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ESTIMATING SHOREBIRD NUMBERS AT MIGRATION STOPOVER SITES

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Abstract. We describe a method for estimating the total number of shorebirds that use a migration stopover site during spring and fall migration. We combined weekly shorebird counts with parameter estimates for detection probability, sampled proportion, and length of stay on the Squaw Creek National Wildlife Refuge. Double sampling was used to determine detection probability and estimated values varied among wetland units from a low of 0.07 to a high of 0.82. The sampled proportion of most wetland units was 100% but was lower in some of the larger units. Length of stay (measured for Pectoral [*Calidris melanotos*] and Least Sandpipers [*C. minutilla*] combined) averaged 10.0 days in spring and 3.7 days in fall. Spring shorebird numbers were approximately five times greater than fall numbers on the Refuge. Annual shorebird numbers varied among years from an estimated low in 2003 of 15 734 to a high in 2002 of 69 570. Peak daily counts during study years averaged only 12% of estimated spring totals and 4% of fall totals. An estimate of shorebird numbers based on summing weekly counts, not corrected for detection probability or sampled proportion, would have been only 21% (spring) to 31% (fall) of the total number of birds. These results reveal that peak counts and nonadjusted counts can significantly underestimate the number of shorebirds that use migration stopover sites in the midcontinent of North America.

Key words: Calidris melanotos, Calidris minutilla, *detectability, Least Sandpiper, length of stay, migration stopover, Pectoral Sandpiper.*

Estimación del Número de Aves Playeras en las Paradas Migratorias

Resumen. Describimos un método para estimar el número de aves playeras migratorias que utilizan sitios de parada durante la migración de primavera y otoño. Combinamos conteos semanales de las aves playeras con estimaciones de los parámetros de la probabilidad de detección, la proporción muestreada y la duración de la estadía en el Refugio Nacional de Squaw Creek. Usamos muestreos dobles para estimar la probabilidad de detección y los valores estimados variaron desde 0.07 hasta 0.82 entre humedales. La proporción del hábitat muestreada fue del 100% en la mayoría de los humedales, pero el valor fue menor en algunas de las unidades de mayor tamaño. La duración de la estadía (medida para *Calidris melanotos* y *C. minutilla*) fue en promedio de 10.0 días en primavera y de 3.7 días en otoño. El número de aves fue aproximadamente cinco veces más alto en la primavera que en el otoño. El número total anual varió entre los años de estudio; la estimación más baja fue de 15 734 individuos en el 2003 y la estimación más alta de 69 570 individuos en el 2002. En promedio, el número diario más alto representó solamente el 12% del total de las aves en primavera y el 4% del total en otoño. Una estimación del número de aves basada sólo en la suma de los conteos semanales, sin estar corregida por la probabilidad de detección o la proporción muestreada, habría representado sólo entre un 21% en primavera y un 31% en otoño del número total de aves. Estos resultados demuestran que conteos del número diario máximo o conteos no ajustados pueden subestimar significativamente el número real de aves que usan paradas migratorias en el centro del continente norteamericano.

INTRODUCTION

The major bird conservation programs, including Ramsar (Ramsar Convention Secretariat 2004), the Western Hemisphere Shorebird Reserve Network (WHSRN; Manomet Center for Conservation Sciences 2005a), and Birdlife International's Important Bird Areas (Birdlife International 2006), all have a common goal of identifying key sites for bird conservation. These programs have established numeric thresholds to qualify proposed sites as part of

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their network of key areas; for example, a common threshold among the programs is a site supporting 1% of a biogeographic population. For a site to be considered as a key site, one must establish that the site supports at least the appropriate threshold number of birds annually based on reliable estimates, with an emphasis on the need for species-specific count data. Conducting an accurate count in support of a site recommendation can be difficult, however, especially at migration stopovers where only a portion of the population is present at any one time, different species and sexes have different migration chronologies, and there is considerable interannual variation in habitat availability and bird numbers. Furthermore, there are no established sampling protocols that address these complicating factors at migration stopover sites.

Nonetheless, the International Shorebird Survey (Harrington et al. 1989, Manomet Center for Conservation Sciences 2005b) has been widely adopted and is almost universally used to count shorebird numbers during migration stopovers in North America. Using this protocol, an observer follows an established route and counts all birds seen along the route. The count may be repeated more than once, usually every 7–10 days during a migration period, and because there is an implicit assumption that length of stay is equal to the interval of time between counts, the individual counts are often summed to get a season-long estimate of shorebird numbers.

Shorebird estimates produced with this protocol, however, can be biased for several reasons. First, not all shorebirds are detected and counted during any census period. The probability of detection (herein called "detectability"), generally less than 1.0, varies as a function of the shorebird species present, distance from the survey route, habitat conditions, observer ability, and environmental variables such as wind, precipitation, and angle of the sun (Buckland et al. 1993). Second, depending on the size, shape, and proximity of the wetland unit to the survey route, some portions of specific wetlands cannot be seen from the survey route; hence, the sampled proportion may be less than 1.0. Finally, one cannot simply add successive counts to get a season-long estimate because the average length of stay of birds may be longer or shorter than the interval of time between successive counts.

We initiated a study of shorebird stopover ecology at Squaw Creek National Wildlife Refuge (hereafter "Refuge") in northwestern Missouri in 2003. Our first study objective was to demonstrate how International Shorebird Surveys, which had begun on the Refuge in 2001, could be expanded by incorporating detectability, sampled proportion of wetlands, and length of stay to produce better estimates of the number of migrating shorebirds that use the refuge during both spring and fall migration. The second objective was to use the improved estimates of shorebird numbers to help the Refuge assess the long-term effects of their habitat management efforts and to support a recommendation for designating the Refuge as a site in the Western Hemisphere Shorebird Reserve Network.

