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Title

Estimating transient populations of unmarked individuals at a migratory stopover site using generalized N-mixture models

Running head

Transient population and dynamic N-mixture models

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ABSTRACT

Migration counts are popular indices used to monitor population trends over time.
 Advanced analytical methods for estimating abundance of unmarked, open populations now incorporate population growth models and simultaneously test for covariate effects on abundance and detection probability. However, estimating population abundance at a staging site is complicated by daily immigration and emigration of unmarked individuals.

2. We applied a set of generalized N-mixture models to simulated count data to test their applicability for transient populations. Using simulated datasets, parameters were unbiased when the apparent survival rate varied within a season or was mis-specified in a model, but not when the immigration or detection probability was mis-specified.

3. With knowledge from the simulated data, we applied these models to daily counts of staging migratory shorebirds and estimated daily abundances accounting for variation in the detection and immigration rates. Daily counts of ruddy turnstones (*Arenaria interpres*) staging at Westhampton Island, New York, were collected during northward migration (1997–1999). We tested the effects of weather and tides on detection probability, and we modelled within-season variation in immigration rates as a function of time.

4. Covariates affecting the detection probability differed among years, but tide height consistently was correlated with detection probability. Accounting for detection and immigration rates, the predicted maximum single-day populations of ruddy turnstones were 172%, 165%, and 129% of the observed counts for each year.

5. *Synthesis and applications*. Management and conservation plans for migratory species require abundance estimates that are near the true population size though they are difficult to obtain. Our study is the first empirical application of the generalized N-mixture model that incorporates temporal trends in immigration and estimates daily abundance of a staging unmarked migratory population. Despite its inherent limitation, we suggest that the generalized N-mixture model can estimate the abundance of transient populations with low individual heterogeneity when counts are intensively surveyed. Correct estimation of population sizes and the environmental factors affecting them can aid the conservation prioritization of species and staging sites. Moreover, the use of generalized N-mixture models can improve our understanding of the environmental factors that shape migratory movements.

KEYWORDS

Dail-Madsen model, daily count data, detection probability, N-mixture model, immigration, ruddy turnstone, seasonal abundance, tidal effect

INTRODUCTION

Abundance estimation is fundamental to addressing many ecological questions, evaluating management actions, and projecting future population numbers (Thomas, 1996; Yoccoz et al., 2001; Sagarin et al., 2006). Indices of relative abundance often are cheaper to

estimate than absolute abundances and often are the goal of monitoring programs with broad spatial or temporal scales (Link & Sauer, 1998; Pollock et al., 2002). Since no wild animal species is perfectly detectable, it is important to untangle true population changes from variable detectability (MacKenzie & Kendall, 2002; Thompson, 2002). When individuals are uniquely identified, mark-recapture/resight methods allow estimation of detection probability (Nichols, 1992; Schwarz & Seber, 1999). For an unmarked population, distance sampling can provide a way to estimate detectability and abundance (Buckland et al., 2005), or N-mixture models can estimate the predicted total number of individuals, using replicate counts over time and space (Schwarz & Seber, 1999; Royle, 2004; Joseph et al., 2009). Analytical methods for estimating abundance of unmarked populations have been expanded to incorporate count data that are spatially correlated, include multiple species, or are from a single survey (reviewed in Dénes et al., 2015).

Generalized N-mixture models, also called dynamic N-mixture models, estimate the population abundance at site *i* at time *t* ($N_{i,t}$) as a result of a Markovian process and $N_{i,t-1}$, thereby relieving the 'population closure' assumption (Dail & Madsen, 2011). In other words, instead of assuming no population changes occur during a study period, these models allow population changes to occur between primary observation periods and incorporate those changes into parameter estimation. Since the generalized N-mixture model was introduced (Dail & Madsen, 2011), studies focused on developing population estimators that incorporate density-dependence, intrinsic population growth rates, and environmental stochasticity into modelling (Zipkin et al., 2014b; Hostetler & Chandler, 2015; Bellier et al., 2016). Empirical application of generalized N-mixture models has been made to estimate population changes across generations (Hocking et al., 2013; Thorson et al., 2014; Zipkin et al., 2014a; Bruggeman et al., 2015; McCaffery et al., 2016), to test environmental effects on local abundances of an elusive bird species (Chandler & King, 2011), or to estimate the emergence

timing of bivoltine butterflies (Matechou et al., 2014). To our knowledge, however, this approach has not been used to estimate a population size that is subject to extreme temporal changes, as occur in migratory populations at staging sites.

Migratory animals congregate into temporary groups throughout their annual cycle on one or more staging sites *en route* between breeding and wintering locations (Newton, 2007). For migratory species, abundance often is estimated during reproductive stages, when intensive monitoring efforts are employed and detection rates are high. Population abundance indices estimated at staging sites potentially are limited because of 1) the few repeated encounters with the same individual (if individuals are identifiable at all) at a staging site, 2) the high rate of population change through immigration and emigration, and 3) the relatively short time spent at a given staging site compared to other life stages for some species. Despite these inherent difficulties, some properties of a migratory population on their staging grounds can facilitate abundance estimation: 1) typically no births occur on a staging site (i.e., immigration is the only source of recruitment); 2) although spatial distribution during migration may be density-dependent (Kelly et al., 2002; Chudzińska et al., 2015; but see Shochat et al., 2002), there is no evidence that within-season changes to immigration rates are dependent on local density at a staging location; and 3) within-season changes of immigration rate typically follow a reasonably predictable bell-shaped trend, although the timing of peak immigration may be dependent on environmental conditions or distinctive by demographic groups (Bednarz et al., 1990; Morris & Glasgow, 2001; Lee et al., 2007; Robson & Barriocanal, 2011).

