AVIAN CONSERVATION
& ECOLOGY

VOLUME 11, ISSUE 2, ARTICLE 11

Hunnewell, R. W., A. W. Diamond, and S. C. Brown. 2016. Estimating the migratory stopover abundance of phalaropes in the outer Bay of Fundy, Canada. *Avian Conservation and Ecology* 11(2):11. http://dx.doi.org/10.5751/ACE-00926-110211

Research Paper

Estimating the migratory stopover abundance of phalaropes in the outer Bay of Fundy, Canada

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ABSTRACT. We investigated the abundance and turnover rate of phalaropes (Red-necked and Red: *Phalaropus lobatus, Phalaropus fulicarius*) in the outer Bay of Fundy, Canada during migratory stopover in 2008, 2009, and 2010. We describe estimation procedures designed to calculate size of the total stopover population of phalaropes, adjusting for length of stay. A total of 29 aerial surveys were flown in two nonoverlapping survey regions situated off Brier Island, Nova Scotia and Grand Manan, New Brunswick. Line transect distance sampling methods were used to obtain abundance estimates at discrete time steps from aerial surveys. Estimated number of phalaropes by date ranged between 6000–88,000 in 2009 and 31,000–127,000 in 2010. To quantify the cumulative number of phalaropes in the study area, the temporal dimension of stopover passage was incorporated by an analysis of radiotelemetry data to estimate length of stay. A total of 27 phalaropes were captured and fitted with radio transmitters between 2008 and 2010. Estimated length of stay in days was 15.2 ± 1.91 for a time-integrated stopover population of 103,496 phalaropes in 2009 and 287,558 in 2010. This is particularly relevant to the conservation status of *P. lobatus* in North America, which has been uncertain since the disappearance of that species from an important stopover site in 1990. Our findings emphasize the need for studies that monitor phalaropes at sea, where they spend the majority of their time, as a means to inform effective management and conservation.

Estimation de l'abondance de phalaropes à des haltes migratoires dans la partie extérieure de la baie de Fundy, Canada

RÉSUMÉ. Nous avons examiné l'abondance et le taux de passage des phalaropes (à bec étroit et à bec large : *Phalaropus lobatus, Phalaropus fulicarius*) dans la partie extérieure de la baie de Fundy, Canada, durant les haltes migratoires de 2008, 2009 et 2010. Nous décrivons la méthodologie employée pour le calcul de la taille de la population de phalaropes de passage, y compris l'ajustement nécessaire pour tenir compte de la durée du séjour des oiseaux. Vingt-neuf relevés aériens ont été effectués au-dessus de deux régions ne se chevauchant pas, l'une au large de l'île Brier en Nouvelle-Écosse, l'autre au large de l'île Grand Manan au Nouveau-Brunswick. Pour obtenir des estimations ponctuelles de l'abondance, un échantillonnage par la méthode des transects et tenant compte de la distance des observations a été choisi. Ces estimations ponctuelles des effectifs de phalaropes variaient de 6 000 à 88 000 en 2009 et de 31 000 à 127 000 en 2010. Pour quantifier le nombre cumulatif de phalaropes dans l'aire d'étude, la dimension temporelle du passage aux haltes a été incorporée en estimant la durée de séjour à l'aide de l'analyse de données radio-télémétriques. Vingt-sept phalaropes ont été capturés et munis d'un émetteur radio de 2008 à 2010. La durée du séjour a été évaluée à 15,2 ± 1,91 jours, ce qui permet l'estimation de la population de passage (qui intègre la durée de séjour) à 103 496 phalaropes en 2009 et à 287 558 en 2010. Ces estimations sont tout particulièrement utiles pour déterminer le statut de conservation de *P. lobatus* en Amérique du Nord, lequel est incertain depuis la disparition de l'espèce d'une importante halte migratoire en 1990. Nos résultats mettent en lumière le besoin de suivis des phalaropes en mer, où ils passent le plus clair de leur temps, afin d'orienter les mesures de gestion et de conservation pour qu'elles soient les plus efficaces possibles.

Key Words: *abundance estimates; aerial line transects; Bay of Fundy; distance sampling; phalarope*

INTRODUCTION

Phalaropes are unique among shorebirds in that they are built for surface swimming with specialized traits including lobed toes and dense belly plumage for an impressive buoyancy (Warnock et al. 2002). Red-necked *Phalaropus lobatus* and Red Phalaropes *P. fulicarius* have Holarctic breeding ranges and spend up to nine months of the year at sea (Rubega et al. 2000, Tracy et al. 2002). Our work focuses on these two pelagic species, hereafter "phalaropes."

In marine environments, phalaropes rely upon oceanographic processes that serve to lift their zooplankton prey to the surface. For example, they have been observed feeding at continental shelf breaks (Haney 1985), major oceanic currents (Murphy 1936), coastal upwelling zones (Briggs et al. 1984, DiGiacomo et al. 2002), edges of pack ice (Orr et al. 1982), and mud plumes created by the benthic feeding of grey whales (Obst and Hunt 1990). Many studies have examined the dynamics of such processes because they play a key role in the formation and persistence of prey patches, concentrating buoyant organisms at the surface

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(Wolanski and Hamner 1988, Franks 1992, Genin 2004) and providing a critical point of contact between marine birds and their prey (Hunt et al. 1998, Yen et al. 2004, Bost et al. 2009).

The Bay of Fundy is a biologically rich marine area that is dominated by strong tidal forcing and provides stopover habitat for phalaropes on migration. During postbreeding migration, mixed flocks feed in tidal eddies generated by fast moving currents over ledges (Brown and Gaskin 1988). Our goal was to conduct targeted surveys for phalaropes in the outer Bay of Fundy, where migrants of *P. lobatus* occur in spatial and temporal overlap with migrants of *P. fulicarius.* Abundance estimates are important because, on account of their pelagic ecology, phalaropes have eluded the major, omnibus shorebird monitoring programs in North America, such as the International Shorebird Survey (ISS) and the Atlantic Canada Shorebird Survey (ACSS), formerly known as the Maritimes Shorebird Survey (MSS). These migration monitoring efforts were originally designed to identify important shorebird staging habitats, but because phalaropes use offshore marine areas, they fall outside the ambit of most periodic survey routines (Brown et al. 2010).

