

INTRODUCTION

Population surveys and resulting maps of distributions, use, and available habitat are broadly used in ecology, while methods to create these maps vary widely (e.g. trend surface analysis, kriging interpolation, inverse distance weighting [IDW] interpolation). Recent work has focused on the best interpolation methods for particular systems (e.g. Dille et al. 2003, Kravchenko 2003, Kratzer et al. 2006) suggesting that one interpolation method is not best for all systems and sampling regimes. There are 2 basic interpolation methods: (1) global interpolation, where every control point is used in estimating

unknown values (e.g. trend surface analysis); and (2) local interpolation, where a sample of known points is used to estimate unknown values (e.g. IDW). The 2 most commonly used interpolation methods are kriging and IDW. A kriging interpolation is a geostatistical method that uses leastsquares linear regression algorithms to estimate continuous variables at unsampled locations (Lo & Yeung 2002, Chang 2006). IDW interpolation assumes that each point is influenced more by nearby points than by those farther away, but it is not an exact interpolation method because interpolated used as it is less physically and computationally laborious than kriging interpolations.

Colonial breeding seabirds are an integral part of the ecosystems they inhabit and are often used as an indicator species for fisheries (Cairns 1987, Piatt et al. 2007, Einoder 2009). Seabirds have also been shown to alter terrestrial systems on breeding islands by adding marine nutrients and by burrowing and trampling vegetation (Mulder & Keall 2001, Bancroft et al. 2005, Fukami et al. 2006). Thus, the ability to quantify changes in seabird breeding densities and colony locations and sizes is extremely important. However, estimating colony area and population size of many crevice- and burrow-nesting seabirds is rife with challenges, most requiring laborious fieldwork and numerous assumptions.

Population surveys used for burrow-nesting seabirds often involve surface counts of attending birds, estimating density of nesting crevices and surface area, transect surveys, and randomized systematic grid surveys (Anker-Nilssen & Rostad 1993, Kampp et al. 2000, Renner et al. 2006). Nocturnal burrownesting seabirds are more difficult to survey, as their surface activities are limited at the breeding colonies to hours of darkness. Published studies on survey methods for these species focus on petrels (Procellariiformes) and suggest that the most reliable methods are playbacks, investigating burrow contents with cameras, and distance sampling using burrow scopes (Ambagis 2004, Lawton et al. 2006). However, playbacks must be done at night, when walking transects over steep or difficult terrain is not feasible. Therefore, most surveys use some form of distance sampling with either grubbing (i.e. searching burrows by hand to confirm whether they are being used for breeding) or burrow-scoping to determine the contents of burrows during the day (Regehr et al. 2007, Barbraud et al. 2009). Colony area, location, and population size are typically estimated using this information.

In Haida Gwaii, British Columbia (Canada), surveys of nocturnal burrow-nesting ancient murrelets *Synthliboramphus antiquus* and Cassin's auklets *Ptychoramphus aleuticus* have been ongoing since 1980 on 29 islands, using either line transects with quadrats or permanent monitoring plots. Both species are blue listed (i.e. categorized as vulnerable) within British Columbia, while the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) also lists ancient murrelets as a species of special concern. Thus, it is of the utmost importance to have accurate estimates of current colony areas, locations, population sizes, and trends. To this

end, the goal of this research was to determine whether using IDW interpolations would improve estimates of colony area and population size for nocturnal burrow-nesting species by evaluating the most reliable method to analyze transect and quadrat data using comparisons of simulated colony sizes and locations between currently employed global interpolation methods (see Rodway et al. 1988, 1990, 1994, Regehr et al. 2007) and IDW interpolations using ArcGIS 9.3 (ESRI). We hypothesized that estimates of colony area and population size are different when different interpolation methods are used and specifically predicted that local interpolation methods (i.e. IDW) provide improved estimates of colony area and population size over global interpolation methods. Additionally, we asked what the limitations were of the established survey protocols given slight differences in survey methods (where global interpolation methods assume areas surrounding unoccupied quadrats are searched for occupied burrows while IDW interpolation methods used only quadrat data) and provide recommendations for improvement. Throughout we define population size as the number of breeding pairs.

known densities, thus the probability of burrow occupancy was 60% when nearby points were occupied, with a density of no more than 0.2 occupied burrows per square meter (i.e. 5 burrows per 5 m \times 5 m cell), as is the mean nesting density observed in Haida Gwaii (Rodway et al. 1988, 1990, 1994).