Large flocks of birds have been counted at major staging sites (Bildstein, 1998; Hurlbert & Liang, 2012), yielding annual indices of population size (e.g., maximum daily count of individuals) and descriptions of population trends (Dunn & Hussell, 1995; Dunn et al., 1997; Knape et al., 2009). Abundance indices of migrating individuals at staging sites

provide important information for ecological understanding and management actions (Bart et al., 2007; Gratto-Trevor et al., 2012). However, few studies have addressed the reliability of annual indices as a measure of population size or incorporated the effects of imperfect detection (Rosenstock et al., 2002). To our knowledge, modelling of daily changes in the population size at a staging site has been purely theoretical (Thompson, 1993; Crewe et al., 2015), or empirical with restrictive assumptions of constant detection probability and spatial homogeneity in abundance (Farmer & Durbian, 2006; Cohen et al., 2009). Consistent monitoring effort across time could justify direct comparison of annual indices, but imperfect detectability must be incorporated into abundance estimation when the absolute population size is of interest. Staging populations are naturally subject to high rates of immigration and emigration as well as imperfect detection. Estimation of an index of the 'true' population abundance requires modelling population changes (i.e., immigration and emigration) and the observation process simultaneously. In the case of annual migration, immigration rates into a staging site tend to increase and then decrease as individuals leave. Therefore, the temporal trends in immigration rate may be modelled as a polynomial function of time (Thompson, 1993; Bunnefeld et al., 2010).

In this study, we applied a set of generalized N-mixture models to both simulated data and daily counts of a migratory shorebird, the ruddy turnstone (*Arenaria interpres*), at a staging site and estimated daily abundances, incorporating within-season variation of immigration rate and detection probability in these models. Various stochastic environmental factors (e.g., weather, habitat), intrinsic factors (e.g., physiological condition of migrants, immigration rate, true survival, emigration rate), and observer effort can affect detectability, creating systematic bias in surveyed counts (Kendall et al., 1996; Rosenstock et al., 2002 and references therein; Hochachka & Fiedler, 2008). Despite these complications, environmental factors can be used to describe variations from seasonal trends in migration (Richardson,

1990). In the case of migrating shorebirds, daily counts at a staging site often are strongly affected by the tidal cycle, where most shorebirds roost at high tides and forage during low tides (Burger et al., 1977; Rogers et al., 2006). Therefore, we considered the effects of daily weather variables and estimated tidal level at the time of survey on detection probability and tested within-season variation in immigration rates as a function of time throughout the migration window. The staging population of ruddy turnstones on Westhampton Island, New York is a good system to test these models because the seasonal trend of immigration rate is expected to be simple with a single peak, based on the monitoring of marked individuals at a nearby staging site (Delaware Bay, USA [1997–2016], A. Tucker, Auburn University, pers. comm.).

Our goal was to show that generalized N-mixture models could be applied to situations such as migratory stopovers when detection and immigration rates are modelled as a function of covariates and expected functional forms. Our study 1) introduces a new application of generalized N-mixture models to estimate the abundance of a staging population where daily movement of unmarked individuals complicates the estimation of a population size, and 2) discusses the unique characteristics of migration counts which may allow the use of the generalized N-mixture model to estimate the true staging population of a species in a specific area.

MATERIALS AND METHODS

Use of the dynamic N-mixture model

The basic structure of the dynamic N-mixture model (Dail & Madsen, 2011) is described as follows,

$$N_{i,1} \sim \text{Poisson}(\lambda_i)$$

- $G_{i,t} \sim \text{Poisson}(N_{i,t-1}\gamma_{i,t})$
- $S_{i,t} \sim \text{binomial}(N_{i,t-1}, \phi_{i,t})$

$$N_{i,t} = G_{i,t} + S_{i,t}$$

 $y_{i,t} \sim \text{binomial}(N_{i,t}, p_{i,t}),$

where the number of individuals at site *i* in the first survey occasion ($N_{i,1}$) is assumed to follow a Poisson distribution with a mean population size at site *i* in the first survey occasion (λ_i), which fluctuates as a function of the apparent survival probability at site *i* from *t* to *t*+1 ($\phi_{i,t}$) and the recruitment rate at site *i* at time *t* ($\gamma_{i,t}$). Therefore, the expected number of individuals at site *i* in time *t* is the sum of individuals newly gained ($G_{i,t}$) and individuals that survived from the previous occasion ($S_{i,t}$). The observed counts at site *i* at time *t* ($y_{i,t}$) are then determined by the expected number of individuals ($N_{i,t}$) and the detection probability ($p_{i,t}$).

We estimated daily abundances within each year's migration window separately. Since no births occurred within our migration windows, we interpreted the daily recruitment rate as the number of individuals arriving at the site between two consecutive survey days ('*immigration*'). We still could not separate deaths from emigrations, thus, we interpreted the apparent survival rate as the probability that an individual survived and stayed on site between survey days ('*persistence*'). Each survey day was treated as a primary period, which is open to immigration and emigration. Because we assumed the immigration rate at time *t* was independent of local abundances at time t - 1 in our study, the number of newly gained individuals at site *i* at time *t* was dependent only on the recruitment rate thus, $G_{i,t} \sim$ Poisson($\gamma_{i,t}$). The N-mixture model uses replicate samples from *i* sites to estimate parameters in the likelihood function and does not require secondary periods.

Simulating within-season patterns of persistence and effects of model misspecification

Because we did not have an *a priori* hypothesis on how the persistence would vary within the migration window, we conducted two sets of simulation studies to test 1) if different within-season patterns of persistence affected the estimation of other parameters and 2) if misspecification of the persistence term in a model biased abundance estimates. First, we simulated a dataset for each of three different persistence scenarios, in which the persistence $(\phi_{i,t})$ was a) constant at 0.5, b) decreasing as a function of date, or c) fluctuating randomly as a function of an environmental variable. Immigration $(\gamma_{i,t})$ was set to a) peak in the middle of the survey period or b) show bimodal peaks of the same height, mimicking a delayed migration scenarios were tested with average detection probability (p) of 1) 0.3 for low detection and 2) 0.8 for high detection. Detection probability also was set to positively and negatively covary with two environmental variables, respectively. Initial abundance at each site was set as '1' (see Supplementary Material S1).

We simulated a count dataset consisting of 14 sites and 47 primary periods without temporal replicates to resemble our field collected dataset and assumed a Poisson mixture for modelling. We first fitted models where the parameter terms were correctly specified to match the parameter values used to simulate the data. The summation of N_i must be bound by an upper limit that is a predicted population size large enough not to affect MLEs but small enough for the model to converge (Dail & Madsen, 2011). For the simulation study, we set the upper limit of the daily population size for any site as 50. Second, we simulated a dataset assuming that persistence decreased with date and immigration peaked in the middle of migration window with the detection probability set the same as above. Then, we fitted three models to the simulated data, in which either the 1) persistence, 2) immigration, or 3) detection probability was mis-specified as constant.