The need for phalarope surveys during the pelagic phase of their ecology was amplified by a conspicuous decline of Red-necked Phalaropes from a reliable stopover site in the 1980s. During postbreeding migration, full migratory passage of the species at this site was estimated at 1-2 million birds (Finch et al. 1978, Vickery 1978, Mercier and Gaskin 1985). Composed wholly of *P. lobatus* and concentrated within a foraging area of approximately 100 km² known as Head Harbour Passage in the western Bay of Fundy, vast flocks staging in the area each year began to decline in the mid-1980s and by 1990 had disappeared altogether (Duncan 1996). Because they have not returned, the crash triggered broad concern for the conservation status of the species (Donaldson et al. 2000, Brown et al. 2001), prompting recommendations to assess remaining numbers of *P. lobatus* in the northeastern U.S. and Canadian Maritimes (Brown et al. 2010). In 2014, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) designated the species as one of Special Concern (http://www.registrelep-sararegistry.gc.ca/species/speciesDetails_e.cfm?sid=1278).

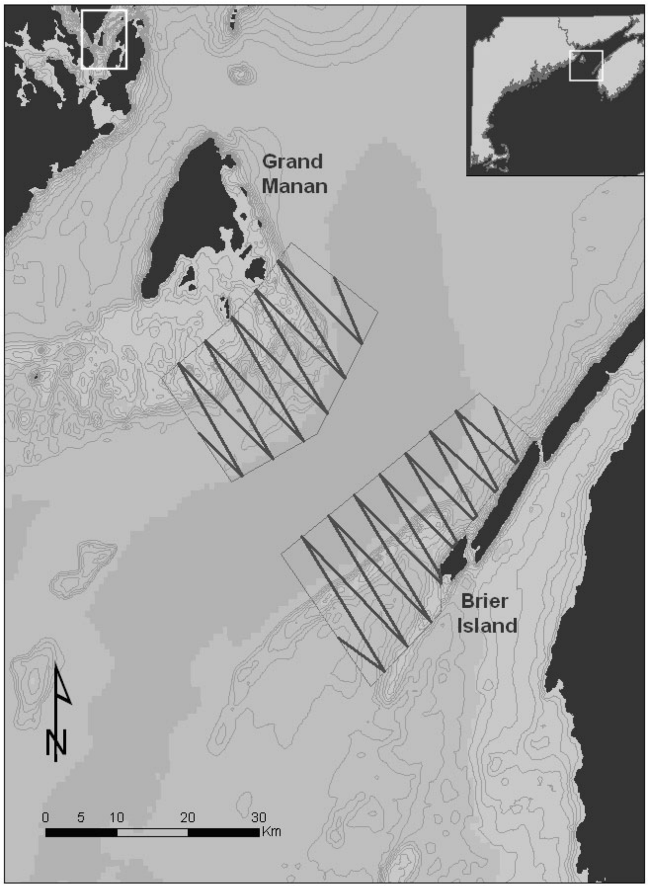
We report the results of estimation procedures designed to calculate the size of the total stopover population of phalaropes in the outer Bay of Fundy, while adjusting for incomplete detection and estimated length of stay. We discuss constraints of aerial surveys for ephemeral, mixed flocks of phalaropes at sea, as well as conservation implications of our present-day findings with respect to the disappearance of *P. lobatus* from the western Bay of Fundy some 25 years ago.

METHODS

Study area

Aerial surveys to estimate stopover abundance and turnover of phalaropes were conducted during postbreeding migration in 2009 and 2010 in the outer Bay of Fundy, Canada. The study area comprised two nonoverlapping survey regions located off Brier Island, Nova Scotia and Grand Manan, New Brunswick (Fig. 1). Characterized by strong tidal forcing and irregular bottom topography, both regions contain ledges and shoals that introduce turbulence into the prevailing axis of tidal flow (Aretxabaleta et al. 2008). As it collides with ledges (e.g., Northwest Rock 44°19'N, 66°24'W), eddies of cool, upwelled water carrying dense prey form, drift, and degrade locally about the ledges (≤ 1100 m), subject to the agency of semidiurnal ebb-flood cycle (Thorne and Read 2013). Phalaropes exhibit positive spatial association with these patches of vertical mixing in the surrounding marine environment (Brown and Gaskin 1988).

Fig. 1. Location of study area in the outer Bay of Fundy, Canada between New Brunswick and the southwestern tip of Nova Scotia. Marine depth contours, range -5 to -100 m, are shown. Aerial line transects (n = 28) were allocated over two nonoverlapping survey regions, "Brier" and "Grand Manan." Strong tidal currents collide with ledges and shoals to generate enhanced vertical mixing in both regions. Note: location of Head Harbour Passage where large flocks of *P. lobatus* staged until the mid-1980s shown in upper left corner.



Aerial surveys were flown in survey regions, herein "Brier" and "Grand Manan," situated on either side of a shipping channel. Steep ledges in both regions host large, mixed flocks of phalaropes, relative to other parts of the surrounding Gulf of Maine (Brown et al. 2010). Both survey regions were demarcated to be of comparable size (633 km² and 531 km², respectively) and configuration with respect to surrounding depth gradients that change abruptly from < 10 m over the ledges to > 220 m in the shipping channel.

Aerial survey design and protocol

To ensure uniform coverage probability within each region, a line transect layout was established in advance of surveys. Following recommendations by Thomas et al. 2007, a systematic design for transect placement was implemented with the total length of transects (458 km) allocated over 28 lines averaging 16 km in length. Exploratory flights had indicated that on average higher densities of phalaropes would be encountered in the Brier region; therefore a larger number of transects was assigned to Brier (n = 16) than Grand Manan (n = 12). To minimize airtime spent in transit between replicate lines, a zig-zag geometry with equal 4-km spacing was selected (Fig. 1). Transects were oriented perpendicular to the prevailing axis of tidal flow and corresponding trend in the spatial distribution of phalaropes. The cross-current orientation was used to prevent spurious imbalances in the set of line-to-object distances obtained from surveys and to give lower variance for the encounter rate across replicate lines (Thomas et al. 2007, Fewster et al. 2009).

