

Red Knot Stopover Population Size and Migration Ecology at Delaware Bay, USA, 2022

A report submitted to the Adaptive Resource Management Subcommittee and Delaware Bay Ecosystem Technical Committee of the Atlantic States Marine Fisheries Commission

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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*). In the late 1990s and early 2000s, the number of Red Knots found at Delaware Bay declined from ~50,000 to ~13,000. Horseshoe crabs have been harvested for use as bait in eel (*Anguilla rostrata*) and whelk (*Busycon*) fisheries since at least 1990, and some avian conservation biologists hypothesized that horseshoe crab harvest levels in the 1990s prevented sufficient refueling for successful migration to the breeding grounds, nesting, 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. We conducted a mark-recapture-resight investigation to estimate the passage population of Red Knots at Delaware Bay in 2022. 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 2022 Red Knot mark-resight dataset

included a total of 1,546 individual birds that were recorded at least once during mark-resight surveys at Delaware Bay in 2022. The passage population size in 2022 was estimated at 39,800 (95% credible interval: 35,013 – 55,355). Although there is broad overlap in the credible intervals for population estimate from 2020–2022, the population estimate for 2022 was below 40,000 birds for the first time since 2011. The 2022 population size estimate will inform harvest recommendations in the next management cycle and decision making by the Atlantic States Marine Fisheries Commission.

1 Acknowledgments

We thank the many volunteers in Delaware and New Jersey who collected mark-resight data in 2022. We are grateful to Henrietta Bellman (Delaware Division of Fish and Wildlife), Stephanie Feigin (Wildlife Restoration Partnerships on behalf of New Jersey Department of Environmental Protection, Division of Fish and Wildlife, Endangered & Nongame Species Program), Lena Usyk (bandedbirds.org), and numerous volunteers in Delaware and New Jersey for data entry and data management. We are grateful to Conor McGowan and Dave Smith for helpful peer reviews as part of U.S. Geological Survey Fundamental Science Practices. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

2 Background

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 spawning of horseshoe crabs, 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 therefore 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*) fisheries (Kreamer and Michels 2009). In the late 1990s and early 2000s the estimated number of Red Knots counted at Delaware Bay declined from ~50,000 to ~13,000 (Niles et al. 2008). The number of horseshoe crabs harvested 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 2022 using mark-resight data on individually-marked birds and a Jolly-Seber model for open populations, as we have each year since 2011.

3 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 2022 according to the methods for mark-resight 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 4) in 2022 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 2022 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 2022” 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 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 2022 is provided in Appendix 1).

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 2.

4 Summary of Mark-resight and Count Data Collected in 2022

Mark-resight encounter data.—The 2022 Red Knot mark-resight dataset included a total of 1,546 individual birds that were recorded at least once during mark-resight surveys at Delaware Bay in 2022; these birds were originally captured and banded with leg flags in five different countries (Table 2). This total is remarkably close to the total detected at Delaware Bay in 2020 (1,587) and 2021 (1, 591) (Table 2).

There was sufficient data for analysis in 9 of the 10 sampling periods in 2022 (≤ 10 May to 3 June; Table 1). In 2022, data beyond 3 June were too sparse for analysis and were not included.

While the number of birds detected in 2022 was similar to the number detected in 2020 and 2021, this number of individuals resighted within a season (i.e., observed in the Bay at least once in a season) was lower than recent years (2018-2019), given the limited use of volunteers for COVID-19 safety concerns. The number of marked birds detected and available for analysis in 2022 was approximately 50% of the number available for analysis in the 2019 ($n = 3,072$ birds) and 40% of the number available for analysis in 2018 ($n = 3,820$).

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 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 5,195 resightings in 2022; 80 were not valid (i.e., no corresponding banding data), for an overall misread rate of 1.5%. 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 2022 but were not in fact present at Delaware Bay in 2022. 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).

