

Individual associations in a wintering shorebird population: do Dunlin have friends?

Jesse R. Conklin¹ and Mark A. Colwell

Department of Wildlife, Humboldt State University, Arcata, California 95521, USA

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ABSTRACT. Among shorebirds, many individuals make migratory and short-distance movements in large flocks, suggesting that stable social groups may persist within populations for days to months. We examined high-tide associations among individual radio-marked Dunlin wintering at Humboldt Bay, California, to determine if flocks represented stable social groups. The rate of co-occurrence of two individuals in the same flock was generally low (\bar{x} = 15% of surveys), and 86% of pairs co-occurred no more than expected by chance. Associations were ephemeral, lasting 1.1 consecutive high tides on average. Variation in co-occurrence reflected individual fidelity to roosts, as well as population-wide differences in space use with precipitation and time of day. Dunlin flock composition was fluid, and individuals appeared to associate by chance according to shared attraction to common roosts. Our findings are consistent with predictions for a highly mobile, generally nonterritorial, long-distance migrant for which stable social associations have no clear benefit.

SINOPSIS. **Asociaciones entre individuos en una población durante el invierno: ¿Tienen amigos los *Calidris alpina*?**

En las especies de aves playeras, muchos individuos migran y también realizan movimientos de corta distancia como parte de bandadas grandes, lo cual podría indicar que grupos sociales estables persisten dentro de poblaciones para un periodo de días hasta meses. Examinamos las asociaciones durante la marea alta entre individuos de *Calidris alpina* marcados con radios cuales inviernaron en la Bahía de Humboldt, California, para determinar si las bandadas representaban grupos sociales estables. La tasa de ocurrencia de dos individuos en la misma bandada generalmente fue baja (\bar{x} = 15% de las muestras), y el 86% de las parejas no se encontraban en la misma bandada en un nivel significativo. Las asociaciones fueron efímeras, durando un promedio de 1.1 mareas altas consecutivas. La variación en la ocurrencia de las parejas en la misma bandada reflejaba la fidelidad a nivel individual a sus dormideros, así como las diferencias a nivel poblacional en el uso del espacio en relación a la precipitación y a la hora del día. La composición de las bandadas de *Calidris alpina* fue fluida y los individuos parecían asociarse al azar de acuerdo a la atracción a dormideros comunes. Nuestros resultados son consistentes con las predicciones hechas para una especie migratoria de larga distancia caracterizada por ser muy móvil y generalmente no-territorial, para la cual las asociaciones sociales estables no tienen un beneficio claro.

Key words: association, *Calidris alpina*, co-occurrence, Dunlin, nonbreeding, roosts, shorebirds

Nonbreeding shorebirds (suborder Charadrii) are among the most gregarious of birds. In many species, individuals make migratory and short-distance movements in large flocks, suggesting that stable social groups may persist within populations for days to months. Understanding social dynamics is essential to conservation of migratory shorebirds because estimates of population size and relative use of different sites often rely on assumptions of random distribution of individuals within a population. The validity of such assumptions would be compromised where persistent individual associations exist (Harrington and Leddy 1982).

The likelihood of stable social groups should vary with interspecific differences in migration strategy and nonbreeding social structure. For example, dominance hierarchies in a population of Ruddy Turnstones (*Arenaria interpres*) led to persistent nonrandom associations among individuals throughout the nonbreeding season (Metcalf 1986). By contrast, the composition of Sanderling (*Calidris alba*) flocks appears to be fluid (Myers 1983, Roberts and Evans 1993). Myers (1983) argued that cohesive social groups were unlikely in Sanderlings because the costs of maintaining associations or excluding other individuals probably outweighed any benefits. However, wintering Red Knots (*C. canutus*) appeared to distribute themselves nonrandomly, even after a round-trip migration to Arctic breeding grounds (Harrington and Leddy 1982).

