <- rep(NA, times = n.occasions)    # number individuals entering
each day
```

```
## daily probability of entering, b, based on normal distribution:
  for(j in 1:n.occasions) {
      s[j] <- (2 * 3.14 * sigma2)^-0.5 * exp(-0.5*(j - mu)^2/sigma2)
      }


## modify s, so that on bad weather days, no birds migrate
  weather <- rbinom(n = n.occasions, size = 1, prob = prob.move)
  s <- s*weather/sum(s)


## daily number of birds entering, with autocorrelation
 for(j in 1:n.occasions){
      x[j] <- rnorm(1, xpred[j], xpred.err)
      xpred[j+1] <- a*x[j]
      b[j] <- rpois(1, lambda = Yi[i]*s[j]*exp(c*(x[j]-(j-
1)/(n.occasions - 1) * xpred[n.occasions]))))
      }
  B <- round(b*Yi[i]/sum(b), digits = 0); plot(B)
  Y <- sum(B)  # Annual total


## The following is based on Kery and Schaub 2011
  p <- rep(p.in, times = n.occasions)
  phi <- rep(phi.in[i], times = n.occasions) # so that survival can
vary among years
  PHI <- matrix(rep(phi, (n.occasions-1)*Y), ncol = n.occasions-1,
      nrow = Y, byrow = T)
  P <- matrix(rep(p, n.occasions*Y), ncol=n.occasions, nrow = Y, byrow
= T)


## NULL files
  CH.sur <- CH.p <- matrix(0, ncol = n.occasions, nrow = Y)
  CH.dur <- NULL


## define a vector with the occasion of entering the population
  ent.occ <- numeric()
  for(t in 1:n.occasions) {
```

```
        ent.occ <- c(ent.occ, rep(t, B[t]))
        }


## Simulate Arrival
  for(j in 1:length(ent.occ)) { #
  CH.sur[j, ent.occ[j]] <- 1 # write 1 when ind. enters the pop
      if(ent.occ[j] == n.occasions) next
      for(t in (ent.occ[j] + 1):n.occasions) {
      # Bernoulli trial: has individual survived occasion?
      sur <- rbinom(1, 1, PHI[j, t-1])
      ifelse(sur ==1, CH.sur[j, t] <- 1, break)
  } # t
  CH.dur[j] <- length(which(CH.sur[j,] == 1)) # number of days
individual survived in reality (avail for capture)
  } # j


## Simulate capture
  for(j in 1:Y) {
      CH.p[j,] <- rbinom(n.occasions, 1, P[j,])
      } #i


## Full capture-recapture matrix
  CH <- CH.sur * CH.p
## Remove individuals never captured
  cap.sum <- rowSums(CH)
  never <- which(cap.sum ==0)
  CH <- CH[-never,]


## Output "Actual" population size (new plus remaining individuals)
  tmp <- as.data.frame(colSums(CH.sur))
  names(tmp) <- "N.Avail"
  tmp$year <- i
  tmp$doy <- row.names(tmp)


## Output detected population size
```

```
  tmp2 <- as.data.frame(colSums(CH))
  names(tmp2) <- "count"
  tmp2$year <- i
  tmp2$doy <- row.names(tmp2)

## merge actual and detected population size
  tmp <- merge(tmp, tmp2, by = c("year", "doy"), all = TRUE)
  tmp$sim <- sim
  tmp$trend <- trend
  tmp$phi.type <- phi.type
  tmp$phi <- paste(phi.in.1, phi.in.2, sep = "")
  out.data <- rbind(out.data, tmp)
  } # end of year loop

write.csv(out.data, file = paste(out.dir, "StopoverData.", trend.type,
".", phi.type, ".", phi.in.1, phi.in.2, ".", sim, ".csv", sep = ""),
row.names = FALSE)


  } # end of simulation function

#####################################################
## Code required to RUN simulation function

nsims <- 100
phi.type <- "linear" # OR "constant", "random", "cyclic"
phi.in.1 <- 0.2 # OR 0.25, 0.3, 0.35, 0.4
phi.in.2 <- 0.7 # OR 0.65, 0.6, 0.55, 0.5

