Bound Together or ~~Falling Apart~~? Foraging Association in Red Knots

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Background

Waders in the Wadden Sea

1 Waders such as red knots *Calidris canutus* gather in large non-breeding flocks in the Wadden Sea, where they forage on the intertidal mudflats

Fig. 1 Red knot — **Fig. 2** Wadden Sea mudflats

Knots Benefit from Sociality

2 Knots can use social information in lab settings to find food[1], and may learn the location of profitable foraging patches by observing flock-mates[2]

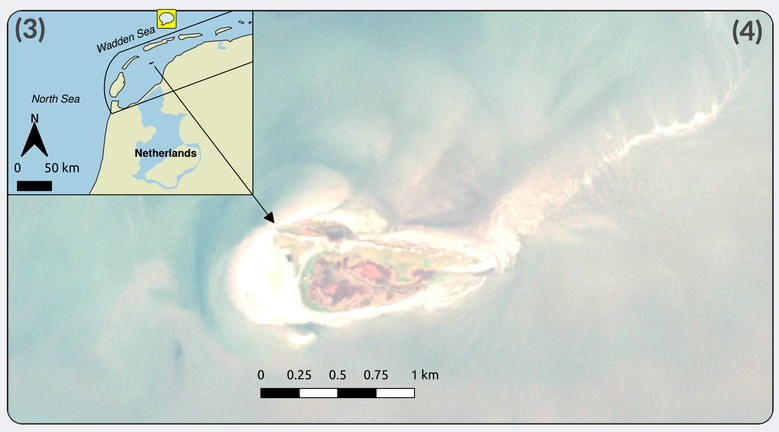

Fig. 3 Study site — **Fig. 4** Island of Griend

Do knots have friends?

3 Knots benefit from association, but do they have friends — persistent, non-random associations — within & between tidal intervals[3,4]?

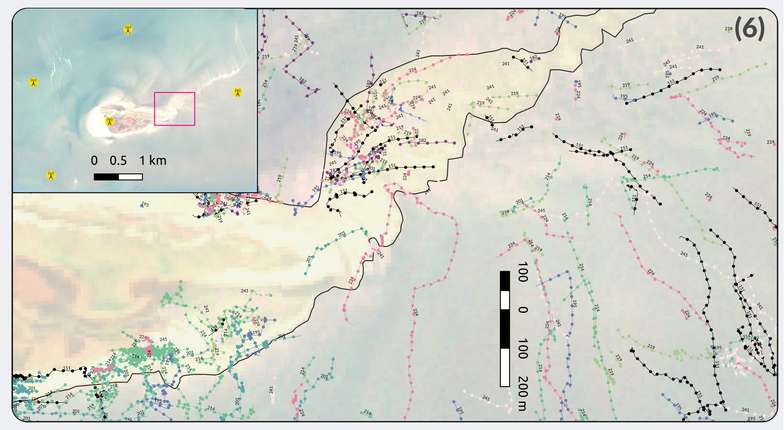

Fig. 5 Tracking towers (black on yellow) — **Fig. 6** Knot positions

Methods

ATLAS Tracking

1 Tagged knots (n = 35) transmit radio signals — tracking tower array (n = 5, Fig. 5) finds position using reference beacon and signal Time of Arrival (ToA);

2 We obtained position data at 1 minute intervals over the tracking period (n = 414,797, Fig. 6).

Tidal Intervals

3 We obtained water-level data and determined tidal intervals (cite) — 35 tidal intervals over 19 calendar days;

4 We grouped each knot's movement tracks by the tidal interval.

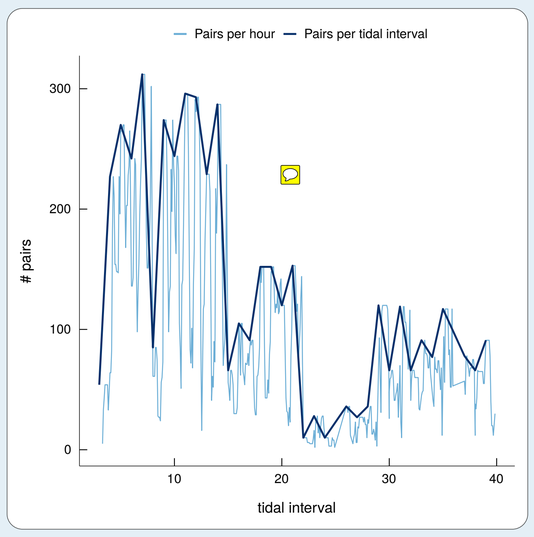

Fig. 7 Number of unique pairs, ie, (a — b), but not (b — a) over the tracking period

