Red Knot Stopover Population Size and Migration Ecology at Delaware Bay, USA, 2023

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Abstract

Red Knots (Calidris canutus rufa) stop at Delaware Bay on the mid-Atlantic coast of North America during northward migration to feed on eggs of horseshoe crabs (Limulus polyphemus). We conducted a mark-recapture-resight investigation to estimate the passage population of Red Knots at Delaware Bay in 2023. We used a Bayesian analysis of a Jolly-Seber model, which accounts for turnover in the population and the probability of detection during surveys. The 2023 passage population size was estimated at 39,361 (95% credible interval: 33,724-47,556). Although there is broad overlap in the credible intervals for population estimates from 2020–2023, the population estimate for 2023 was below 40,000 birds for only the second time since 2011. Horseshoe crabs have been harvested for use as bait in eel (Anguilla rostrata) and whelk (Busycon) fisheries since at least 1990. In the late 1990s and early 2000s, the number of Red Knots counted during aerial surveys at Delaware Bay declined from ~50,000 to ~13,000 and some avian conservation biologists hypothesized that horseshoe crab harvest levels in the 1990s prevented sufficient refueling for successful migration to the Arctic breeding grounds, reproduction, and survival for the remainder of the annual cycle. Since 2013, the harvest of horseshoe crabs in the Delaware Bay region has been managed using an Adaptive Resource Management (ARM) framework. The objective of the ARM framework is to manage sustainable harvest of Delaware Bay horseshoe crabs while maintaining ecosystem integrity and supporting Red Knot recovery with adequate stopover habitat for Red Knots and other migrating shorebirds. For annual harvest recommendations, the ARM framework requires annual estimates of horseshoe crab population size and the Red Knot stopover population size. The 2023 population size estimate will inform harvest recommendations in the next management cycle for decision making by the Atlantic States Marine Fisheries Commission.

1. Introduction

Red Knots (*Calidris canutus rufa*) stop at Delaware Bay during northward migration to feed on eggs of horseshoe crabs (*Limulus polyphemus*). The northward migration of *C. c. rufa* coincides with the onset of spawning of L. polyphemus, whose eggs are an excellent food resource for a migrating Red Knots because they have a high energy content and are easily digestible (Karpanty et al. 2006, Haramis et al. 2007). Horseshoe crabs are thus an important food resource for Red Knots as well as other shorebirds at Delaware Bay.

Horseshoe crabs have been harvested since at least 1990 for use as bait in American eel (*Anguilla rostrata*) and whelk (*Busycon sp.*) fisheries (Kreamer and Michels 2009). In the 1990s and early 2000s the estimated number of Red Knots

Table 1. Dates for mark-resight survey periods (3-day sampling occasions) for Red Knots (*C. c. rufa*) at Delaware Bay in 2023. The same sampling periods have been used at Delaware Bay since 2011. Data from survey period 10 were not used in the 2023 analysis because the mark-resight data were sparse in this period.

Survey		Survey	
period	Dates	period	Dates
1	≤10 May	6	23-25 May
2	11-13 May	7	26-28 May
3	14-16 May	8	29-31 May
4	17-19 May	9	1-3 June
5	20-22 May	10	4-6 June

counted at Delaware Bay during aerial surveys declined from ~50,000 to ~13,000 (Niles et al. 2008). The number of horseshoe crabs harvested began to increease around 1990, peaked in the late 1990s, and then declined in the early 2000s. Avian conservation biologists hypothesized that unregulated harvest of horseshoe crabs from Delaware Bay in the 1990s prevented sufficient refueling during stopover for successful migration to the breeding grounds, nesting, and survival for the remainder of the annual cycle (Baker et al. 2004, McGowan et al. 2011).

The Atlantic States Marine Fisheries Commission (ASMFC) has managed the horseshoe crabs in the Delaware Bay region since 1998 and in 2012 adopted an Adaptive Resource Management (ARM) framework, which explicitly incorporates shorebird objectives in horseshoe crab (hereafter "crab" or "crabs") harvest regulation (McGowan et al. 2015b). The ARM framework was designed to constrain the harvest so that the number of spawning crabs would not limit the number of Red Knots stopping at Delaware Bay during migration. To achieve multiple objectives simultaneously, the ARM framework requires an estimate each year of both the crab population and the Red Knot stopover population size to inform harvest recommendations (McGowan et al. 2015a). Therefore, we estimated the stopover population size in 2023 using markresight data on individually-marked birds and a Jolly-Seber model for open populations, as we have each year since 2011.

