

Bound together or falling apart? Foraging associations in Red Knots

Pratik R. Gupte^{1,2,*}, Selin Ersoy^{2,1}, Allert I. Bijleveld²

¹ Groningen Institute for Evolutionary Life Sciences, University of Groningen, Nijenborgh 7, 9747AG Groningen, Netherlands

² Dept. Coastal Systems, Royal Netherlands Institute for Sea Research, <please fill address>

*Correspondence: Pratik R. Gupte, p.r.gupte@rug.nl

Abstract

Shorebirds feeding on the intertidal mudflats of the Wadden Sea often forage socially; this allows them to avoid predation, and increase efficiency in locating food patches and assessing their quality. Foraging is restricted to brief windows of opportunity created by the tidal cycle, when waders such as red knots *Calidris canutus islandica* can access the buried macrozoobenthos. Like other waders, red knots form large foraging flocks, and have been shown to use social information in lab studies to find food. However, it remains unresolved whether knot flocks show fission–fusion dynamics, where individual association is random and fleeting, or if there is some social structure in the form of non-random association, where individuals have an affinity for certain neighbours over others. Modern tracking methods enable the investigation of this aspect of wader sociality in more detail than was available to previous studies. Here, we present work that uses high frequency (1 minute interval) tracking with the ATLAS system of 38 adult red knots from the summer of 2017, and addresses the question of whether knots form non-random foraging associations, i.e., do red knots have friends? Ultimately, our work aims at a better understanding of the social dynamics of group-living foragers.

Keywords: Foraging, social networks, intertidal systems, shorebirds, time-of-arrival tracking

Introduction

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Methods

Knot capture and tracking

We captured xx Red Knots *Calidris canutus islandica*, hereafter knots, on the island of Griend (coordinates here) in the Dutch Wadden Sea (Fig. 1a) on the nights of 20 -- 23 August, 2017, using previously/well established mist-netting techniques for nocturnally foraging waders. We took body mass and the following morphometric measurements of each individual: some measurements here: wing length, tarsus length, bill length. We chose a subset of yy knots based on some criteria here, body mass were chosen to be fitted with radio transmitter tags (manufacturer, place, mass in g, % of mean knot mass).

We attached ATLAS tags to the dorsal surface of each individual using a safe but strong glue (manufacturer, place, exact active composition; Fig. 1b). Tags were programmed to transmit a unique signal at a frequency of 1 Hz. These signals were received by a network of xx receivers (Fig. 1a, 1c), and the position of the tag was calculated based on the time of arrival of the signal (see reference for details on ToA tracking). The receiver network reported tag positions along with the position timestamp, variance in the X and Y coordinates, and the covariance of the coordinates.

The study period lasted 24 August -- 31 October, when we removed the ATLAS receivers to avoid storm damage over the winter. We retrieved knot position data at the end of the study period, and filtered it to include only the first 30 tracking days (24 August -- 23 September) to reduce computation load. We averaged individual positions to the nearest minute to further ease computation. Thus we obtained on average xx positions (range: yy -- zz) over a mean xx days (range: yy -- zz) for xx knots, with a mean position interval of xx minutes (range: yy -- zz).

Tidal period and data filtering

To place our analyses in the context of the tidal cycle, we obtained sea level measurements at one minute intervals from Harlingen (coordinates here, Fig. 1a, data provider name, citation_if_possible), xx km from Griend, over the period 24 August -- 23 September, and calculated high and low tide times. We defined a tidal period as the time between consecutive high tides, and assigned the tidal period to each observation in the tracking data. Our data spanned 59 tidal periods with a mean duration of xx hours (range: yy -- zz).

We identified the number of 1 minute positions expected from knots in each tidal period (the duration of the tidal period in minutes), and calculated the ratio of observed to expected positions. We then filtered the tracking data to include only those knots that had an observed:expected ratio ≥ 0.3 per tidal period, and then selected only those tidal periods in which > 5 knots had been included. As a result, we obtained 36 tidal periods from xx August -- xx September, with an average of xx knots (range: xx -- yy; after filtering) observed in each tidal period.

Track segmentation and interaction scores

We calculated the first passage time (cite) for a radius of 250 m at each track point over the tidal periods, and then filtered out points with an FPT₂₅₀ of < 10 minutes, reasoning that these points did not comprise foraging behaviour (cite some papers, see the tide simulation setup at NIOZ). After removing tracks with < 60 foraging points, we segmented the remainder of the remaining 615 tracks based on the FPT₂₅₀ using the Lavielle method (cite), allowing for a minimum segment length of 3 points, and a maximum of 40 segments in each track. Following this, we corrected for potential over-segmentation, i.e., spatially proximate track points classified into different segments, by merging consecutive segments with median coordinates < 250 m apart. This resulted in an average of xx segments (range: yy -- zz, $n = zz$) per track per tidal period.

For each knot within each tidal period, which we now refer to as the focal bird, we calculated the distance matrix between its segment median positions and the segment median positions of every other bird in turn (which we called non-focal birds), and checked whether focal and non-focal segments overlapped in time, assigning a value of 0 if there was no spatio-temporal overlap. We counted the number of associations between focal and non-focal birds as the number of cells in each focal -- non-focal distance matrix that had a distance < 250 m and thus obtained the empirical pairwise association matrix for each tidal period.

Testing association strength

We then calculated the Wilkinson coherence score (cite) for each focal -- non-focal pair from the empirical pairwise association matrix of each tidal period as in (cite myers_space_1983). To test whether pairwise coherence scores were different from that expected by chance, we generated a null expectation in the form of 100 simulated random pairwise coherence score matrices for each tidal period; this was done by random permutation of the row order of the empirical pairwise coherence matrix, and averaging of the resultant 100 simulated matrices. We then compared empirical pairwise coherence scores pooled over the tidal periods (i.e., the full tracking period) to simulated coherence scores using a two-sample Kolmogorov Smirnov test (cite). Only pairs which were present in ≥ 5 tidal periods were used in this analysis.

All method were implented in the R (cite) statistical environment using the following packages: *VulnToolkit* (cite) to find high tide times, *recurse* (cite) to find first passage time, and *segclust2d* (cite) for Lavielle segmentation.

Results

We obtained ≥ 5 coherence scores for 720 of a possible 1,260 pairwise associations (57%; mean: xx scores, range: yy – zz scores). We found that only 9.5% ($n = 69$) of pairwise associations were more coherent than than expected by chance, while 37.2% ($n = 268$) of pairs cohered less than expected from the null. 53.2% ($n = 383$) of pairs' coherence was not significantly different from that of the null.

References

Figures

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Fig. 1 a. Location of the study site in the Dutch Wadden Sea showing Griend, Harlingen, ATLAS radio receiver tower locations, and 95% MCP of knot observations, b. Individual xx showing radio transmitter deployment on knots, and c. radio receiver tower of the ATLAS system.