



STAGING BEHAVIOR IN RED KNOT (*CALIDRIS CANUTUS*) IN DELAWARE BAY: IMPLICATIONS FOR MONITORING MASS AND POPULATION SIZE

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ABSTRACT.—Many migratory birds use staging sites to gain essential resources to fuel their ongoing migration. Understanding staging strategies reveals much about migration systems and is essential if one is concerned with monitoring population trends and mass gains, two of the principal methods for assessing the “health” of a migratory population. In spring 2004, we investigated the staging behavior in Delaware Bay of Red Knot (*Calidris canutus*) using mark–recapture techniques and resightings of birds marked in the preceding spring. Individuals staged for 11–12 days, which declined to 8–10 days late in the season. Arrivals were asynchronous, but departures tended to be synchronized. A simple sensitivity analysis showed that the mark–recapture analysis estimated length of stay to within +10% and confirmed biases in monitoring trends and mass gains using peak counts and mass-on-date regressions. Alternative methods using staging duration to estimate passage population size and mass gains were shown to be unbiased. Using these methods, we estimated a passage population size in 2004 of 18,000 Red Knot that arrived at an average mass of 111 g and, on average, gained mass at 7.2 g day^{−1}. Thus, in 2004, the passage population was substantially smaller than the recent peak count of 50,360 in 1998, which confirms a significant decline in the number of Red Knot staging in Delaware Bay. Use of refined techniques such as these is essential if management decisions such as those in Delaware Bay are to be based on firm scientific advice. *Received 24 November 2006, accepted 17 June 2008.*

Key words: *Calidris canutus*, Delaware Bay, mark–recapture models, mass gain, passage population size, Red Knot, staging ecology, turnover.

Comportamiento Migratorio en Etapas de *Calidris canutus* en la Bahía Delaware: Implicancias para el Monitoreo del Peso y el Tamaño Poblacional

RESUMEN.—Muchas aves migratorias usan sitios de parada para adquirir recursos energéticos esenciales a lo largo de sus rutas migratorias. El entendimiento de esta estrategia de migración en etapas, revela mucho sobre el sistema de migración y es esencial para monitorear las tendencias poblacionales y los aumentos en el peso corporal, dos de los principales métodos utilizados para determinar la “salud” de una población migratoria. En la primavera de 2004, investigamos el comportamiento migratorio en etapas de *Calidris*

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canutus, utilizando técnicas de marcado y recaptura y de avistamiento repetido de aves marcadas durante la primavera anterior. Los individuos pararon por 11–12 días, tiempo que disminuyó a 8–10 días durante la etapa más tardía de la época migratoria. Las llegadas fueron asincrónicas, pero las partidas tendieron a estar sincronizadas. Un análisis simple de sensibilidad mostró que el método de marcado y recaptura estimó el tiempo de parada dentro de +10% y confirmó los sesgos en las tendencias de monitoreo y aumento de peso que utilizan picos de conteo y regresiones entre la fecha y el peso corporal. Los métodos alternativos que utilizan la duración de la parada para estimar el tamaño de la población de paso y las ganancias en peso no presentaron sesgos. Utilizando estos métodos, estimamos que el tamaño de la población de paso en 2004 fue de 18,000 individuos que llegaron con un peso promedio de 111 g y que en promedio ganaron peso a una tasa de 7.2 g día⁻¹. Así, en 2004 la población de paso fue substancialmente menor que la del pico de conteo reciente de 50,360 individuos en 1998, lo que confirma una disminución significativa en el número de individuos de *C. canutus* que paran en la Bahía Delaware. El uso de estas técnicas refinadas es esencial si se espera que las decisiones de manejo, como las tomadas en la Bahía Delaware, tengan una base científica sólida.

MIGRATION PUTS GREAT demands on birds, and many long-distance migrants must pause at highly productive passage sites to acquire sufficient energy reserves to complete their migration. Such sites can be of critical importance to the ongoing survival or likelihood of successful breeding of individuals (Sandberg and Moore 1996, Ydenberg et al. 2002, Bêty et al. 2003, Baker et al. 2004). This is especially true for Arctic-breeding species, for which prompt arrival in the Arctic is crucial for successful breeding in the short summer. Understanding strategies of arrival, residency, and departure at passage sites is of considerable interest when understanding the migration process and its population consequences. Moreover, because deterioration or loss of passage sites can have severe population-level consequences (Dolman and Sutherland 1995, Piersma and Baker 2000), understanding strategies of use of passage sites is of considerable applied importance.

Worldwide, many passage sites are threatened in one way or another (Davidson et al. 1991, International Wader Study Group 2003), and ongoing monitoring is required. Two of the principal methods used to assess the “health” of populations of migratory birds are trends in counts and rates of mass gain (Madsen and Mortensen 1987, Baker et al. 2004, Skagen 2006, Atkinson et al. 2007). Assessing biases in these approaches is essential if conservation action is to be both scientifically grounded and likely to succeed, yet both these measures may be affected by migration strategies. Clearly, peak counts will underestimate the total passage population if there is a high degree of turnover (Moser and Carrier 1983, Kersten and Smit 1984, Spiekman 1990), but trends in migration strategies have the potential to mask or exaggerate true population trends. Likewise, rates of mass gain are not immune from variation in migration strategies. Plots of average body mass against capture date underestimate true mass gains if individuals arrive at different times (Zwarts et al. 1990). Similarly, mass changes in individuals retrapped within the season are problematic, because the likelihood of recapture increases with length of stay, and long-staying individuals may employ different mass-gain strategies than short-staying individuals (Winker et al. 1992). Therefore, proper interpretation of counts and mass-gain rates requires an understanding of migration strategies and, in particular, turnover, arrival synchrony, and duration of stay.