2. Methods

Red Knots have been individually marked at Delaware Bay and other locations in the Western Hemisphere (e.g., Argentina, Brazil, Canada, Chile) with engraved leg flags since 2003. Each leg flag is engraved with a field-readable, unique 3-character alphanumeric code (Clark et al. 2005). Mark-resight data (i.e., sight records of individually-marked birds and counts of marked and unmarked birds) were collected on the Delaware and New Jersey shores of Delaware Bay in 2023 according to the methods for markresight investigations of Red Knots at Delaware Bay (Lyons 2016). This protocol has been used at Delaware Bay since 2011.

Surveys to locate leg-flagged birds were conducted on 20 beaches (Appendix 1) in 2023 according to the sampling plan, i.e., every three days in May and early June (Table 1). During these resighting surveys, agency staff and volunteers surveyed the beach and recorded the field- readable alphanumeric combinations detected on leg-flagged birds.

As in previous years (Lyons 2022), all flag resightings were validated with physical capture and banding data available in the data repository at http://www.bandedbirds.org/. Resightings without a corresponding record of physical capture and banding (i.e., "misread" errors) were discarded and not included in the analysis. However, banding data from Argentina are not available for validation purposes in bandedbirds.org; therefore, all resightings of orange engraved flags were included in the analysis without validation using banding data. We also omitted resightings of 12 flagged individuals in 2023 whose flag codes were accidentally deployed in both New Jersey and South Carolina (Amanda Dey, New Jersey Division of Fish and Wildlife, pers. comm., 31 May 2017) because it is not possible to confirm individual identity in this case. Section 4 "Summary of Mark-resight and Count Data Collected in 2023" describes additional quality control procedures and the potential for other types of errors in the mark- resight dataset.

While searching for birds marked with engraved leg flags, observers also periodically used a scan sampling technique to count marked and unmarked birds in randomly selected portions of Red Knot flocks (Lyons 2016). As part of the scan sampling protocol to estimate the marked-unmarked ratio (Lyons 2016), observers checked a random sample of birds for marks (leg flags), and recorded 1) the number of

	No. of flagged individuals detected							
Banding country (flag color)	2019	2020	2021	2022	2023			
USA (light green)	2,368	1,255	1,292	1,281	843			
USA (dark green)	351	161	118	118	141			
Argentina/Uruguay (orange)	216	89	81	66	48			
Canada (white)	156	52	78	62	41			
Brazil/Paraguay (dark blue)	35	21	17	14	14			
Chile (red)	10	9	5	5	4			
Total	3,136	1,587	1,591	1,546	1,091			

Table 2. Number of leg-flagged Red Knot (*C. c. rufa*) detected at Delaware Bay from 2019–2023 by banding country (flag color). Flag colors were designated by country by the Pan American Shorebird Program (Howes et al. 2016). USA uses both light green and dark green leg flags.

individually-marked birds, and 2) the number of birds checked for marks in each sample.

To estimate stopover population size, we used the methods of Lyons et al. (2016) to analyze 1) the mark-resight data (flag codes), and 2) data from the scan samples of the marked-unmarked ratio. Lyons et al. (2016) relied on the "superpopulation" approach developed by Crosbie and Manly (1985) and Schwarz and Arnason (1996). The superpopulation is defined as the total number of birds present in the study area on at least one of the sampling occasions over the entire study, i.e., the total number of birds present in the study area at any time between the first and last sampling occasions (Nichols and Kaiser 1999). In this superpopulation approach, passage population size is estimated each year using the Jolly-Seber model for open populations, which accounts for the flow-through nature of migration areas and probability of detection during surveys.

In our analyses for Delaware Bay, the days of the migration season were aggregated into 3-day sampling periods (a total of 10 sample periods possible each season, Table 1). Data were aggregated to 3-day periods because this is the amount of time necessary to complete mark-resight surveys on all beaches in the study (a summary of the mark-resight data from 2023 is provided in Appendix 2).

