Journal of Applied Ecology 2007
44, 196–209

Shorebird roost-site selection at two temporal scales: is human disturbance a factor?

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Summary

1. Roost-site selection in shorebirds is governed by ambient factors, including environmental conditions and human disturbance. Determination of the extent to which these factors affect roost use and the associated implications for shorebird habitat protection is important for conservation strategies and informed management of human recreational use of these habitats. Shorebird conservation as a whole is a high priority world-wide because a large proportion of shorebird species is in decline. However, little is understood about the consistency of roost use by different species, what conditions affect species-specific roost-site selection, and at what spatial and temporal scales conditions influence selection.

2. We studied high-tide roost-site selection by eight species of non-breeding shorebirds on a critically important stopover and wintering refuge. We calculated spatial and temporal variability in roost use for each species based on counts and consistency of incidence. We then examined roost-site selection in relation to structural, environmental and human disturbance factors, and how this varied across spatial and temporal scales.

3. Most roosts were used less than 50% of the time, although larger roosts were used more consistently. This varied among species, with red knot *Calidris canutus* tending to concentrate at a few roosts and American oystercatcher *Haematopus palliatus*, dowitcher *Limnodromus griseus* and *Limnodromus scolopaceus* and ruddy turnstone *Arenaria interpres* more diffusely distributed among roosts.

4. At an annual scale, the principal factors affecting shorebird presence at roosts were roost length (size), local region, substrate and aspect. The extent and direction of these effects varied among species. Among years, red knots avoided roosts that had high average boat activity within 1000 m, but disturbance did not appear to be a factor for other species.

5. Daily roost use was influenced primarily by wind speed and the ability of roosts to provide shelter from the wind. Only dowitchers appeared to track daily disturbance, avoiding prospective roosts when boat activity within 100 m was high.

6. *Synthesis and applications*. Our findings emphasize the need to consider species-specific differences in temporal- and spatial-scale effects of roost-site selection factors, including human disturbance, when employing conservation measures for shorebirds. We suggest that conservation management should aim to provide a wide range of potential roosts (both natural and artificial) that could be used under different wind conditions and that are within reasonable travelling distance of preferred feeding areas. Roost use is often highly variable, and monitoring efforts must take this into account before making inferences about changes in use or selection of roost sites.

Key-words: habitat selection, high-tide roost, human disturbance, recreational boats

Journal of Applied Ecology (2007) **44**, 196–209
doi: 10.1111/j.1365-2664.2006.01248.x

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Introduction

Because intertidal feeding grounds are typically only available during low tides, shorebirds using coastal habitats tend to aggregate at roosts during high tides to preen and rest (Hale 1980). Roost-site selection may be governed by any one or more factors, including energy limitations (Warnock & Takekawa 1996; Burton & Evans 1997; Rogers *et al*. 2006; Van Gils *et al*. 2006), predation risk (Cresswell 1994; Rogers *et al*. 2006), disease, abiotic conditions (Cramp & Simmons 1983; Burton, Evans & Robinson 1996; Rehfisch, Insley & Swann 2003; Rogers *et al*. 2006), habitat limitation (Gill, Norris & Sutherland 2001), demographic structure (Rehfisch *et al*. 1996; Rehfisch, Insley & Swann 2003) and human disturbance (Pfister, Harrington & Lavine 1992; Kirby, Clee & Seager 1993; Webb & Blumstein 2005). The configuration and availability of high-tide roosts can affect the fitness of shorebirds by determining the profitability of accessing high-quality foraging areas (Van Gils *et al*. 2006). Extensive movements among roosts might also deplete crucial energy stores (Rehfisch *et al*. 1996) and increase predation risk (Lima 1998a). However, little is known about the relative importance of individual environmental, biological and anthropogenic factors to roost-site selection in shorebirds (Rehfisch *et al*. 1996), the temporal and spatial scales at which these factors influence selection (Sanzenbacher & Haig 2002; Rehfisch, Insley & Swann 2003), or the consistency and fidelity of roost use within and among years (Pearce-Higgins 2001; Colwell *et al*. 2003).