Delaware Bay is one of the most important spring passage sites for shorebirds in the western Atlantic flyway, supporting an estimated 1 million shorebirds each spring as they feed on the eggs of Horseshoe Crabs (*Limulus polyphemus*) (Harrington 1996, Castro and Myers 1993). Concurrent commercial exploitation of the crabs (Odell et al. 2005, Whitmore and Cole 2005) and marked declines in Red Knot (*Calidris canutus rufa*) (Baker et al. 2004,

2005; Morrison et al. 2004; Niles et al. 2007) have led to intense scrutiny of counts and mass gains in an attempt to identify causes and possible remedies of the shorebird declines. However, basic migration parameters such as length of stay in Delaware Bay are poorly known, making the assessments described above difficult. We used resightings of individually marked Red Knot to estimate length of stay and assess the degree to which turnover affects estimates of passage population size and rate of mass gain. We also aimed to provide general advice for monitoring of passage populations.

METHODS

Field Methods

During May–June 2003, 1,385 Red Knot were captured and fitted with plastic flags bearing an alphanumeric code allowing individual recognition in the field (see Clark et al. 2005). In May–June 2004, teams of observers scanned flocks of Red Knot within Delaware Bay for these flagged individuals. Flocks form on a relatively small number of bay beaches, which enables a large proportion of the population to be checked for flags and generates high resighting rates. Nearly complete coverage of the bay was achieved approximately every two days. About every five days, samples of Red Knot were caught, weighed, and released; every seven days, an aerial survey provided bay-wide estimates of the numbers present.

Analysis of Field Data

Mark–recapture analysis of staging duration.—The time elapsed between the first and last sightings of an individual provides a crude estimate of length of stay; mark–recapture methods that estimate and account for the probability of resighting are more informative (Kaiser 1999, Schaub et al. 2001). In this context, arrival and departure from a passage site are analogous to recruitment into and mortality from the local population. Once these rates have been estimated, it is possible to calculate the length of time individuals have been present before resighting and the length of time they will remain after resighting; the sum of these is the estimated duration of stay at the passage site. Although calculation of these rates is possible in standard mark–recapture programs such as MARK (White and Burnham 1999), the precision of the estimates cannot be determined because the covariance between arrival and departure probabilities is nonzero and unknown (Schaub et al. 2001). The program SODA (Stop Over Duration Analysis, version 1; Schaub et al. 2001) solves this problem by bootstrapping the resighting history. However, SODA does not perform model

selection. Therefore, it is necessary to use both programs, first applying MARK to determine the appropriate model for arrival and departure processes, then running these in SODA to obtain estimates of stopover duration with measures of variation. Observations indicate that birds probably arrive in groups and stay for similar periods, which makes the use of the SODA methods more appropriate than, for example, those of Efford (2005). However, we used a sensitivity analysis to consider potential biases in the SODA methods (see below).

Resighting data from 2004 were summarized into a resighting history and were analyzed with Pradel recruitment and survival models in MARK, version 4.1 (White and Burnham 1999). A very small number of marked individuals from 2003 were captured, but these encounters were not used in compiling the resighting history so as to maintain uniform reporting. Throughout, we use the following model notation: survival [S], reporting [p], recruitment rates [f]; we tested eight basic model structures with each parameter being either constant [subscript c] or time-dependent [subscript t]. Models were overdispersed, so \hat{c} was estimated from survival-only models by bootstrapping and used to scale Pradel models. The best model was selected on the basis of the quasi-Akaike's information criterion (qAIC; Burnham and Anderson 1998) and then used in SODA. Because there was potentially large variation in arrival and departure patterns, we computed 1,000 bootstrapped estimates of staging parameters in SODA. For each observation period, SODA produces an estimate of the length of time birds present on that day have been present, how long they will remain, and, by summation, how long those individuals will stay. It thus provides a way of tracking the daily shifts in staging behavior of the individuals present.

Rates of mass gain in 2004.—Using least-squares regression, we fitted the following linear relationship between date of capture (t , in days) and mass (m , in grams) of the i^{th} bird caught on date t :

$$m_{it} = s_{\text{DATE}} \cdot t + c_{\text{DATE}} + \varepsilon_{it} \quad (1)$$

Coefficient s_{DATE} has been used as an estimate of the daily rate of mass gain. However, this method (hereafter called “the date method”) is a biased estimator of an individual's rate of mass gain, because s_{DATE} is influenced by both the mass gain of individuals already present and the introduction into the population of new arrivals with low mass (Zwarts et al. 1990). The constant c_{DATE} has no biological meaning. An intuitively more appropriate method is to ascertain the slope of the relationship between body mass and residence time (t' , in days since arrival):

$$m_{it'} = s_{\text{TIME}} \cdot t' + c_{\text{TIME}} + \varepsilon_{it'} \quad (2)$$

where t' is derived from the SODA estimates of time since arrival. Because both mass and time since arrival are calculated across the whole population present at any given time, s_{TIME} should provide an estimate of the rate of mass gain that is not biased by asynchronous arrival. Additionally, the constant c_{TIME} provides an estimate of mass upon arrival. We apply this method (hereafter called “the time method”) and the date method to capture data from 2004 and SODA estimates of time since arrival. Results are presented as means \pm SE.

Passage population size in 2004.—Bishop et al. (2000) provided the following equation for estimating the total passage

population (\hat{N}) from the total number of birds on day i (\hat{W}_i), the detection probability (D), and the estimated stopover duration (L , in days):

$$\hat{N} = \frac{\sum_{i=1}^n \hat{W}_i}{D \cdot L} \quad (3)$$

In their study, in which length of stay averaged two to three days, they estimated that 10% of individuals stayed for less than one day and were missed by shorebird counts, giving $D = 0.9$. Given the significantly longer staging period of Red Knot in Delaware Bay, it is unlikely that an individual will arrive and leave between counts. In this context, $D = 1$ and the method simplifies to that of Frederiksen et al. (2001), though there could be other sources of error to cause $D < 1$.