¹Corresponding author. Email: conklin.jesse@gmail.com

Furness and Galbraith (1980) reported similar findings for color-marked Redshanks (*Tringa totanus*).

Since these observations, few investigators have examined associations among individual nonbreeding shorebirds, despite the increased use of radio-telemetry that allows continuous monitoring of associations. We describe patterns of high-tide association among radio-marked Dunlin (*C. alpina pacifica*) wintering at Humboldt Bay, California, and examine the influence of season, time of day, age, and roost site fidelity on these associations.

METHODS

Study area. Humboldt Bay is a Western Hemisphere Shorebird Reserve Network international site (<http://www.whsrn.org/>) in coastal northern California. The bay is 22.5 km long and 7.2 km wide at its widest point, with 62.4 km² area of water overlaying tidal flats at mean high tide. Two uneven high and low tides occur every 24 h, with nocturnal high tides lower than diurnal high tides in winter. The bay consists of three basins, with Arcata Bay being the largest and northernmost (Fig. 1). The wintering population of Dunlin at Arcata Bay includes about 10,000–12,000 individuals (JRC, unpubl. data), and the high fidelity of radio-marked Dunlin to Arcata Bay (Conklin and Colwell 2007) suggests that little mixing occurs with Dunlin wintering in south Humboldt Bay. We identified 86 roost sites used by radio-marked Dunlin during high tide (Fig. 1), with 25 used only by day, 27 only at night, and 34 both day and night (Conklin and Colwell 2007).

Radio-telemetry. For details of radio attachment, tracking, and GIS methods, see Conklin and Colwell (2007). We captured Dunlin at a tidal flat where dense feeding flocks formed before rising tides forced them off the bay. We staggered captures throughout each year, and the number of days tracked per bird varied from 1 to 38 d. As a result, the number of Dunlin with active radios at any time varied from two to nine. We determined Dunlin age by plumage, and sex by culmen length (Page 1974). We tracked birds during the 2 h bracketing predicted high tides. From 24 November 2003–11 March 2004 (hereafter Yr 1), we tracked 22 individuals during 102 diurnal and 66 nocturnal high tides. From 2 December 2004 to 15 March 2005 (Yr

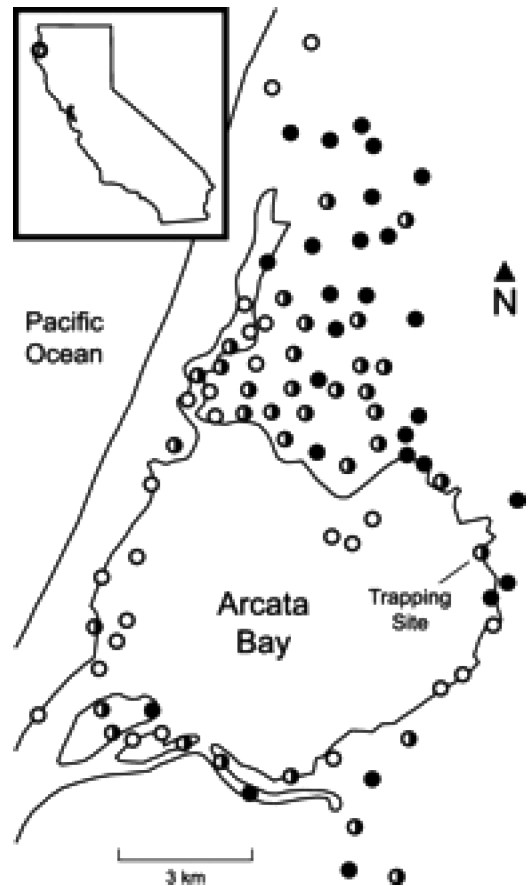


Fig. 1. Arcata Bay study area and locations of 86 high-tide roosts (open circle = day roost, filled circle = night roost, and half-filled circle = day and night roost) used by radio-marked Dunlin at Arcata Bay, California.