We used the 'pcountOpen' function and the 'constant model' setting in R package 'unmarked' to fit models (Fiske & Chandler, 2011). With the 'constant model' setting, parameter values can vary as a function of covariates, but are otherwise constant, allowing parameters to be separately estimable (Fiske & Chandler, 2011). For each of the scenarios, we predicted conditional daily abundance at each site for each date, using 'ranef' and 'predict' functions in R package 'unmarked' (Fiske & Chandler, 2011). Daily total predicted abundance for the entire study area was calculated as the sum of predicted abundances from each of 14 sites for a given day. We repeated each scenario 500 times and reported parameter estimates and predicted abundances in relation to the true values.

Daily counts of ruddy turnstones

We applied this model to daily counts of ruddy turnstones collected at Westhampton Island, New York, during northward migration in 1997–1999 (Houghton, 2005). Ruddy turnstones migrate long distances between Arctic breeding grounds and temperate wintering grounds along the Atlantic and the Pacific coasts (Nettleship, 2000). Northward migration begins in March, and at an important stopover site just south of our study site, the Delaware Bay, USA, the peak single day counts of migrating birds typically occurred in late May (Clark et al., 1993). Northward migration is usually more contracted and relatively synchronous except for immature birds migrating later than adults (Nettleship, 2000).

Field counts were conducted on 44 days in 1997 (May 7–Jun 23), 46 days in 1998 (Apr 30–Jun 19), and 50 days in 1999 (Apr 29–Jun 20). During each migration window (1997–1999), we counted ruddy turnstones on 6–7 transects in West Hampton Dunes (40.46° N, 72.43° W), and 7–8 transects on the adjoining Westhampton Beach (40.47° N, 72.40° W). West Hampton Dunes is a village that was largely washed away during winter storms in the winter of 1992–1993 and was mostly undeveloped during this study (Cohen et al., 2009). Westhampton Beach was a highly developed part of the same barrier island. Each transect

constituted a site, and therefore, we had total 13, 15, and 14 replicate sites for the three years, respectively. Not all transects were surveyed every day, and our dataset comprised 302, 288, and 637 transect-survey data points for the three years. Transects were perpendicular to the shoreline with 420 m between each transect. Transects within either Westhampton Beach or West Hampton Dunes were surveyed in sequence within a few hours on any given day, reducing the potential double counting of the same birds moving between sites. The length of the transects varied depending on the width of the beach at a survey point (ca. 50–100 m). The transects in West Hampton Dunes ran from the water's edge on the ocean to the dense vegetation or the water's edge on the bay. The transects in Westhampton Beach ran from the water's edge on the ocean to the seaward edge of the dense vegetation due to human development. Observers surveyed by foot between 05:00 and 14:30 every day, except for days with heavy rain, and recorded the number of ruddy turnstones seen. Our transects included both foraging and roosting habitat for migrating shorebirds. Previous surveys on the other side of Long Island Sound showed that ruddy turnstones use the beach habitat for both foraging and roosting regardless of the tide height (Placyk & Harrington, 2004). Therefore, our survey design incorporated both foraging and roosting flocks.

Covariate effects on parameter estimates using ruddy turnstone data

For modelling with field collected data, we considered the effects of survey-specific (time of day, tidal height) and day-specific covariates (daily total precipitation, daily average wind direction, and daily maximum wind speed) on detection probability. We predicted that the detection probability would be higher when the environmental condition is favorable for foraging (i.e., with less precipitation and lower wind speed, and when northwesterly wind pushes the water's edge down the ocean beach and exposes more foraging habitat). We obtained daily precipitation data from a weather station at Francis S. Gabreski Airport

(40.84° N, 72.63° W) and daily wind data from a weather station at John F. Kennedy Intl. Airport (40.66° N, 73.78° W). We obtained publicly available tidal information for Moriches Inlet on Long Island, New York (40.45° N, 72.45° W; http://tides.mobilegeographics.com/). Our study site experienced two low tides and two high tides each day. We used tidal information and 'The rule of twelfths' (Getchell, 1994) to interpolate predicted tidal height at the time of each survey. For immigration rate, we tested four different structures: 1) single peak in the middle of migration window, 2) bimodal peaks of the same height, 3) a shallow peak followed by a taller peak, and 4) a tall peak followed by a shallower peak (see Supplementary Material S2). Survival rates at a staging site are assumed to be high given the short time spent there and the adaptive predator-avoidance behaviour shown by shorebirds (Ydenberg et al., 2004; Cohen et al., 2009). Because our simulation study showed little effect of differing persistence on abundance estimation, we assumed a constant persistence within each migration window. Initial abundance and the immigration rate were allowed to vary between the more natural West Hampton Dunes and the developed Westhampton Beach.

First, to choose a distribution for the observed initial abundance, we used Akaike Information Criteria (AIC, Burnham & Anderson, 2002) and compared models with Poisson, zero-inflated Poisson, and negative binomial distributions with all remaining parameters held constant. Retaining the best distribution from above, we compared models with different temporal structure of immigration and various covariates on detection probability (survey time, tidal height, time + tide, time × tide, daily total precipitation, daily mean wind speed, and daily mean wind direction). Parameter estimation can be sensitive to the K-value, which is the upper limit of the daily population size for any site that the model is set to allow (Kéry, 2018). For all models, we set the K-value to 120% of the maximum daily count observed within a season for any transect, so that it proportionally increases with greater observed counts.

Using the best fit model, we predicted daily abundance of ruddy turnstones at each transect for each survey and calculated the daily total predicted abundance for the entire study area as the sum of predicted abundance on each transect for a given day. Similarly, we reported the sum of 95% confidence interval endpoints around the daily total predicted abundances. Finally, we tested if the difference between the daily total counts observed at the field and the observable daily total abundance predicted from the best fit model significantly differed from 0 using a paired t-test. We fitted all models in the R environment (R version 3.3.2, R Core Team, 2016) installed on a 134-node system with 24 cores ('Newriver') at Virginia Tech.