Bishop et al. (2000) assumed that \hat{W}_i and L are independent. In our situation, SODA produces daily estimates of stopover duration, L_i . Under certain situations, it may be inappropriate to simply average the L_i across days to obtain L to insert into Equation 3. For example, in the simple case of one arrival cohort with right-skewed stopover duration, the individuals present in the last few days of the passage period will have the longest stopover duration. A value of L derived by averaging L_i across days would produce a biased estimate of mean stopover duration for the population and would lead to an underestimation of passage population size. Taking an average of L_i weighted by the number of birds present on day i should reduce this problem. We evaluate this by comparing passage population size estimates calculated with unadjusted and weighted mean stopover-duration estimates.

Linear interpolation was used to convert weekly aerial counts into daily estimates of local population size. These and estimates of staging duration from SODA were analyzed according to the standard Bishop et al. (2000) method, and our weighted version, to provide estimates of the total number of Red Knot passing through Delaware Bay in 2004.

Sensitivity Analysis

The analyses described above provide only a snapshot of the extent to which variation in migration strategy affected results in 2004. To aid in the interpretation of previous results, and to evaluate the need for caution in future studies, we performed a simple sensitivity analysis of the effects of variation in arrival synchrony on stopover duration estimates and methods of estimating passage population size and rates of mass gain. The sensitivity analysis was based on a stochastic model population of birds with date and mass values drawn from normal distributions and marking, capture, and resighting based on binomial probabilities. The stochastic model assumes that birds spend similar amounts of time at the stopover site, allowing us to consider how violating the SODA assumption that departure probability is independent of time affects the accuracy of SODA results. All parameters were based on published information, knowledge of the system, or results from the present study (Table 1). Six scenarios of increasingly asynchronous arrival were generated by allocating individuals randomly to one of five arrival groups (Table 1). The mean arrival date across the whole population was constant (day 18), but the frequency distribution of arrival dates shifted from unimodality to bimodality. The model was structured with individuals arriving at 0001 hours, being resighted at 1200 hours, and departing at 2359 hours.

TABLE 1. Model variables and parameters for the sensitivity analysis. For arrival date, the six scenarios show increasing asynchrony. Arrival is centered around five days, with the proportion of the population arriving on each varying among scenarios.

Variable	Value
Total passage population	24,000
Percentage of population marked	7.0
Daily probability of resighting	0.15 ^a
Staging duration, days (mean, variance)	12.5, 2.0 ^b
Arrival mass, g (mean, variance)	112.0, 16.0 ^c
Linear rate of mass gain, g day ⁻¹ (mean, variance)	4.5, 1.0 ^c
Arrival date (day [frequency]), (variance = 2)	
Scenario 1	10 (0), 14 (0), 18 (100), 22 (0), 26 (0)
Scenario 2	10 (0), 14 (25), 18 (50), 22 (25), 26 (0)
Scenario 3	10 (11), 14 (22), 18, (33), 22 (22), 26 (11)
Scenario 4	10 (14), 14 (29), 18, (14), 22 (29), 26 (14)
Scenario 5	10 (25), 14 (25), 18, (0), 22 (25), 26 (25)
Scenario 6	10 (50), 14 (0), 18 (0), 22 (0), 26 (50)

^aResults give the two-day resighting probability as 0.27, from which daily probability is calculated.

^bSee results.

^cSource: Robinson et al. 2003.

Resighting histories were created for the period between the first and last days that marked birds were resighted. On day 5 and each fifth day thereafter, a catch of ≤ 100 individuals was simulated. The model was run 50 times for each arrival scenario. Data from each run of each scenario were analyzed in the same way as the 2004 data, and the results were compared with the initial model parameters.

RESULTS

Of the 1,385 Red Knot individually flagged in 2003, 573 (41%) were resighted at least once in Delaware Bay in May–June 2004. Up to 116 marked individuals were seen per day (Fig. 1), and over the course of the season 1,326 individual resightings were made (i.e., each marked individual was seen, on average, 2.3 times). On those days when at least one marked individual was seen, $\geq 29\%$ had not been seen on an earlier day. Fifty percent of marked individuals were resighted on only one day; for the remaining 287 individuals that were seen on multiple days, the minimum apparent staging duration (time between first and last days seen) ranged from 2 to 30 days (mean = 7.1 days).

Mark-recapture analysis of staging duration.—Because all sites were checked only every two days, resighting data were summarized into 16 two-day recording periods, from 10–11 May to 9–10 June 2004. The initial analysis in MARK (Table 2) found that the best-fitting model had time-dependent survival and recruitment with a constant reporting rate of 0.27 ± 0.03 (95% confidence interval [CI]: 0.22–0.34). This model was applied in SODA to derive estimates of staging parameters (Fig. 2). Estimates for the first and last three periods are based on extremely small samples of

TABLE 2. Results of fitting Pradel survival and recruitment models to resightings of Red Knot in Delaware Bay in 2004 in the program MARK. Notation: S = survival, p = reporting rate, f = recruitment rate, and subscripts c and t indicate constant or time-dependent parameters. $qAIC_c$ = quasi-Akaike's information criterion corrected for small sample size, $\Delta qAIC_c$ = change in $qAIC_c$ between models, and $qDeviance$ = quasi-deviance. Models are scaled with $\hat{c} = 3.953$.