2), we tracked 25 individuals during 97 diurnal and 84 nocturnal high tides. We defined day as the period from 30 min before sunrise to 30 min after sunset, and night as the remainder of the 24-h cycle. When possible, we estimated the number of Dunlin in the associated flock of each bird detected by telemetry. An individual contributed a maximum of one data point per high-tide survey.

Data summary and analysis. We defined co-occurrence as two individuals (Dunlin pairs) in the same flock. We analyzed pairs with at least 8 d (range = 8–33 d) of overlap in their tracking periods because, for among-pair comparisons, 8 d was the point where the standard

deviation of co-occurrence reached an asymptote. Because roost fidelity and habitat use differed between day and night (Conklin and Colwell 2007), we analyzed the two periods separately (102 diurnal and 81 nocturnal pairs). For each survey, we recorded a pair as either together (in the same roosting or flying flock) or apart (in different flocks, or only one of the pair detected). We disregarded surveys where neither bird was detected, but this occurred infrequently, with detection rates of 94% and 86% during diurnal and nocturnal surveys, respectively (Conklin and Colwell 2007). For each pair, we calculated a rate of co-occurrence (number of surveys together/number of total surveys), and averaged these for a population measure. We compared diurnal and nocturnal co-occurrence using the Wilcoxon paired-sample test ($N = 76$ pairs with adequate samples day and night).

We defined co-occurrence at the scale of the flock, and thus could have missed important associations if the population contained structure at a larger scale. To examine the effect of spatial scale, we recalculated diurnal co-occurrence based on whether a pair of Dunlin occurred at roosts whose geometric centers were ≤ 500 m, ≤ 750 m, and $\leq 1,000$ m apart. The effect of these scale adjustments was minimal. At the original and 500-m scales, average diurnal co-occurrence was 0.23, and increased slightly to 0.27 at 750 m, and 0.30 at 1,000 m. Therefore, we believe the roost was an appropriate scale for evaluating co-occurrence.

Our final sample included 36 Dunlin (18 first-yr and 18 adults; 23 males, three females, and 10 unknown sex). For each individual, we defined a primary roost as the one most often visited, and considered day and night separately. Only one bird had the same diurnal and nocturnal primary roost. We examined co-occurrence according to year, age, primary roost, and capture flock using Mann-Whitney two-sample tests. We could not evaluate the effect of sex due to the small number of females in the sample. To examine within-season trends, we determined the temporal midpoint of each pair's potential co-occurrence period, with 24 November being day 1 of the season and 11 March day 109. To examine environmental effects, we calculated mean daily precipitation (National Weather Service; <http://www.weather.gov/climate>) and mean verified peak tide height (National

Oceanic and Atmospheric Administration; <http://tidesonline.nos.noaa.gov>) for each pair.

Fidelity to primary roosts varied among individuals (Conklin and Colwell 2007). To examine the relationship between co-occurrence and the extent of movement among roosts, we divided pairs into three classes: (1) both members had fidelity less than the population mean, (2) one member each had above- and below-average fidelity, and (3) both members had above-average fidelity. We evaluated differences in co-occurrence among classes using Kruskal-Wallis nonparametric analysis of variance.

To compare observed rates of co-occurrence to expected values, we used a statistic described by Wilkinson (1985):

$$\chi^2 = \frac{(N_{ij} - \sum_{k=1}^{86} P_{ik}P_{jk}T)^2}{\sum_{k=1}^{86} P_{ik}P_{jk}T},$$

where N_{ij} is the number of times Dunlin i and j were observed together, T is the lesser of the number of times Dunlin i and j were observed, respectively, and P is the proportion of observations that Dunlin i spent at roost k ($df = 1$). The statistic compares observed co-occurrence to the expected value if two birds each randomly visited roosts in proportion to their observed use of specific roosts. The null model retains important biological information (roost preferences of individual birds) that is lost in simulations where birds are allowed to occur at roosts at random (Cairns and Schwager 1987, Roberts and Evans 1993). Thus, it discriminates between co-occurrence resulting from mutual attraction between birds, and that resulting from two birds coincidentally using the same locations without regard to each other.