METHODS

STUDY AREA

Our study was conducted in northwestern Missouri along the Missouri River, about 50 km north of St. Joseph and west of Mound City (40°10′N, 95°15′W). The study area, the greater "Squaw Creek ecosystem," encompasses Squaw Creek National Wildlife Refuge, Bob Brown State Conservation Area, Big Lake State Park, and two private wetland complexes north of the Refuge. These areas exist in close proximity and collectively form a large complex that contains a variety of wetland types, including managed wetlands, moist soil units, natural lakes, and sheetwater wetlands (LaGrange and Dinsmore 1989). Radio-tracking since 1993 has shown that birds frequently move back and forth on a daily basis between the Refuge and surrounding wetland areas (Farmer and Parent 1997). Thus, this complex of wetlands functions as a single migration stopover site, although the relative amount of habitat provided by the individual areas, as well as the distribution of shorebirds, varies annually with precipitation and management. While our study included all these areas, the shorebird count data and population estimates presented herein pertain solely to the Refuge, the most important component of the complex as measured by the number of shorebirds counted in our shorebird surveys.

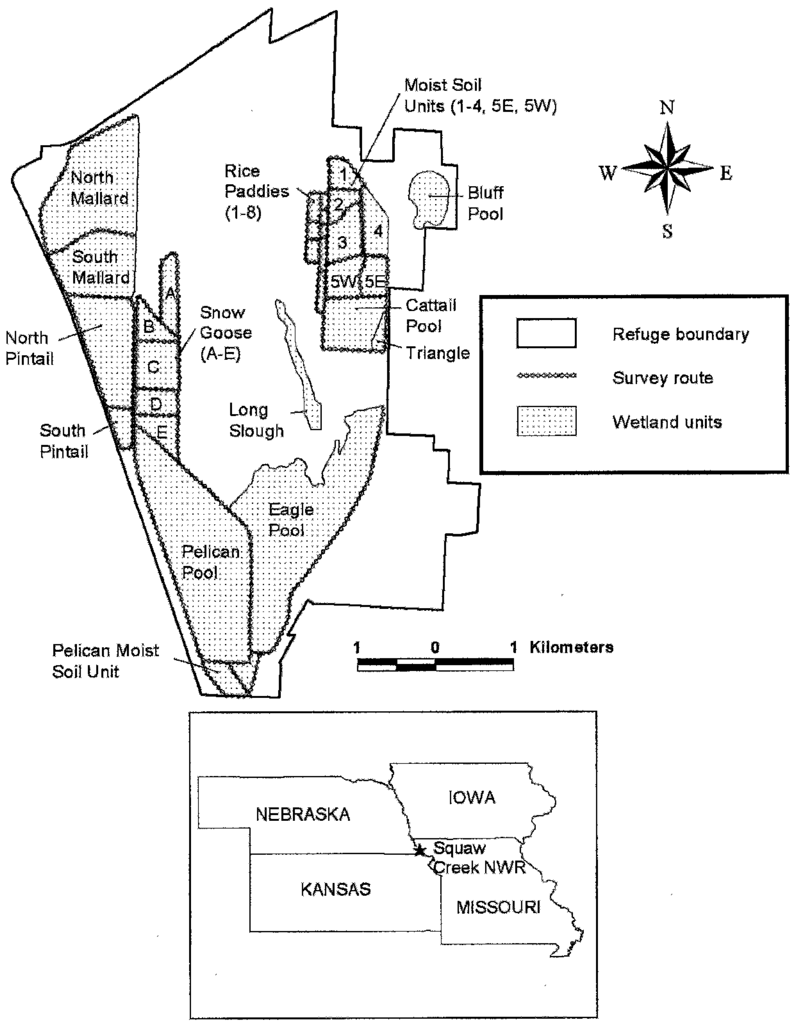

FIGURE 1. Wetland units, International Shorebird Survey route used to conduct weekly shorebird counts, and Refuge boundaries at the Squaw Creek National Wildlife Refuge, Missouri.

SHOREBIRD SURVEYS

Periodic (approximately weekly) shorebird surveys have been conducted on the Refuge since the fall of 2001 and are ongoing. These surveys are conducted following International Shorebird Survey protocol. All surveys are performed by driving the route shown in Figure 1, and stopping where and when necessary to count shorebirds seen along the route. There are no significant disturbance or road effects (e.g., flushing birds away from the route into inaccessible areas), and the elevated route along unit dikes generally improves visibility. This route is surveyed weekly during fall and spring shorebird migration. To control environmental factors that potentially affect detectability, surveys are always conducted between sunrise and 12:00 when the wind is less than 16 kph and no rainfall or fog is present. Surveys to date have been conducted by FD and other experienced shorebird observers. All shorebirds are counted from a vehicle using binoculars, or spotting scopes when necessary, and identified to species. The total number of each species for each wetland unit is recorded.

DETECTABILITY

We estimated detectability using double sampling (Cochran 1977, Eberhardt et al. 1979, Eberhardt and Simmons 1987), combining weekly extensive surveys with more intensive "flush" counts on selected wetland units. The flush counts were conducted immediately following the survey at the selected wetland unit. Generally, two or more observers (not including the person who conducted the survey) walked abreast through the selected unit and attempted to flush all shorebirds and record the numbers of individuals by species. If an individual shorebird could not be identified to species, the observer used a generic descriptor (e.g., *Tringa* spp., or "peeps" for small unidentified shorebirds). It was difficult to make accurate counts of flushed shorebirds if the sampled area was too large, because flushed individuals could land elsewhere in the sample area without being seen by the observers, and thus get counted multiple times. To minimize this error in larger wetland units, we agreed *a priori* on a specific subarea to be sampled, and both the survey and flush count were conducted in that subarea. We did not explicitly account for error in estimating flock size, which varies with flock size (B. Harrington, Manomet Center for Conservation Sciences, pers. comm.). Since most flocks that we encountered were small (<100 individuals), we assumed there was no consistent under- or overestimation and that this error was imbedded in the measured observer error. The number of observers and the actual people involved in the flush counts varied among units and occasions depending on who was available to participate on a given day. Some units were double sampled on more than one occasion. Counts by different observers were assumed to be independent and both occasions and observers were treated as replicates. For each unit that was double sampled, we computed a mean detectability (d), which was the mean of the ratios (survey-count/flush-count) from all sampling occasions and observers.