Model	$qAIC_c$	$\Delta qAIC_c$	Number of parameters	$qDeviance$
$S_t p_c f_t$	1,339.5	0.0	19	101.1
$S_t p_t f_c$	1,348.4	8.9	25	97.5
$S_c p_t f_t$	1,353.0	14.4	24	105.1
$S_t p_t f_t$	1,358.8	19.3	31	95.1
$S_t p_c f_c$	1,374.3	34.8	13	148.3
$S_c p_c f_t$	1,376.9	37.5	12	153.0
$S_c p_t f_c$	1,406.2	66.7	17	171.9
$S_c p_c f_c$	1,449.3	109.8	3	243.7

resighted birds ($n < 10$) and should be interpreted with caution. Otherwise, total staging duration was in the range 11–12 days for much of May and declined in late May–early June to 8–10 days. There were concurrent trends in time since arrival and time to departure: between 12–13 and 26–27 May, time since arrival increased in a near-linear fashion (Fig. 2B) at a rate of 0.6 day day⁻¹, indicative of $\sim 20\%$ new arrivals per day throughout this period. On 28–29 May, the marked decrease in time since arrival and increase in time to departure suggest a major turnover of the local population. Precision of staging estimates from SODA varied throughout the season because of insufficient resightings, heterogeneity in the behavior of the individuals encountered, or both.

Rates of mass gain in 2004.—In spring 2004, 1,240 Red Knot were captured and weighed. The date method gave a significant positive relationship between catch date and body mass ($F = 539.9$, $df = 1$ and 1,238, $P < 0.0001$, $R^2 = 0.30$) giving $\hat{s}_{DATE} = 2.7 \pm 0.1$ g day⁻¹ (Fig. 3A). The time method gave a significant positive

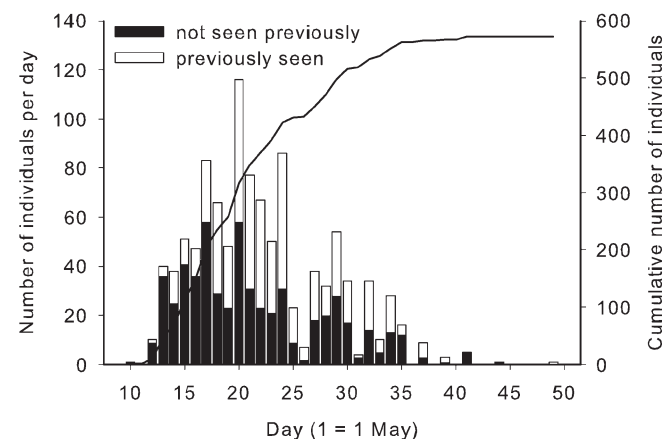


FIG. 1. Daily pattern of the number of individually marked Red Knot resighted in Delaware Bay in May–June 2004. The number is split into those already seen on a previous day (black bars) and those not seen previously (white bars). The cumulative number of individuals seen is also shown (line).

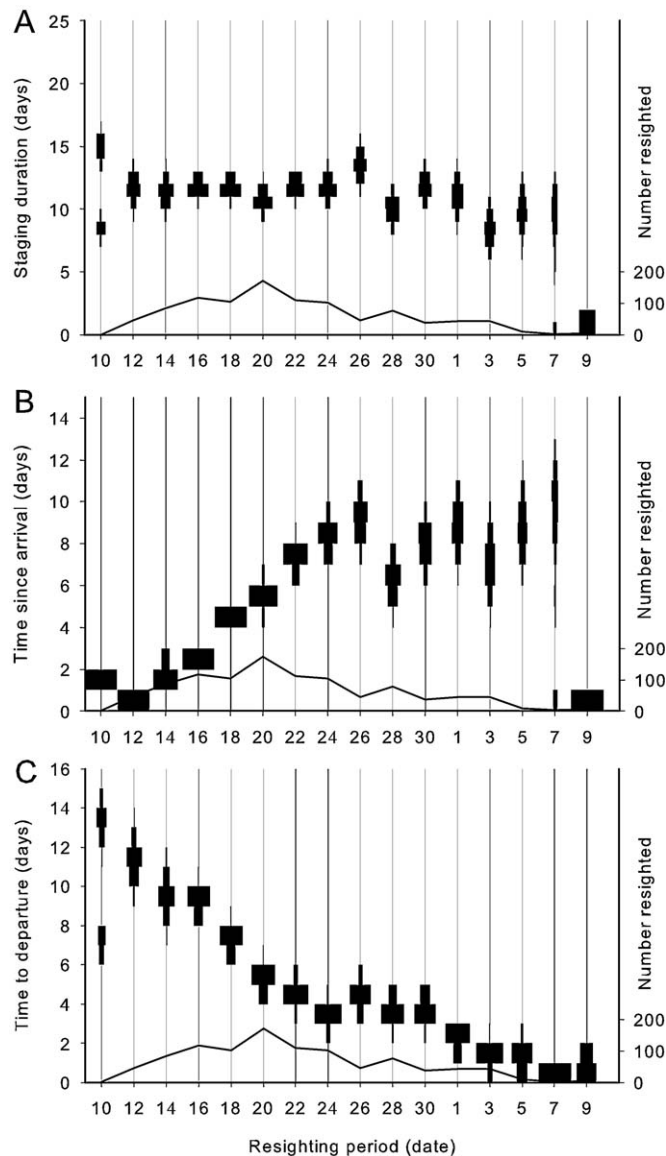


FIG. 2. Mark-recapture estimates of (A) total time staging, (B) time since arrival, and (C) time to departure of individually marked Red Knot resighted during two-day periods in Delaware Bay in May–June 2004. Each kite diagram indicates the relative frequency distribution of the respective staging variable for any individuals resighted during that period (based on 1,000 resampled estimates from SODA). Also shown is the number of individuals resighted per day.

relationship between estimated time since arrival and body mass ($F = 666.4$, $df = 1$ and $1,238$, $P < 0.0001$, $R^2 = 0.35$), giving $\hat{s}_{\text{TIME}} = 7.2 \pm 0.3 \text{ g day}^{-1}$ and $\hat{c}_{\text{TIME}} = 111.1 \pm 1.8 \text{ g}$ (Fig. 3B).