Although opportunities depended on weather and fog, we conducted all surveys independently of tidal stage on days with optimal conditions of zero fog and sea state (Beaufort scale) of 0-3. Time needed to complete a full survey was no more than 3 hours; mean duration (h) was 2.67 (max 3.03). Surveys were flown throughout the migration of postbreeding phalaropes in the study area, a period that typically spans 8–10 weeks beginning in mid-July and tapering off by mid- to late September (Orr et al. 1982, Rubega et al. 2000, Tracy et al. 2002).

The survey platform was a twin-engine aircraft with low wings and flat-sided windows flying at a speed of 100 knots. Surveys were flown at varying altitude; range 80–182 m, mean (± st dev) 126.9 ± 21.5 in 2009 and range 94–169 m, mean 128.7 ± 11.2 in 2010. Phalarope flocks were visually identified from the air by an observer stationed in aft seats, scanning to one side of the aircraft. A global positioning system (GPS) including two Garmin units (GPSMap 76, eTrex Vista Cx) was used to log position, altitude, and speed at 5-s intervals and to store a specific waypoint whenever a flock sighting occurred.

Sighting data included flock size and downward viewing angle to the detected flock. To facilitate taking angle measurements, a set of bins demarcating the search strip were used to collect sightings from the air. We used two plexiglass angle boards to define the bins based on vertical angle measurements: 30°-35°-40°-50°-60°-70°-80° (Bengston et al. 1996). Fitted in both windows, the boards denoted the bins with marks calibrated to observer height. A second set of strips on the trailing edge of the aircraft wing was used as a peripheral aid to maintain standard head alignment. Viewed through the angle boards, each flock was assigned a sighting bin number as it passed abeam within the field of view.

The observer scanned continually to one side of transects, alternating between left and right seats as needed to maintain a glare free prospect of the search strip. Downward visibility was limited by the flat-sided windows. Width of the search strip was determined by an available field of view, which was bounded below at 30° and above at 80°. Sitting upright, the observer could not search within a viewing angle of 30° from the vertical. Thus at any altitude, a near-line blind strip beneath the plane obscured flocks from view. Other than bounding it at 80° for flocks near horizon, no attempt was made to delimit the search strip.

Because time to process flock sightings from the air was limited, we confined bin classification to the geometric centroid of flock clusters, as recommended in Buckland et al. 2001. Because species composition of flocks could not be discerned from the air, sightings were recorded as "phalaropes" and examined together (cf. Herr et al. 2009). Whenever a flock sighting occurred, the observer announced flock size and sighting bin number through headset microphone to a digital voice recorder. Spoken-entry data were uploaded to a WAV file, which generated a time code to reference each sighting in a survey.

Perpendicular distances (x) were calculated from measurements of angle (a) and altitude (H) at the time a sighting was made, using basic trigonometry $x = H \cdot \tan(a)$. We employed a procedure of discretizing viewing angles, obtained in situ as grouped data using bins, by rounding to the nearest midpoint articulating each bin (e.g., flocks assigned to bin 3 were rounded to 45°). This allowed us to achieve an ungrouped perpendicular distance, calculated from a rounded angle and stored altitude at the time a sighting was made, for each flock. All flock positions, eastings and northings relative to the flown line, were georeferenced in ArcGIS 10 (ESRI).

To evaluate the species composition of mixed flocks on the water, we conducted boat-based surveys in 2010. All boat-based surveys were carried out opportunistically on calm days with flat seas (Beaufort 0-1) and confined to accessible areas (≤ 10 km²) around the Brier Island ledges.

Model fitting and analysis

A detection function for phalaropes was estimated from the perpendicular distances of detected flocks to the flown line by means of conventional distance sampling methods, described in Buckland et al. 2001 and 2004. Because it is expected that a proportion of objects will be missed, analysis procedures specify a flexible, semiparametric model for the detection function $g(x)$ and use model fit to infer this proportion (Thomas et al. 2010). Standard estimators describe change in detection relative to an assumed intercept; detection is assumed to be certain on the line itself at zero distance, $g(0) = 1$.

For the distance detections gathered here, visibility on the line itself was not possible. Because of the flat-sided windows, a near-line blind strip existed such that distances 0–46 m were hidden from view while distances 47–105 m were intermittently available, depending on survey altitude. When detection probability is subject to the anatomy of a blind strip, left-truncation may ensure a plausible shape for detection curves (Alldredge and Gates 1985, Quang and Lanctot 1991). We considered left truncating at x = 100 m to retain the assumption $g(0) = 1$, but 477 flock sightings would have been discarded by this move. Therefore, we employed an offset method of rescaling distance data to the minimum observable distance (x_{min}) from the flown line, computed from the minimum viewing angle (a_{min} = 30) and altitude (H) at the time of each sighting. In this way, detection functions were offset and detection was assumed to be certain, or nearly so, at the nearest visible distance from the line, $g(x_{min}) = 1$. To implement this, all perpendicular distances were rescaled accordingly: $x_{offset} = x - x_{min}$ (Laake et al. 2008*b*).

We analyzed the data separately by survey region and by year (Brier 2009, 2010, Grand Manan 2009, 2010), enabling a comparison of detection parameters estimated at levels relevant to this study. The decision to conduct separate analyses by year was unambiguous because it was not meaningful to obtain pooled estimates of abundance across years. Desired gains in precision by fitting a separate detection function by region, however, were formally evaluated. Resulting Akaike weights were checked throughout the model fitting routine to confirm whether this improved model fit (Buckland et al. 2001). We estimated detection probability "globally" (region:yr), using poststratification to obtain abundance estimates by survey date. This level of temporal resolution in the data was of intrinsic interest in calculating the size of the stopover population.