Marked-ratio data.—In 2022, 541 marked ratio scan samples were collected: 330 and 211 samples in Delaware and New Jersey, respectively (Appendix 3). In 2020 and 2021, respectively, 734 and 564 marked-ratio scan samples were collected.

Aerial and ground count data.—Aerial surveys were conducted on 22 and 26 May 2022 (Table 3; data provided by S. Feigin, Wildlife Restoration Partnerships on behalf of New Jersey Department of Environmental Protection, Division of Fish and Wildlife). The aerial survey on 22 May was affected by the Dover Air Show, which prevented the plane from surveying some of the northern study sites on the Delaware shore (H. Bellman, Delaware Division of Fish and Wildlife, pers. comm.). Ground and boat surveys were also conducted in Delaware and New Jersey on 22 and 26 May 2022 (Table 3).

5 Summary of 2022 Migration

The pattern of arrivals of Red Knots at Delaware Bay in 2022 shows one large peak of arrivals about 18 May, with approximately 25% of all birds that stopped in the bay in 2022 arriving between 17 and 19 May (Fig. 1a). The numbers of birds arriving in the preceding (15 May) and following (21 May) 3-day periods were also relatively large (approximately 20% of all arrivals in each). In 2022, few birds (<10%) arrived before 14 May or after 28 May.

Stopover persistence is the probability that a bird present at Delaware Bay during sampling period i is present at sampling period $i + 1$. In 2022, stopover persistence started off relatively high (Fig. 1b). Stopover persistence declined around 18 May and again around 21 May, indicating some early departures and turnover in the population. A second peak in stopover persistence around 24 May indicated few departures in this sampling period. After 24 May, persistence declined sharply, indicating synchronous departures of the remaining birds between 27 and 30 May.

Following Lyons et al. (2016), we used the Jolly-Seber model to estimate stopover duration. Stopover duration declined slightly in 2022 for the third year in a row. In 2022, estimated average stopover duration was 9.4 days (95% credible interval (CI) 8.6 – 10.9 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), and 10.3 days in 2021 (9.0 – 12.1). 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 that birds remained in the study area. Sampling periods in this analysis are 3 consecutive days in which the data are aggregated (Table 1). To estimate stopover duration in 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 (i.e., the time step in the mark-recapture model).

Probability of resighting in 2022 was relatively low early in the season, less than 20% in four of the first five sampling periods (10 – 21 May, Fig. 1c). Probability of resighting increased steadily after 21 May until the end of the season, when it peaked at approximately 50%.

In 2022, 8.4% of the stopover population carried engraved leg flags (95% CI: 7.4% – 9.7%) (Fig. 2). This is similar to the 2021 estimate (8.2% with leg flags [95% CI: 7.0%–9.1%]) and slightly lower than the 2020 estimate (9.6% with leg flags [95% CI: 8.8%–10.3%]).

6 Stopover Population Estimation

The passage population size in 2022 was estimated at 39,800 (95% credible interval: 35,013 – 51,355). Unlike the aerial survey, this superpopulation estimate accounts for turnover in the

population and probability of detection. The 2022 stopover population estimate is slightly lower than the 2021 estimate and is below 40,000 for the first time since 2011 when this mark-resight analysis began (Table 4). However, there was wide overlap of the confidence intervals for the stopover population estimates in recent years (Table 4).

Like 2020–2021 population estimates, the 2022 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 2020–2022 compared to earlier years (early 2021 notwithstanding).

The time-specific stopover population estimates in 2022 increased steadily from the beginning of the season and peaked around 18–21 May (approximately 20,700 birds; Fig. 1d). Time-specific estimates declined to approximately 13,500 for 24 – 27 May and then declined steadily until 2 June (Fig. 1d).