Animal and specifically bird distributions at breeding colonies vary widely and are unknown for many species, thus we employed 2 different algorithms to simulate bird distributions on each island. The first algorithm starts in the first cell *(0,0)* and sequentially places breeding pairs in each cell, with a baseline probability of occupancy of 0.6. This probability is incremented by up to an additional 0.4 if each of the 4 neighboring cells is occupied (i.e. 0.1 increase per occupied neighbor cell). The process is repeated until all breeding pairs have been placed in a cell. This method produces a distribution of occupied burrows consisting of loosely clustered colonies (i.e. dispersed colonies, Fig. 1a).

The second method produces a more tightly clustered distribution of occupied burrows (i.e. clustered colony, Fig. 1b). This algorithm starts in a random cell, checking to see if the cell is first habitable, then completely occupied (i.e. 5 or fewer breeding pairs occupying it). If the cell is habitable and is not completely occupied, whether the breeding pair settles in that cell is based on the probability of settling (P_s) , such that $P_s = (n + 1)/(N + 1)$, where *n* is the number of breeding pairs present in the cell and *N* is the maximum number of breeding pairs per cell *(N* = *5)*. If the cell is uninhabitable, occupied, or the breeding pair does not settle, a new cell, in a random direction *d* cells away, is selected and the process is repeated until all breeding pairs have been distributed on the island. The probability of selecting a new cell *d* cells away from the current cell (P_d) follows a Poisson distribution, such that *Pd*

(i.e. quadrats with at least 1 breeding pair) and inactive (i.e. quadrats with 0 breeding pairs) quadrats and those perpendicular to the shore were placed halfway between active and inactive transects. Thus, when surveyed quadrats were all inactive, colony boundaries were delineated by searching the surrounding 25 m^2 cells halfway to the nearest quadrat or shoreline. When any of these surrounding cells were active, the area was included in the colony boundaries. Colony area was estimated by summing the number of 25 m^2 cells within the colony boundaries and multiplying by 0.0025. Population densities were estimated using mean values for ancient murrelets in Haida Gwaii (Rodway et al. 1994) and are presented in Table 1. Population size was then estimated by summing assigned population densities within each quadrat sampled along the transect lines (Table 1), where low density is 0 to 2 burrows quadrat−1, medium is 3 to 4 burrows quadrat−1; and high is 5 burrows quadrat⁻¹.

Colony mapping—local interpolation

We interpolated colony area and population size from our simulated transect and quadrat data using an IDW interpolation in ArcGIS 9.3, where Z-field (i.e. a magnitude value for each point) was the number of occupied burrows and cell size was $5 \text{ m} \times 5 \text{ m}$. We used a power of 2, a fixed radius of 500 m, and the minimum number of sampled points was set at 6. We calculated colony area (in ha) by summing the number of $5 \text{ m} \times 5 \text{ m}$ cells with occupied burrows >0 from the interpolated map's attribute table data and multiplied by 0.0025. Again using the attribute table data, we calculated population size (number of breeding pairs) by multiplying the interpolated number of occupied burrows by the number of cells with that burrow occupancy, and then summed this product.

Survey structure evaluation

We evaluated the probability of detecting colonies using a survey structure where transects are located 200 m apart, with 25 $m²$ quadrats located every 30 m along those transects by assigning each of the 1600 simulations (i.e. 800 clustered and 800 dispersed simulations) as having occupied areas surveyed or not. We calculated the probability of surveying occupied areas for each colony area/population size simulation group by summing the number of simulations with occupied areas surveyed and dividing by 100 (the number of simulations within each group).