All detection probability analysis was performed in program DISTANCE, version 6.1 Beta 1 (Thomas et al. 2010). Model fitting was based on a set of key functions and series adjustment terms to improve fit. Data grouping was enlisted at the analysis stage to address any evidence of heaping in the data relative to estimated detection curves. We explored data groupings and right truncation widths as a means to diagnose model fit and capture disparity between observed probability of detection and the fitted curve of estimated detection models. Where appropriate, Akaike's Information Criterion (AIC) was used for model selection, while chi-squared goodness-of-fit was used to evaluate function forms with respect to data groupings. To generate estimates of density (D) and abundance (N) of phalaropes by survey date under each of the four (region:yr) detection functions used, expected flock size $E(s)$ was needed along with estimated density of flocks. Accordingly, flock size was estimated globally (region:yr) using the size biased-regression method in which ln(cluster size) is regressed against estimated $g(x)$.

Estimating length of stay

To adjust for turnover or length of stay, we derived a correction factor based on an analysis of radio-marked birds in the study area. In 2008, 2009, and 2010, a total of 27 phalaropes were fitted with VHF radio transmitters (1.2 grams, 6 wk lifespan, Holohil Systems, Ltd.). Full description of materials and methods designed to capture phalaropes at sea is given in Ronconi et al. 2010. Tags were deployed in mid- to late August of each year. From the first date of deployment, aerial telemetry to monitor the site tenure of radio-marked birds was conducted every other day at high altitude, 650 m, for a signal range of 8–10 km. Time needed to relocate tagged birds in the study area was ≤ 15 min. After 1 hr, telemetry ceased until the following attempt. If a signal could not be relocated after three consecutive attempts, the bird was considered to have migrated on the day of its last detection.

Measured as the elapsed number of days between capture and final detection at a site, minimum length of stay may be estimated from the observation times of radio-marked birds (Iverson et al. 1996), but this neglects precapture site tenure on the part of birds. Therefore, we used encounter sampling (Otis et al. 1993) and program DISTANCE (Thomas et al. 2010) to estimate length of stay (Farmer and Durbian 2006). We assumed that (1) the probability of a bird being caught was proportional to its length of stay, (2) a bird had an equal probability of being caught at any juncture of its stay, and (3) marked birds were representative of unmarked birds (Lehnen and Krementz 2005). Under these assumptions, we fitted a probability density function to the observation times and used the DISTANCE parameter "effective strip width," μ , i.e., that distance for which as many objects are detected beyond μ as are missed within μ for a given model (Buckland et al. 2001), as an estimate for length of stay in days. As the effective proportion of recorded observation times, this gave an estimate that factored in the likelihood of birds being captured upon arrival and successfully relocated until departure from the study area.

Calculating size of stopover population

As snapshots of phalarope abundance at discrete time steps, each aerial survey was used to track fluctuations in stopover population size across the survey period. In both years, the survey period from initial to final survey date was divided into subintervals, days, to find a cumulative number of phalaropes for all values of date and abundance, "bird days." Hence if b_1 is the estimated abundance on survey date t_1, as determined from the detection model, bird days was found by numerical integration of coordinate pairs $(t_1,b_1,t_2,b_2...t_f\ ,b_f)$. Stopover population was estimated by *pop* = *bd*/*LOS*, where *pop* = stopover population, *bd* = bird days and *LOS* = estimated length of stay in days (Farmer and Durbian 2006).

Variance of total stopover population size estimates arose from multiple components: survey date abundance estimates (b_t) generated by the detection models, and estimated length of stay, also derived from a detection function model. We report associated coefficients of variation and 95% confidence limits for the abundance estimates and estimated length of stay.

RESULTS

Aerial line transect surveys were conducted from 31 July to 14 September in 2009 and 26 July to 12 October in 2010. In all, we flew 29 surveys (15 in 2009; 14 in 2010) for a total of 12,667 km and 2159 flock sightings recorded. Time intervals between surveys ranged from 1–8 days, mean (± st dev) 3.7 ± 2.6 in 2009 and 2–11 days, mean 6.4 ± 2.8 in 2010. Fog in the study area prevented the first survey until the end of July in both years. On three occasions, survey effort was curtailed by fog that formed near Grand Manan and we flew transects in Brier only. On three occasions we flew back-to-back surveys in the course of a single day to assess changes in phalarope habitat specificity with respect to tidal stage. In 2010, the time frame for surveys (78 days) was protracted relative to that in 2009 (45 days) as flocks remained in the study area until mid-October. In response, we continued to fly surveys until October 12.

A combination of global detection models was fitted to the data partitioned by year (2009; 2010). Candidate models with lowest AIC were based on a half-normal key with simple polynomial or cosine adjustment terms. Nested within respective years, we compared models fitted to the data pooled across regions (Brier, Grand Manan) with estimating detection probability separately by region. Summed AIC values from models fitted to the region-specific data (2571 in 2009, 4104 in 2010) were consistently less than AIC values from models fitted to the region-pooled data (2591 in 2009, 4118 in 2010). Therefore on the basis of improved model fit, we focused our analysis on models fitted to the data separately by region:yr.

Table 1. Parameter estimates (*p, ESW*) for detectability of phalarope flocks from detection functions fitted with various data groupings. Global detection functions were fitted to data pooled across survey dates at four levels (region:yr). All models used a half-normal key with simple polynomial or cosine adjustment terms. For each model, *p* refers to the estimated average detection probability and *ESW* refers to the effective strip width. Standard error (SE) and %CV are reported for *p*. The chosen data grouping for each of the four models was ranked by highest Chi-*p values* and on basis of fit at the left-edge of the detection curve.