With the mark-resight superpopulation approach, we first estimated the number of birds that were carrying leg flags, and then adjusted this number to account for unmarked birds using the estimated proportion of the population with flags. The estimated proportion with leg flags is thus an important statistic. We used the scan sample

data (i.e., the counts of marked birds and the number checked for marks) and a binomial model to estimate the proportion of the population that is marked. To account for the random nature of arrival of marked birds at the study area and the addition of new marks during the season, we implemented the binomial model as a generalized linear mixed model with a random effect for the sampling period. More detailed methods are provided in Lyons et al. (2016) and Appendix 3.

3. Summary of Mark-resight and Count Data Collected in 2023

3.1 Mark-resight encounter data

The 2023 Red Knot mark-resight dataset included a total of 1,091 individual birds that were recorded at least once during mark-resight surveys at Delaware Bay in 2023; these birds were originally captured and banded with leg flags in five to seven different countries (Fig. 1). This total is ~30% lower than the total detected at Delaware Bay in 2020 (1,587), 2021 (1,591), and 2022 (1,546; Table 2).

There were sufficient data for analysis in 9 of the 10 sampling periods in 2023 (≤10 May to 3 June; Table 1). In 2023, data beyond 3 June were too sparse for analysis and were not included.

One assumption of the mark-resight approach is that individual identity of marked birds is recorded without error (see Lyons 2016 for discussion of all model assumptions). As noted above, some field-recording errors are evident when sight records are compared to physical capture records



Figure 1 Number of birds detected for the first time (in 2023) by banding country (flag color). Colors correspond to leg-flag colors assigned to countrys in the Pan American Shorebird Program (Howes et al. 2016). USA uses both light and dark green flags.

Table 3. Number of Red Knots (*C. c. rufa*) detected during 2023 aerial and ground surveys of Delaware Bay (Delaware and New Jersey combined). Data were provided by W. Pitts, New Jersey Department of Environmental Protection.

	Total
Aerial survey	
2023-05-16	5,029
2023-05-22	12,713
2023-05-26	11,785
Ground/Boat Surveys	
2023-05-22	22,266
2023-05-26	21,448

available from bandedbirds.org. Again, any engraved flag reported by observers that did not have a corresponding record of physical capture was omitted. Field observers submitted 3,379 resightings in 2023; 34 were not valid (i.e., no corresponding banding data), for an overall misread read of 1.1%. These invalid resightings were removed before analysis, but a second type of "false positive" is still possible, i.e., false positive detection of flags that were deployed prior to 2023 but were not in fact present at Delaware Bay in 2023. It is not possible to identify this second type of false positive with banding data validation or other quality assurance/quality control methods (Tucker et al. 2019).

3.2 Marked-ratio data ("scan samples" in Appendix 3)

In 2023, 504 marked ratio scan samples were collected: 326 and 178 samples in Delaware and New Jersey, respectively (Appendix 4). In 2020, 2021, and 2022, there were 734, 564, and 541 marked-ratio scan samples collected, respectively.



Figure 2 Estimated Jolly-Seber (JS) model parameters from a mark-resight study of Red Knots (C. c. rufa) at Delaware Bay in 2023: (a) proportion of stopover population arriving at Delaware Bay, (b) stopover departure probability, (c) probability of resighting, and (d) time-specific population size. Dates on the x-axis represent sampling occasions (3-day survey periods, Table 1). Triangles in (d) are aerial survey (triangle point up) and ground counts (triangle point down).

3.3 Aerial and ground count data

Aerial surveys of the Delaware and New Jersey shore were conducted on 16, 22, and 26 May 2023 (Table 3; data provided by W. Pitts, New Jersey Department of Environmental Protection, Division of Fish and Wildlife). Ground and boat surveys of the Delaware and New Jersey shore also were conducted on 22 and 26 May 2023.

4. Summary of 2023 Migration

A substantial number of Red Knots arrived early in 2023, with ~20% of all birds that stopped in Delaware Bay this year arriving by 10 May (Fig. 2a). This is a larger proportion of early arrivals than last year: in 2022, <10% arrived before 14 May (Lyons 2022). Arrivals in 2023 peaked around 15

May, with another ~25% of all birds arriving between 13 and 16 May 2023. Approximately 50% of all birds in the 2023 stopover populations thus had arrived by 16 May, which is slightly earlier than the long-term pattern of arrivals; in many years the peak of arrivals has been closer to 18 May (J. Lyons, personal observation, 2023-09-23).