Statistical comparison of interpolation methods

For each of the 800 island simulations, we estimated proportional error for both the estimated colony area and population size using the formula: proportional error = $(x - y)/y$ where *x* is the estimated term and *y* is the known term. We evaluated which interpolation method most accurately predicted colony area and population size by considering 2 *a priori* candidate models composed of 2 variables of interest (interpolation method and known population size nested within island size) in 4 separate analyses. Our models were ranked using Akaike's information criterion for small sample sizes $(QAIC_c)$, corrected for overdispersion by including an estimate of model deviance $(\hat{c}$ = model deviance/df) for the global model, and $QAIC_c$ weights *(wi*) were used to evaluate model likelihood (Burnham & Anderson 2002). When the best supported model received a weight less than 0.9, we used model averaging to generate parameter estimates and unconditional standard errors, which were used with parameter likelihoods to draw inferences from our data set (Johnson & Omland 2004). We used generalized linear mixed models with a maximum pseudo-likelihood fitting method (allowing for inter-model comparisons), a negative binomial distribution, log link function, and a Kenward-Rogers approximation in SAS 9.2 (proc GLIM-MIX; SAS Institute), where the nested term 'known population size (island size)' was included in all models as a random effect. In addition, we evaluated the probability that a quadrat would fall within an occupied area at each population and island size and present survey structure guidelines.

RESULTS

Comparison of interpolation methods

Overall, IDW interpolation methods estimated colony area and population size with higher accuracy than global interpolation methods (Figs. 2 & 3). Using global interpolation methods and dispersed colony simulations, proportional error ranged

between -0.14 and 24.14 (8.38 ± 0.43) and between 0.34 and 77.44 (32.46 ± 1.46) for colony area and population size, respectively. Using IDW interpolation methods and dispersed colony simulations, proportional error ranged between −1.00 and 12.45 (1.48 \pm 0.13) and between −1.00 and 1.37 (−0.39 ± 0.03). This represents an average decrease in proportional error of 82% and 99% when using IDW interpolation methods versus global interpolation me thods. Similarly, when clustered, proportional error ranged between −1.00 and 9.82 (2.19 ± 0.17) and between −1.00 and 27.41 (5.89 ± 0.41) for colony area and population size with global interpolation methods, and between and −1.00 and 51.24 (2.38 ± 0.34) and between −1.00 and 7.60 (−0.34 ± 0.06) for colony area and population size with IDW interpolation methods. This corresponds to an 8% increase and a 94% decrease in proportional error when using IDW interpolation methods compared to global interpolation methods for colony area and population size estimates. Thus, global interpolation methods regularly over estimated both colony area and population size, while IDW interpolation methods overestimated colony area but underestimated population size slightly. This trend was mostly supported by our AIC analyses that revealed that for colony area in dispersed colonies, the top candidate model did not include the term interpolation method (Table 2); in clustered colonies, the top candidate model included the term interpolation method, but weighted parame-

ter estimates and associated standard errors for the term interpolation method overlap with 0, suggesting that this effect was weak (Table 3). For population size, the top candidate model included the term Table 2. Summary of 4 candidate model sets describing precision of colony area and population size estimates within 3 simulated islands (10, 50, and 500 ha) with 3 known population sizes (500, 1000, and 50 000 breeding pairs) in relation to interpolation method (Method: global or inverse distance weighting), where known population size was nested within island size (Pop(Island)) and was included in all models as a random effect ($n = 1600$). *K*: number of parameters; AIC_c: Akaike's information criterion for small sample sizes; *wi*: Akaike weight

Parameter Summed Weighted para- SE

Survey structure evaluation

We found that when colonies were dispersed and global interpolation methods were used, there was a 100% probability of surveying occupied sites at all population and island sizes, whereas when IDW interpolation methods were used, there was between 76 and 100% (93 \pm 0.07%) probability of surveying occupied sites (Fig. 4a). When colonies were highly clustered, there was between 75 and 100% (94 \pm 0.07%), and between 18 and 100% (67 \pm 0.21%) probability of surveying occupied sites when using global and IDW interpolation methods, respectively (Fig. 4b). In both cases, the lowest probability of sur-

> veying an occupied area occurred for the small population and large island size simulation group.