Passage population size in 2004.—The peak aerial count of Red Knot in Delaware Bay in 2004 was 13,315 on 25 May, and birds were present from at least 12 May to 8 June, a period of 28 days. This is more than twice the estimated staging period and alone confirms that peak counts must underestimate passage population size. The standard method of Bishop et al. (2000) gave an

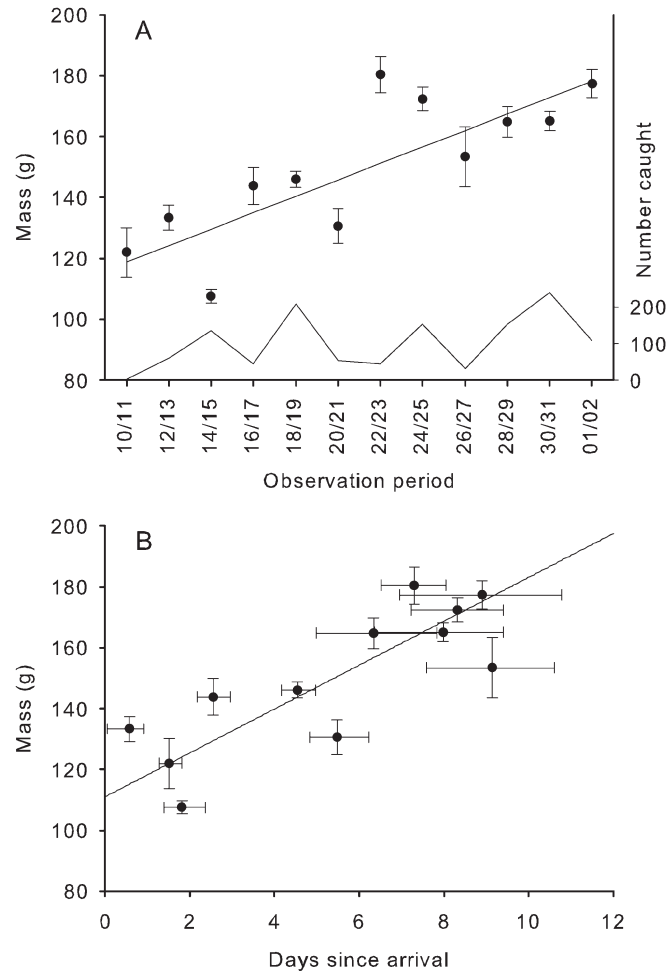


FIG. 3. A comparison of two methods of determining the rate of mass gain of Red Knot in 2004: (A) the date method and (B) the time method. Lines were fitted to raw data (see equations) and here, for reference, mean points ($\pm 95\%$ confidence interval) are given for each two-day period. In panel B, x-axis error bars (median $\pm 95\%$ percentiles of bootstrap estimates) are shown to indicate the precision with which time since arrival was estimated. Panel A shows the number of individuals caught and weighed per two-day period.

estimated passage population size of 17,931 individuals (95% CI: 12,973–22,889). The modified method using the weighted mean staging duration gave a slightly lower figure of 17,707 individuals (95% CI: 12,800–22,614). Both methods were $\geq 30\%$ higher than the peak count.

Sensitivity Analysis

The stochastic model generated realistic patterns of arrival and departure. Although many of the trends in stopover parameters are intuitive, the example outputs (Fig. 4) are informative in illustrating the magnitude of these trends, the influence of resighting effort, and the extent of biases. For example, in the absence of an underlying trend in staging duration, the apparent mean staging duration increased from 12.5 days to 17 days, an increase of 36%

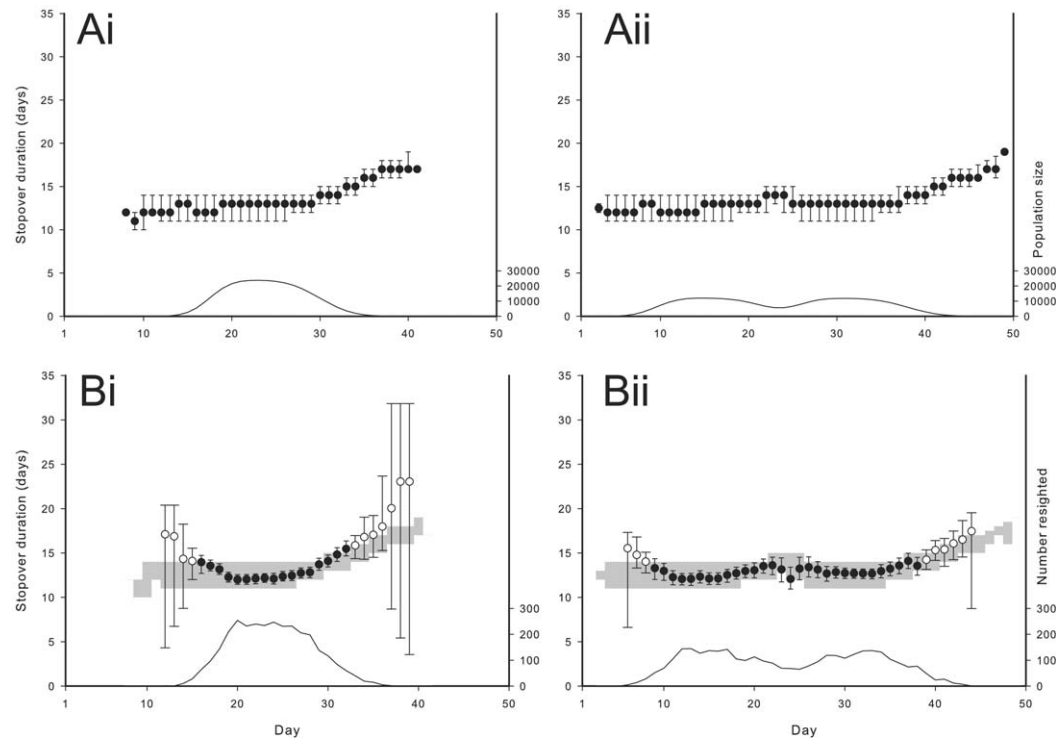


FIG. 4. Details and outputs from the sensitivity model for the extreme cases of (i) synchronous (scenario 1) and (ii) asynchronous (scenario 6) arrivals. (A) The trend (median and quartiles) in stopover duration for all individuals present (thin line) on each day, and (B) the SODA-estimated stopover duration (median and quartiles) based on resighted individuals (thin line). In panel B, open symbols show predictions for days when <50 individuals were resighted and gray shading indicates the interquartile range of model data.