7 References

- Baker, A. J., P. M. González, T. Piersma, L. J. Niles, I. de Lima Serrano do Nascimento, P. W. Atkinson, N. A. Clark, C. D. T. Minton, M. K. Peck, and G. Aarts. 2004. Rapid population decline in Red Knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271:875–882.
- Clark, N.A., S. Gillings, A.J. Baker, P.M. González, and R. Porter. 2005. The production and use of permanently inscribed leg flags for waders. *Wader Study Group Bull.* 108: 38–41.
- Crosbie, S. F., and B. F. J. Manly. 1985. Parsimonious modelling of capture-mark-recapture studies. *Biometrics* 41:385–398.
- Haramis, G. M., W. A. Link, P. C. Osenton, D. B. Carter, R. G. Weber, N. A. Clark, M. A. Teece, and D. S. Mizrahi. 2007. Stable isotope and pen feeding trial studies confirm the value of horseshoe crab *Limulus polyphemus* eggs to spring migrant shorebirds in Delaware Bay. *Journal of Avian Biology* 38:367–376.

- Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52:225–248.
- Karpanty, S. M., J. D. Fraser, J. Berkson, L. J. Niles, A. Dey, and E. P. Smith. 2006. Horseshoe crab eggs determine red knot distribution in Delaware Bay. *Journal of Wildlife Management* 70:1704–1710.
- Kéry, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. 1st ed. Academic Press, Boston.
- Lyons, J.E. 2016. Study design guidelines for mark-resight investigations of Red Knots in Delaware Bay. Unpublished report. U.S. Fish and Wildlife Service Division of Migratory Bird Management, Laurel, MD. 13 pp.
- Lyons, J.E., W.P. Kendall, J.A. Royle, S.J. Converse, B.A. Andres, and J.B. Buchanan. 2016. Population size and stopover duration estimation using mark-resight data and Bayesian analysis of a superpopulation model. *Biometrics* 72:262-271.
- Lyons, J. E. 2022. Red Knot stopover population size and migration ecology at Delaware Bay, USA, 2021. Delaware Division of Fish and Wildlife, Dover, DE. 18 pp. Available at: <https://dnrec.alpha.delaware.gov/fish-wildlife/conservation/shorebirds/research/>
- McGowan, C. P., J. E. Hines, J. D. Nichols, J. E. Lyons, D. R. Smith, K. S. Kalasz, L. J. Niles, A. D. Dey, N. A. Clark, P. W. Atkinson, C. D. T. Minton, and W. L. Kendall. 2011. Demographic consequences of migratory stopover: linking Red Knot survival to horseshoe crab spawning abundance. *Ecosphere* 2:Article 69.
- McGowan, C. P., J. E. Lyons, and D. R. Smith. 2015a. Developing objectives with multiple stakeholders: Adaptive management of horseshoe crabs and red knots in the Delaware Bay. *Environmental Management* 55:972–982.
- McGowan, C. P., D. R. Smith, J. D. Nichols, J. E. Lyons, J. Sweka, K. Kalasz, L. J. Niles, R. Wong, J. Brust, M. Davis, and B. Spear. 2015b. Implementation of a framework for multi-species, multi-objective adaptive management in Delaware Bay. *Biological Conservation* 191:759–769.
- Kreamer, G., and S. Michels. 2009. History of horseshoe crab harvest on Delaware Bay. Pages 299–313 in J. T. Tanacredi, M. L. Botton, and D. R. Smith, editors. *Biology and Conservation of Horseshoe Crabs*. Springer, New York, NY.
- Nichols, J. D., and A. Kaiser. 1999. Quantitative studies of bird movement: a methodological review. *Bird Study* 46:S289–S298.
- Niles, L. J., H. P. Sitters, A. D. Dey, P. W. Atkinson, A. J. Baker, K. A. Bennett, R. Carmona, K. E. Clark, N. A. Clark, C. Espoz, P. M. González, B. A. Harrington, D. E. Hernández, K. S. Kalasz, R. G. Lathrop, R. N. Matus, C. D. T. Minton, R. I. G. Morrison, M. K. Peck, W. Pitts,