RESULTS

When the models matched the data in our simulations, all parameters were correctly estimated with three different structures of persistence, and predicted daily abundance closely matched true abundance, regardless of detection probability (Figure 1,2). Parameters were correctly estimated even when we mis-specified the persistence as constant in the model (Figure 3A). Models with mis-specified immigration, however, estimated the mean immigration rate to be higher and the mean persistence rate to be lower than their true values (Figure 3B). Models with mis-specified detection probability estimated the initial abundance and immigration rate to be higher and detection probability to be lower than true values (Figure 3C). Predicted daily abundances departed from the true abundance when immigration or detection probability were mis-specified, but not when persistence was mis-specified (Figure 4). The results were the same whether immigration was modelled with a unimodal or bimodal distribution (see Supplementary Material S3).

We detected ruddy turnstones on 11–25% of the surveys (74/302 in 1997, 61/288 in 1998, and 68/637 in 1999). The entire northward migration was observed for all years (i.e., we estimated a population size of 0 at the beginning and end of our time series). Pooling

counts from all transects, the observed maximum single-day count was 108 birds on May 26th in 1997, 154 birds on May 24th in 1998, and 346 birds on May 28th in 1999.

Based on the best fit model for the ruddy turnstone data, immigration rates varied as a function of quadratic effects of date in all three years (Table 1). Immigration rate varied from 0.03–2.50 individuals per day per transect among three years (Table 2). In all three years, immigration rates were higher at the less developed West Hampton Dunes than in Westhampton Beach, illustrated by the negative estimates of 'subsite' (Table S4-1). Significant negative effects of date² indicate that the immigration rates initially increased and then decreased toward the end of the migration window (Table S4-1). The persistence rate was near 90% in all three years (Table 2). Mean detection probability ranged between 21%–53% among years (Table 2) and was higher earlier in the day, at higher tides, lower wind speeds, and with more north-westerly wind (Table S4-1). Daily total precipitation had variable effects on detection probability among years (Table S4-1).

We observed few or no birds at the beginning and end of each migration season, and therefore, our estimates of initial abundance from the best model were imprecise (Table 2). Greater immigration rates in 1998 contributed to a higher migration peak compared to 1997, but a higher detection probability that year reduced the disparity between the observed and predicted counts (Figure 5). Accounting for imperfect detection and trends in immigration rate, the predicted maximum single-day population of ruddy turnstones was 186 birds in 1997, 254 birds in 1998, and 445 birds in 1999, 172%, 165%, and 129% of the observed counts, respectively (Figure 5). The difference between the counts that we observed in the field and the model-predicted abundances corrected for detection was not significantly different from 0 for the first two years and only marginally different in 1999 (1997: t=0.426, df=171, p=0.671; 1998: t=1.413, df=126, p=0.16; 1999: t=1.998, df=559, p=0.046; Figure S4-1).

DISCUSSION

Long-term ecological monitoring with standardized count surveys plays an important role in detecting population changes over time (Link & Sauer, 1998). Standardized survey methods can produce abundance estimates that are comparable across time and space, but, they cannot correct the observation errors. Depending on the purpose, sometimes it is preferable to use the estimated abundance over daily maximum counts because the modelling incorporates observation processes into the population process, thereby producing an estimate and not just an index of the population size (Dail & Madsen, 2011; Hostetler & Chandler, 2015). Dénes et al. (2015) nicely summarized the fast-developing suite of N-mixture models extended to handle the overdispersion or spatial correlation of counts, open population assumptions, and a varying degree of survey frequency, and compared those to established methods such as generalized linear models and distance sampling. At the same time, recent studies raised significant caution of over-fitting N-mixture models in regard of the model's key assumptions (Dennis et al., 2015; Barker et al., 2018; Duarte et al., 2018; Kéry, 2018; Link et al., 2018). We are addressing each of these assumptions below.

The **first** assumption of generalized N-mixture models is that the data match the distributional assumptions of the model and that the counts from every survey occasion, except for the initial survey, are from a binomial distribution. The 'binomial assumption' does not allow a double-counting of the same individual, identification errors, or movements among sites within a primary period, all of which can increase the chance of over-counting, especially without individually identifiable markings. However, we argue that an open beach habitat with very little visual obstruction and the relatively conspicuous plumage of ruddy turnstones precluded identification errors. Besides, our survey did not include birds in flight

nor left much time for birds to move between adjacent transects and get counted multiple times within a primary period. **Second**, the model also assumes that individuals are detected independently from each other, and the abundance and detection are not confounded. The unavoidable positive correlation between the abundance and detectability casts an issue when the false negative can underestimate the abundance of a rare species (Delaney & Leung, 2010; McCarthy et al., 2013). During the three survey years, we counted 5 or less ruddy turnstones in 49% of 203 surveys where the species was detected, which suggests that the probability of detecting one individual did not differ from that of detecting a flock. Third, the dynamic N-mixture model assumes that the survival and recruitment rates are independent and identically distributed among individuals. However, the movement or mortality rates of individuals often fluctuate as a function of population density, and renders this assumption easily violated (Sæther et al., 1999). A previous simulation study showed bias in parameter estimates when the model ignores the existing density-dependence (Bellier et al., 2016). We disregarded this issue in our case study, because ruddy turnstones migrate usually in small flocks (<20 individuals), and the density-dependent immigration into a staging site is rarely documented in birds (Fleischer, 1983; Nettleship, 2000). Last, the model assumes that there is no remaining heterogeneity of detection probability that is not accounted by the covariates in the model. This assumption is particularly unrealistic considering various factors that can potentially cause the variation in detectability, including the environmental stochasticity, individual heterogeneity across different age, sex, and life stages, as well as seasonal trends and observer effects. Migrant shorebirds make a short stay at stopover sites for a single purpose: refuelling for their next flight. Naturally, the spatial distribution of individuals is strongly dependent on the foraging quality of littoral habitat and less on the idiosyncratic or demographic factors (Recher, 1966; Clark et al., 1993). In this study, we assumed that the detectability was determined by the tidal cycle and daily weather conditions but otherwise

constant across beach transects throughout the migration window. Thus, we relied on the fact that the open beach provides relatively homogeneous landscape where the inhabitants are readily observable regardless of the observer's experience level or the true abundance. We leave it up to the readers to decide whether this assumption of ours was reasonable or worth taking for a population estimate which would not be available otherwise.