Double sampling was not conducted on all units because no shorebirds were present on some units when flush counts could be scheduled. Those units that were not double sampled were assigned a detectability value, which was the mean detectability for all units in the same vegetation cover class. Every wetland unit was classified as having light, moderate, or heavy vegetation cover (Fig. 2). In most cases it was easy to classify a wetland unit's vegetation cover because the Refuge's wetlands occur in natural groupings that correspond with historic management regimes. Nevertheless, we were also interested in characterizing the vegetation cover classes in quantitative terms, to determine the vegetation attributes that affected our perceptions of both cover and detectability. We measured two aspects of vegetation structure: 1) canopy cover (Daubenmire 1959), which estimates horizontal vegetation structure; and 2) visual obstruction (Robel et al. 1970), which incorporates both horizontal and vertical vegetation structure. Random points were selected in wetland units representing each vegetation cover class, and at each point four visual obstruction readings (north, south, east, and west of the point) and one estimate of canopy cover (centered on the point) were made. The point data were pooled across the wetland units in each vegetation class to compute a mean visual obstruction reading and canopy cover for each vegetation cover class. Differences in visual obstruction and canopy cover among vegetation classes were evaluated with a t-test ($\alpha = 0.05$) for independent, unequal-sized groups.

SAMPLED PROPORTION

Depending on the landscape, some portions of several wetland units could not be seen from the survey route. These areas were typically blocked from view by features such as dikes or tall vegetation (e.g., cattails or trees); hence, shorebirds using these areas were never counted. We estimated the sampled proportion for each wetland unit based on inspection of aerial photos and field reconnaissance of each unit. The estimate was not the proportion of the entire wetland area, but an estimate of the proportion of suitable shorebird habitat that could be seen from the survey route.

LENGTH OF STAY

We estimated the length of stay for Least Sandpipers (*Calidris minutilla*) and Pectoral Sandpipers (*C. melanotos*) during both the spring and fall migration periods using radiotelemetry. These species were selected for study because they are abundant on the Refuge and differ with respect to body size, migration

FIGURE 2. Photos (taken in early May) of Squaw Creek National Wildlife Refuge wetland units with different vegetation conditions and shorebird visibility. Top panel: Moist Soil Unit 1 in the "light" vegetation class. Common plant species are spikerush (*Eleocharis* spp.) and wild millet (*Echinochloa* spp.). Middle panel: One of the Rice Paddy units in the "moderate" vegetation class. Common plant species are spikerush and river bullrush (*Scirpus fluviatilis*) averaging 4–6 inches tall. Bottom panel: A Rice Paddy unit in the "heavy" vegetation class. The dominant plant species is arrowhead (*Sagittaria latifolia*), which averages about 9 inches tall in the photo.

distance, and breeding systems, all of which potentially affect migration strategies. Radio-transmitters were glued to clipped-feather stubble on the birds' backs with cyanoacrylate glue (Raim 1978, Warnock and Warnock 1993). Shorebird migration takes place during about a five-week field season in both spring and fall; therefore, we attempted to attach radios to approximately four birds of each species per week (including both males and females of Pectoral Sandpipers) to incorporate sexual differences in migration chronology as well as other factors that might affect temporal variation in length of stay across the migration period.

Each bird was located twice daily from the ground; the first observation was in the morning, generally between 08:00 and 10:00 CST, and the second was in the afternoon, generally between 16:00 and 20:00. When a bird's signal was not detected through ground tracking we searched from aircraft (Gilmer et al. 1981). Prior experience with tracking shorebird movements in the area (Farmer and Wiens 1999) led us to conduct aerial searching along parallel transects covering the Missouri River floodplain, up to 50 km from the bird's last known location. If a bird's signal was found, the location was recorded and further ground tracking resumed from that point. If the bird was not located, it was assumed to have left the study area.

The observation time for each radio-tagged bird was measured as the elapsed time between its release and the time its radio signal was last detected. Length of stay (the mean time between arrival and departure from the study area) was estimated from the observation times (Farmer and Wiens 1999, Lehnen and Krementz 2005) based on length-biased sampling methods (Cox 1969, Otis et al. 1993). This approach assumes that: 1) a shorebird has an equal probability of being captured at any time during its stay, and 2) the overall probability of a shorebird being captured during its stay is proportional to its length of stay. Program DISTANCE (Laake et al. 1996) was used to fit alternative function forms to the probability density of the observation times for a group of individuals, and second-order Akaike's information criterion (AIC_c; Anderson et al. 2001) was used to select the best-fitting function form. Length of stay was estimated by taking the inverse of $f(0)$, the estimated y-intercept of the best-fitting probability density function. The 95% confidence limits for length of stay estimates were computed by taking the inverse of the confidence limits on $f(0)$ computed by program DISTANCE. Likelihood ratios were used to test for differences in capture dates and length of stay among species.

ESTIMATING TOTAL SHOREBIRD NUMBERS

For a given survey date, t, the shorebird count for a wetland unit was divided by detectability to calculate the number of shorebirds that were likely present in the portion of the unit that was sampled. This calculation produces the best unbiased estimate of the number of shorebirds present if, as in this study, the relationship between survey and flush counts is linear and passes through the origin, and the variance of the flush counts is proportional to the survey counts (Cochran 1977). This result was then divided by the sampled proportion to extrapolate the total number of shorebirds that were present in the entire unit on the survey date. The extrapolated number was then totaled across all wetland units as:

$$b_t = \sum_{j=1}^{m} \left(\frac{s_{tj}}{d_j}\right) \frac{1}{p_j}, \qquad (1)$$

where b_t = the estimated number of shorebirds on survey date t, s_{tj} = the survey count in wetland unit j on date t, d_j = the mean detectability in wetland unit j, p_j = the sampled proportion of wetland unit j, and m = the number of wetland units.

Second, the total number of bird-days for the migration season was computed by integrating b_t across the interval of time between an initial and final survey date:

$$bd = \int_{t=1}^{f} b_t, \qquad (2)$$

where bd = the number of bird-days for the migration season, b_t = the estimated number of shorebirds on survey date t, t = survey date (beginning at 1 on the first survey date), and f = the final survey date.

We used the "Area Under" (ARU) function in SYSTAT v. 10 (SPSS 2000), which uses the trapezoidal rule, to do this integration based on

TABLE 1. Shorebird counts varied among years, but were consistently higher during spring migration than in fall migration of the same year at Squaw Creek National Wildlife Refuge, Missouri. The range of survey dates and number of surveys per survey period also varied among years.