- R. A. Robinson, and I. L. Serrano. 2008. Status of the red knot (*Calidris canutus rufa*) in the Western Hemisphere. *Studies in Avian Biology* 36:xviii+185.
- Royle, J. A., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. Academic Press, Amsterdam.
- Royle, J. A., and R. M. Dorazio. 2012. Parameter-expanded data augmentation for Bayesian analysis of capture–recapture models. *Journal of Ornithology* 152:521–537.
- Schwarz, C. J., and A. N. Arnason. 1996. A general methodology for the analysis of capture–recapture experiments in open populations. *Biometrics* 52:860–873.
- Seber, G. A. F. 1965. A note on the multiple-recapture census. *Biometrika* 52:249–259.
- Tucker, A. M., C. P. McGowan, R. A. Robinson, J. A. Clark, J. E. Lyons, A. DeRose-Wilson, R. Du Feu, G. E. Austin, P. W. Atkinson, and N. A. Clark. 2019. Effects of individual misidentification on estimates of survival in long-term mark–resight studies. *The Condor: Ornithological Applications* 121:1-13.

Table 1. Dates for mark-resight survey periods (3-day sampling occasions) for Red Knots (*C.c. rufa*) at Delaware Bay in 2022. The same sampling periods have been used at Delaware Bay since 2011. Data from survey period 10 were not used in the 2022 analysis because the mark-resight data were sparse in this period.

Survey period	Dates	Survey 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

Table 2. Number of Red Knot (*C. c. rufa*) flags detected at Delaware Bay from 2019–2022 by banding location (flag color).

Banding location (flag color)	<i>No. flagged individuals detected</i>			
	2019	2020	2021	2022
U.S. (lime green)	2,368	1,255	1,292	1,281
U.S. (dark green)	351	161	118	118
Argentina (orange)	216	89	81	66
Canada (white)	156	52	78	62
Brazil (dark blue)	35	21	17	14
Chile (red)	10	9	5	5
Total	3,136	1,587	1,591	1,546

Table 3. Number of Red Knots (*C.c. rufa*) detected during aerial and ground surveys of Delaware Bay in 2022. Data provided by S. Feigin, Wildlife Restoration Partnerships on behalf of the New Jersey Department of Environmental Protection, Division of Fish and Wildlife, Endangered & Nongame Species Program.

	Delaware	New Jersey	Total
Aerial/Ground Surveys			
22 May 2022	280	11,834	12,114
26 May 2022	1,054*	8,660	9,714
Ground/Boat Surveys			
22 May 2022	132	10,812	10,944
26 May 2022	1,054	8,996	10,050

* Delaware ground survey total from 26 May 2022 (1,054 birds) was used here rather than the aerial count of the Delaware shore on the same day because the aerial count (875 birds) was lower than the corresponding ground count.

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

Year	Stopover population ^a (mark-resight N^*)	95% CI Stopover pop- ulation N^*	Peak-count index [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

^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.