DISCUSSION

Overall we found that IDW interpolations greatly improved estimates of population size for nocturnal burrownesting species such as Cassin's auklets and ancient murrelets, but neither interpolation method improved estimates of colony area. Specifically, we found that global interpolation methods greatly overestimated population size especially when populations were small. Overestimating small populations can be very dangerous, especially when declining populations of threatened or endangered species are involved. Global interpolation methods had the highest probability of successfully detecting a colony; however, these methods are extremely labor intensive, requiring burrow searches surrounding unoccupied quadrats, resulting in higher financial costs and less efficient survey times.

Population estimates, trends, and colony areas and locations are all important aspects of managing animal populations and assessing their risk of extinction (Butchart & Bird 2010). These data are often used to determine whether a population is at risk of being extirpated, needs to be protected, is recovering, or whether particular habitats can be developed (Conway & Simon 2003, Borsa et al. 2010, Cadiou et al. 2010, Camp et al. 2010). Yet, because of the effort required to fully estimate populations, long-term trend data are only available at specific sites, typically the locations of field stations. Methods used to survey and monitor at field stations are normally very labor intensive and thus not effective for large-scale monitoring (e.g. capture−mark−recapture studies). The ability to detect, estimate, and confidently make informed decisions concerning the management of a population is critical. Here, we found that with consistent use of an established and efficient survey protocol, together with a relatively simple interpolation method, we were able to achieve accurate estimates of colony area and population size that are comparable across island and breeding population sizes.

Unlike field studies, we assumed perfect knowledge of the contents of each burrow encountered and that every occupied burrow in our transect quadrats was discovered. It is unlikely that every occupied nest site will be found during a survey and that every burrow encountered will have known contents. It is because of this that sampling protocols involving double sampling and/or double observers are recommended (Taylor & Pollard 2008). We advocate these methods in the field to obtain the most precise data possible. Additionally, having experienced field crews who are able to train new team members and ensure data collection is consistent among years and islands is also of the utmost importance.

We acknowledge that IDW interpolation methods led to a low detection probability on large islands with small populations. Global interpolation methods did not reveal this same flaw, because we assumed that in all cases when an occupied burrow existed outside of an unoccupied quadrat, observers would find it and confirm the presence of a small *Acknowledgements*. We thank R. Ydenberg, M. Hipfner, M. Lemon, and J. Barrett for advice and discussions pertaining to various aspects of this study, and 3 anonymous reviewers for comments on an earlier version of this manuscript.

LITERATURE CITED

- Ambagis J (2004) A comparison of census and monitoring techniques for Leach's storm petrel. Waterbirds 27: 211−215
- Anker-Nilssen T, Rostad OW (1993) Census and monitoring of puffins *Fratercula arctica* on Rost, N Norway, 1979−1988. Ornis Scand 24: 1−9
- Bancroft WJ, Garkaklis MJ, Roberts JD (2005) Burrow building in seabird colonies: a soil-forming process in inland systems. Pedobiologia 49: 149−165
- Barbraud C, Delord K, Marteau C, Weimerskirch H (2009) Estimates of population size of white-chinned petrels and grey petrels at Kerguelen Islands and sensitivity to fisheries. Anim Conserv 12: 258−265
- Borsa P, Pandolfi M, Andrefouet S, Bretagnolle V (2010) Breeding avifauna of the Chesterfield Islands, Coral Sea: current population sizes, trends, and threats. Pac Sci 64: 297−314
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information theoretic approach. Springer-Verlag, New York, NY
- Butchart SHM, Bird JP (2010) Data deficient birds on the IUCN Red List: What don't we know and why does it matter? Biol Conserv 143: 239−247
- Buxton RT (2010) Monitoring and managing recovery of nocturnal burrow-nesting seabird populations on re cently predator-eradicated Aleutian Islands. MSc thesis, Memorial University of Newfoundland, St. John's
- Cadiou B, Bioret F, Chenesseau D (2010) Response of breeding European Storm Petrels *Hydrobates pelagicus* to habitat change. J Ornithol 151: 317−327
- Cairns DK (1987) Seabirds as indicators of marine food sup-