Knot Co-occurrence

5 We calculated co-occurrence over unit time between two individuals i and j as c_{ij}

$$c_{ij} = n_{250}/N$$

Where

n_{250} = number of positions where i and j are ≤ 250 m apart

N = number of positions where i and j positions are both known;

6 Pairwise co-occurrence was calculated over the tidal interval, and in each hour within each tidal interval.

Results

Co-occurrence is low over the tracking period

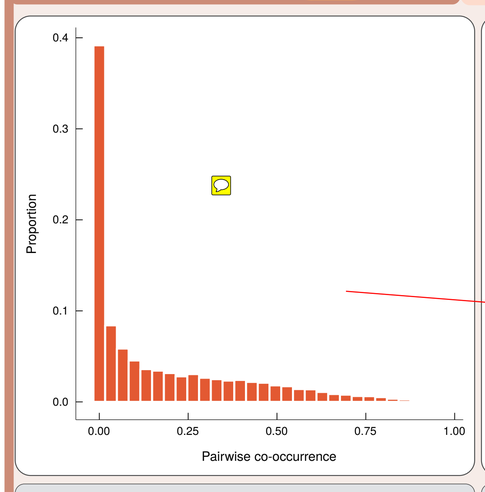

Fig. 8 Red knot pair-wise co-occurrence distribution

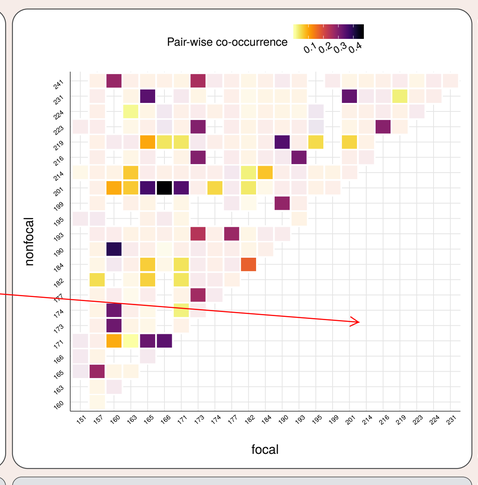

Fig. 9 Knot pair-wise co-occurrence between unique pairs

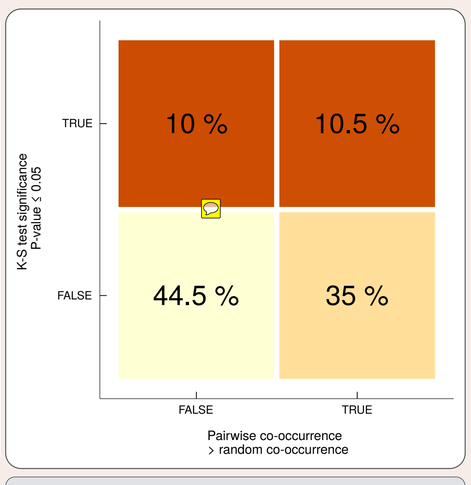

Fig. 10 Proportions of pair-wise co-occurence values *vs* significance

1 Pairwise knot co-occurrence is mostly low, with a mean of 0.14 ± 0.3 SD **(Fig. 8)**

2 ~80% pairwise co-occurrence distributions are not different from the overall distribution of co-occurrences **(Fig. 9, 10)**

3 10.5% of pairwise co-occurrences were significantly higher than expected by chance; the same number were significantly lower than expected by chance **(Fig. 10)**

Results: within tidal period

Co-occurrence is tidally forced and fleeting

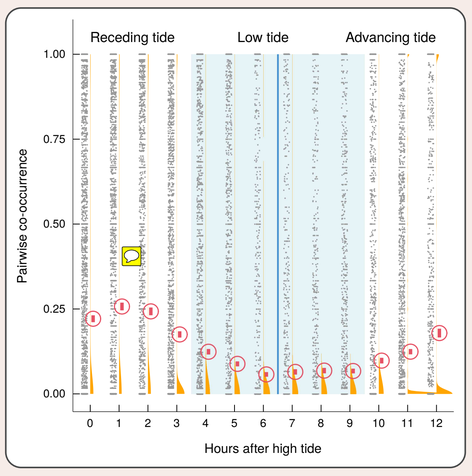

Fig. 8 Mean population co-occurrence at each hour after high tide. Low tide occurs ~6 hours post high tide (HT)