One limitation of the statistic is its sensitivity to the number of days included in the comparison. For our data, the likelihood of a significant result was positively correlated with the number of days of potential co-occurrence. We believe this resulted from the dependence of roost choice upon environmental conditions (Conklin et al., in press) because the chance that roost choice would be decoupled from associated environmental conditions increased as the number of days in the randomization increased, inflating the chance that birds would appear at different roosts. To equalize this bias among pairs, we

restricted data to eight consecutive days chosen randomly from the available data for each pair.

To understand the strength of associations, we calculated (1) the proportion of co-occurrences on one high-tide survey that persisted to the next survey, and (2) the average run of co-occurrence (number of consecutive surveys the pair was together). To evaluate whether temporal patterns of co-occurrence deviated from random, we conducted, for each diurnal pair, a runs test for randomness (Zar 1999), where n_1 = number of high tides the pair was together, n_2 = number of high tides the pair was apart, and u = number of runs.

RESULTS

Flock size. During diurnal high tides, radio-marked Dunlin ($N = 36$) occurred in flocks ranging in size from 1 to 8,000 individuals. For each individual, flock size was highly variable from one diurnal high tide to the next; mean standard deviation was 69% of flock size (range = 32–100%). Mean flock size for individual Dunlin ranged from 831 to 4257 birds ($\bar{x} = 2522$).

Pairwise co-occurrence. Co-occurrence was low (Fig. 2; $\bar{x} = 0.15$), with no pairs co-occurring during more than 50% of high tides

and six pairs (8%) never occurring together. Diurnal co-occurrence ($\bar{x} = 0.23$; $N = 102$ pairs) was higher ($z = 6.4$, $P < 0.001$) than nocturnal co-occurrence ($\bar{x} = 0.05$, $N = 81$ pairs). During the day, 86% of pairs co-occurred at least once (max = 0.62). At night, 73% of pairs never co-occurred. Co-occurrence of one pair was 0.82, but neither bird was detected away from the nocturnal roost they shared so their association was consistent with independent attraction to the same roost. Diurnal co-occurrence of this pair was below average (0.21), suggesting that their nocturnal association was an artifact of roost choice.

Diurnal co-occurrence was higher in Yr 1 than in Yr 2 ($z = 2.4$, $P = 0.02$; Table 1), but nocturnal co-occurrence did not differ between years ($z = 0.07$, $P = 0.94$). Diurnal co-occurrence declined throughout the season in Yr 1 ($r^2 = 0.10$, $P = 0.04$), but not in Yr 2 ($r^2 = 0.002$, $P = 0.76$). There was no seasonal trend in nocturnal co-occurrence ($r^2 = 0.0004$, $P = 0.85$).

Diurnal peak tides were higher ($t_{100} = 3.1$, $P = 0.003$) in Yr 1 ($\bar{x} = 2.22$ m) than Yr 2 ($\bar{x} = 2.16$ m), but nocturnal high tides did not vary ($t_{79} = 1.85$, $P = 0.07$) between years (Y1 $\bar{x} = 1.85$ m, Y2 $\bar{x} = 1.88$ m). Pairs experienced higher tides during the day ($\bar{x} = 2.21$ m) than at night ($\bar{x} = 1.87$ m; paired $t_{75} = 22.3$,