## determine cycle.amp for cyclic sims (amplitude) to get desired
range in phi

cycle.amp <- NULL
if(phi.in.1 == 0.2) {(cycle.amp  <- 0.25)}
if(phi.in.1 == 0.25) {(cycle.amp  <- 0.2)}
if(phi.in.1 == 0.3) {(cycle.amp  <- 0.15)}
```

```
if(phi.in.1 == 0.35) {(cycle.amp  <- 0.1)}
if(phi.in.1 == 0.4) {(cycle.amp  <- 0.05)}


X <- c(1:nyears)
  trend.pd     = 0
  cycle.1  = 5
  d1       = 2/(cycle.1) # ensures full sin cycle completed


for(i in 1:nsims) {
  phi.in <- NULL
  if(phi.type == "constant") {
  phi.in <- rep(phi.in.1, times = nyears) }
  if(phi.type == "random") {
  phi.in <- runif(n = nyears, min = phi.in.1, max = phi.in.2) }
  if(phi.type == "linear") {
  phi.in <- seq(from = phi.in.1, to = phi.in.2, length = nyears) }
  if(phi.type == "cyclic") {
  phi.in <- 0.45 + trend.pd*X + cycle.amp*sin(d1*(X-1)*pi) }


## RUN simulation function
for(s in 1:nsims) {
simul.js(nyears = nyears, Y1 = 1000, trend = trend, trend.err = 0.45,
nb.annual.size = 5, ndays = 65, mean.sigma2 = 50, sd.sigma2 = 10,
sd.mu = 2.25, c = 1.6, a = 0.2, phi.in = phi.in, phi.in.1 = phi.in.1,
phi.in.2 = phi.in.2, p.in = 0.3, prob.move = 0.85, xpred.err = 1.25,
sim = s, phi.type = phi.type, out.dir = out.dir)
} # end of for loop
```

Simulation Parameterization

Table D 1. Values of simulation model parameters that varied among simulated datasets, where: 'trend' specifies the rate of population trend simulated (log scale); 'phi.type' specifies whether daily probability of survival was simulated to be constant, vary randomly or cyclically, or to increase linearly over time; 'phi.in' specifies the rate or range in survival probability simulated; 'phi.in.1' and 'phi.in.2' are the minimum and maximum values of survival, respectively; and 'cycle.amp' specifies the amplitude of cyclical change required to simulate the desired range in survival.

trend	phi.type	phi.in	phi.in.1	phi.in.2	cycle.amp
-0.012 / 0/ 0.0096	constant	0	0	0	
		0.2	0.2	0.2	
		0.5	0.5	0.5	
		0.7	0.7	0.7	
-0.012 / 0/ 0.0096	random	0.2–0.7	0.2	0.7	
		0.25–0.65	0.25	0.65	
		0.3–0.6	0.3	0.6	
		0.35–0.55	0.35	0.55	
		0.4–0.5	0.4	0.5	
-0.012 / 0/ 0.0096	linear	0.2–0.7	0.2	0.7	
		0.25–0.65	0.25	0.65	
		0.3–0.6	0.3	0.6	
		0.35–0.55	0.35	0.55	
		0.4–0.5	0.4	0.5	
-0.012 / 0/ 0.0096	cyclic	0.2–0.7	0.2	0.7	0.25
		0.25–0.65	0.25	0.65	0.2
		0.3–0.6	0.3	0.6	0.15
		0.35–0.55	0.35	0.55	0.1
		0.4–0.5	0.4	0.5	0.05

Appendix E. Real and Simulated Data Summaries, for Simulations with Variable Survival Probability and Stopover Duration.

Table E 1. Mean, median, coefficient of variation (CV), minimum and maximum of migration counts for White-throated Sparrow (*Zonotrichia albicollis*) collected daily at the tip station of the Long Point Bird Observatory, Ontario, Canada, during spring migration from 1961–2011.