The trade-off between data collection and the complexity of analytical modelling often decides how ecologists approach a question, and ever-more complex modelling is not the solution to all questions (Field et al., 2016). We agree with the valid concerns on the use of N-mixture models, and we simply argue that the unique characteristics of a stopover population and intensive daily surveys may provide the 'adequate' (Link et al., 2018) or 'better quality' (Barker et al., 2018) data that this modelling approach requires. When the population lacks uniquely identifiable individuals and mark-resight methods are impractical, generalized N-mixture models can estimate daily abundances of unmarked migratory populations at a staging site, using environmental effects and temporal trends to predict detection probability and immigration rate, on an important condition that there are adequate data. In our case study of ruddy turnstones, the use of the generalized N-mixture model did not change the estimated date of peak migration. However, its use showed that the total daily abundance of migrating individuals on site was significantly higher than the observed maximum counts because the joint modelling of observation and population processes produced an estimate that accounted for imperfect detection.

In a similar sense, generalized N-mixture models may be broadly applicable to various other taxa, such as migratory ungulates and insects, when mark-resight methods are infeasible. Use of generalized N-mixture models also provides an opportunity to test potential covariates on parameters simultaneously. Within a season, detection probability often varies as a function of habitat quality, observer experience, and sampling effort, which could be

incorporated into the modelling (Wang & Finch, 2002; Diefenbach et al., 2003; Wintle et al., 2005). Creative applications of the generalized N-mixture models also have answered new questions on phenology and the number of reproductive attempts (Cornulier et al., 2009; Matechou et al., 2014). However, it is important to note that the missed information from not marking the individuals brings much stricter model assumptions that can rarely be met (Dennis et al., 2015; Barker et al., 2018; Duarte et al., 2018; Kéry, 2018; Link et al., 2018).

Given the uncertainty around the use of generalized N-mixture models, we suggest that one may choose alternative methods such as spatial distance sampling models that accommodate for temporary emigration (Mizel et al., 2017) or open populations (Sollmann et al., 2015), or daily occupancy models (Ruete et al., 2017), depending on the survey design. When possible, comparing population size estimates and demographic rates estimated with multiple complementary methods would refine overall estimates (Bennetts et al., 1999a; Dreitz et al., 2002; Priol et al., 2014; Baker et al., 2016). In the case of migrating birds, recent analytical development has focused on augmenting the traditional capture-recapture-resight data with simple count data to estimate the staging population size and stopover duration (Matechou et al., 2013; Lyons et al., 2016). When at least part of the population is uniquely marked and resighted, integrating information from both marked and unmarked groups of individuals can bring the population estimates closer to the true population size. When resident and transient individuals co-occur, joint use of analyses for unmarked and marked animals can also differentiate use among different groups (Peele et al., 2015).

The benefits of using the generalized N-mixture models, as with any other models, come with the premise that the model fits the data. From the methodological point of view, the biggest limitation of the generalized N-mixture model is that there is no good way to test for the model fit. For a staging population, estimating population sizes specific to days and weeks can greatly increase the number of survey occasions and thus computation time.

Moreover, traditional parametric bootstrapping methods can take a very long time with Nmixture models and does not guarantee a reliable diagnostic (Duarte et al., 2018). Recently, alternative goodness-of-fit measures were introduced for static N-mixture models but not for the dynamic or generalized N-mixture models (Knape, 2017). Therefore, we relied on a graphical check as well as a paired t-test of observed counts vs. expected abundance (i.e., the estimated abundance multiplied by the estimated detection probability) to assess model fit in our study.

Our simulation study highlights the importance of correctly estimating the detection probability to estimate true abundance more accurately. On the other hand, our simulation showed that different structures for persistence (i.e., the probability that an individual survives and stays on site between survey days) or even mis-specifying it in a model did not bias predicted daily abundance. In the ideal case, one should simultaneously test different structures of initial abundance (λ), population processes (ϕ and γ), and detection probability (p). However, our models failed to converge when we simultaneously tested the effects of covariates on the persistence parameter (Kwon, unpublished data). It is likely that our transects did not provide sufficient spatial replication to simultaneously test covariate effects on all four parameters. Based on our simulation study, however, we are confident that assuming a constant persistence within the migration window would have limited effects on the abundance estimation. Our measure of persistence from the generalized N-mixture model represents the combined probability of surviving and remaining on site and differs from the traditional estimator of 'minimum stopover duration', which often is calculated as the time between first capture and last sighting (Kaiser, 1999). Recent estimates of stopover durations increasingly are derived from a survival estimate corrected for imperfect detection (Kaiser, 1999; Pledger et al., 2009; Henkel & Taylor, 2015; Lyons et al., 2016). Stopover duration likely is dependent on seasonal timing, weather conditions, habitat quality, food availability,

predation risks, an individual's condition, and migration distance pre- and post-staging (Alerstam, 2011). Within-season systemic changes in stopover duration can bias daily population estimates, as detection probability of individuals increases with longer stopovers (Crewe et al., 2015). Therefore, we recommend careful investigation of the persistence term before assuming its structure.

The northward migration of ruddy turnstones is thought to occur earlier for adults than for immature birds (Nettleship, 2000). However, a single-peak immigration model consistently fit better than a double-peak immigration model for our three years of data. Similar observations were made with a larger staging population of ruddy turnstones in Delaware Bay, USA, where birds steadily immigrated, often creating a single migration peak (Burger, 1986; Clark et al., 1993; Tucker, pers. comm.). Although we expected a second peak, it is possible that only certain demographic groups of birds stop at our site or that the temporal segregation among different demographic groups is limited or non-existent. Additional field data on the migration ecology of the species and more elaborate simulations with different migration strategies could help discern among options.

The effects of environmental covariates on the detection probability generally matched our hypotheses, except for the positive correlation with tide height in all three years and the positive correlation with daily total precipitation during the first two years. Local staging populations of ruddy turnstones have been shown to use beaches for both foraging and roosting (Placyk & Harrington, 2004). Therefore, it is possible that the high tide and consequently narrower beach facilitated detection of the birds. With precipitation, relatively high precipitation events (>20ml/day) in the first two years occurred near the peak of migration, whereas, in 1999, the single high precipitation event occurred at the end of migration (Kwon et al., unpublished data), which explains the patterns that we detected.