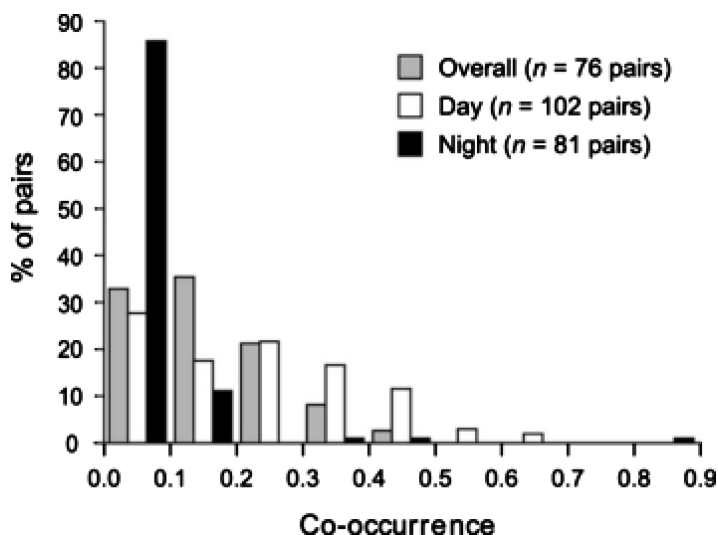


Fig. 2. Frequency distributions of overall ($\bar{x} = 0.15$), diurnal ($\bar{x} = 0.23$), and nocturnal ($\bar{x} = 0.05$) pairwise co-occurrence of Dunlin at Arcata Bay, California.

Table 1. Diurnal and nocturnal mean pairwise co-occurrence of Dunlin by year, age, primary roost, capture flock, and roost fidelity.

	Day		Night	
	<i>N</i>	Co-occur	<i>N</i>	Co-occur
All pairs	102	0.23	81	0.05*
Year				
1	41	0.28*	35	0.04
2	61	0.20	46	0.05
Age				
Same	45	0.28	36	0.06
Different	57	0.21	45	0.04
Primary roost				
Same	29	0.30*	4	0.41*
Different	73	0.20	77	0.03
Capture flock				
Same	13	0.27	12	0.08
Different	89	0.22	69	0.04
Roost fidelity ^a				
Low-low	35	0.18*	28	0.05
High-low	56	0.25	39	0.03
High-high	11	0.31	14	0.09

Significant differences indicated by *

^aIndicates primary roost fidelity of the two individuals; either below ("low") or above ("high") the population mean.

$P < 0.001$). Throughout the season, diurnal peak tides decreased ($r^2 = 0.46$, $P < 0.001$) and nocturnal peak tides increased ($r^2 = 0.43$, $P < 0.001$). Mean peak tide was not significantly correlated with either diurnal ($r^2 = 0.01$, $P = 0.36$) or nocturnal ($r^2 = 0.04$, $P = 0.07$) co-occurrence.

Daily precipitation was higher ($t_{100} = 3.1$, $P = 0.003$) in Yr 1 ($\bar{x} = 0.74$ cm) than in Yr 2 ($\bar{x} = 0.49$ cm), and decreased during the season during both Yr 1 ($r^2 = 0.2$, $P = 0.003$) and Yr 2 ($r^2 = 0.51$, $P < 0.001$). Diurnal co-occurrence was positively correlated with mean daily precipitation in Yr 1 (Fig. 3a; $r^2 = 0.22$, $P = 0.02$), but not in Yr 2 (Fig. 3b; $r^2 = 0.01$, $P = 0.6$). Nocturnal co-occurrence was not correlated with precipitation ($r^2 = 0.01$, $P = 0.29$).

Pairs that shared a primary roost co-occurred more frequently than pairs with different primary roosts (Table 1; day: $z = 2.8$, $P = 0.002$; night: $z = 3.2$, $P < 0.001$). Co-occurrence did not differ between same-age and different-age pairs (day: $z = 1.4$, $P = 0.83$; night: $z = 1.3$, $P = 0.1$) or between pairs captured from the same flock and those captured on different

days (day: $z = 1.03$, $P = 0.31$; night: $z = 1.2$, $P = 0.12$). Pairs where both members had higher than average roost fidelity co-occurred more frequently than other pairs during the day ($H_2 = 6.6$, $P = 0.04$), but not at night ($H_2 = 1.2$, $P = 0.55$).