Survey period	Range of dates	No. of surveys	No. of shorebirds
2001			
Fall	03 Aug–12 Sep	6	2347
2002			
Spring	19 Mar–23 May	18	28 789
Fall	03 Aug–09 Oct	9	1334
2003			
Spring	24 Mar–19 May	9	4868
Fall	12 Aug–22 Sep	7	544
2004			
Spring	01 Apr–17 May	8	19 611
Fall	20 Aug–12 Oct	9	1041

coordinate pairs ($t_1, b_1, t_2, b_2, t_3, b_3 \ldots t_f, b_f$). The total number of shorebirds visiting the Refuge during the migration season was then estimated as:

$$pop = \frac{bd}{LOS}, \tag{3}$$

where pop = estimated total number of shorebirds, bd = total bird-days computed with equation 2, and LOS = estimated length of stay in days.

Using calculated mean values for detectability and length of stay in the above equations, we derived point estimates of spring and fall populations. However, both detectability and length of stay are random variables. Therefore, we also derived 95% confidence limits for estimated populations by performing a simulation based on the following assumptions: 1) that detectability was uniformly distributed between the high and low values calculated for each wetland, and 2) that $f(0)$ was asymptotically normally distributed with mean and variance as calculated by program DISTANCE. Based on these assumptions, we estimated the population by selecting a uniform random deviate for detectability of each wetland, computing the b_t for each time period, and integrating these values to get an estimate of bird-days (equation 2), which we then divided by LOS, computed as the inverse of a normal random deviate of $f(0)$. This process was repeated to produce a vector of 10 000 population estimates, which was sorted to identify the 2.5% and 97.5% quantiles.

RESULTS

SHOREBIRD SURVEYS

Many more shorebirds were counted during the spring survey periods than in the fall surveys (Table 1), which on the Refuge was at least partly a response to the greater amount of habitat that was available in the spring. Shorebirds were not equally distributed among the Refuge wetland units (Table 2). While there was interannual variation in the distribution of shorebirds and shorebird habitat among units, six units consistently received the highest shorebird usage (Table 2). These wetland units (North Mallard, South Mallard, Snow Goose B, Moist Soil Unit 1, Moist Soil Unit 2, and the Rice Paddies [the Rice Paddies are really eight separate units, but they are surveyed as a whole]) accounted for an average of 68% (annual values from 51% to 77%) of shorebirds in the spring and 63% (annual values from 54% to 70%) in the fall. The single exception to this pattern of shorebird distribution occurred in the spring of 2002, when the water level in Pelican Pool (one of two large units on the Refuge) was drawn down, resulting in a substantial increase in the amount of available habitat and shorebird use.

The initial surveys conducted in 2001 and 2002 did not identify shorebird species. In 2003 and 2004, more than 24 species of shorebird were detected during surveys (Table 3). About half (46% of shorebirds in spring and 54% in fall) of all individuals were Lesser Yellowlegs (*Tringa flavipes*) and Pectoral Sandpipers. The

TABLE 2. The number of shorebirds varied by wetland unit at Squaw Creek National Wildlife Refuge, Missouri. Six wetland units, North Mallard, South Mallard, Snow Goose B, Moist Soil Unit 1, Moist Soil Unit 2, and Rice Paddies, accounted for 68% of shorebirds in spring and 63% of shorebirds in fall. See Fig. 1 for location of wetland units.

	2001	2002		2003		2004	
Wetland unit	Fall	Spring	Fall	Spring	Fall	Spring	Fall
Eagle Pool	0	452	81	220	1	6	0
Cattail Pool	178	51	245	42	5	1779	53
Long Slough	0	150	0	0	8	0	0
South Mallard	0	3597	195	89	1	2797	0
North Mallard	0	1209	62	3	359	5864	0
North Pintail	0	271	65	1	9	0	0
South Pintail	0	43	0	0	0	0	0
Snow Goose A	0	1496	0	172	9	21	10
Snow Goose B	533	4766	386	1604	14	2261	0
Snow Goose C	32	173	0	8	15	8	35
Snow Goose D	0	1647	0	88	0	928	120
Snow Goose E	0	778	0	31	0	1466	99
Pelican Pool	0	7066	0	53	0	2	0
Moist Soil Unit 1	1419	1283	209	812	4	1746	363
Moist Soil Unit 2	0	15	3	14	2	131	200
Moist Soil Unit 3	0	303	0	0	0	0	0
Moist Soil Unit 4	0	1	0	0	6	0	0
Moist Soil Unit 5E	0	5	0	14	2	115	87
Moist Soil Unit 5W	152	6	12	0	80	2	46
Pelican Moist Soil Unit	0	1226	0	4	25	3	28
Rice Paddies	0	4099	26	1209	4	2482	0
Bluff Pool	0	0	0	500	0	0	0
Triangle	33	152	50	0	0	0	0
Total	2347	28 789	1334	4864	544	19 611	1041

five most abundant species in spring (Lesser Yellowlegs, Pectoral Sandpipers, White-rumped Sandpipers [*Calidris fuscicollis*], Least Sandpipers, and dowitchers [*Limnodromus* spp.]) accounted for 80% of all individuals, and the five most abundant species in fall (Lesser Yellowlegs, Pectoral Sandpipers, Killdeer [*Charadrius vociferous*], Least Sandpipers, and dowitchers) accounted for 86% of all birds. Thus, the Refuge's shorebird community was dominated by a few shorebird species.

DETECTABILITY

We estimated detectability in the spring of 2003 and 2004 in 10 Refuge wetland units and five similar-sized wetland units on nearby private and State wetland complexes (Table 4). We focused sampling efforts on the wetland units that had the highest shorebird usage (North and South Mallard, Moist Soil Units 1 and 2, and the Rice Paddies). Individual replicate samples (including the off-Refuge samples) were grouped by vegetation class to estimate mean detectability values for each vegetation class, which were used to represent unsampled wetland units (Table 4).