Depending on the question of interest, an index of relative abundance may suffice. However, an abundance estimate that is representative of the entire area of interest can improve management decisions, especially when the goal is to maintain a certain number of individuals in a population (USFWS, 1996; Elphick et al., 2001). Abundance indices that are close to true population sizes are becoming more important as we see pervasive population declines related to climate change and habitat degradation (Humbert et al., 2009; Belant et al., 2016). Especially for species whose breeding locations are either unknown or inaccessible, abundance estimates at staging sites can be used to track population trends over time (Niles et al., 2008; Amano et al., 2010). Besides, the sum of initial abundance, N[i, 1], and the total number of individuals newly immigrated into the population in a given season or a year, $\sum_{i=1}^{t} \sum_{t=2}^{t} G$, might be used as an estimate of the 'superpopulation size' for species that the lack of individual marking hinders more rigorous modelling of the population size (Lyons et al., 2016). Despite recent critiques on the N-mixture modelling in general, we suggest that the application of the generalized N-mixture model might be useful to provide new abundance estimates of transient populations, and thereby, provide a new way to attain abundance estimates during a volatile stage of an annual cycle.

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AUTHORS' CONTRIBUTIONS

L.M.H collected the data. E.K. and R.E.S analysed the data. E.K, D.H.C., S.M.K., and J.D.F. wrote the paper. All authors contributed to manuscript revisions and gave final approval for publication.

DATA ACCESSIBILITY

Data and modelling information available via the Dryad Digital Repository https://doi.org/10.5061/dryad.bc1k2b3 (Kwon et al., 2018).

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Table 1. Model selection results for ruddy turnstone abundance during northward migration of 1997–1999 on Westhampton Island, New York. λ_{i1} is initial abundance at transect *i*, γ_{it} is immigration at transect *i* and time *t*, ϕ_{it} is persistence, and p_{it} is detection probability. The initial abundance was set to be the same among transects or vary by two subsites, West Hampton Dunes and Westhampton Beach. Covariates tested for the detection probability: tide = predicted tidal height at the time of each survey, time = time of day, rain = daily total precipitation, wind_D = daily average wind direction, and wind_S = daily maximum wind speed. Temporal structure tested for the immigration rate: bifh = bimodal peaks with higher front peak, bish = bimodal peaks with the same height, bibh = bimodal peaks with higher second peak. Dots indicate no covariate effect. Persistence, ϕ_{it} was set constant in all models. Models with different distribution mixture (Poisson, zero-inflated Poisson, negative binomial) were compared first with all parameters held constant. Distribution mixture with the lowest AIC was carried for testing covariate effects.

1997				K	AIC	ΔAIC
Poisson				4	2133.89	0
Zero-infla	ted Poisson			5	2135.90	2.01
Negative	binomial			5	2135.91	2.02
λ_{i1}	Yit	$\boldsymbol{\phi}_{it}$	<i>p</i> _{it}			
subsite	subsite+date+date ²	•	tide+rain	10	1505.49	0
subsite	subsite+date+date ²			8	1601.89	96.40
subsite	subsite+bifh	•	tide+rain	9	1789.84	284.35
subsite	subsite+bish		tide+rain	9	1803.26	297.77

	subsite	subsite		tide+rain	8	1803.30	297.81
	subsite	subsite+bibh		tide+rain	9	1803.94	298.45
				tide+rain	6	1990.69	485.20
				tide+wind _D	6	2031.32	525.83
	•		•	tide+wind _s +wind _D	7	2033.32	527.83
	•		•	tide	5	2035.42	529.93
				tide+wind _s	6	2036.93	531.44
			•	time+tide	6	2037.42	531.93
				time×tide	7	2039.02	533.53
4			•	tide+rain+wind _s +wind _D	8	2095.02	589.53
				tide+rain+wind _s	7	2102.34	596.85
				tide+rain+wind _D	7	2103.08	597.59
				time	5	2135.08	629.59
	1998				K	AIC	ΔΑΙΟ
	Poisson				4	2355.68	0
	Zero-infla	ated Poisson			5	2357.68	2.00
	Negative	binomial			5	2357.73	2.05
	λ _{i1}	Yit	$\boldsymbol{\phi}_{it}$	<i>P</i> _{it}			
	subsite	subsite+date+date ²		time×tide+rain+wind _s +wind _D	14	1543.76	0