Human disturbance, or the temporary loss of habitat because of human activities (Nisbet 2000), has gained increasing attention as a probable determinant of roost-site selection in shorebirds (Pfister, Harrington & Lavine 1992; Kirby, Clee & Seager 1993; Burton, Evans & Robinson 1996; Durrell *et al*. 2005). Disturbance can affect birds by increasing energetic costs, limiting access to profitable areas and enhancing predation risk (Fox & Madsen 1997; Bechet, Giroux & Gauthier 2004). Studies have shown human disturbance of roosting shorebirds to be related to local population declines (Pfister, Harrington & Lavine 1992; Tubbs, Tubbs & Kirby 1992), lowered body condition (Durrell *et al*. 2005), regional habitat shifts (Burton, Evans & Robinson 1996) and local avoidance behaviour (Kirby, Clee & Seager 1993). One source of disturbance that has been connected to long-term roost abandonment in shorebirds is boat traffic (Burton, Evans & Robinson 1996). Species with high roost-site fidelity and minimal movement among roosts might be most at risk from human disturbance and therefore require particular attention (Rehfisch, Insley & Swann 2003). Yet there is a shortage of empirical data concerning the local and regional movement patterns of avian species in general (Wiens 1994) and shorebirds in particular (Haig, Mehlman & Oring 1998; Sanzenbacher & Haig 2002).

Little is known about the spatial scale at which shorebirds react to human disturbance or other factors that may affect roost-site selection. The issue of spatial and temporal scales has long been recognized as an important consideration when looking at behavioural processes such as habitat selection (Wiens 1976; Wiens, Rotenberry & Van Horne 1987). Habitat selection models can be scale dependent, and individuals may show multiscale responses to a single resource (Turner, Gardner & O'Neill 2001; Thompson & McGarigal 2002). Individual species' responses to human disturbance in particular are highly likely to be scale dependent, as studies of response to natural predation risk have been shown to be sensitive to scale (Lima 1998b). Reaction to human disturbance can be further confounded by habituation, about which very little is currently understood (Nisbet 2000), particularly with respect to the spatial and temporal scales at which habituation may influence behaviour and habitat selection (Webb & Blumstein 2005).

Several studies have demonstrated that avian reactions to human disturbance can be affected by the temporal context in which the disturbance takes place. McGowan, Cresswell & Ruxton (2002) found that red knot *Calidris canutus* responsiveness to disturbance was affected by small-scale temporal variation in the environment, such as changes in windspeed and air temperature. Ronconi & St Clair (2002) observed that black guillemots *Cepphus grylle* were more vulnerable to boat disturbance during low tides than high tides, leading to setback recommendations that varied as much as 2 km between tidal stages. Cliff-nesting seabirds react differently to human visitor groups that vary in size and their reactions have been shown to fluctuate temporally (Beale & Monaghan 2005). One way to determine the scales at which individual species make habitat decisions is to take an organism-centred approach, defining the scale of observation and measurement on the basis of characteristics of the study animal (Wiens 1976; Mitchell, Lancia & Gerwin 2001; Thompson & McGarigal 2002).

We studied high-tide roost-site selection in eight species of non-breeding shorebirds on a critically important stopover and wintering refuge in South Carolina, USA. We calculated the spatial and temporal variability in roost use for each species. We examined roost-site selection at two temporal scales: (i) among years (i.e. selection among roosts) and (ii) within years (i.e. daily selection within roosts). At the annual scale, we determined the relationships between the occupancy of shorebirds at roosts, structural characteristics of the roost and the average level of boating disturbance within the vicinity of roosts at three spatial scales. At the daily temporal scale, we examined the relationships between daily occupancy of shorebirds at each roost, environmental conditions and daily levels of boat disturbance within the vicinity of roosts at the same three spatial scales. Our objectives were to determine the extent to which different factors affected roost-site selection, the scales at which these factors operated and how these compared among species.

Methods

Our study was conducted on the Cape Romain National Wildlife Refuge (CRNWR), approximately 50 km north of Charleston, South Carolina, USA (33·10°N, 78·43°W). The CRNWR contains nearly 26 000 ha of protected saltmarsh, shallow bays and barrier islands, 11 300 ha of which have been assigned protection under the National Wilderness Preservation System. The refuge is included in the Western Hemispheric Shorebird Reserve Network (WHSRN) because of its importance as a breeding, stopover and overwintering site for shorebirds (Marsh & Wilkinson 1991). Wetlands on the refuge are mainly comprised of saltmarsh habitats, dominated by saltmarsh cordgrass *Spartina alterniflora* interspersed with other perennial marsh grasses and rushes. Bays on the refuge are shallow, depths averaging slightly more than 2 m at high tide, with more than 50% exposed as tidal flats during low tide. There are several uninhabited barrier islands and oyster *Crassostrea virginica* shell rakes are found throughout the refuge. The islands provide the only sandy beach roosting habitat for shorebirds. The rakes are located primarily along the Intra Coastal Waterway (ICW), at the mouths of tidal creeks and at the bay perimeter.