Variable	Mean	Median	CV	Min	Max
Annual Count	571	471	0.51	100	1160
Daily Count	15	4	1.88	0	141
Proportion 0-Observation Days	0.19	0.19	0.44	0	0.35
Observation Days/Season	44	43	0.18	31	70

Table E 2. Mean, median and coefficient of variation (CV) of annual population size among 100 simulated datasets for each set of factor levels. Datasets were simulated to have either a declining population trend (-1.2 %year^{-1}; "Decline"), no population change (0 %year^{-1}; "NoChange") or an increasing population trend (0.96 %year^{-1}; "Increase"). Survival probability remained constant or varied randomly, cyclically or increased linearly over time.

Survival	*phi*	Mean			Median			CV		
		Decline	NoChange	Increase	Decline	NoChange	Increase	Decline	NoChange	Increase
Constant	0	291	333	358	242	280	302	0.62	0.62	0.63
	0.20	293	332	370	245	275	311	0.64	0.63	0.65
	0.50	304	343	386	251	291	319	0.64	0.62	0.63
	0.70	310	353	386	259	295	328	0.62	0.63	0.63
Random	0.20–0.70	566	631	711	452	524	579	0.70	0.69	0.69
	0.25–0.65	551	614	683	450	504	560	0.67	0.66	0.67
	0.30–0.60	539	609	681	440	509	561	0.66	0.64	0.65
	0.35–0.55	546	601	662	458	497	553	0.64	0.65	0.64
	0.40–0.50	524	598	668	438	500	562	0.64	0.63	0.63
Cyclic	0.20–0.70	590	661	743	457	514	586	0.74	0.74	0.72
	0.25–0.65	569	638	705	458	512	572	0.68	0.69	0.69
	0.30–0.60	553	620	688	458	510	572	0.66	0.67	0.66
	0.35–0.55	538	599	660	444	506	560	0.65	0.64	0.64
	0.40–0.50	526	607	649	438	505	543	0.63	0.65	0.63
Linear	0.20–0.70	554	647	726	454	514	567	0.69	0.69	0.72
	0.25–0.65	544	626	692	448	509	560	0.65	0.68	0.70
	0.30–0.60	539	610	690	452	502	560	0.63	0.67	0.69
	0.35–0.55	531	601	673	446	507	552	0.64	0.63	0.66
	0.40–0.50	522	600	667	440	501	568	0.62	0.64	0.63

Table E 3. Mean, median and coefficient of variation (CV) of daily population size among 100 simulated datasets for each set of factor levels. Datasets were simulated to have either a declining population trend (-1.2 %year^{-1}; "Decline"), no population change (0 %year^{-1}; "NoChange") or an increasing population trend (0.96 %year^{-1}; "Increase"). Survival probability remained constant or varied randomly, cyclically or increased linearly over time.

Survival	phi	Mean			Median			CV		
		Decline	NoChange	Increase	Decline	NoChange	Increase	Decline	NoChange	Increase
Constant	0	6	7	8	0	1	1	3.12	3.13	3.14
	20	6	7	8	1	1	1	3.09	3.07	3.09
	50	7	7	8	1	1	1	3.00	2.96	2.99
	70	7	8	8	1	1	1	2.92	2.95	2.95
Random	0.20–0.70	11	13	14	3	3	4	2.11	2.11	2.12
	0.25–0.65	11	12	14	3	3	4	2.08	2.11	2.12
	0.30–0.60	11	12	14	3	3	3	2.10	2.10	2.10
	0.35–0.55	11	12	13	3	3	3	2.08	2.09	2.09
	0.40–0.50	11	12	13	3	3	3	2.08	2.11	2.09
Cyclic	0.20–0.70	12	13	14	3	4	4	2.13	2.13	2.15