subsite subsite+bish . time×tide+rain+wind ₃ +wind ₀ 13 1606.17 62.4 subsite subsite+bibh . time×tide+rain+wind ₃ +wind ₀ 13 1705.54 161.7 subsite subsite+date+date ² . . 8 1772.45 228.6 subsite subsite . time×tide+rain+wind ₃ +wind ₀ 12 1829.66 285.9 . . . time×tide+rain+wind ₃ +wind ₀ 10 2085.10 541.3 . . . time×tide+rain+wind ₃ +wind ₀ 9 2087.34 543.5 . . . time×tide+rain+wind ₃ +wind ₀ 9 2096.20 552.4 . . . time×tide+rain+wind ₃ +wind ₀ 9 2096.20 552.4 . . . time×tide+rain+wind ₃ 9 2159.23 615.4 . . . time×tide+rain+wind ₃ 8 2159.24 671.6 . . . time×tide+rain+wind ₃ 8 2215.78 672.0 . . .	subsite	subsite+bifh	•	time×tide+rain+wind _s +wind _D	13	1576.42	32.66
subsite subsite+bibh . time×tide+rain+wind_p+wind_p 13 1705.54 161.7 subsite subsite+date+date ² . . 8 1772.45 228.6 subsite subsite subsite . time×tide+rain+wind_p+wind_p 12 1829.66 285.9 . . . time×tide+rain+wind_p+wind_p 10 2085.10 541.3 . . . time×tide+rain+wind_p+wind_p 9 2087.34 543.5 . . . time×tide+rain+wind_p+wind_p 9 2096.20 552.4 . . . time×tide+rain+wind_p 9 2096.20 552.4 . . . time×tide+rain 8 2105.92 662.1 . . . time×tide+rain 8 2159.23 615.4 . . . time×tide+rain 8 2159.24 671.6 . . . time×tide+rain 8 2159.24 671.6 time×tide 5	subsite	subsite+bish		time×tide+rain+wind _s +wind _D	13	1606.17	62.41
subsite subsite subsite . 8 1772.45 228.6 subsite subsite . time×tide+rain+wind_s+wind_p 12 1829.66 285.9 . . . time×tide+rain+wind_s+wind_p 10 2085.10 541.3 . . . time×tide+rain+wind_p+wind_p 9 2087.34 543.5 . . . time×tide+rain+wind_p 9 2096.20 552.4 . . . time×tide+rain+wind_p 9 2096.20 552.4 . . . time×tide+rain+wind_p 8 2105.92 562.1 . . . time×tide+rain+wind_p 8 2159.23 615.4 . . . time×tide+rain 8 2159.24 615.4 . . . time×tide 7 2215.42 671.6 . . . time×tide+wind_s 8 215.78 672.0 . . . time . time 5 2344.85 801.0	subsite	subsite+bibh		time×tide+rain+wind _s +wind _D	13	1705.54	161.78
subsite subsite itime×tide+rain+wind_r+wind_r 12 1829.66 285.9 . . time×tide+rain+wind_r+wind_r 10 2085.10 541.3 . . time×tide+rain+wind_r+wind_r 9 2087.34 543.5 . . time×tide+rain+wind_r 9 2087.34 543.5 . . time×tide+rain+wind_r 9 2096.20 552.4 . . . time×tide+wind_r 8 2105.92 562.1 . . . time×tide+rain+wind_r 9 2159.23 615.4 time×tide+rain 8 2159.24 615.4 time×tide+rain 8 2159.24 615.4 time×tide+wind_r 8 2215.78 672.0 time×tide+wind_r 8 2235.12 691.3 2344.85 801.0 </td <td>subsite</td> <td>subsite+date+date²</td> <td></td> <td></td> <td>8</td> <td>1772.45</td> <td>228.69</td>	subsite	subsite+date+date ²			8	1772.45	228.69
. . time×tide+rain+wind _y +wind _p 10 2085.10 541.3 . . time×tide+rain+wind _p 9 2087.34 543.5 . . time×tide+rain+wind _p 9 2096.20 552.4 . . time×tide+wind _p +wind _p 9 2096.20 552.4 . . time×tide+wind _p 8 2105.92 562.1 . . time×tide+wind _p 8 2105.92 562.1 . . time×tide+rain+wind _p 9 2159.23 615.4 . . time×tide+rain 8 2159.24 615.4 . . time×tide 7 2215.42 671.6 . . time×tide 7 2215.42 671.6 . . . time×tide 8 2215.78 672.0 . . . time 5 235.12 691.3 . . . time 5 2344.85 801.0 1999 K AIC AIC <	subsite	subsite		time×tide+rain+wind _s +wind _D	12	1829.66	285.90
. . timextide+rain+windp 9 2087.34 543.5 . . timextide+rain+windp 9 2096.20 552.4 . . timextide+windp 8 2105.92 562.1 . . timextide+windp 8 2105.92 562.1 . . timextide+rain 8 2105.92 562.1 . . . timextide+rain 9 2159.23 615.4 . . . timextide+rain 8 2159.24 615.4 . . . timextide+rain 8 2159.24 615.4 . . . timextide 7 2215.42 671.6 . . . timextide 7 2215.78 672.0 . . . time 5 2237.08 693.3 time 5 2344.85 801.0 1999 K AIC AAIC Poisson 4 3635.07 1.9				time×tide+rain+wind _S +wind _D	10	2085.10	541.34
. . time×tide+winds+windp 9 2096.20 552.4 . . time×tide+windp 8 2105.92 562.1 . . time×tide+rain+winds 9 2159.23 615.4 . . time×tide+rain+winds 9 2159.24 615.4 . . . time×tide+rain 8 2159.24 615.4 . . . time×tide+rain 8 2159.24 615.4 . . . time×tide 7 2215.42 671.6 . . . time×tide 7 2215.42 672.0 . . . time×tide+winds 8 2215.78 672.0 . . . time 5 2235.12 691.3 . . . time+tide 6 2237.08 693.3 . . . time 5 2344.85 801.0 1999 K AIC AAIG Poisson 4 3635.07 1.9 <td></td> <td></td> <td></td> <td>time×tide+rain+wind_D</td> <td>9</td> <td>2087.34</td> <td>543.58</td>				time×tide+rain+wind _D	9	2087.34	543.58
. . time×tide+wind _D 8 2105.92 562.1 . . time×tide+rain+wind _S 9 2159.23 615.4 . . time×tide+rain 8 2159.24 615.4 . . time×tide+rain 8 2159.24 615.4 . . time×tide+rain 8 2159.24 615.4 . . . time×tide 7 2215.42 671.6 . . . time×tide+wind _S 8 2215.78 672.0 . . . tide 5 2235.12 691.3 . . . time+tide 6 2237.08 693.3 . . . time 5 2344.85 801.0 1999 K AIC AAIG Poisson 4 3635.07 4 3635.07				time×tide+wind _s +wind _D	9	2096.20	552.44
. . time×tide+rain+winds 9 2159.23 615.4 . . time×tide+rain 8 2159.24 615.4 . . time×tide 7 2215.42 671.6 . . time×tide 7 2215.42 671.6 . . . time×tide 8 2215.78 672.0 . . . time×tide+winds 8 2215.78 672.0 . . . tide 5 2235.12 691.3 . . . time+tide 6 2237.08 693.3 . . . time 5 2344.85 801.0 1999 K AIC AAIC Poisson 4 3635.07 4 3635.07				time×tide+wind _D	8	2105.92	562.16
. . time×tide+rain 8 2159.24 615.4 . . time×tide 7 2215.42 671.6 . . time×tide 7 2215.42 671.6 . . . time×tide 8 2215.78 672.0 . . . time×tide+winds 8 2215.78 672.0 . . . tide 5 2235.12 691.3 . . . time+tide 6 2237.08 693.3 . . . time 5 2344.85 801.0 1999 K AIC AAIG Poisson 4 3635.07 4 3635.07				time×tide+rain+wind _s	9	2159.23	615.47
. . time×tide 7 2215.42 671.6 . . time×tide+winds 8 2215.78 672.0 . . time×tide+winds 8 2215.78 672.0 . . tide 5 2235.12 691.3 . . . time+tide 6 2237.08 693.3 . . . time 5 2344.85 801.0 1999 K AIC ΔAIC Poisson 4 3635.07 3637.04 1.9				time×tide+rain	8	2159.24	615.48
. . time×tide+winds 8 2215.78 672.0 . . tide 5 2235.12 691.3 . . time+tide 6 2237.08 693.3 . . . time+tide 6 2237.08 693.3 . . . time 5 2344.85 801.0 1999 K AIC AAI Poisson 4 3635.07 Zero-inflated Poisson 5 3637.04 1.9				time×tide	7	2215.42	671.66
. . tide 5 2235.12 691.3 . . time+tide 6 2237.08 693.3 . . time+tide 5 2344.85 801.0 1999 K AIC ΔAIC Poisson 4 3635.07 1.9 Zero-inflated Poisson 5 3637.04 1.9				time×tide+wind _s	8	2215.78	672.02
. . time+tide 6 2237.08 693.3 . . . time 5 2344.85 801.0 1999 K AIC ΔAIC Poisson 4 3635.07 Zero-inflated Poisson 5 3637.04 1.9				tide	5	2235.12	691.36
. . . time 5 2344.85 801.0 1999 K AIC ΔAIC Poisson 4 3635.07 Zero-inflated Poisson 5 3637.04 1.9	•			time+tide	6	2237.08	693.32
1999 K AIC ΔAI Poisson 4 3635.07 3637.04 1.9				time	5	2344.85	801.09
Poisson 4 3635.07 Zero-inflated Poisson 5 3637.04 1.9	1999				K	AIC	ΔΑΙΟ
Zero-inflated Poisson 5 3637.04 1.9	Poisson				4	3635.07	0
	Zero-infl	ated Poisson			5	3637.04	1.97