^f 26 May

^g 22 May

^h 27 May

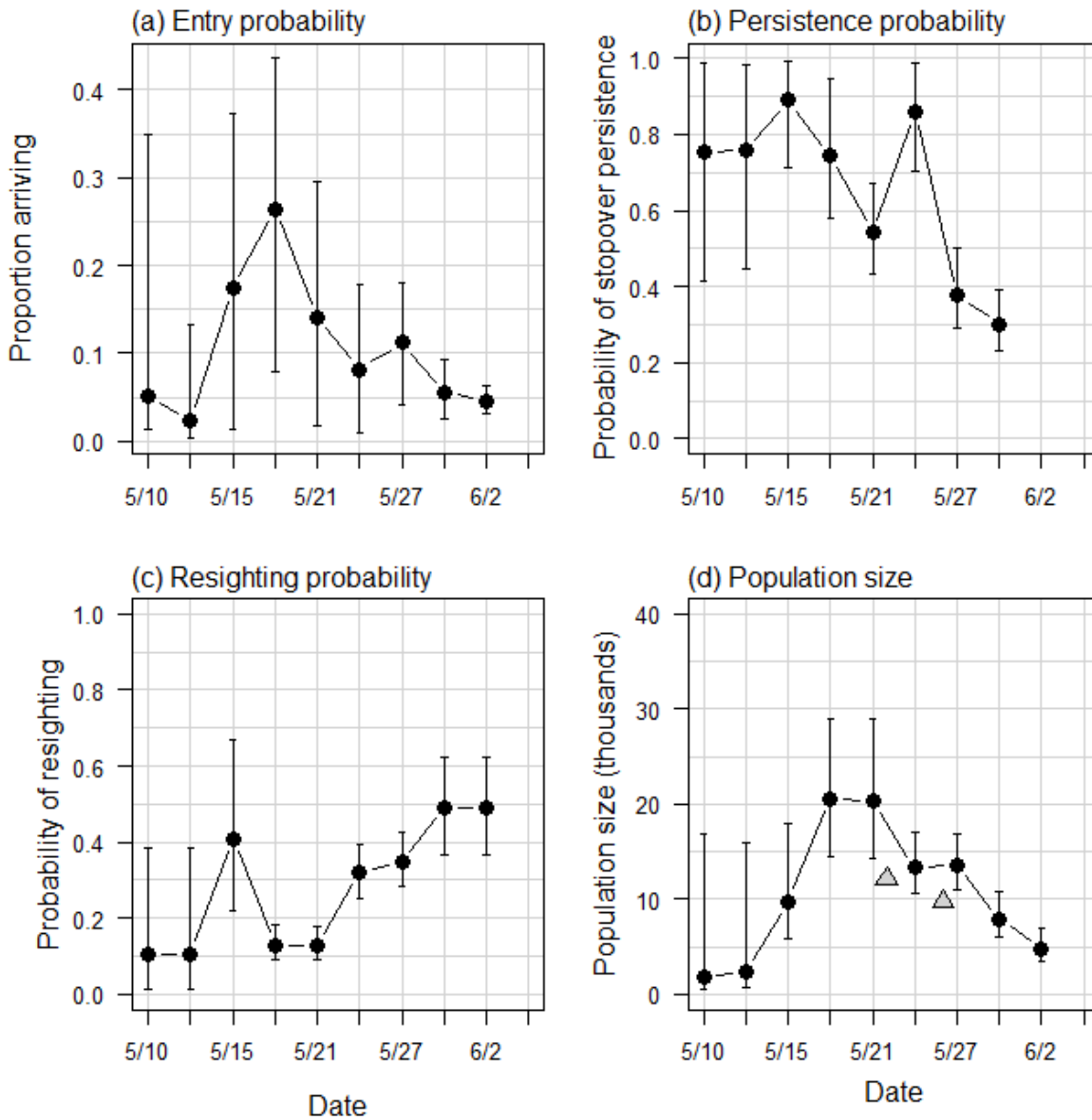


Figure 1. Estimated Jolly-Seber (JS) model parameters from a mark-resight study of Red Knots (*C.c. rufa*) at Delaware Bay in 2022: (a) proportion of stopover population arriving at Delaware Bay, (b) stopover persistence, (c) probability of resighting, and (d) time-specific stopover population size. Dates on the x-axis represent sampling occasions (3-day survey periods, Table 1). Triangles in (d) are total counts conducted on 22 May 2022 (sum of aerial counts for both Delaware (DE) and New Jersey (NJ) and 26 May 2022 (sum of ground count of DE and aerial count of NJ).