Canopy cover and visual obstruction were measured in two units from the light cover class (Triangle [$n = 10$] and Snow Goose B [$n = 13$]), three units from the moderate cover class (Moist Soil Unit 2 [$n = 11$], Rice Paddy 8 [$n = 14$], and Snow Goose E [$n = 10$]), and three units from the heavy class (Rice Paddy 4 [$n = 15$], Snow Goose A [$n = 15$], and Snow Goose D [$n = 16$]). Canopy cover estimates were 5% ± 11% ($n = 23$), 17% ± 17% ($n = 35$), and 25% ± 22% ($n = 46$) in the light, moderate, and heavy classes, respectively. Canopy cover was significantly different ($t = 5.4$, $P < 0.001$) between the light and moderate classes, but not between the moderate and heavy classes ($t = 1.85$, $P \approx 0.08$). Visual obstruction estimates were 0.9 ± 3.1 cm ($n = 92$), 1.6 ± 4.9 cm ($n = 140$), and 10.6 ± 22 cm ($n = 184$) in the light, moderate, and heavy cover classes, respectively. In contrast to canopy cover, visual obstruction

TABLE 3. At least 23 shorebird species were counted during the study on the Squaw Creek National Wildlife Refuge, Missouri, but the Refuge's shorebird community was dominated by a few species. About half (46% of shorebirds in spring and 54% in fall) of all individual shorebirds were Lesser Yellowlegs and Pectoral Sandpipers.

Species	2003		2004		Total	
	Spring	Fall	Spring	Fall	Spring	Fall
American Golden-Plover (*Pluvialis dominica*)	200	1	0	0	200	1
Piping Plover (*Charadrius melodus*)	0	0	0	0	0	0
Semipalmated Plover (*Charadrius semipalmatus*)	17	0	183	2	200	2
Killdeer (*Charadrius vociferus*)	130	118	87	96	217	214
American Avocet (*Recurvirostra americana*)	1	1	2	0	3	1
Greater Yellowlegs (*Tringa melanoleuca*)	75	2	93	11	168	13
Lesser Yellowlegs (*Tringa flavipes*)	964	213	5722	312	6686	525
Solitary Sandpiper (*Tringa solitaria*)	0	19	2	53	2	72
Willet (*Catoptrophorus semipalmatus*)	6	6	0	0	6	6
Spotted Sandpiper (*Actitis macularia*)	79	12	203	13	282	25
Hudsonian Godwit (*Limosa haemastica*)	45	0	55	0	100	0
Sanderling (*Calidris alba*)	0	0	1	0	1	0
Dunlin (*Calidris alpina*)	9	0	48	0	57	0
Pectoral Sandpiper (*Calidris melanotos*)	566	135	4093	204	4659	339
White-rumped Sandpiper (*Calidris fuscicollis*)	856	0	3311	16	4167	16
Baird's Sandpiper (*Calidris bairdii*)	28	4	649	32	677	36
Western Sandpiper (*Calidris mauri*)	0	0	5	0	5	0
Semipalmated Sandpiper (*Calidris pusilla*)	83	3	194	1	277	4
Least Sandpiper (*Calidris minutilla*)	587	24	2282	116	2869	140
Stilt Sandpiper (*Calidris himantopus*)	15	0	98	12	113	12
Dowitcher spp. (*Limnodromus* spp.)	484	0	893	149	1377	149
Buff-breasted Sandpiper (*Tryngites subruficollis*)	0	1	0	0	0	1
Common Snipe (*Gallinago gallinago*)	101	4	178	14	279	18
Wilson's Phalarope (*Phalaropus tricolor*)	82	1	177	1	259	2
Other (unidentified)	536	0	1335	9	1871	9
Total	4864	544	19 611	1041	24 475	1585

differed significantly between the moderate and heavy classes ($t = 3.90$, $P < 0.001$), but there was no significant difference between the light and moderate classes ($t = 1.33$, $P \approx 0.20$).

SAMPLED PROPORTION

The proportion of available habitat sampled ranged from 0.1–1.0 of each wetland unit (Table 4). These values changed substantially for the Pelican Pool during the study period. Normally, only a small fraction (0.1) of this pool's shorebird habitat is observable from the survey route. However, the pool was drained in 2002 prior to spring migration and a larger portion of its surface (0.5), which is normally too deep to be used by shorebirds, was suitable habitat and visible from the route in that year.

LENGTH OF STAY

During 2003 and 2004 we radio-tagged 75 Pectoral Sandpipers (37 in spring, 38 in fall) and 76 Least Sandpipers (37 in spring, 39 in fall) to estimate length of stay. Lengths of stay estimates in spring were similar for the two species (10.5 days for Pectoral and 9.7 days for Least Sandpipers; Table 5). In fall, Pectoral Sandpipers had a slightly longer length of stay (4.9 days, versus 3.6 days for Least Sandpipers). There were no significant differences among years for either species.

Observation times in spring varied inversely with capture date for both species (Fig. 3), a temporal trend that has previously been seen for Pectoral Sandpipers (Farmer and Wiens 1999). We partitioned both species into "early" and "late" subgroups (defined by median capture date: $<$29 April = early; $\geq$29 April = late) and estimated length of stay for both subgroups. The length of stay for early migrating individuals was significantly longer (23.0 days for Pectoral Sandpipers, 21.0 days for Least Sandpipers) than that of late migrants (6.8 days for Pectoral Sandpipers, 6.3 days for Least Sandpipers). Differences between species were not significant. In fall, late migrating Pectoral Sandpipers had a slightly longer

TABLE 4. Wetland units at the Squaw Creek National Wildlife Refuge, Missouri varied in terms of their vegetation cover, detectability of shorebirds, and sampled proportion of suitable habitat. Each wetland unit was assigned to a vegetation class (L = light, M = moderate, H = heavy vegetation cover) based on field inspection and the sampled proportion was estimated from maps and field inspection. Detectability for each unit was estimated by double sampling the unit or by using the mean value for that unit's vegetation class. Detectability for each vegetation class was estimated by taking the mean of samples (*n*) from all units assigned to that vegetation class.