Stopover departure probability is the probability that a bird present at Delaware Bay during sampling period *i* departs before sampling period *i*+1. In 2023, departure probability was relatively high early in the season, indicating substantial turnover in the stopover population (Fig. 2b). In many years, departure probability is often $\leq 10\%$ early in the season, indicating that early-arriving birds remain in the bay. In 2023, departure probability was above 20% by 12 May, relatively high for early in the season and indicating

Table 4. Red Knot (*C. c. rufa*) stopover (passage) population estimate using mark-resight methods compared to a peak-count index using aerial- or ground-survey methods at Delaware Bay. The mark-resight estimate of stopover (passage) population, N^* , accounts for population turnover during migration. The peak-count index, a single count on a single day, does not account for turnover in the population. "AG" indicates a combination of aerial and ground counts used to formulate the peak-count index. CI = credible interval.

	Stopover		
	population ^a		Peak-count index
Year	(mark-resight N*)	95% CI N*	(aerial [A]; ground [G])
2011	43,570	(40,880 – 46,570)	12,804 (A) ^b
2012	44,100	(41,860 – 46,790)	25,458 (G) ^c
2013	48,955	(39,119 – 63,130)	25,596 (A) ^d
2014	44,010	(41,900 – 46,310)	24,980 (A) ^c
2015	60,727	(55,568 – 68,732)	24,890 (A) ^c
2016	47,254	(44,873 – 50,574)	21,128 (A) ^b
2017	49,405 ^e	(46,368 – 53,109)	17,969 (A) ^f
2018	45,221	(42,568 – 49,508)	32,930 (A) ^b
2019	45,133	(42,269 – 48,393)	30,880 (A) ^g
2020	40,444	(33,627 – 49,966)	19,397 (G) ^c
2021	42,271	(35,948 – 55,210)	6,880 (AG) ^h
2022	39,800	(35,013 – 51,355)	12,114 (AG) ^g
2023	39,361	(33,724 – 47,556)	22,266 (G) ^g

^a passage population estimate for entire season, including population turnover

^b 23 May

^c 24 May

^d 28 May

^e Data management procedures to reduce bias from recording errors in the field; data from observers with greater than average misread rate were not included in the analysis.

^f26 May

^g 22 May

^h 27 May

high turnover in the population. Departures continued at a steady pace until 24 May when mass depatures began and continued to the end of May (Fig. 2b).

Following Lyons et al. (2016), we used the Jolly-Seber model to estimate stopover duration. Stopover duration in 2023 was similar to 2022, but slightly lower than during 2019 – 2021. In 2023, estimated average stopover duration was 9.2 days (95% credible interval (CI), 8.2 - 10.4 days). The stopover duration estimate (and 95% CI) was 12.1 days in 2019 (11.6 - 12.5), 10.7 days in 2020 (9.9 - 11.7), 10.3 days in 2021 (9.0 - 12.1), and 9.4 days in 2022 (8.6 - 10.9 days). This method of estimating stopover duration provides a coarse measure in our Delaware Bay study, however, because it is derived from the estimated number of sampling periods (i.e., the time step in the markrecapture model) that birds remained in the study area. Each sampling period in this analysis is 3 consecutive days in which the data are aggregated (Table 1). To estimate stopover duration in number of days at Delaware Bay with this method, we first estimate the number of sampling periods that each bird remained in the study area and then multiply this by 3 (the number of days in each period). The resolution of the stopover duration estimate is thus limited by the resolution of the sampling periods.

Probability of resighting in 2023 was relatively low for much of the season, remainging below 30% from 10 May until 24 May (Fig. 2c). Probability of resighting higher during 27 May to 2 June (~40–50%) at the end of the season.

In 2023, 6.8% of the stopover population carried engraved leg flags (95% CI: 5.9–7.9%; Appendix 5 Fig. A5). This is slightly lower than 2022 (8.4%, 95% CI: 7.4%–9.7%) and suggests a declining trend in the proportion with flags. The proportion of the population with leg flags has historically been closer to 10% and was as high as 9.6 percent (95% CI: 8.8%–10.3%) in 2020 (Lyons 2020).