Region: Year	Data grouping	Right-truncation (m)	*p*	SE	%CV	*ESW*	GoF Chi-p
Brier 2009	six unequal bins	340	0.372	0.013	3.60	126.50	0.001
Brier 2009	ten 34-m bins	340	0.378	0.018	4.80	128.37	0.070
Brier 2009	fifteen 23-m bins	350	0.368	0.018	4.99	128.82	0.890
Brier 2009	eight 40-m bins	320	0.397	0.020	5.14	126.97	0.522
Grand Manan 2009	six unequal bins	340	0.299	0.014	4.61	101.80	0.000
Grand Manan 2009	ten 34-m bins	340	0.298	0.020	6.65	101.15	0.000
Grand Manan 2009	eight 40-m bins	320	0.322	0.014	4.36	102.95	0.072
Grand Manan 2009	ten 30-m bins	300	0.326	0.024	7.27	97.68	0.098
Brier 2010	six unequal bins	340	0.331	0.015	4.54	112.63	0.036
Brier 2010	ten 34-m bins	340	0.317	0.013	4.08	107.82	0.000
Brier 2010	seven 40-m bins	280	0.410	0.016	3.95	114.79	0.010
Brier 2010	six mixed bins[†]	360	0.318	0.010	3.12	114.38	0.258
Grand Manan 2010	six unequal bins	340	0.281	0.013	4.50	95.67	0.000
Grand Manan 2010	ten 34-m bins	340	0.261	0.011	4.18	88.83	0.005
Grand Manan 2010	seven 40-m bins	280	0.346	0.015	4.35	96.80	0.048
Grand Manan 2010	six mixed bins[†]	360	0.261	0.008	2.90	94.06	0.429

[†] 6 mixed distance bins: 34-m bin followed by a 46-m bin and four equal 70-m bins.

Empirical line-to-object distances obtained from surveys exhibited a nonuniform pattern of detection relative to the left-edge of fitted curves, characterized by a "shortage" of sightings in the first bin, followed by a spike or "surplus" in the second. We anticipated a lack of fit between observed detection and estimated detection curves owing to the presence of a blind strip and varying survey altitude. Thus we used the offset method and rescaled distance data to accommodate the blind strip. However, visual inspection of offset detection curves revealed a remaining lack of fit. Rounding to favored values can cause heaping in distance data (Buckland et al. 2001) and we judged that the aerial sighting process led to visibility bias affecting the first and second sighting bins, which induced a systematic lack of fit. Various data groupings were enlisted to alleviate heaping and achieve a robust fit for each model. After regrouping the data into distance classes that spread line-to-object distances across the spiked pattern, we selected a data grouping that achieved best fit overall.

To evaluate the various groupings used with each model, we did not rely upon selection criteria such as AIC, which is not valid to select among data groupings used with the same model (Buckland et al. 2001). Care was taken not to evaluate model fit solely on the basis of chi-squared tests either, which can be sensitive to the choice of distance classes underlying the test (Fewster et al. 2008). Thus for the Brier 2009 model, the data grouping that yielded best fit as assessed by chi-squared test consisted of 15 bins out to a right-truncation of 350 m (*p-value* = 0.890). Nevertheless, a set of 8 bins out to 320 m (*p-value* = 0.522) was selected as the most optimal data grouping, especially in the critical realm of fit at the left-edge of the detection curve (Fig. 2). Once detection functions were offset to accommodate the blind strip, 98% of flock sightings occurred at ≤ 340 m.

Parameter estimates for probability of detection *p* and effective strip width *ESW* remained stable over the various data groupings used with each (region:year) model, indicating a good overall fit (Table 1). Probability of detection estimated by each of the four chosen models was: 0.39, 0.31 in Brier 2009, 2010 and 0.32, 0.26 in Grand Manan 2009, 2010. Corresponding point estimates for density *(D)* and abundance *(N)* of phalaropes by survey date are given in Table 2.

Fig. 2. Comparison of data groupings enlisted to achieve robust model fit for the same detection function. Brier 2009 analysis set shown, i.e., distance data obtained from surveys flown in Brier, 2009. Figures show observed probability of detection in each distance class (histograms) against expected probability of detection (blue lines) estimated by the fitted model. Eight 40 m-distance bins out to 320 m achieved most optimal fit on basis of χ2 p-value as well as visual inspection of fit at the left-edge of the detection curve.

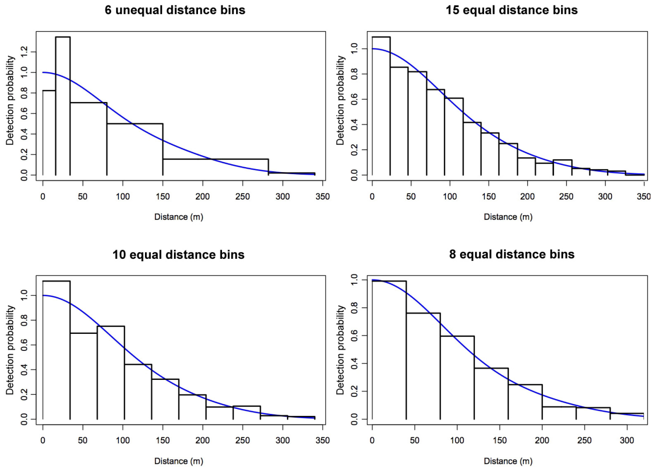


Table 2. Point estimates for the density *(D)* and abundance *(N)* of phalaropes by survey date based on detection models fitted to each of four dataset partitions (region:yr). Density refers to number of phalaropes per square kilometer. Percent coefficient of variation in *D* and *N* as estimated by the four models was: 13.58, 23.70, 18.70, 16.45 for Brier 2009, 2010, GM 2009, 2010, respectively. Standard error (SE) for density and confidence intervals (95% CI) for abundance estimates are shown. Inference about the abundance of phalaropes by survey date was restricted to the covered region only: 175 km^2 in Brier, 145 km^2 in Grand Manan.