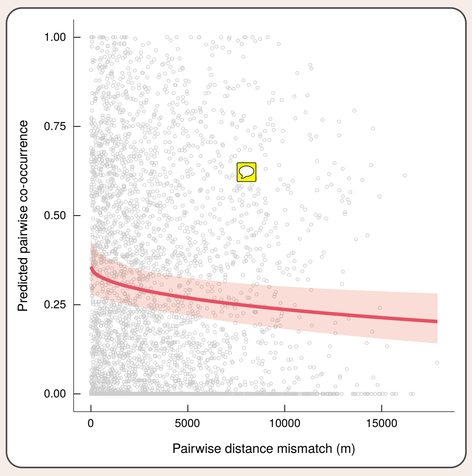

Fig. 9 Pair-wise co-occurrence during the advancing tide (9 — 12 hours post HT) as a function of pair-wise distance mismatch

4 Mean population co-occurrence is highest during the receding tide (0 — 3 hours post high tide, mean ± 95% CI = 0.22 ± 0.008) and the advancing tide (10 — 12 hours post high tide, mean ±, 95% CI = 0.12 ± 0.007) and lowest around low tide (4 — 9 hours post high tide, mean ± 95% CI = 0.11 ± 0.005);

5 Within each pair, co-occurrence in the receding tide, i.e., at the start of a tidal interval, does not predict co-occurrence in the advancing tide, i.e., the end of a tidal interval (GLMM estimate = 0.31, z-value = 1.738, p-value = 0.08);

6 Pair-wise co-occurrence in the advancing tide is well predicted by the distance mismatch (difference in distance travelled between individuals in a pair) in the foraging period (4 — 9 hours post high tide) (GLMM estimate = -0.006, z-value = -2.72, p-value = 0.006).

Discussion

1 Red knot co-occurrence is low between tidal intervals, and pairs rarely associate more than would be expected by chance, suggesting that knots, like other waders[3,4], have no 'friends', i.e., that knot flocks are randomly mixed with no persistent non-random associations;

2 Over a tidal interval, the co-occurrence of the population drops to its lowest around low tide, when the area of exposed mudflats is highest. Co-occurrence is highest at high tide, when available surface area is lowest, suggesting that wader density and association is a result of environmental, and not social, drivers;

3 Low co-occurrence at low tide, when waders forage suggests that information transfer in knot flocks

a. happens at the high tide roost when most knots are closely associated, and takes the form of coarse-grained information on which individuals are 'informed'[2] about the location of rich foraging patches,

b. occurs at a smaller temporal scale than we can measure, and takes the form of locally successful or informed individuals — temporary 'producers' — rather than consistently more successful foragers — informed 'leaders';

4 Current technology produces position error, restricting our ability to accurately track individuals at very fine spatial scales — improvements here would enable testing of co-occurrence at smaller distances;

5 Finally, association may occur at larger scales than tested here[5], however, this introduces questions of scale selection.

Acknowledgements We thank Emma Penning, Eva Kok, Frank van Marseveen, & Anne Dekinga for the tracking data. Thanks also to Bram Fey, Hein de Vries, Dave Huijsman & NIOZ technical staff for the ATLAS system. Thanks to Rijkswaterstaat for Harlingen harbour water level data.

References **1.** Bijleveld et al. 2015. Benefits of foraging in small groups: An experimental study on public information use in red knots *Calidris canutus*. *Behav. Processes*. **2.** Bijleveld et al. 2010. Beyond the information centre hypothesis: communal roosting for information on food, predators, travel companions and mates? *Oikos*. **3.** Myers 1983. Space, time, and the pattern of individual associations in a group-living species: sanderlings have no friends. *Behav. Ecol. Sociobiol.* **4.** Conklin & Colwell 2008. Individual associations in a wintering shorebird population: do dunlin have friends? *J. Field. Ornith.* **5.** Harrington and Leddy 1982. Are wader flocks random grouping? A knotty problem. *Wader Study Group Bull.*