During the day, 14 of 102 pairs co-occurred more frequently than expected at random (Table 2). These 14 pairs were distributed proportionately in our sample with regard to year ($\chi^2_1 = 0.4$, $P = 0.51$), age ($\chi^2_1 = 1.8$, $P = 0.18$), primary roost ($\chi^2_1 = 0.9$, $P = 0.35$), and capture flock ($\chi^2_1 = 0.4$, $P = 0.54$), that is, same-age, same-primary roost, and same-capture flock pairs were no more likely to co-occur nonrandomly than other pairs. Pairs were no more likely to co-occur nonrandomly as roost fidelity increased ($\chi^2_2 = 3.9$, $P = 0.14$).

Diurnal and nocturnal co-occurrence of the same Dunlin pair were not correlated ($r^2 = 0.01$, $P = 0.55$, $N = 76$). At night, only one of 81 pairs co-occurred more frequently than expected, and this pair was not among the 14 pairs that co-occurred more than expected during the day.

Persistence of associations. Associations between individual Dunlin were ephemeral (Table 3). Considering all high tides, the average duration of association was 1.1 consecutive tides, and only three of 296 runs (1%; maximum = 6 tides) exceeded four consecutive tides. Few (7%) diurnal high-tide associations persisted to the subsequent nocturnal high tide. Nocturnal associations, although less frequent, were more likely (44%) to persist to the subsequent diurnal high tide. Considering day and night separately, 40% of diurnal associations reoccurred on the next diurnal high tide, and 39% of nocturnal associations reoccurred on the next nocturnal high tide. Only eight of 250 diurnal (3%; maximum = 9 d) and one of 31 nocturnal (3%; maximum = 5 nights) runs of co-occurrence exceeded four consecutive high tides.

The runs test indicated that likelihood of co-occurrence on a given diurnal high tide was generally independent of the previous high tide. For 92% of pairs (70 of 76 pairs co-occurring at least twice), the temporal pattern of co-occurrence did not differ from random.

DISCUSSION

We found no evidence of stable social groups within the Dunlin population at Arcata Bay.