	0.25–0.65	11	13	14	3	3	4	2.11	2.12	2.11
	0.30–0.60	11	12	14	3	3	4	2.10	2.11	2.11
	0.35–0.55	11	12	13	3	3	3	2.08	2.11	2.10
	0.40–0.50	11	12	13	3	3	3	2.08	2.09	2.09
Linear	0.20–0.70	11	13	14	3	3	4	2.11	2.11	2.13
	0.25–0.65	11	13	14	3	3	4	2.11	2.09	2.11
	0.30–0.60	11	12	14	3	3	4	2.10	2.09	2.12
	0.35–0.55	11	12	14	3	3	3	2.08	2.10	2.10
	0.40–0.50	11	12	13	3	3	3	2.08	2.09	2.11

Table E 4. Mean, median and coefficient of variation (CV) of the number of 0-observation days among 100 simulated datasets for each set of factor levels. Datasets were simulated to have either a declining population trend (-1.2 %year^{-1}; "Decline"), no population change (0 %year^{-1}; "NoChange") or an increasing population trend (0.96 %year^{-1}; "Increase"). Survival probability remained constant or varied randomly, cyclically or increased linearly over time.

Survival	*phi*	Mean			Median			CV		
		Decline	NoChange	Increase	Decline	NoChange	Increase	Decline	NoChange	Increase
Constant	0	0.55	0.54	0.53	0.55	0.53	0.53	0.23	0.24	0.24
	0.2	0.53	0.52	0.51	0.53	0.52	0.51	0.25	0.26	0.26
	0.5	0.51	0.49	0.48	0.51	0.49	0.48	0.27	0.27	0.28
	0.7	0.50	0.49	0.47	0.50	0.49	0.47	0.27	0.29	0.29
Random	20–70	0.35	0.33	0.33	0.34	0.32	0.32	0.45	0.44	0.45
	25–65	0.34	0.33	0.33	0.34	0.32	0.32	0.43	0.43	0.45
	30–60	0.34	0.33	0.32	0.33	0.32	0.31	0.42	0.42	0.43
	35–55	0.34	0.33	0.32	0.33	0.32	0.31	0.42	0.42	0.42
	40–50	0.34	0.33	0.32	0.33	0.32	0.31	0.41	0.42	0.43
Linear	20–70	0.35	0.34	0.33	0.34	0.33	0.33	0.44	0.45	0.45
	25–65	0.34	0.33	0.33	0.33	0.33	0.32	0.43	0.44	0.44
	30–60	0.34	0.33	0.33	0.33	0.32	0.32	0.42	0.43	0.43
	35–55	0.34	0.33	0.32	0.33	0.32	0.31	0.41	0.42	0.43
	40–50	0.34	0.33	0.32	0.33	0.32	0.31	0.40	0.42	0.42
Cyclic	20–70	0.35	0.34	0.33	0.35	0.34	0.33	0.45	0.46	0.47
	25–65	0.34	0.34	0.33	0.34	0.33	0.32	0.44	0.45	0.45
	30–60	0.34	0.33	0.32	0.33	0.32	0.31	0.43	0.44	0.44
	35–55	0.34	0.33	0.32	0.33	0.33	0.31	0.42	0.42	0.43
	40–50	0.34	0.33	0.32	0.33	0.32	0.31	0.41	0.42	0.42

Table E 5. Mean, median and coefficient of variation (CV) of the number of observation days each season among 100 simulated datasets for each set of factor levels. Datasets were simulated to have either a declining population trend (-1.2 %year^{-1}; "Decline"), no population change (0 %year^{-1}; "NoChange") or an increasing population trend (0.96 %year^{-1}; "Increase"). Survival probability remained constant or varied randomly, cyclically or increased linearly over time.

Survival	phi	Mean			Median			CV		
		Decline	NoChange	Increase	Decline	NoChange	Increase	Decline	NoChange	Increase
Constant	0	35	36	36	36	37	37	0.18	0.18	0.17
	0.2	35	36	36	36	37	37	0.18	0.18	0.175
	0.5	35	36	37	36	37	38	0.18	0.17	0.17
	0.7	36	36	36	36	37	37	0.18	0.18	0.17