The Cape Romain region is currently the third most popular site for recreational shrimp baiting in South Carolina (Low 1998), a human activity that has increased substantially in the region over the last two decades. Recreational shrimp baiting entails placing bait balls (fish meal/clay aggregates) on the bay or tidal creek bottoms to attract shrimp, which are then captured by cast nets or seines from small boats with outboard engines. The CRNWR has experienced a sharp increase in shrimp-baiting trips: in 1988, 96 shrimp baiting trips; 1993, 6896 trips; 1997, 20 419 trips (Low 1998). Based on trailer counts, more than 300 boats have been estimated to be on CRNWR waters during a single day [S. Cofer-Shabica, United States Fish and Wildlife Service (USFWS), personal communication]. The shrimp-baiting season lasts 60 days, beginning on the second Friday of September, and is set to coincide with the period when larger Atlantic white shrimp *Penaeus setiferus* are moving offshore.

SHOREBIRD COUNTS

We used high-tide aerial photographs taken in January 1999 (1 : 24 000; USFWS) to identify potential roost sites along bays for shorebird surveys. The criteria for designation as a potential roost site were: (i) exposure at high tide, (ii) lack of vegetation, (iii) sand or shell substrate and (iv) a minimum area of 100 m^2. These criteria were based on knowledge of basic shorebird roosting biology, i.e. the visibility required for predator defence and an area large enough to support a medium to large flock (≥ 100 birds). Sites were removed from sampling if they proved to be inappropriate after initial visits (i.e. had tree or tall shrub growth along the margin of the roost) and several sites were added in 2000. We sampled 16 potential roosts in 1999 and 32 potential roosts in 2000, 2001 and 2002.

We conducted 23 surveys between 1999 and 2002. Each survey consisted of 15–32 roost counts and varied according to year (fewer roosts were surveyed in 1999) and accessibility because of weather conditions (island sites were difficult to survey during high winds). Each survey took 3–8 high-tide cycles and was completed within a 3–10-day period. Because of practical constraints, the order in which roosts were surveyed was not randomized but initiated in several different regions of the refuge.

The methods used for counting birds at roost sites were based on those described by Marsh & Wilkinson (1991). We conducted all counts within 2 h of high tide, when birds tended to be concentrated on roosts. Counts rarely included birds on the marsh-facing side, which may have provided roosting habitat for some individuals (Marsh & Wilkinson 1991), although when we were able to observe marsh-facing banks we noted that shorebird numbers were low (i.e. generally < 10 individuals). During surveys each roost site was approached by boat at a tangential angle, to minimize disturbance (Burger & Gochfeld 1981). In the case of large flocks, flock size, by species, was initially estimated by groups of five birds in case of premature flushing. Birds were then counted individually to obtain a second estimate of flock size. Marsh & Wilkinson (1991) determined that counts from the two methods tend to differ by less than 5%. All counts conducted from the boat were made with 8× or 10× magnification binoculars, and flocks on front beaches were surveyed on foot, using 60× magnification spotting scopes in addition to binoculars.

We estimated the locations of all boats within 1000 m of each roost during each survey. From a stationary, spatially referenced position (Trimble Geo Explorer II® GPS, Trimble Navigation Ltd, Sunnyvale, CA), we obtained azimuth readings coupled with Bushnell Rangefinder distance readings, which were later used to map the location of each boat (GPS Pathfinder Office V.2.90®; Trimble Navigation Ltd). Prior to shorebird counts, wind speed and direction were recorded using an anemometer (accuracy to 0·80 km h^{-1}). Sampling time periods were noted and used to derive minutes past sunrise, moon phase, minutes before or after low tide, and water depth at low tide (Tides and Currents software package V.2·5; Nobeltec, Portland, OR). Several habitat variables were also estimated for each roost site: slope (degrees; ElectraLevel Electronic Water Level, Zircon Corporation, Campbell, CA), presence or absence of a north-, south-, east- or west-facing slope that terminated at a shoreline, and substrate (shell, sand or both).