λ_{i1}	Ϋ́it	$\boldsymbol{\phi}_{it}$	<i>p</i> _{ii}			
subsite	subsite+date+date ²	•	time×tide+rain+wind ₃ +wind _D	12	2937.18	0
subsite	subsite+date+date ²		time+tide+rain+wind _s	12	2962.49	25.31
subsite	subsite+bifh		time×tide+rain+wind _s +wind _D	13	3180.91	243.73
subsite	subsite		time+tide+rain+wind _s	10	3243.61	306.43
subsite	subsite+bish		time×tide+rain+wind _s +wind _D	13	3431.14	493.96
			time+tide+rain+winds	8	3598.72	647.45
			time+tide+rain+wind _s +wind _D	9	3599.75	648.48
			time+tide+rain	7	3599.88	648.61
			time+tide+wind _s	7	3601.66	650.39
			time+tide+rain+wind _D	8	3601.84	650.57
			time+tide+wind _s +wind _D	8	3601.94	650.67
			time+tide	6	3602.10	650.83
			time×tide	7	3603.85	652.58
			time+tide+wind _D	7	3603.88	652.61
			time	5	3608.35	657.08
			tide	5	3629.30	678.03

Table 2. Average parameter estimates and 95% confidence intervals from the best model on estimating daily abundance of ruddy turnstones during spring migration of 1997–1999 on Westhampton Island, New York. Immigration rate is the number of gained individuals per day per study area. 95% CI for the initial abundance was inestimable for 1999.

	1997			1998			1999		
	Estimate	Lower	Upper	Estimate	Lower	Upper	Estimate	Lower	Upper
Initial abundance, $\lambda_{\mathrm{i},\mathrm{l}}$	0.00	0.00	Inf	0.00	0.00	Inf	0.00	-	-
Immigration rate, $\gamma_{i,t}$	0.03	0.003	0.22	2.50	1.85	3.38	0.60	0.22	1.67
Persistence, $oldsymbol{\phi}_{\mathrm{i},\mathrm{t}}$	0.90	0.88	0.91	0.89	0.87	0.91	0.91	0.89	0.93
Detection probability, <i>p</i> _{i,t}	0.33	0.30	0.36	0.53	0.46	0.61	0.21	0.17	0.24

Figure legends

Figure 1. Boxplots showing the distribution of parameter estimates from generalized Nmixture models with the probability that an individual survived and stayed on site between survey days (ϕ , 'persistence') being A) constant, B) decreasing with date, or C) fluctuating with a stochastic environmental factor. Each scenario was tested with the detection probability of 80% ('High P') or 30% ('Low P') and was simulated 500 times. Red lines indicate the true value of each parameter. Blank panels are when there was no covariate effect to estimate. Fitted model matches the model used to generate the dataset. Immigration was set to peak in the middle of the survey period, and detection probability covaried with two environmental variables. Environmental covariate for persistence represented 'date' (B) or a 'stochastic environmental factor' (C).

Figure 2. Comparison of true abundance (blank circle) to predicted abundance (filled circle) from three scenarios of persistence. Models used for analyses and models used to generate dataset were matched. Mean abundances are shown with the standard error.

Figure 3. Boxplots showing the distribution of parameter estimates from generalized Nmixture model where A) persistence, B) immigration, or C) detection probability was misspecified in the model as 'constant'. Each scenario was tested with the detection probability of 80% ('High P') or 30% ('Low P') and was simulated 500 times. Dataset for each scenario was simulated so that persistence decreased over time, immigration peaked in the middle of the survey period, and detection probability covaried with two environmental variables. Red lines indicate the true value of each parameter. Blank panels are when there was no covariate effect to estimate.

Figure 4. Comparison of true abundance (blank circle) to predicted abundance (filled circle) from three scenarios where A) persistence, B) immigration, or C) detection probability was mis-specified in the model as 'constant'. Mean abundances are shown with the standard error.

Figure 5. Daily observed counts (black) and predicted abundance (red) of ruddy turnstones during spring migration of 1997–1999 on Westhampton Island, New York. Predicted abundances are shown with the 95% confidence intervals.











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