Random	0.20–0.70	39	40	40	40	40	41	0.17	0.16	0.16
	0.25–0.65	39	39	40	40	40	41	0.16	0.16	0.16
	0.30–0.60	39	39	40	40	40	41	0.16	0.16	0.155
	0.35–0.55	39	39	40	40	40	40	0.16	0.16	0.16
	0.40–0.50	39	39	40	39	40	41	0.16	0.16	0.16
Linear	0.20–0.70	39	40	40	40	41	41	0.17	0.16	0.17
	0.25–0.65	39	40	40	40	41	41	0.16	0.16	0.16
	0.30–0.60	39	39	40	40	40	40	0.16	0.16	0.16
	0.35–0.55	39	39	40	40	40	41	0.16	0.16	0.16
	0.40–0.50	38	39	40	39	40	41	0.16	0.16	0.15
Cyclic	0.20–0.70	39	40	40	40	41	41	0.17	0.17	0.17
	0.25–0.65	39	40	40	40	41	41	0.17	0.16	0.16
	0.30–0.60	39	39	40	40	40	41	0.17	0.16	0.16
	0.35–0.55	39	39	40	40	40	40	0.16	0.16	0.15
	0.40–0.50	39	39	39	40	40	40	0.16	0.16	0.16

Table E 6. Mean (SD) of Pearson correlation coefficients of quantile-quantile (QQ) scores among 100 simulated migration count datasets with real white-throated sparrow (*Zonotrichia albicollis*) migration count data collected during spring migration at the tip station of the Long Point Bird Observatory in Ontario, Canada (1961–2011). A correlation coefficient of one suggests quantiles of each dataset originate from a similar distribution of counts. Survival was simulated to remain constant, or to vary randomly, linearly or cyclically over time. A daily probability of survival of zero suggests all birds departed the count site within 24 hours (i.e., no stopover).

		Population Trend Type		
Survival	Survival Probability	Decline	No Change	Increase
Constant	0	0.92 (0.06)	0.92 (0.05)	0.93 (0.05)
	0.20	0.93 (0.04)	0.93 (0.04)	0.93 (0.05)
	0.50	0.93 (0.04)	0.93 (0.04)	0.94 (0.04)
	0.70	0.94 (0.04)	0.93 (0.05)	0.93 (0.05)
Random	0.20–0.70	0.98 (0.03)	0.97 (0.04)	0.97 (0.03)
	0.25–0.65	0.97 (0.03)	0.98 (0.02)	0.98 (0.03)
	0.30–0.60	0.98 (0.03)	0.97 (0.03)	0.98 (0.03)
	0.35–0.55	0.98 (0.02)	0.97 (0.03)	0.98 (0.03)
	0.40–0.50	0.98 (0.02)	0.98 (0.03)	0.97 (0.04)
Linear	0.20–0.70	0.98 (0.03)	0.98 (0.02)	0.98 (0.02)
	0.25–0.65	0.97 (0.03)	0.98 (0.03)	0.98 (0.03)
	0.30–0.60	0.97 (0.03)	0.97 (0.03)	0.98 (0.03)
	0.35–0.55	0.97 (0.03)	0.98 (0.03)	0.97 (0.04)
	0.40–0.50	0.98 (0.02)	0.98 (0.03)	0.97 (0.03)
Cyclic	0.20–0.70	0.98 (0.02)	0.98 (0.03)	0.98 (0.02)
	0.25–0.65	0.97 (0.03)	0.97 (0.03)	0.98 (0.03)
	0.30–0.60	0.98 (0.02)	0.98 (0.03)	0.97 (0.03)
	0.35–0.55	0.98 (0.02)	0.97 (0.03)	0.97 (0.03)
	0.40–0.50	0.98 (0.03)	0.97 (0.03)	0.97 (0.04)

Appendix F. Regional Trends Simulation and Parameterization.

Simulation Code

Note that R uses as a default the "Mersenne-Twister" random number generator, from Matsumoto and Nishimura (1998). A twisted GFSR with period 2^19937-1 and equidistribution in 623 consecutive dimensions (over the whole period). The 'seed' is a 624-dimensional set of 32-bit integers plus a current position in that set (see ?Random in R).