(Fig. 4A), because of the departure of short-staying individuals. The SODA outputs (Fig. 4B) illustrate a general problem: parameter estimates were inaccurate and imprecise when based on few marked individuals. These periods were excluded for further consideration of the effects of arrival patterns on errors.

With increasing asynchrony, peak counts seriously underestimated passage population size (Table 3). Although the Bishop

method was not biased with respect to arrival patterns, it consistently underestimated population size. Using the weighted average staging duration reduced but did not eliminate this problem (Table 3). The date method underestimated mass gain by 30% even with the most synchronous arrival considered, and by ~70% where arrivals were asynchronous (Table 3). The time method performed better, but in some cases slope was still underestimated

TABLE 3. Sensitivity of various passage parameters to analytical methods and increasing variance in arrival patterns. Peak count and the four “Bishop” rows indicate the percentage by which different measures underestimated passage population size (superscripts M and S indicate calculations using the direct model values and the SODA estimates of staging duration, respectively; subscript WT indicates calculations using weighted mean staging duration, and \hat{S}_{DATE} , \hat{S}_{TIME} , and \hat{C}_{TIME} indicate the percentage accuracy by which the rate of mass gain and arrival mass were estimated). Figures are the median (quartiles in parentheses) calculated across all 50 model runs for each scenario.

Parameter	Arrival scenario					
	1	2	3	4	5	6
Arrival date SD	± 2.0	± 3.5	± 5.0	± 5.6	± 6.6	± 8.3
Peak count	−1.0 (−0.9, −1.1)	−9.6 (−9.3, −10.0)	−25.4 (−24.8, −25.9)	−32.1 (−31.5, −36.7)	−45.9 (−45.4, −46.5)	−50.3 (−49.8, −50.5)
Bishop ^M	−9.8 (−8.9, −10.6)	−8.2 (−7.7, −8.7)	−7.0 (−6.6, −7.4)	−7.0 (−6.2, −7.8)	−6.9 (−6.4, −7.5)	−7.4 (−6.8, −8.1)
Bishop ^S	−11.8 (−9.3, −14.8)	−13.8 (−10.7, −16.5)	−15.1 (−12.5, −17.6)	−13.6 (−9.5, −18.7)	−11.6 (−9.4, −13.7)	−7.8 (−5.3, −10.2)
Bishop ^M _{WT}	−2.5 (−2.5, −2.6)	−2.5 (−2.5, −2.6)	−2.6 (−2.5, −2.6)	−2.6 (−2.5, −2.6)	−2.5 (−2.5, −2.6)	−2.5 (−2.5, −2.6)
Bishop ^S _{WT}	−1.7 (−0.8, −3.2)	−3.3 (−2.3, −4.2)	−4.7 (−4.0, −6.0)	−5.1 (−3.9, −6.5)	−5.6 (−4.3, −6.7)	−2.9 (−1.4, −4.4)
\hat{S}_{DATE}	−30.3 (−28.2, −32.7)	−50.4 (−49.2, −51.4)	−62.7 (−61.7, −64.7)	−64.1 (−62.4, −65.9)	−67.4 (−65.8, −69.1)	−69.5 (−68.9, −71.6)
\hat{S}_{TIME}	−7.0 (−4.3, −11.0)	−7.5 (−4.5, −12.8)	−17.7 (−10.1, −23.7)	−15.1 (−10.0, −22.2)	−12.5 (−2.1, −16.9)	−0.3 (−5.7, 5.4)
\hat{C}_{TIME}	1.4 (0.6, 2.6)	0.2 (−1.0, 1.9)	2.6 (1.1, 4.2)	2.8 (1.0, 4.4)	1.8 (0.1, 3.2)	0.2 (−0.8, 2.1)