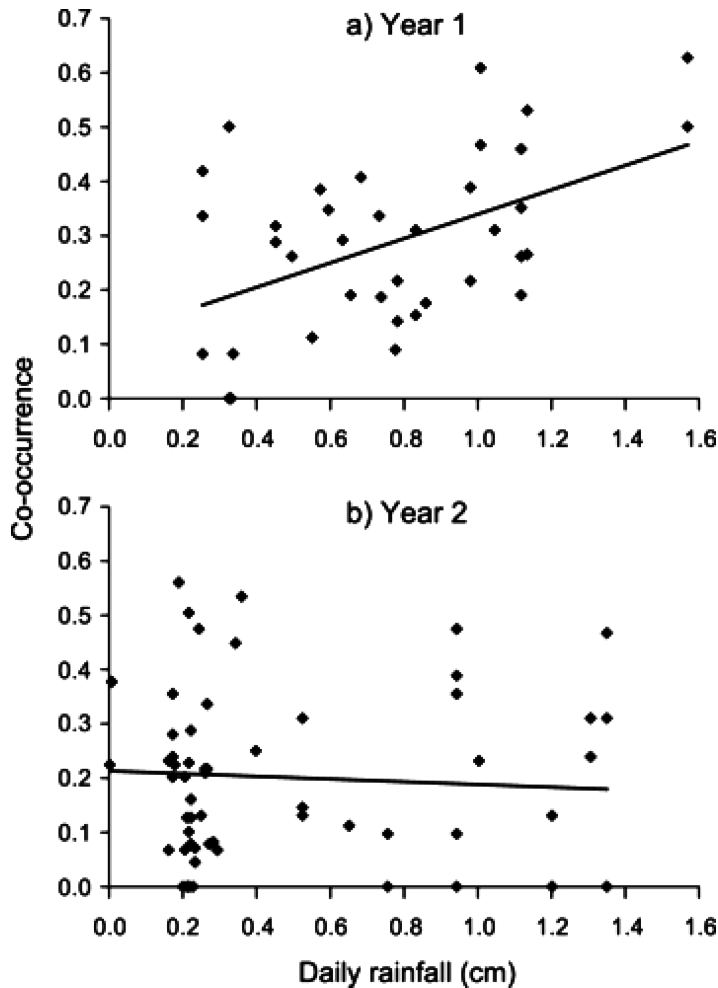


Fig. 3. Diurnal co-occurrence of Dunlin at Arcata Bay was significantly correlated with precipitation in Yr 1 ($N = 41$ pairs), but not in Yr 2 ($N = 61$ pairs).

Pairs did not move among roosts together, and ephemeral associations appeared to result from common roost choice rather than persistent flock composition. Similar results have been reported for Sanderlings (Myers 1983, Roberts and Evans 1993); both Dunlin and Sanderling flocks appear to represent random samples of individuals in the population. This is surprising because *Calidris* sandpipers move about in conspicuous flocks, so movements by individuals are clearly not independent of the movements of others. Even without selection pressure to maintain cohesive groups (Myers 1983), associations should persist until there is a reason for individuals to separate. The ephemeral nature of

high-tide associations suggests that: (1) Dunlins are not severely limited by roost choice, (2) numerous individual strategies of space use exist in the population, or (3) randomness itself may be a strategy.

At Arcata Bay, roost use by Dunlin differed between diurnal and nocturnal high tides (Conklyn and Colwell 2007). During the day, Dunlin roosted in large flocks, but often switched roosts between consecutive high tides. At night, Dunlin occurred in small flocks, but were more faithful to their roosts. Assuming fluid flock composition, these patterns predict precisely the differences in co-occurrence we observed: most diurnal pairs roosted together occasionally,

Table 2. Diurnal co-occurrence of Dunlin was greater than expected by chance for 14% of pairs that were distributed evenly by year, age, primary roost, capture flock, and roost fidelity (no significant χ^2 comparisons).

	N	> random	= random	% > random
All pairs	102	14	88	14
Year				
1	41	4	37	10
2	61	10	51	16
Age				
Same	45	9	36	20
Different	57	5	52	9
Primary roost				
Same	29	2	27	7
Different	73	12	61	16
Capture flock				
Same	13	3	10	23
Different	89	11	78	12
Roost fidelity ^a				
Low-low	35	2	33	6
High-low	56	9	47	16
High-high	11	3	8	27

^aIndicates primary roost fidelity of the two individuals; either below (low) or above (high) the population mean.

but not consistently, whereas nocturnal pairs exhibited either very high or very low co-occurrence, depending on whether they shared a primary roost.

Many studies have revealed high-roost site-fidelity among nonbreeding *Calidris* sandpipers (Warnock and Takekawa 1996, Rehfisch et al. 1996, 2003, Dias et al. 2006, Leyrer et al. 2006). Site fidelity may be one strategy by which individuals maintain social groups. Conversely, site fidelity may naturally result from groups remaining together. The relationship between

site fidelity and co-occurrence may, therefore, often be difficult to disentangle. However, Dunlin at Arcata Bay exhibited relatively low fidelity to roosts, particularly during the day (Conklin and Colwell 2007), providing the opportunity to examine individual associations without the confounding effect of site fidelity.

Previous studies have shown that individual mobility influences the rate of co-occurrence with other individuals. For Ruddy Turnstones, co-occurrence increased with seasonal increases in mobility (Metcalf 1986). Although stable associations persisted during these times, individuals came into contact with more of the population, increasing overall co-occurrence. Perhaps by the same mechanism, highly mobile Sanderling pairs co-occurred at higher rates than less mobile pairs, despite the lack of stable associations (Roberts and Evans 1993). Our study demonstrates that the relationship between mobility and co-occurrence is not necessarily static. During the day, more sedentary pairs had higher co-occurrence, apparently because shared fidelity to a roost increased their association. However, at night, higher fidelity did not result in higher overall co-occurrence because smaller flocks limited the number of other individuals encountered.