```
# Definition of terms
Y1.region: Annual population size in year 1
abund.dist = "equal" or "unequal"; how is abundance distributed among regions/sites
nregions = 4; number of regions to simulate
nsites = 3, 5, or 10; number of sites in each region
prob.site
Species
write.summ = TRUE; whether or not to write summary to output file
SpeciesCode = CAWA or WTSP
site.err =
out.dir: specifies output directory
trend =  1, 2, or 4; whether trend same across regions (1) or varies (2, 4)
nyears = 40; number of years to simulate
sday
sday.err
m.spread = 0
m.spread.err
m.peak
m.peak.err
day.err
weath.pois = 1.2
prob.move,
```

```
prob.move.err = 0.05

max.similar.days = 2

####################################

## Beginning of R code

## Required packages


require(lattice)
require(reshape2)
require(reshape) # for rename()


##########################
## Define the function


sim.daily <- function(Y1.region, abund.dist, nregions = 4,
nsites, prob.site, Species, write.summ = TRUE, SpeciesCode,
site.err, out.dir = "", trend, nyears = 40, sday, sday.err,
m.spread = 0, m.spread.err, m.peak, m.peak.err, day.err,
weath.pois = 1.2, prob.move, prob.move.err = 0.05,
max.similar.days = 2)  {

## Set up null dataframe for output

daily.data<- as.data.frame(matrix(nrow = 1, ncol = 9))
names(daily.data) <- c("SpeciesCode", "region", "site", "year",
"day", "doy", "count",  "Y1.site", "Y1.region")

## FIRST LOOP = REGIONS

for (r in 1:nregions) {
```

```
## generate vector of annual regional abundances, based on
starting pop size in region and region-specific trend.

log.Y.region<- log(Y1.region[r] * (1 + trend[r])^(0:(nyears -
1)))
Y.region<- exp(log.Y.region)


## SECOND LOOP = YEARS
## Distribute annual regional abundance among sites


for(i in 1:nyears) {
Y.site<- rmultinom(1, size = Y.region[i], prob = prob.site)


## THIRD LOOP = SITES


for(s in 1:nsites) {


Yi <- Y.site[s]


## Add RANDOM SITE-SPECIFIC YEAR EFFECT on log scale


log.Yi<- log(Yi) + rnorm(1, 0, site.err[r,s])


## Back-transform to response scale


  Yi <- exp(log.Yi)
## Distribute annual total (Yi) through days in a year


## Determine number of days in season.  Allow normal variation
around sday, and determine eday accordingly
s.day<- round(sday[r,s] + rnorm(1, 0, sday.err[r,s])) # site-
specific error
e.day<- abs(s.day)  # creates first and last day, centered on 0
ndays<- e.day - s.day + 1  # number days
days<- seq(s.day, e.day)
```

```
## Set up distribution of birds across days in a year.  Assumes
bell-shaped (normal) distribution, with peak number birds moving
through mid-season

spread<- dnorm(seq(s.day, e.day), rnorm(1, m.spread,
m.spread.err[r,s]),
     rnorm(1, m.peak, m.peak.err[r,s])) # allows spread to vary
among years
spread<- spread/sum(spread)  # so values of spread add to 1
plot(spread)

## Add first level of noise to daily counts: random site-specific
error in daily counts on log scale

Yij_avail<- Yi * spread
log.Yij_avail<- log(Yij_avail) + rnorm(length(Yij_avail), 0,
day.err[r,s])
Yij_avail<- exp(log.Yij_avail)

## Second level of noise on daily counts: add Poisson

Yij_avail<- rpois(ndays, Yij_avail)

## The following ensures the sum of daily counts adds up to
annual counts (or close to it).

if(sum(Yij_avail) > 0) {
     Yij_avail<- round(Yij_avail/sum(Yij_avail) * Yi, digits =
0)}

##  Set up a weather variable, based on uniform distribution with
added Poisson variability, to allow adjacent days to have more
similar weather conditions.  Limit to a given maximum number of
days with similar weather conditions.
```

```
weather<- runif(ndays, 0, 1)
weather.pois<- rpois(20*ndays, weath.pois)
weather.pois<- subset(weather.pois, weather.pois> 0)
weather.pois[which(weather.pois>max.similar.days)] <-
max.similar.days
weather.pois<- weather.pois[1:ndays]
weather<- rep(weather, weather.pois)
weather<- weather[1:ndays] ## subset, so vector is same length as
number of days in year


## Set up a probability that birds will move through/stop at a
site on a given day, given they are available to move ( =nwm).