Brier 2009					Brier 2010				
Date	*D*	SE	*N*	95% CI	Date	*D*	SE	*N*	95% CI
July 31	38.9	5.29	6824	5234 - 8897	July 26	102.2	24.23	17,896	11,289 - 28,370
Aug 1	199.3	27.05	34,877	26,749 - 45,474	July 31	249.9	59.23	43,745	27,594 - 69,348
Aug 6	168.9	22.93	29,570	22,679 - 38,554	Aug 11	426.0	100.96	74,565	47,036 - 118,210
Aug 8	402.9	54.70	70,512	54,080 - 91,936	Aug 13	142.0	33.65	24,855	15,679 - 39,402
Aug 9	164.6	22.35	28,811	22,097 - 37,565	Aug 18	210.2	49.80	36,786	23,204 - 58,315
Aug 12	142.9	19.41	25,020	19,190 - 32,623	Aug 25	409.0	96.92	71,583	45,155 - 113,480
Aug 20	173.3	23.52	30,328	23,260 - 39,543	Aug 30	267.0	63.27	46,728	29,476 - 74,076
Aug 27	177.6	24.11	31,086	22,679 - 38,554	Sept 9	119.3	28.27	20,878	13,170 - 33,098
Sept 1	168.9	22.93	29,570	22,679 - 38,554	Sept 13	335.1	79.42	58,658	37,002 - 92,990
Sept 2	238.2	32.34	41,701	31,983 - 54,371	Sept 23	539.7	127.89	94,449	59,579 - 149,730
Sept 9	60.6	8.23	10,615	8141 - 13,840	Sept 27	176.1	41.73	30,820	19,442 - 48,859
Sept 10	56.3	7.64	9857	7560 - 12,851	Oct 3	147.7	35.00	25,849	16,306 - 40,978
Sept 14	38.9	5.29	6824	5234 - 8897	Oct 12	181.8	43.07	31,815	20,069 - 50,435

Grand Manan 2009					Grand Manan 2010				
Date	*D*	SE	*N*	95% CI	Date	*D*	SE	*N*	95% CI
Aug 1	194.5	36.39	28,216	19,595 - 40,628	July 26	90.6	14.90	13,141	9525 - 18,130
Aug 8	125.3	23.43	18,173	12,621 - 26,167	July 31	527.7	86.82	76,525	55,466 - 105,580
Aug 12	118.7	22.20	17,216	11,956 - 24,790	Aug 11	202.5	33.32	29,373	21,290 - 40,526
Aug 20	6.5	1.23	956	664 - 1377	Aug 13	373.1	61.38	54,109	39,219 - 74,653
Aug 27	32.9	6.16	4,782	3321 - 6886	Aug 18	234.5	38.58	34,011	24,652 - 46,924
Sept 1	75.8	14.18	10,999	7639 - 15,838	Aug 25	138.6	22.80	20,098	14,567 - 27,728
Sept 2	46.1	8.63	6695	4650 - 9641	Aug 30	559.7	92.08	81,163	58,828 - 111,980
Sept 10	19.7	3.70	2,869	1993 - 4132	Sept 9	79.9	13.15	11,595	8404 - 15,997
Sept 14	3.2	0.61	478	332 - 689	Sept 13	346.5	57.00	50,244	36,417 - 69,320
					Sept 23	298.5	49.11	43,287	31,375 - 59,722
					Sept 27	282.5	46.47	40,968	29,694 - 56,523
					Oct 3	154.6	25.43	22,417	16,248 - 30,927

Distance sampling methods may be used to infer abundance to a wider area in which line transects are evenly distributed or, more conservatively, to an area demarcated by the line transects themselves. We observed high percent coefficient of variation in the daily abundance estimates generated by detection models. Therefore, we opted to restrict inference about the abundance of phalaropes to the strip of sea repeatedly overflown by aerial surveys, i.e., the covered region only. Our line transects were laid out in two survey regions with an area of 633 km^2 (Brier) and 531 km^2 (Grand Manan). Within each area, we delimited a search strip by the length of transects (250 km in Brier, 207 km in Grand Manan) and width of transects (700 m given the available field of view). Accordingly, area of the covered region only was 175 km^2 in Brier and 145 km^2 in Grand Manan.

Component sources of uncertainty in our density estimates were detection probability and cluster size. Cluster size was responsible for the largest percent of variance: 85.7, 98.3 in Brier 2009, 2010 and 84.9, 96.9 in Grand Manan 2009, 2010. In correcting for size bias, expected flock size was: $E(s) \pm SE$ = 138 ± 17.3, 163 ± 38.3 in Brier 2009, 2010 and 67 ± 11.5, 104 ± 16.9 in Grand Manan 2009, 2010. Estimated density of phalaropes/km^2 in 2009 ranged from low (39 in Brier, 3 in Grand Manan) to high (403 in Brier, 195 in Grand Manan) with peak densities occurring in early August. In 2010, density ranged from low (102 in Brier, 80 in Grand Manan) to high (540 in Brier, 560 in Grand Manan), with peaks occurring in late July, late August and late September.

Prior to finding the cumulative number of phalaropes for all values of date and abundance, "bird days," the sum of *N* values by date in Brier and Grand Manan was taken to derive a combined abundance *(Total N)* across the study area for each survey date in 2009 and 2010. It must be emphasized that in 2009, three survey attempts were curtailed because of fog over Grand Manan; abundance estimates were returned for Brier only on 31 July, 6 August, and 9 August. As snapshots of stopover abundance at discrete time steps, the combined abundance values used to calculate size of the total stopover population, adjusting for length of stay, are given in Table 3.

Among the 27 phalaropes fitted with a radio tag, species ratio differed widely across years with numbers of Red-necked to Red 7:0, 5:3, 0:12 in 2008, 2009, 2010. We fitted a probability density function to the pooled observation times from all individuals and all years to estimate length of stay. The model with lowest AIC_c was based on a uniform key with cosine adjustment term. Estimated length of stay in days (*LOS* ± SE) was 15.2 ± 1.9 with 95% confidence limits at 11.8 - 19.7.