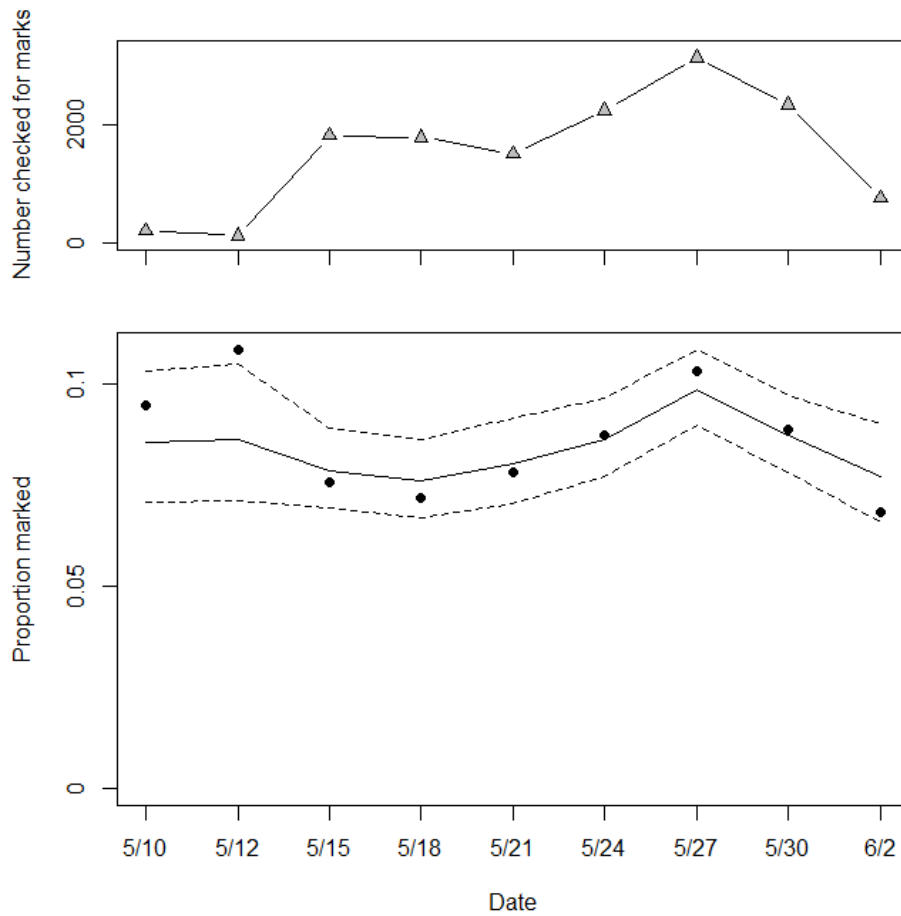


Figure 2. Estimated proportion of the Delaware Bay stopover population of Red Knots (*C.c. rufa*) carrying leg flags in 2022 (overall average and 95% credible interval: 0.084 [0.073, 0.095]). The marked proportion was estimated from marked-ratio scan samples for each 3-day sampling period. The dates for the sampling periods are shown in 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 at 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; filled circles show (number with marks/number scanned).

Appendix 1. Summary (“m-array”) of Red Knot (*C.c. rufa*) mark-resight data from Delaware Bay, USA, 2022. NR = never resighted.

Sample	Dates	Resighted	Next resighted at sample								NR
			2	3	4	5	6	7	8	9	
1	≤10 May	17	3	3	0	2	0	0	0	0	9
2	11-13 May	22		8	1	0	1	0	1	0	11
3	14-16 May	309			37	19	25	22	6	1	199
4	17-19 May	199				23	22	10	5	1	138
5	20-22 May	206					39	13	13	3	138
6	23-25 May	366						118	34	1	213
7	26-28 May	465							85	14	366
8	29-31 May	339								51	288
9	1-3 June	174									

Appendix 2. 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 t remains 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 1.

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:

$$m_s \sim \text{Bin}(C_s, \pi), \quad (1)$$

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

$$\widehat{N}^* = \widehat{M}^* / \widehat{\pi} \quad (2)$$

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 (\widehat{M}_t^*) 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:

$$m_{s,t} \sim \text{Binomial}(C_{s,t}, \pi_t) \quad (3)$$

for s in $1, \dots, n_{\text{samples}}$ and t in $1, \dots, n_{\text{occasions}}$

$$\text{logit}(\pi_t) = \alpha + \delta_t$$

$$\delta_t \sim \text{Normal}(0, \sigma_{\text{occasions}}^2)$$

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 .