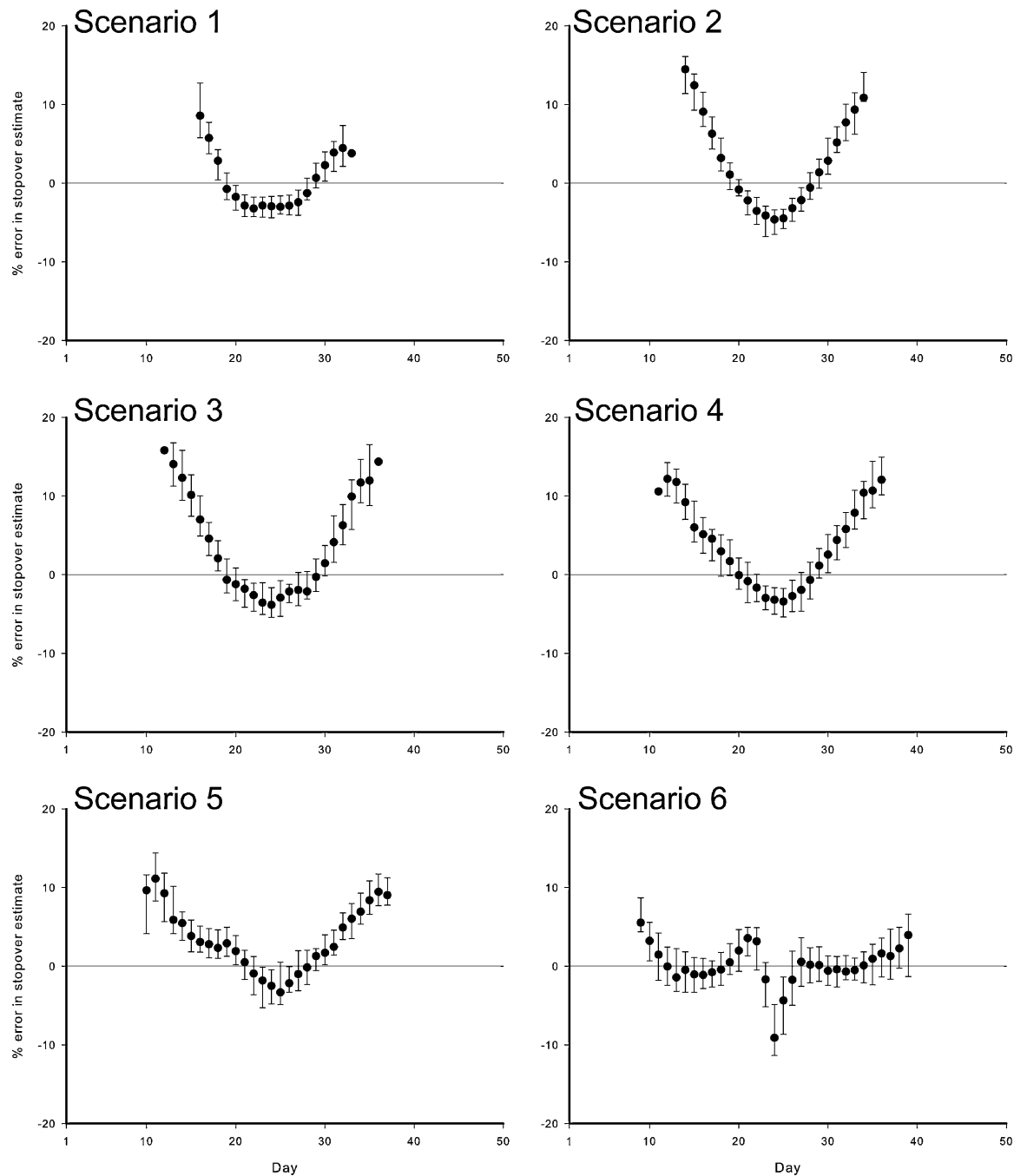


FIG. 5. Errors in SODA estimates of total stopover duration expressed as a percentage of the actual stopover duration of all individuals present on each day for six scenarios of increasingly asynchronous arrival. Points and bars indicate medians and quartiles calculated across the 50 runs for each arrival scenario. Days on which ≤ 50 individuals were resighted are omitted.

by $\leq 18\%$ (Table 3). These inaccuracies were likely caused by errors in estimates of time since arrival. Arrival mass was predicted well (Table 3). Figure 5 shows the temporal pattern of errors in total stopover duration estimates. Generally, in the middle of the passage periods, stopover duration was estimated well, but toward the beginning and end of the passage periods there was a tendency toward overestimation of $+10\%$, in this case $+1$ day.

This may explain the slight underestimation of the weighted average Bishop method. Closer examination of the SODA outputs showed this to be a result of overestimation of time since arrival at the end of the passage period and of time to departure at the beginning of the period. The overestimation of time since arrival also explains the tendency for a slightly lower-than-expected rate of mass gain.

DISCUSSION

Our main finding is that individual Red Knot spent, on average, 11–12 days during their spring staging in Delaware Bay in 2004. As with other studies that have employed mark–recapture techniques (Kaiser 1999, Schaub et al. 2001), this figure is longer than the 7.1-day average period between the first and last sightings of marked individuals. The sensitivity analysis suggests that we can be relatively confident in these results for the middle part of the season but that there could be errors of up to +10%, or +1 day, at the beginning and end of the passage period. The sensitivity analysis also confirms the serious underestimation and inherent bias in assessment of mass gain based on the date method. Under the scenarios tested here, the time method provided less-biased estimates of the rate of mass gain. Although some errors remain, these are not in the time method *per se* but in the estimates of time since arrival used in its calculation. We estimate that after arriving at a mass of 111.1 g, Red Knot gained mass at a rate of 7.2 g day⁻¹ in 2004. Further work is needed to validate this method and to investigate the influence of variation in mass gain through the season.

Staging duration, mass gain, and passage population size in 2004.—We estimate mean staging duration at 11–12 days, which compares well with results of two radiotelemetry studies in 2004. Eight birds, judged to be recent arrivals on the basis of mass, were fitted with radiotransmitters and located almost daily and remained, on average, for a further 12.5 days (range: 10–15 days; Delaware Division of Fish and Wildlife unpubl. data). Separately, 48 radiotagged individuals of varying body mass (mean = 137.8 g, range: 103.8–199.0 g) were detected for a further 12.4 days, on average (range: 2–22 days). These telemetry results may overestimate length of stay as a result of handling effects (e.g., Warnock and Bishop 1998, Warnock et al. 2004). On the other hand, they may underestimate length of stay if reporting rate is <1. However, most birds were registered almost daily, so there is likely little difference between the time between first and last registration and the actual staging duration.