GIS PROCESSING

The 1999 aerial photographs were orthorectified (UTM projected coordinate system, NAD83 datum). Differential correction of all 1999 boat positions was conducted using Charleston, South Carolina, base station files.

Positions from 2000 to 2002 were not corrected under the assumption that a 5–15 m accuracy in open habitats (Roper 2005) was acceptable given the scale of our study. A feature layer depicting roosts surveyed was constructed (ArcGIS, V.8·3, ESRI Inc., Redlands, CA). Roost boundaries were delineated based on image coloration and knowledge of the site, and roost length was calculated using a line drawn along the edge of the shoreline approximately 5 m from the water's edge. A point feature layer representing boat activity was overlaid on the roost layer, and numbers of boats within 100-, 500- or 1000-m buffers around each roost were tallied for each sample. Roosts were grouped into six regions in order to account for local conditions that may have affected roost selection, such as proximity to forage areas (Van Gils *et al*. 2006): Bull's Bay, Marsh Island, White Banks, Raccoon Key, Outer Beaches, and Cape Romain Harbor.

STATISTICAL ANALYSES

Consistency of roost use

We analysed count data of eight relatively abundant species or species groups: American oystercatcher *Haematopus palliatus*, short-billed dowitcher *Limnodromus griseus* and long-billed dowitcher *Limnodromus scolopaceus*, dunlin *Calidris alpina*, small 'peep' sandpipers (small calidrid sandpipers including the semipalmated sandpiper *Calidris pusilla*, western sandpiper *Calidris mauri* and least sandpiper *Calidris minutilla*), red knot, ruddy turnstone *Arenaria interpres*, sanderling *Calidris alba* and whimbrel *Numenius phaeopus*. We determined species incidence and spatial concentration as defined by Colwell *et al*. (2003). Species incidence is the proportion of total surveys conducted at a roost in which at least one individual of the species is present, and is reported for each species as the mean and SD among surveys. We used linear regression to analyse the relationship between roost size and incidence. Spatial concentration is the proportional abundance of a species among roosts, as calculated using the Shannon–Wiener index ($H' = -\sum_1^N p_i \ln p_i$), where p_i is a species' proportional abundance at N roosts surveyed during a sample period, with possible values ranging from 0·0 (all individuals occurring at one roost) to approximately 3·4 (depicting an even distribution among 32 roosts). We did not count birds on each roost during every survey (i.e. roost counts ranged from 15 to 32 roosts per survey), thus our H' values do not provide a true estimate of the degree of concentration of each species. However, they do provide an indication of relative concentrations of our focal species.

Roost-site selection

Inferences about the relationships among abiotic habitat parameters, shrimp-baiting activities and shorebird roost site use were derived from an information-theoretic approach (Burnham & Anderson 1998). We defined two sets of candidate models prior to analysis based on biological knowledge about potential correlates of habitat selection on a seasonal scale. One set of models was used to make inferences about selection among roosts among seasons, and the second set was used to make inferences about selective use of each roost within seasons. We used polytomous logistic regression to model count data as a function of predictor variables. This method allowed us to model relationships of response variables with more than two response levels. Two or three flock-size categories were defined for each species prior to analysis, based on distribution of the data. These categories were treated as ordinal data and served as the dependent parameters in models.

Akaike's information criterion adjusted for small sample size ($\mathrm{AIC_c}$) was used to determine the best approximating model of habitat selection at each scale (Burnham & Anderson 1998). Models that fell within two $\mathrm{AIC_c}$ points of the lowest-ranked model were considered strong candidates. We present parameter estimates and 95% confidence intervals of the weighted averages from all strong candidate models, and incorporated model-selection uncertainty in our estimates of variance and hence confidence intervals (Burnham & Anderson 1998). All P-values presented were derived from the strongest candidate model, and we accepted significance at $P \le 0{\cdot}05$. We also present 95% confidence limits of odds ratios for all significant parameters derived from the strongest candidate model. Odds ratios can be defined as the change in odds for having a flock present when there is an increase of one unit in the corresponding parameter (SAS Institute 1999). Odds ratios could not be calculated for parameters that were incorporated in an interaction.