5. Stopover Population Estimation

The passage population size estimate for 2023 was 39,361 (95% credible interval: 33,724 – 47,556; Table 4). Unlike the aerial survey, this superpopulation estimate accounts for turnover in the population and probability of detection. The 2023 stopover population estimate is similar to the 2022 population estimate, lower than the 2021 estimate, and below 40,000 for the second time since 2011,

the first year of our mark-resight estimation procedures were used at Delaware Bay (Table 4). However, there was wide overlap of the confidence intervals for the stopover population estimates in recent years (Table 4).

Like 2020–2022 population estimates, the 2023 estimate is slightly lower than the 2018 and 2019 estimates (Table 4) and the confidence interval is wider. The wide confidence intervals are due in part to the low probability of resighting for many of the sampling periods during 2020–2023 compared to earlier years (early 2021 notwithstanding).

The time-specific stopover population estimates in 2023 increased steadily from the beginning of the season and peaked around 18–21 May (~18,300; Fig. 1d), similar to 2022. After the peak, time-specific estimates declined steadily until 2 June (Fig. 2d).

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State	Beach	Longitude	Latitude
DE	Port Mahon	-75.4021	39.1831
DE	Pickering Beach	-75.4087	39.1377
DE	Kitts Hummock	-75.4048	39.1130
DE	Ted Harvey Wildlife Area	-75.4019	39.0864
DE	North Bowers	-75.3973	39.0630
DE	South Bowers	-75.3860	39.0498
DE	Brockenbridge	-75.3638	39.0359
DE	Mispillion	-75.3131	38.9519
DE	Slaughter Beach	-75.3146	38.9282
DE	Fowlers Beach	-75.2633	38.8766
DE	Prime Hook Beach	-75.2467	38.8604
NJ	Gandys/Money Island	-75.2417	39.2767
NJ	Fortescue	-75.1675	39.2233
NJ	North Reeds	-74.8908	39.1228
NJ	South Reeds	-74.8922	39.1138
NJ	Cooks	-74.8941	39.1082
NJ	Kimbles	-74.8948	39.1049
NJ	Bay Cove	-74.8965	39.1008
NJ	Pierces Point	-74.9013	39.0897
NJ	Villas and Norburys	-74.9298	39.0449

Appendix 1. Locations around Delaware Bay, USA, where mark-resight surveys were conducted to estimate Red Knot (*C. c. rufa*) stopover population size in 2023. DE = Delaware and NJ = New Jersey.

			Next resighted at sample								
Sample	Dates	Resighted	2	3	4	5	6	7	8	9	NR
1	≤10 May	62	9	1	1	9	3	3	0	0	36
2	11-13 May	83		7	4	7	1	1	0	0	63
3	14-16 May	99			17	9	2	4	0	0	67
4	17-19 May	166				32	17	6	2	0	109
5	20-22 May	277					49	17	4	0	207
6	23-25 May	269						42	6	0	221
7	26-28 May	261							35	2	224
8	29-31 May	142								13	129
9	1-3 June	35									

Appendix 2. Summary ("m-array") of Red Knot (*C. c. rufa*) mark-resight data from Delaware Bay, USA, 2023. NR = never resighted.

Appendix 3. Statistical Methods to Estimate Stopover Population Size of Red Knots (*C. c. rufa*) Using Mark-Resight Data and Counts of Marked Birds

We converted the observations of marked Red Knots into encounter histories, one for each bird, and analyzed the encounter histories with a Jolly-Seber (JS) model (Jolly 1965, Seber 1965, Crosbie and Manly 1985, Schwarz and Arnason 1996). The JS model includes parameters for recruitment (β), survival (φ), and capture (p) probabilities; in the context of a mark-resight study at a migration stopover site, these parameters are interpreted as probability of arrival to the study area, stopover persistence, and resighting, respectively. Stopover persistence is defined as the probability that a bird present at time tremains at the study area until time t + 1. The Crosbie and Manley (1985) and Schwarz and Arnason (1996) formulation of the JS model also includes a parameter for superpopulation size, which in our approach to mark-resight inferences for stopover populations is an estimate of the marked (leg-flagged) population size.