Wetland unit	Vegetation class	Detectability			Sampled proportion
		n	Mean	Range	
Refuge units:					
Eagle Pool	L				0.10
Cattail Pool	M				0.75
Long Slough	L				0.25
South Mallard	H	3	0.07	0.06–0.10	0.75
North Mallard	M	1	0.51		0.75
North Pintail	H				0.75
South Pintail	H				0.75
Snow Goose A	H				1.00
Snow Goose B	L				1.00
Snow Goose C	H				1.00
Snow Goose D	H				1.00
Snow Goose E	M				1.00
Pelican Pool	L				0.10, 0.50[a]
Moist Soil Unit 1	L	5	0.82	0.46–0.97	1.00
Moist Soil Unit 2	M	2	0.26	0.19–0.34	1.00
Moist Soil Unit 3	M	1	0.34		0.50
Moist Soil Unit 4	H				0.50
Moist Soil Unit 5W	H				0.75
Moist Soil Unit 5E	H	2	0.12	0.11–0.14	0.75
Pelican Moist Soil Unit	M				1.00
Rice Paddies	M	8	0.60[b]	0.40–0.80	1.00
Rice Paddies	H	5	0.10[b]	0.06–0.13	1.00
Bluff Pool	H	2	0.14	0.12–0.16	0.25
Triangle	L	1	0.63		1.00
Off-refuge units:					
Nodaway Sanctuary	M	2	0.58	0.51–0.68	
Middle Marsh A	H	2	0.14	0.13–0.15	
Middle Marsh B	M	2	0.44	0.39–0.50	
Bigelow 2-2	M	1	0.46		
Bigelow 2-3	M	1	0.36		
Vegetation class:					
Light cover		6	0.79	0.46–0.97	
Moderate cover		18	0.50	0.34–0.80	
Heavy cover		16	0.10	0.06–0.14	

[a] Pelican Pool was drained in 2002 and its sampled fraction was much higher that year (0.5).
[b] The Rice Paddies contain units that are heavily vegetated as well as moderately vegetated, however they are surveyed as a single unit. Therefore, we applied a detectability = 0.6 for all survey data and consequently underestimated the shorebird usage of these eight units.

observation time (Fig. 4), but when the data were combined with those for Least Sandpipers, there were no differences in length of stay between early and late birds. The length of stay estimates for both species combined were based on reanalysis with the larger sample size and are not simply an average of the separate estimates. Because of the larger sample size and smaller confidence limits, the combined length of stay estimates were used to make population estimates.

ESTIMATES OF TOTAL SHOREBIRD NUMBERS

Estimates were derived for every season from fall 2001 to fall 2004. Spring numbers were

TABLE 5. Shorebirds remained at the Squaw Creek National Wildlife Refuge, Missouri longer in early than in late spring (early spring was defined as <29 April and late spring was ≥29 April), and longer during spring than in fall. Shown are measured observation times (time between release of a radio-tagged shorebird and when its radio signal was last detected), estimated length of stay (total time spent at site), and 95% confidence limits for length of stay for Pectoral and Least Sandpipers captured in 2003 and 2004. Sample sizes in parentheses are the number of radio-tagged birds.

Species and season		Observation time (days)	Length of stay (days)	95% CL (days)
Pectoral Sandpiper				
Spring	(*n* = 37)	8.2	10.5	6.9–16.2
Early	(*n* = 17)	11.9	23.0	13.2–39.0
Late	(*n* = 20)	4.9	6.8	5.1–9.2
Fall	(*n* = 38)	3.9	4.9	3.4–7.2
Least Sandpiper				
Spring	(*n* = 37)	7.2	9.7	7.2–13.1
Early	(*n* = 18)	10.6	21.1	12.6–35.0
Late	(*n* = 19)	3.9	6.3	4.4–9.0
Fall	(*n* = 39)	3.4	3.6	2.6–5.0
Combined				
Spring	(*n* = 74)	7.7	10.0	7.1–12.7
Early	(*n* = 35)	11.2	21.6	15.0–31.3
Late	(*n* = 39)	4.1	6.8	5.9–8.1
Fall	(*n* = 77)	3.7	4.0	3.1–5.1

substantially higher than fall numbers in all years (Table 6). Generally, spring numbers were approximately five times (range = 3.5–8.5) higher than fall numbers, which paralleled seasonal differences in habitat availability in the greater Squaw Creek ecosystem. The relatively low spring numbers in 2003 were a response to the lack of habitat on the refuge in that year; 2003 was one of the two driest years on the Refuge in the last two decades (R. Bell, Squaw Creek National Wildlife Refuge, pers. comm.).

We used two methods to estimate spring numbers, which differed based on how length of stay was calculated (Table 6). The first method used the mean value of length of stay (equation 3), which generally produced a lower estimate. In the second approach, bird-days (*bd*) were computed (equation 2) for both an early and a late period, defined by the median capture date of April 29. Each of these estimates was then divided by the estimated length of stay for the early (<29 April) or late (≥29 April) period and the results were added to get the total. Population estimates based on this latter method were higher, mainly because the temporal distribution of shorebirds was skewed—a majority of shorebirds arrived during the late period, which was associated with a shorter length of stay (Table 5).

DISCUSSION

Our estimates of shorebird numbers for Squaw Creek National Wildlife Refuge are substantially higher than what would be derived using peak counts or other methods that do not properly account for detectability, sampled proportion of available habitat, and turnover rates. During the study years, peak daily counts in spring (5123 in 2002, 1633 in 2003, and 8065 in 2004) averaged only 12% of the calculated spring totals each year. Peak fall counts (521 in 2001, 378 in 2002, 145 in 2003, and 201 in 2004) averaged only 4% of the estimated fall totals. The lower percentage represented by peak counts in fall is due to the shorter length of stay, and hence a higher turnover rate, during this time period.