Annual roost selection

The response variable in each model for predicting roost selection across years consisted of the flock-size category of each species at each roost site (Table 1). Responses consisted of either two or three flock-size categories. For instance, dunlin tended to be present only in large flocks, whereas dowitcher was often found in small or large flocks (Table 1). The four candidate models included a reduced model, containing only roost structural characteristics and region, and three disturbance models, which also incorporated the number of boats, averaged across years, around each roost at three spatial scales. Models included one or more of the following general roost characteristics: slope, presence or absence of north, south, east and west shore-facing slope, substrate, length, region and average number of boats within 100, 500 and 1000 m of the roost. Continuous variables were standardized by subtracting the mean for the entire sample and dividing by the SD prior to analysis to aid in interpretation of parameter estimates. Counts of boats within 100, 500 and 1000 m were not independent from one another and were therefore correlated ($r > 0{\cdot}50$). Thus we did not include a global

Table 1. Flock-size categories and number of counts representing each category (*n*) used in logistic regression analyses for predicting abiotic and anthropogenic effects on high-tide roost site use by shorebirds on Cape Romain National Wildlife Refuge, South Carolina, USA

	Flock size categories*						
	0*	*n*	1*	*n*	2*	*n*	Range
Dowitcher	0	414	1–40	121	> 40	83	0–1154
American oystercatcher	0	405	1–25	119	> 25	94	0–276
Peep sandpiper	0	458	1–10	97	> 10	63	0–589
Ruddy turnstone	0	340	1–10	176	> 10	102	0–123
Sanderling	0	456	1–10	96	> 10	66	0–1070
Dunlin	0	527	> 0	91			0–1145
Red knot	0	558	> 0	60			0–1450
Whimbrel	0	566	> 0	52			0–15

*Number of individuals per flock.

model in our model sets to avoid problems associated with collinearity.

Daily roost selection

A set of candidate models was constructed to predict flock presence at an individual roost within a season. We used stratified conditional logistic regression (i.e. stratified by roost), which includes an intercept term for each roost in each model to adjust for variability in average use among roosts (SAS Institute Inc. 2003). However, because the stratification procedure can only be employed with binary data, the response variable in this set of models was either 0 (no individual present) or 1 (at least one individual present). We tested six candidate models, including a reduced model containing only roost strata and year, an environmental model that included roost and environmental parameters, and three disturbance models that additionally incorporated the number of boats around each roost at three spatial scales. We also included an environmental model that did not include roost strata, to test our assumption that there was high variability in use among roosts.

Independent variables in these models included one or more of the following: Julian date (days after the new year), tide level (cm), wind speed (km h^{-1}), wind direction (north, south, east or west), shelter (whether or not the roost provided shelter from the wind), shelter–wind speed interaction, moon phase (proportion of the moon illuminated that night), minutes past sunrise, tidal stage (rising or falling) and number of boats within 100, 500 and 1000 m. In each model we also included year, to account for any annual differences in roost use. Moon phase was included because it may influence feeding and roosting schedules (Dodd & Colwell 1998). The shelter variable was calculated based on the aspect of each roost and the wind direction on a particular day; for instance, if a roost provided a north-facing slope on a day with prevailing southerly winds, it was categorized as sheltered for that day. We acknowledge that some birds may have used the back, or inland, sides of beaches or rakes for shelter from wind. However, we were unable to observe these individuals. Continuous variables were standardized, and boat counts within 100, 500 and 1000 m were not included in a global model, as above.

Model fit

The full models in each set were examined to obtain a goodness-of-fit measure. For seasonal roost-site selection models, fit was based on model concordance ratings, and for species with only two response categories (i.e. individuals or no individuals) also by prediction accuracy, as indicated by classification error (SAS Institute 1999). For determining classification error, model responses that had a predicted probability greater than or equal to 0·50 were classified as ‘event’ responses (i.e. flocks present; SAS Institute 1999). Fit for the stratified, daily roost-selection models was based on the adjusted generalized coefficient of determination.