We chose to use 3-day periods, rather than days, as the sampling interval for the JS model given logistical constraints on complete sampling of the study area; multiple observations of the same individual in a given 3-day period were combined for analysis. A summary (m-array) of the mark-resight data is presented in Appendix 2.

We made inference from a fully-time dependent model; arrival, persistence, and resight probabilities were allowed to vary with sampling period [$\beta_t \phi_t p_t$]. In this model, we set $p_1 = p_2$ and $p_{K-1} = p_K$ (where K is the number of samples) because not all parameters are estimable in the fully-time dependent model (Jolly 1965, Seber 1965, Crosbie and Manly 1985, Schwarz and Arnason 1996).

We followed the methods of Royle and Dorazio (2008) and Kéry and Schaub (2012, Chapter 10) to fit the JS model using the restricted occupancy formulation. Royle and Dorazio (2008) use a state-space formulation of the JS model with parameter-expanded data augmentation. For parameter-expanded data augmentation, we augmented the observed encounter histories with all-zero encounter histories (n = 2000) representing potential recruits that were not detected (Royle and Dorazio 2012). We followed Lyons et al. (2016) to combine the JS model with a binomial model for the counts of marked and unmarked birds in an integrated Bayesian analysis. Briefly, the counts of marked birds (m_s) in the scan samples are modeled as a binomial random variable:

$$m_s \sim Bin(C_s, \pi),$$
 (1)

where m_s is the number of marked birds in scan sample *s*, C_s is the number of birds checked for marks in scan sample *s*, and π is the proportion of the population that is marked. Total stopover population size $\widehat{N^*}$ is estimated by

$$\widehat{N^*} = \widehat{M^*}/_{\widehat{\pi}} \tag{2}$$

where $\widehat{M^*}$ is the estimate of marked birds from the J-S model and $\widehat{\pi}$ is the proportion of the population that is marked (from Eq. 1). Estimates of marked subpopulation sizes at each resighting occasion $t\left(\widehat{M}_t^*\right)$ are available as derived parameters in the analysis. We calculated an estimate of population size at each mark-resight sampling occasion \widehat{N}_t^* using \widehat{M}_t^* and $\widehat{\pi}$ as in equation 2. To better account for the random nature of the arrival of marked birds and addition of new marks during the season, we used a time-specific model for proportion with marks in place of equation 1 above:

$$m_{s,t} \sim Binomial(C_{s,t}, \pi_t)$$
(3)
for s in 1, ..., $n_{samples}$ and t in 1, ..., $n_{occasions}$
 $logit(\pi_t) = \alpha + \delta_t$
 $\delta_t \sim Normal(0, \sigma_{occasions}^2)$

where m_s is the number of marked birds in scan sample s, C_s is the number of birds checked for marks in scan sample s, δ_t is a random effect time of sample s, and π_t is the time-specific proportion of the population that is marked. Total stopover population size $\widehat{N^*}$ was estimated by summing time-specific arrivals of marked birds to the stopover (B_t) and expanding to include unmarked birds using estimates of proportion marked:

$$\widehat{N^*} = \sum \widehat{B_t} / \pi_t$$

Time-specific arrivals of marked birds are estimated from the Jolly-Seber model using $\widehat{B_t} = \widehat{\beta_t} \widehat{M^*}$ where $\widehat{M^*}$ is the estimate of the number of marked birds and $\widehat{\beta_t}$ is the fraction of the population arriving at time *t*.





Figure A4. Number of Red Knot (*C. c. rufa*) marked-ratio scan samples (n =) collected in Delaware Bay in 2023 by field crews in Delaware (blue, n = scan samples) and New Jersey (orange, n = scan samples) and date.

Appendix 5. Marked proportion.



Figure A5. Estimated proportion of the Delaware Bay stopover population of Red Knots (*C. c. rufa*) carrying leg flags in 2023 (overall average and 95% credible interval: 0.068 [0.059, 0.079]). The marked proportion was estimated from marked-ratio scan samples for each 3-day sampling period (Table 1). The upper panel shows the sample size (number scanned, i.e., checked for marks) for each sample period. The bottom panel shows the estimated proportion marked for each sample occasion, which was estimated with the generalized linear mixed model described in Appendix 2. Solid and dashed lines are estimated median proportion marked and 95% credible interval, respectively; open circles show (number with marks/number scanned).