Table 3. Combined abundance (*Total N*) of phalaropes in the study area by survey date, based on the sum of *N* by survey date in both Brier and Grand Manan. Results of numerical integration to find bird days (BD) and quantify stopover population size (pop) adjusting for length of stay are given. Estimated length of stay (*LOS*) was derived by fitting a probability density function to the observation times of radiomarked birds (n = 27) captured in 2008, 2009, and 2010.

2009		2010	
Date	*Total N*	Date	*Total N*
Jul 31[†]	6824	July 26	31,037
Aug 1	63,093	July 31	120,270
Aug 6[†]	29,570	Aug 11	103,938
Aug 8	88,685	Aug 13	78,964
Aug 9[†]	28,811	Aug 18	70,797
Aug 12	42,236	Aug 25	91,681
Aug 20	31,284	Aug 30	127,891
Aug 27	35,868	Sept 9	32,473
Sept 1	40,569	Sept 13	108,902
Sept 2	48,396	Sept 23	137,736
Sept 9	10,615	Sept 27	71,788
Sept 10	12,726	Oct 3	48,266
Sept 14	7302	Oct 12	31,815
Survey period = 45 days		Survey period = 49 days	
BD	1,573,142	BD	4,370,889
LOS	15.2	*LOS*	15.2
pop	103,496	pop	287,558
		Survey period = 78 days	
		BD	6,743,654
		LOS	15.2
		pop	443,661

[†] Indicates no data available from Grand Manan because presence of fog; Brier survey only.

Estimated size of the total stopover population of phalaropes in 2009 was 103 thousand. The time frame for surveys in 2009 was 45 days. By contrast, in 2010 the time frame was 78 days because flocks remained in the study area and we continued to fly surveys until mid-October. Based on consensus as to the timing of phalarope migration in the region (Orr et al. 1982, Rubega et al. 2000, Tracy et al. 2002), it was unusual to observe large flocks in the region beyond September. However, our aerial survey coverage suggests that the stopover site tenure of postbreeding phalaropes in the Bay Fundy may be subject to more variation than previously thought. For comparison, we report stopover population size in 2010 for a 49-day period ending on September 13th (287 thousand), and for the full 78-day period (443 thousand), assuming a constant length of stay of 15 days.

Species ratios were gathered for a sample of flocks encountered opportunistically near the Brier ledges in 2010. Between 21 July and 31 August, we conducted 12 boat trips on calm days with flat seas (Beaufort 0-1), during which we were able to approach and photograph 43 flocks resting or feeding on the water. Taken together, the proportion of phalaropes positively identified as *P. lobatus* was 53%.

DISCUSSION

In this study, the choice of survey platform introduced several factors that likely influenced our stopover abundance estimates. An aircraft was critical to achieving our goal of obtaining comprehensive abundance data on small, highly mobile migratory birds at sea. Brown and Gaskin (1988) characterized the ecology phalaropes in the outer Bay of Fundy as closely tied to the Brier ledges, which act as "tidal pumps" and provide a nexus for phalarope flocks in the region. Quantitative evidence provided by Thorne and Read (2013) substantiates their hypothesis. However, our aerial perspective revealed that large flocks occur in "off-ledge" areas as well, and that while the ledges provide a focal point for their collective movements, flocks shift widely about them (100s km^2) in the span of hours. The dynamic nature of this system imparts a complexity to phalarope occurrence patterns and has a large bearing on the choice of platform to assess them comprehensively.

Aircraft provide certain advantages over boats for surveys at sea, notably an ability to cover large areas (100s of km^2) in a short time window (hours), but trade-offs to the increased encounter rate include reduced observer acuity overall (Caughley 1974, Pollock and Kendall 1987, Marsh and Sinclair 1989, Pollock et al. 2006). As a remedy, boat-based surveys allow for detailed observation at close range, but boats must operate with some dependence on "hotspots" as a means of encountering mobile assemblages of birds at sea. As such, they are confined to small search areas (10–15 km^2), a feature that limits the utility of boats for surveying phalaropes in the outer Bay of Fundy. In sum, the primary drawback of aircraft for surveys is incomplete detection whereas for boats the problem is one of incomplete coverage. Given the high mobility of phalarope flocks, we concluded that aerial surveys allow for a more synoptic picture.

Our results highlight several issues to be considered when designing studies of small marine birds using aerial line transect methods. The speed of an aircraft allows greater coverage, but entails an increased chance of missing target objects in the search strip. As near-line objects pass through the field of view up to 4x faster than objects near-horizon (Fleming and Tracey 2008), higher altitude allows more time for visual detection. On the other hand, if higher altitude imposes a nontrivial distance between observer and objects below, it reverts to the same drawback brought about by lower altitude, which reduces distance to target objects, but affords less time to process sightings from the air (Buckland et al. 2001).

These are classic pitfalls known to affect aerial surveys and, potentially, to introduce visibility bias into estimation procedures used to obtain abundance estimates from them (Laake et al. 2008*a*). In our case, a key consideration for the utility of distance sampling is a requirement for uniform distances (Fewster et al. 2008). Our empirical distance data showed that features of the aerial sighting situation led to visibility bias that may have translated into a violation of the uniform requirement, interfering with our estimators of detection probability. We discuss two scenarios that likely gave rise to a spiked pattern in our distance data: (1) impaired downward visibility induced by the flat-sided windows, such that detections in the first sighting bin were harder to obtain than in the second (Laake et al. 2008*b*). In a plane with flat-sided windows, it is generally easier for an observer to search slightly away from the first sighting bin and to favor the second; (2) influence of animal movement and in particular, evasive movement from the flightpath. If flocks flushed away from the first sighting bin and into the second before being recorded, this would also give rise to the nonuniform pattern of detection reported here. In support of scenario 2, phalaropes were observed to flush from the flightpath during surveys. Paradoxically, this response served as a valuable cue for visual detection (cf. Southwell et al. 2008).