There are various published estimates of length of stay across many shorebird species and locations, but findings are difficult to generalize, partly because of differences in study design. Direct estimates vary from short stopovers of one to three days by Dunlin (*C. alpina*) and Western Sandpipers (*C. mauri*) (Butler et al. 1987, Iverson et al. 1996, Warnock and Bishop 1998, Warnock et al. 2004), to 15 days by Sanderling (*C. alba*; Scott et al. 2004) to approximately 14–31 days in recaptured Dunlin (Goede et al. 1990). At least in the last case, the estimate may be biased because it relies on capturing each individual twice, which is more likely for longer-staying individuals (Winker et al. 1992). Two indirect estimates exist for Red Knot, based on an assessment of the length of stay required to gain sufficient body mass: individuals in Mauritania must stage for one month (Zwarts and Piersma 1990), and individuals in Australia for 57 days followed by 25 days in China (Battley et al. 2005). Such long periods are to be expected in more southerly locations, with staging becoming more compressed closer to the breeding grounds (Piersma et al. 2005). Staging duration is clearly highly variable and depends on geography, prevailing weather (especially wind conditions; Butler et al. 1997), arrival condition, and local food supply. Our estimates fall within this broad range, and the sensitivity analysis suggests that SODA

provides reliable estimates of stopover duration to within +10%. Nonetheless, there could be other sources of bias. For example, it is conceivable that the marked population resighted in 2004 could contain a disproportionate number of long-staying individuals, because long-staying individuals would have been present during more catching occasions than short-staying individuals in 2003.

Our estimates of arrival mass and mass gain correspond with other studies of Delaware Red Knot: captive individuals gained mass at 3–11 g day⁻¹ (Haramis et al. 2007), and between 1998 and 2005, the mean mass of newly arrived birds (those captured before 12 May) was 112 g (R. A. Robinson unpubl. data). This rate of mass gain is substantially higher than those published for other Red Knot populations (Piersma et al. 2005), perhaps partly because we have been able to account for turnover. Kvist and Lindström (2003) demonstrated that high rates of mass gain are common among shorebirds. Successfully gaining body mass during staging is critical, and a body mass of 180–200 g at departure enhances the probability of an individual being seen in a subsequent year (Baker et al. 2004). From an arrival mass of 111 g, and with 11 days of mass gain at 7.2 g day⁻¹, an individual can successfully reach 190 g. However, we also find that individuals arriving later stage for a shorter period and must, therefore, fatten more rapidly. Evidence from within-year retraps suggests that this is exactly what they do (Robinson et al. 2003, Atkinson et al. 2007), though there may be future costs associated with operating at such physiological extremes (Baker et al. 2004).

To manage a population in decline, such as *Calidris canutus rufa*, it is imperative to know with confidence the passage population size. For 2004, we estimate that ~18,000 passed through Delaware Bay. The true figure could be higher still, depending on the assumption of what proportion of the population is detected by counts and whether our estimates of staging duration are at all overestimated. Our figure is 30% higher than the peak count for 2004. In three published studies, total passage population size was two, three, and seven times the recorded peak count (Moser and Carrier 1983, Kersten and Smit 1984, and Spiekman 1990, respectively). Worldwide, >146 countries designate sites as Ramsar sites (under the Convention on Wetlands of International Importance) or Special Protection Areas (under the EC Directive 79/409 on the Conservation of Wild Birds) if a site regularly holds ≥1% of a waterbird's flyway population. Assessments of the degree of turnover are needed to determine the true importance of sites. The sensitivity analysis suggests that ≥50 individuals must be resighted per day if stopover estimates are to be reliable, but this is expensive and may be impractical for some species and sites. Fortunately, in Delaware Bay, the proximity at which shorebirds can be approached and the extent to which they are concentrated in a small number of sites permits unusually high resighting rates. Since 2004, resighting >100 individuals per day is common.

Arrival asynchrony.—Several pieces of evidence point to asynchronous arrival of Red Knot in Delaware Bay. First, our estimates of time since arrival only increase by ~0.6 day per observation day. If arrivals were synchronous, for each subsequent day time since arrival should increase by one day. That it does not indicates a gradual arrival of Red Knot each day. Second, changes through the season in the precision with which SODA estimated time since arrival may also be indicative of heterogeneity in behavior of resighted birds. The other explanation is variation in sample

size, but, at least during the middle part of the study period, the daily number of birds resighted was consistently high. In support of these results, field observations during mid- to late May, 2000–2007, found lean individual Red Knot within Delaware Bay (Atkinson et al. 2007), which indicates recent arrivals. Finally, frequency distributions of the mass of samples of captured birds are multimodal and indicate multiple arrivals (Robinson et al. 2003).

Whether asynchrony relates to sex differences, as in Western Sandpipers (Warnock and Bishop 1998, Bishop et al. 2004), is unknown. Asynchrony could arise because Red Knot staging in Delaware Bay come from at least three distinct molting–wintering locations (Atkinson et al. 2005, 2006) and one might expect strategies to vary among populations, given the different costs that individuals will experience en route to Delaware Bay. Since 2004, feather samples for molecular sexing and stable-isotope analysis have been taken from all uniquely marked individuals. In the future, it should be possible to separate effects of sex and wintering location on the pattern of staging.

Implications of asynchrony for monitoring.—The sensitivity analysis we performed is relatively simple, and though it is based on realistic population parameters for Delaware Bay, we considered only simple patterns of arrival. However, the results illustrate how biased different methods can be under even simple patterns of arrival. If arrival patterns are constant across years, figures such as peak counts and rates of mass gain derived by the date method might suffice as useful indices. But where there is potential for changes in arrival patterns, more robust methods such as the Bishop et al. (2000) method for estimating passage population size and our time method for estimating the rate of mass gain are needed. In Delaware Bay, there is variability in arrival synchrony between years (R. A. Robinson pers. comm.), which limits the usefulness of peak counts and the date method for monitoring purposes. Unfortunately, this is the first year for which staging duration estimates are available for Delaware Bay Red Knot, so it is not possible to correct census data from other years to derive a more accurate trend using passage population estimates. However, our passage population estimate for 2004 is substantially lower even than peak counts from the 1990s, which means that change in synchrony and length of stay cannot, alone, explain the unquestionable decline. The time method cannot be used retrospectively, which makes it difficult to assess trends in rates of mass gain without modeling (e.g., Atkinson et al. 2007).

There is still much to be learned concerning stopover ecology of migratory birds, and mark–recapture techniques such as those used here are powerful tools. They also provide valuable insights into the causes of population declines and aid in the formulation of management actions to reverse declines.

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