Simply adding successive survey counts to obtain total seasonal numbers gives 28 789 birds in spring 2002 and 19 611 birds in spring 2004, although more shorebirds actually stopped at the Refuge during spring 2004. The misleading sum of survey counts reflects the higher frequency of surveys in 2002: every three days on average in spring 2003, compared to every six days in spring 2004. It is difficult to plan and maintain a fixed interval of time between successive counts due to weather and other unpredictable factors, and sometimes it

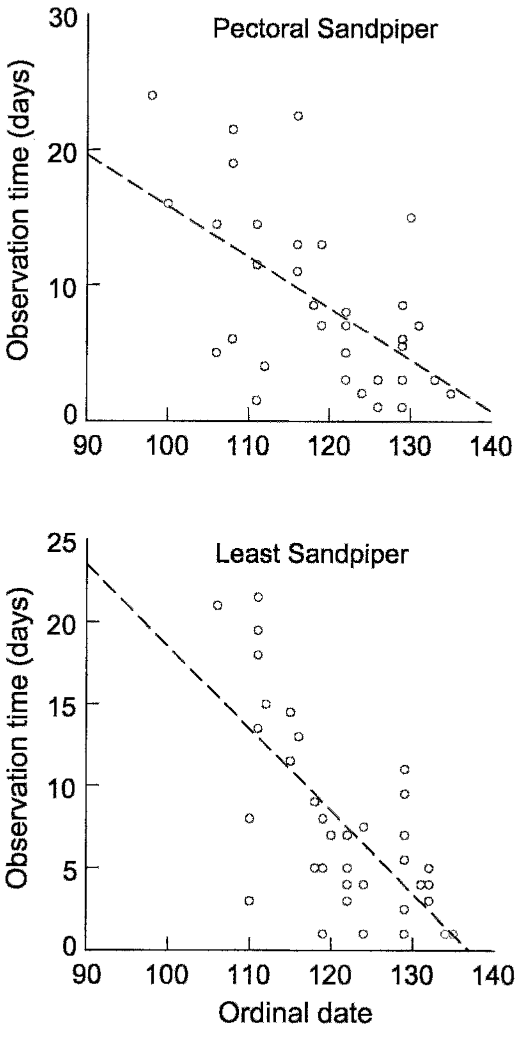

FIGURE 3. Length of spring observation times vs. capture date for Pectoral and Least Sandpipers at the Squaw Creek National Wildlife Refuge, Missouri, 2003 and 2004. Shorebirds arriving at the Refuge earlier stayed longer than those arriving later. Ordinal date 90 = 31 March and ordinal date 140 = 20 May.

may even be desirable to conduct counts more frequently than originally planned. Therefore, integrating the survey counts through time rather than simply adding successive counts is a more robust approach for producing comparable totals.

However, even if successive counts were integrated over the season, but not adjusted for detectability or sampled proportion of wetlands, the resulting spring totals would average only 21% of the estimated spring numbers. The fall totals, computed similarly without taking into account detectability and sampled proportion, would average only 31% of the estimated fall numbers. Hence, ignoring detectability and sampled proportion of suitable habitat introduces significant bias. The fall bias was lower, likely due to the higher relative abundance of fall birds in smaller (with higher sampled proportion), more open (i.e., less vegetation cover) wetland units in the fall.

The combined effect of detectability and sampled proportion of wetlands on population estimates was significant, but the two parameters were not equal in their effect. Detectability was more than three times as important as sampled proportion for obtaining accurate population estimates at the Refuge. For instance, our estimate of the spring 2004 population was 62 000 shorebirds. Ignoring detectability and sampled proportion would have yielded an alternative estimate of 11 700 shorebirds. Of the difference between these two estimates (62 000 − 11 700 = 50 300), 76% (38 228 birds) was due to detectability and 24% (12 072 birds) was due to sampled proportion. These relative effects of detectability and sampled proportion on obtaining accurate population estimates are specific to the Refuge and cannot be assumed to apply to other sites that may have a different mix of shorebird species or wetland conditions.

Given the importance of detectability, the ideal approach would be to double sample and estimate detectability for every wetland unit, thereby avoiding the necessity of using vegetation classes as we did. This may not always be feasible, however, as was the case in our study. Our survey protocols minimized the effects of observer and environmental variability, and we believe that detectability varied among units as a function of observation distance (related to wetland size) and vegetation cover. However, the wetland units on the Refuge are similar; they are small, roughly the same size, and have good access from dikes on one or more sides. Hence, we believe that vegetation cover probably had the most influence on the detectability estimates.

Vegetation was patchily distributed in all sampled wetland units, as evidenced by the relatively high standard deviation for visual obstruction and canopy cover measurements.

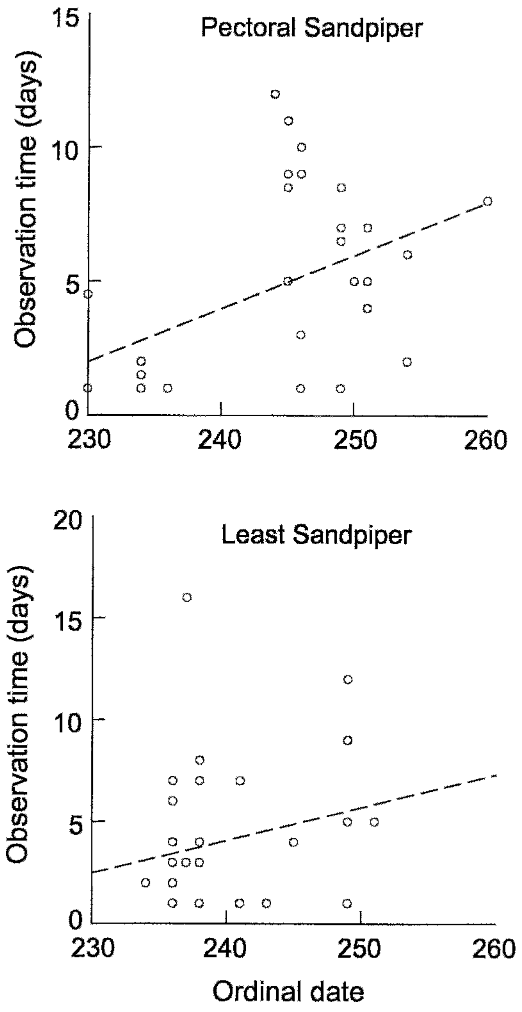

FIGURE 4. Length of fall observation times vs. capture date for Pectoral and Least Sandpipers at the Squaw Creek National Wildlife Refuge, Missouri, 2003 and 2004. There is some indication that later-arriving birds stay longer, but this is not a significant trend. Ordinal date 230 = 18 August and ordinal date 260 = 17 September.