In the absence of mark-recapture methods, it is difficult to gauge whether either scenario was severe enough to cause genuine nonuniformity in our data (Borchers et al. 2006). We speculate that a mixture was at play and a potential outcome is that our estimators for detection probability are positively biased. When estimators for detection probability are too high, compensation for abundance will be too low, and the degree to which abundance is underestimated is proportional to the true detection probability (Laake et al. 2008*a*). Nevertheless, our results clearly show there has been a significant decline in numbers of *P. lobatus* that pass through the Bay of Fundy. Based on previous counts, total stopover passage at Head Harbour from July–September included some 2 million migrants of *P. lobatus,* with daily densities of 5000-20,000 birds/km² (Mercier and Gaskin 1985). By contrast, highest recorded density comprising both species of phalarope as evaluated in the present study was 560 birds/km². Even without applying a species ratio to the abundance estimates reported here, this amounts to a steep reduction in numbers of *P. lobatus* observed at Head Harbour prior to their abrupt disappearance in the 1980s.

The upheaval of phalaropes from Head Harbour in the 1980s remains a matter of speculation in terms of demography. Although the event has been characterized as a disproportionate local decline, consensus from literature is that its impact on the species in North America is unknown (Duncan 1996, Rubega et al. 2000, Brown et al. 2010). The level of uncertainty is reflected in a population size estimate for *P. lobatus* in North America: in their reassessment of population size and trend of 52 species and 75 taxa of shorebirds occurring in North America, Andres et al. (2012) report the figure for *P. lobatus* at 2.5 million. They note that the estimate is highly problematic because it includes historic counts from Head Harbour prior to the disappearance and has not been revised from compilations on shorebird numbers in North America, first published in 2001 (Morrison et al. 2001) and updated in 2006 (Morrison et al. 2006).

Explanatory frameworks for the Head Harbour disappearance can be broken into two categories: (1) population crash; (2) shift in migratory stopover pathway. In support of the first hypothesis, Nisbet and Veit (2015) have proposed the largest part of the decline at Head Harbour was well underway by 1984 and thus can be linked to El Nino-Southern Oscillation (ENSO) events affecting the wintering area. The authors noted that severe ENSO conditions depleted marine ecosystems in the eastern tropical Pacific in 1982/1983. In the Western Hemisphere, the only known major wintering area for *P. lobatus* is the Humboldt Current off Ecuador, Peru, and northern Chile (Murphy 1936, Rubega et al. 2000, but see Haney 1985). Although migrants of *P. fulicarius* winter here too, those that pass through Fundy in autumn are thought to winter in the Canary and Benguela Currents off West Africa (Cramp and Simmons 1982).

This may in part explain why there was not a crash in the outer Bay of Fundy where, based on summary assessments from Brier Island (Brown and Gaskin 1988), smaller assemblages of phalaropes (10s of thousands) occurred through the 1970s and 1980s and no strict segregation of species, such as that distinguishing Head Harbour, has been reported. However, any perception that the outer Fundy stopover population was insulated from the decline at Head Harbour bears scrutiny: anecdotal observations suggest that *P. fulicarius* often outnumbered *P. lobatus*, by as much as 95:5, at the Brier ledge areas prior to the Head Harbour disappearance, but the species ratio changed measurably, at times approaching 1:20, in its aftermath in 1990 (Brown 1991). As evaluated for the present study, species ratio at the Brier ledges was found to be closer to 50:50 overall in 2010.

Others have proposed a local disturbance affecting prey availability as being responsible for the Head Harbour disappearance (Brown et al. 2010), leading to a shift in migratory pathway and supplying migrants elsewhere. In 1990, there was some indication that zooplankton density was low at Head Harbour in August. Against this, more rigorous plankton tows returned extremely high density values in October (Duncan 1996). The second hypothesis would be better substantiated if population trends observed on Arctic breeding grounds had remained stable overall, but this is not the case for either species of phalarope: survey counts are sparse, but declines were reported at Arctic breeding sites (La Pérouse Bay, Manitoba; Prudhoe Bay, Alaska) in the wake of ENSO 1982/1983 (see Nisbet and Veit 2015). Although the authors acknowledge these declines to be far less pronounced and sustained than the Head Harbour crash, such findings undermine a shift hypothesis because breeding populations of *P. lobatus* should have remained stable if not increasing had 1–2 million birds simply altered their migratory stopover pathway.

None of the above frameworks has sufficient scope without quantitative information on phalarope populations on the breeding grounds, wintering areas, and critical stopovers between. This study provides the first attempt to obtain comprehensive estimates of phalarope stopover abundance in the Atlantic, while adjusting for estimated length of stay. Our work provides baseline information essential for evaluating the importance of the Bay of Fundy to phalaropes in general. Recent geolocator evidence gathered by Smith et al. 2014 offers an intriguing example of a trans-Atlantic Ocean migratory route in which the Bay of Fundy provided a stopover to a bird breeding in Shetland, UK (Smith et al. 2014). We urge the development of surveys to track phalaropes at sea, where they concentrate reliably and spend the majority of their time.

Responses to this article can be read online at:
http://www.ace-eco.org/issues/responses.php/926

Acknowledgments:

Sincere thanks to the team at the Grand Manan Whale and Searbird Research Station, especially Andrew Westgate, Sarah Wong, and Zach Swaim for their skill and persistence in the field. Aerial surveys were made possible by Atlantic Charters of Grand Manan and we thank Klaus and Peter Sonnenberg for their expertise as pilots. Special thanks to Christopher Julian, for design of tools used in the *field, and Reid Gillis for long hours of boat maneuvering under challenging conditions. Brier Island Whale and Seabird Cruises generously provided boat-based support and we are grateful to Harold Graham for housing as well. Funding was provided by U.S. Fish & Wildlife Service Region 5, Manomet Center for Conservation Sciences, and Environment Canada. Many insightful discussions contributed to the design of this study; in particular, we thank Dan McCauley, John Chardine, Lesley Thorne, and Charles Duncan. We greatly thank Carina Gjerdrum, Rob Ronconi, and Julie Paquet for helpful reviews of this manuscript.*

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Sponsored by the Society of Canadian Ornithologists and Bird Studies Canada
Parrainée par la Société des ornithologistes du Canada et Études d`oiseaux Canada