Results

CONSISTENCY OF ROOST USE

We conducted 618 roost counts (1999 $n = 69$, 2000 $n = 301$, 2001 $n = 124$, 2002 $n = 124$), yielding observations of more than 60 000 individuals of our focal species. Consistency of roost use by focal species differed among roosts (Table 2). Six roosts (19% of roosts sampled) supported flocks of 100 or more total focal individuals in more than 50% of our samples. One roost in particular, Sandy Point South, harboured exceptionally high numbers of shorebirds on a regular basis, with 73% of the counts tallying 500 or more individuals. However, many sites (41%) showed large fluctuations in use and supported flocks between 4% and 40% of the time. In general, roosts that harboured larger flocks appeared to be used more consistently than those that harboured smaller flocks. This assertion was supported by incidence ratings, which increased for all species at longer roosts, where the largest flocks tended to congregate (Fig. 1). Concentration among roosts differed by species, with

Table 2. Consistency of high-tide roost use on Cape Romain National Wildlife Refuge, South Carolina, USA, 1999–2002

			Proportion of samples*		
Roost	Total counts	Median count	$n > 25$	$n > 100$	$n > 500$
AV1	21	4·0	0·24		
AV2	22	14·5	0·36	0·05	
AV3	22	48·0	0·64	0·32	
BA	23	155·0	0·87	0·61	0·13
BI	15	0·0			
BP	20	213·0	0·90	0·65	0·25
CM	19	0·0			
CN	18	15·5	0·39	0·22	
CPN	21	7·0	0·29	0·10	
CPS	21	0·0			
CS	21	164·0	0·71	0·57	0·10
KEY	21	173·0	0·90	0·71	
MD	21	69·0	0·86	0·38	
ME	22	125·5	0·64	0·59	0·09
MI	21	1·0	0·05		
MN	19	0·0	0·26	0·16	
MS	18	58·5	0·72	0·44	
MW	23	0·0	0·04	0·04	
SPN	14	80·0	0·57	0·43	0·07
SPS	22	776·5	0·95	0·86	0·73
WBEE	18	1·5	0·17	0·06	
WBEN	18	0·0			
WBES	18	0·5	0·22	0·11	
WBEW	18	42·5	0·50	0·39	
WBME	16	0·0			
WBMN	18	0·0	0·17	0·11	
WBMS	18	7·0	0·39	0·28	
WBMW	18	8·0	0·44	0·17	
WBWE	18	0·0			
WBWN	18	0·0			
WBWS	18	0·0	0·06		
WBWW	18	1·0	0·17		

*Proportion of samples during which > 25, > 100 and > 500 total focal shorebirds were counted.

red knot, dunlin and whimbrel tending to concentrate in fewer roosts, and ruddy turnstone, American oystercatcher and dowitcher spread more evenly among roosts (Table 3).

Table 3. Focal species concentration among roosts as represented by mean Shannon–Wiener indices ($H' = -\Sigma p_i \ln p_i$) for each shorebird survey. Each survey took 3–8 days to complete and covered 15–32 roosts. A 0·0 score indicates that all individuals counted during a survey occurred at a single roost, whereas larger scores indicate a more even distribution among roosts (Colwell *et al.* 2003)

	Mean H'	SD
Red knot	0·37	0·35
Dunlin	0·62	0·58
Whimbrel	0·86	0·76
Sanderling	1·02	0·28
Peep sandpiper	1·06	0·32
Dowitcher	1·42	0·41
American oystercatcher	1·57	0·52
Ruddy turnstone	1·95	0·37

SELECTION ACROSS YEARS

The best predictor models for roost use across years differed among species (Table 4), ranging in fit from good to excellent: American oystercatcher, 70·5% concordance; ruddy turnstone, 75·1%; dowitcher, 77·4%; dunlin, 78·8%; peep sandpiper, 79·6%; whimbrel, 84·0%; red knot, 89·8%; sanderling, 91·7%. Prediction accuracy for dunlin was 85·0%, red knot 92·1% and whimbrel 91·6%. The best model for American oystercatcher, dowitcher, red knot, whimbrel and ruddy turnstone included abiotic roost characteristics as well as average number of boats recorded within 1000 m (Table 4). Sanderling flocks were best predicted by the model that included roost characteristics and average number of boats within 100 m. The best models for dunlin and peep sandpiper included only roost characteristics. However, the only species for which strong model support suggested a relationship between boat abundance and habitat selection (i.e. ≥ 2·0 AIC point difference between competing models) were red knot and sanderling.