Appendix 3. Marked-ratio scan samples of Red Knots (*C.c. rufa*).

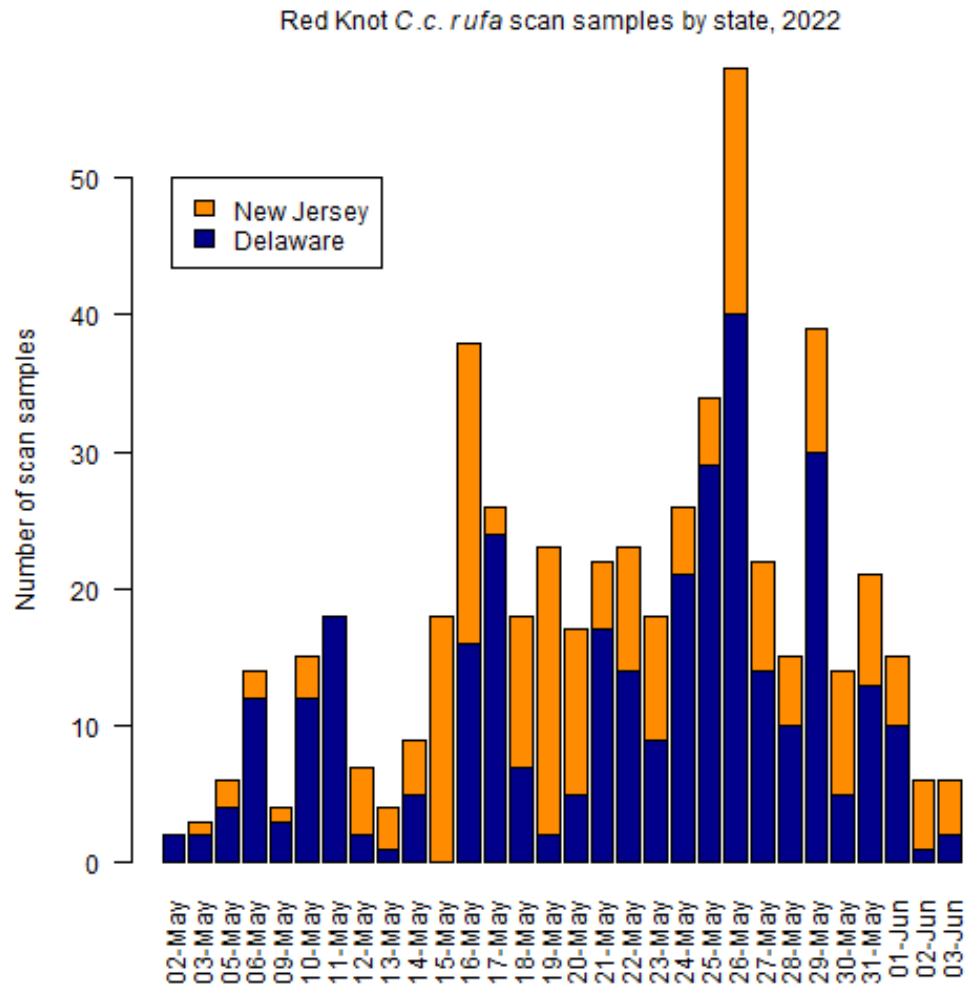


Figure A3.1. Number of Red Knot (*C.c. rufa*) marked-ratio scan samples (n = 541) collected in Delaware Bay in 2022 by field crews in Delaware (blue, n = 330 scan samples) and New Jersey (orange, n = 211 scan samples) and date.

Appendix 4. Locations around Delaware Bay, USA, where mark-resight surveys were conducted to estimated Red Knot (*C.c. rufa*) stopover population size in 2022.

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