Seasonal trends in co-occurrence may result from changing environmental conditions that influence space use. For example, co-occurrence of Sanderlings increased as beach erosion reduced availability of foraging sites (Myers 1983). We expected co-occurrence to increase with tide height because higher tides reduce available habitat and may constrain Dunlin to fewer roosts. Accordingly, both co-occurrence and peak tides were higher during the day than at night. However, tide height was unrelated to variation in both diurnal and nocturnal co-occurrence. We

Table 3. Most high-tide associations between two Dunlins did not persist to the next high tide.

	Persisted ^a	Separated ^b	% Persisted	N runs	Mean run (no. of tides) ^c
Day-night	13	184	7	296	1.11
Night-day	21	27	44		
Day-day	173	258	40	250	1.54
Night-night	19	30	39	31	1.65

^aPair observed together on both high tide a and $a + 1$.

^bPair observed together on high tide a and apart on high tide $a + 1$.

^cNumber of consecutive high tides pair was observed together.

also predicted a positive relationship between co-occurrence and precipitation. Use of grazed pastures by Dunlin has been strongly tied to precipitation (Colwell and Dodd 1997, Shepherd 2001, Evans Ogden 2002), and diurnal high-tide Dunlin flocks were larger in pasture than in other habitats in our study (Conklin and Colwell 2007). Accordingly, both precipitation and diurnal co-occurrence were higher in Yr 1 than in Yr 2. However, within-year variation in diurnal co-occurrence was related to precipitation only in Yr 1. Precipitation had little apparent influence on space use at night; pasture was the primary high-tide habitat during both wet and dry periods (JRC, unpubl. data), and there was no evidence of large congregations (Conklin and Colwell 2007). Accordingly, nocturnal co-occurrence did not vary with rainfall or year.

Although the relationship between predation pressure and individual associations has yet to be explicitly studied, frequent attacks by raptors (JRC, pers. obs.), particularly Peregrine Falcons (*Falco peregrinus*), may have contributed to the randomness of diurnal Dunlin flocks in our study. Shorebird flocks often coalesce in the presence of raptors (Myers 1984), and such behavior could arguably increase co-occurrence. However, these defensive congregations may be temporary and variable in membership, particularly because raptors separate flocks into smaller groups for easier capture. At night, Dunlin use different anti-predator strategies, occurring in smaller flocks (Evans Ogden 2002, Conklin and Colwell 2007) and remaining motionless rather than flushing when disturbed (Mouritsen 1992). These strategic differences predict lower overall co-occurrence, but greater persistence of association at night, consistent with our observations.

Between successive high-tide observations, birds generally departed to feed on tidal flats, returning to roosts when flooding tides inundated the bay. Although we lack low-tide co-occurrence data, mixing of the population occurs at this time and 50–90% of the local Dunlin population often occurs in a single feeding flock (JRC, pers. obs.). Thus, individuals come into contact with most others in the population during the course of a nonbreeding season, and probably over much shorter intervals. This may explain why birds captured in the same feeding flock, a potential source of bias in our study, were no more likely to co-occur than other pairs.

The lack of persistent associations in Dunlin flocks places them with Sanderlings as extreme examples of openness in shorebird social groups. Many of the reasons to expect this pattern in Sanderlings (Myers 1983) apply to Dunlin as well, including high mobility, lack of obvious individual plumage characteristics, long-distance migration with age- and sex-related timing differences, and apparent lack of reciprocal or nepotistic behavior. Persistent associations are more likely in less migratory species that demonstrate long-term defense of nonbreeding territories, such as oystercatchers and curlews (Colwell 2000). However, considerable temporal and spatial variation in association patterns may exist even within a species due to the influence of weather, time of day, predation pressure, and availability of roosting or foraging sites.

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