## linear relationship between prob moving and weather
pm<- weather


## adds threshold: below certain weather condition, no birds move


pm[which(pm < (1 - prob.move[i]))] <- 0


## set up blank vector for number of birds that actually move


Yij<- rep(0, length(Yij_avail))


## Now loop though days, calculate the number that move (nm)
based on binomial distribution. Number that actually want to move
(nawm) needs to be the same as number want to move (nwm) in first
time step.


Yij_wantmove<- Yij_avail


## LOOP THROUGH DAYS = FOURTH LOOP


for(d in 1:ndays) {
```

```
      ## each individual has a binomial probability of moving
      Yij[d] <- rbinom(1, Yij_wantmove[d], round(pm[d], digits
=3))
      ## add left-over individuals to next day's number that want
to move
if(d <= (ndays-1)) { Yij_wantmove[d + 1] <- Yij_avail[d + 1] +
Yij_wantmove[d] - Yij[d]}
  } # end of day loop


tmp.df<- data.frame(SpeciesCode = SpeciesCode, region = r, site =
s, year = i, day = c(1:length(Yij)), doy = days, count = Yij,
Y1.site = Yi, Y1.region = Y.region[i] )# this is the regpopn size
for year i, AFTER random and poisson error in trend


daily.data<- rbind(daily.data, tmp.df) # daily counts for one
year, merged with other years
daily.data<- subset(daily.data, !is.na(day)) # ensure no NA
counts/days


  } # end of site loop
  } # end of year loop
  } # end of region loop


return(daily.data)


  } # end of simulation function
```

Simulation Parameterization

Table F 1. Parameter values for the simulation function to approximate Canada Warbler and White-throated Sparrow data. For trend = 1 (national population change), -1.2 %year^{-1}, or a 20 % decline in 20 years was simulated. For trend = 2, 2 regions declined by -1.2 %year^{-1}, and two regions increased by 0. 96 %year^{-1}, or a 20 % increase in 20 years. For trend = 4, each region was assigned a different trend: 1) -1.2 %year^{-1}, 2) 0. 96 %year^{-1}, 3) -3.6 %year^{-1} (50 % decline in 20 years), and 4) 2.2 %year^{-1} (50 % increase in 20 years). Starting abundance was distributed either equally or unequally among sites and regions.

Parameter	No. Sites	Canada warbler		White-throated sparrow	
		Equal	Unequal	Equal	Unequal
Y1.region	3	225	c(260, 35, 145, 225)	600	c(2230, 6460, 1420, 30)
	5	375	c(435, 60, 240, 375)	1000	c(3716, 10767, 2367, 50)
	10	1500	c(1730, 230, 970, 1500)	2000	c(7430, 21530, 4730, 100)
prob.site	3	1/nsites	c(0.55, 0.30, 0.15)	1/nsites	c(0.55, 0.30, 0.15)
	5	1/nsites	c(0.05, 0.10, 0.20, 0.25, 0.40)	1/nsites	c(0.05, 0.10, 0.20, 0.25, 0.40)
	10	1/nsites	c(0.1, 0.04, 0.2, 0.13, 0.05, 0.08, 0.11, 0.09, 0.17, 0.03)	1/nsites	c(0.1, 0.04, 0.2, 0.13, 0.05, 0.08, 0.11, 0.09, 0.17, 0.03)
site.err		0.1	N(0.16, 0.05)	0.51	N(0.30, 0.08)
trend		1, 2 **OR** 4	1, 2 **OR** 4	1, 2 **OR** 4	1, 2 **OR** 4
sday		-23	-23	-34	-34
sday.err		1	1	2	2
m.spread.err		3	3	0.2	0.2
m.peak		6	6	12	12
m.peak.err		1.5	1.5	0.8	0.8
day.err		1	N(1, 0.3)	0.8	N(1.2, 0.15)
prob.move		0.7	0.7	0.85	0.85

Curriculum Vitae

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