In spite of the combination of high variation and our small sample size, however, two patterns emerged from these vegetation data. Canopy cover was significantly different between the light and moderate classes, and visual obstruction differed significantly between the moderate and heavy classes. Thus, at low levels (<15% cover) of vegetation abundance on the Refuge, canopy cover was the most important determinant of detectability, but at higher levels of vegetation abundance (>15% cover), vegetation height and vertical structure became an increasingly important determinant of detectability. These specific numerical results for vegetation measurements probably do not apply outside the Refuge, but it seems likely that both canopy cover and height are important to consider when using vegetation abundance to classify wetland units with respect to detectability.

Detectability estimates from the springs of 2003 and 2004 were used to calculate the spring 2002 and fall populations for all years. This is a potential source of error because vegetation conditions vary annually and seasonally on the Refuge depending on changing water conditions and management activities. However, the spring habitat conditions in 2002 were very similar to those in 2004, especially on the units that had the highest shorebird counts. One exception was Pelican Pool, which was drained and had substantial shorebird use in 2002 (sampled proportion was modified for that year and vegetation cover was assumed to be "light" in all years). With respect to vegetation growth, detectability should have been lower in all wetland units in the fall period. However, other factors (e.g., changing water levels and management) also affect fall vegetation conditions in suitable portions of wetland units. We believe that the spring detectability estimates fairly represented fall conditions, but if there was error associated with this assumption, we likely overestimated detectability and underestimated shorebird numbers in fall.

Our estimates of shorebird numbers for the Squaw Creek National Wildlife Refuge assume that length of stay estimates for Pectoral and Least Sandpipers are representative of length of stay for all species. Length of stay has not been estimated for most of the other species that occur at the Refuge. Skagen and Knopf (1994) reported observation times for two study years for White-rumped (7.0 days in both years) and Semipalmated Sandpipers (3.4 and 9.7 days; average = 6.7 days), and these values are similar to the observation times that we measured in the spring for Least and Pectoral Sandpipers. Hence, we believe that the lengths of stay for White-rumped and Semipalmated Sandpipers are similar to the values reported herein. Furthermore, Pectoral, Least, White-rumped, and Semipalmated Sandpipers com-

TABLE 6. Spring, fall, and total shorebird population estimates for Squaw Creek National Wildlife Refuge, Missouri, by year. Length of stay was estimated two ways: 1) by pooling all birds for the season ("season mean"), and 2) by splitting ("split") the spring into early (<29 April) and late (≥29 April) periods, making separate estimates, and then summing the estimates for both periods. Bird-days were computed by integrating survey counts over the time between the first and last surveys. The "estimated population" column is a point estimate based on mean values for detectability and length of stay. The 95% CL (confidence limits) are the 2.5% and 97.5% quantiles of 10 000 simulations, rounded to the nearest 10 birds. Yearly totals are the sum of spring (season mean) and fall estimates.

Year and season	Length of stay	Bird-days	Estimated population	95% CL
2001				
Fall	Season mean	27 936	6984	5320–8800
2002				
Spring	Season mean	572 872	57 170	39 920–74 690
	Split		64 420	49 460–79 470
	Early	196 194		
	Late	376 678		
Fall	Season mean	49 603	12 400	9440–15 640
Total			69 570	49 360–90 330
2003				
Spring	Season mean	122 481	12 250	8450–15 950
	Split		15 230	11 800–18 670
	Early	27 420		
	Late	95 061		
Fall	Season mean	13 939	3484	2650–4400
Total			15 734	11 100–20 350
2004				
Spring	Season mean	620 672	62 000	43 130–81 390
	Split		78 410	60 600–95 900
	Early	128 286		
	Late	492 386		
Fall	Season mean	29 109	7277	5520–9190
Total			69 277	48 650–90 580

prised about half (49%) of all individual shorebirds counted in this study. The remaining 51% of shorebirds, however, included species from different families, with different social systems and migration distances. On that basis alone one might expect some differences in lengths of stay, although Pectoral and Least Sandpipers vary with regard to some of these factors yet have a similar length of stay at the Refuge. Although no data are available, we can explore the possible consequences of an error in the assumption about length of stay. The effect of an error in the length of stay for the other 51% of individuals would vary among years and between seasons, but generally the higher spring population estimates are not particularly sensitive to this value. For instance, the spring 2004 estimates would vary by about 3500 individuals per day of error in the length of stay. If the other 51% of shorebirds had a length of stay of 8.0 days (rather than the assumed 10.0 days), the point estimate would be approximately 69 150 (rather than 62 000).

An additional factor that may have biased our estimates of length of stay is the effect of capture and handling time. Warnock and Bishop (1997) found that the length of stay of Western Sandpipers (*Calidris mauri*) was significantly longer at the site of capture compared to individuals that had been previously radio-tagged elsewhere. Although we have no data to shed light on the possible magnitude of this effect in our study, such a bias would mean that our length of stay estimates were too long and consequently the number of shorebirds was really higher than our estimates.

Our estimates of shorebird numbers are based on parameter estimates, the values of which are dependent on the specific habitat conditions and shorebird species assemblage found on Squaw Creek National Wildlife Refuge. We would not expect our values of detectability to apply, for example, to surveys conducted along coastal beaches. Nevertheless, the Refuge is not unlike many other wetland complexes in the midcontinent of North America with respect to both habitat conditions and the mix of shorebird species. Moreover, we believe that the approach we used is broadly applicable to other stopover sites. In some cases it might be necessary to modify specific techniques to fit a new situation; for example, it might be difficult to perform flush counts and more feasible to estimate detectability using other techniques such as double observer methods (Nichols et al. 2000).

Our results demonstrate that shorebird surveys conducted without adjustment for detectability, sampled proportion of suitable habitat, and other factors can significantly underestimate the number of shorebirds using stopover sites in this important shorebird region. Depending on one's objectives for conducting a shorebird survey, it may be desirable to invest the additional resources needed to estimate detectability, sampled proportion of suitable habitat, and length of stay to obtain a more accurate estimate of total numbers.

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