A strong roost length effect was evident for predicting presence of all focal species, with longer roosts more

Table 4. Candidate logistic regression models for predicting shorebird roost counts on Cape Romain National Wildlife Refuge, South Carolina, USA. ΔAIC values reflect the difference in score from the best performing model. Models including roost characteristics included parameters associated with roost structure, and models including environmental conditions took into account ambient variables such as wind speed and direction

		American oystercatcher			Dowitcher			Red knot			Whimbrel			Dunlin			Sanderling			Ruddy turnstone			Peep sandpiper		
Model ID	k*	LL†	ΔAIC$_c$	w_i††	LL	ΔAIC$_c$	w_i	LL	ΔAIC$_c$	w_i	LL	ΔAIC$_c$	w_i	LL	ΔAIC$_c$	w_i	LL	ΔAIC$_c$	w_i	LL	ΔAIC$_c$	w_i	LL	ΔAIC$_c$	w_i
Selection among roosts (annual roost selection)																									
Roost characteristics	14	976·34	1·7	0·19	884·86	1·2	0·23	254·57	3·7	0·11	277·39	2·1	0·18	415·68	0·0	0·34	508·68	4·2	0·10	1021·44	0·6	0·25	708·18	0·0	0·34
Roost characteristics + average boats 100 m	15	976·25	2·7	0·11	884·79	2·3	0·14	254·21	4·5	0·07	276·33	2·1	0·17	415·54	1·0	0·21	503·39	0·0	0·78	1021·42	1·7	0·14	708·17	2·0	0·13
Roost characteristics + average boats 500 m	15	974·62	1·0	0·26	883·92	1·4	0·21	252·96	3·2	0·14	276·57	2·4	0·15	415·54	1·0	0·21	508·42	5·0	0·06	1020·09	0·4	0·28	707·25	1·1	0·20
Roost characteristics + average boats 1000 m	15	973·57	0·0	0·44	882·53	0·0	0·42	249·75	0·0	0·68	274·19	0·0	0·50	415·26	0·7	0·24	508·52	5·1	0·06	1019·71	0·0	0·33	706·24	0·1	0·33
Selection within roosts (daily roost selection)																									
Roost only	36	483·06	60·3	0·00	438·14	28·3	0·00	178·30	19·9	0·00	195·54	63·6	0·00	317·59	86·2	0·00	222·42	23·4	0·00	477·01	20·2	0·00	384·72	0·0	0·30
Environmental conditions only	16	726·98	344·4	0·00	734·71	365·1	0·00	357·39	229·2	0·00	265·86	174·1	0·00	421·21	230·0	0·00	670·91	512·1	0·00	804·00	387·3	0·00	677·29	316·6	0·00
Roost + environmental conditions	47	408·59	0·7	0·29	399·13	3·5	0·13	154·21	0·0	0·31	121·28	3·5	0·09	217·14	0·0	0·35	186·12	1·3	0·25	442·64	0·0	0·35	363·12	0·4	0·25
Roost + environmental conditions + boats 100 m	48	408·58	2·1	0·15	394·26	0·0	0·74	153·98	1·1	0·18	116·45	0·0	0·51	216·42	0·6	0·26	183·50	0·0	0·48	442·52	1·2	0·19	361·86	1·1	0·17
Roost + environmental conditions + boats 500 m	48	408·52	2·0	0·15	399·09	4·8	0·07	153·41	0·5	0·24	119·12	2·7	0·13	217·08	1·3	0·19	186·03	2·5	0·14	442·49	1·2	0·20	361·87	1·1	0·17
Roost + environmental conditions + boats 1000 m	48	406·52	0·0	0·41	399·13	4·9	0·07	153·13	0·3	0·27	117·68	1·2	0·27	216·96	1·2	0·20	186·02	2·5	0·14	441·96	0·7	0·26	362·59	1·9	0·12

*The number of estimable parameters in the model including intercept(s) and error term. In seasonal models for American oystercatcher, dowitcher, peep sandpiper, ruddy turnstone and sanderling, $k = k + 1$ to account for a third-response category.

†LL, $-\alpha$ log-likelihood of the model, given the data (Burnham & Anderson 1998).

††Akaike model weights (Burnham & Anderson 1998).

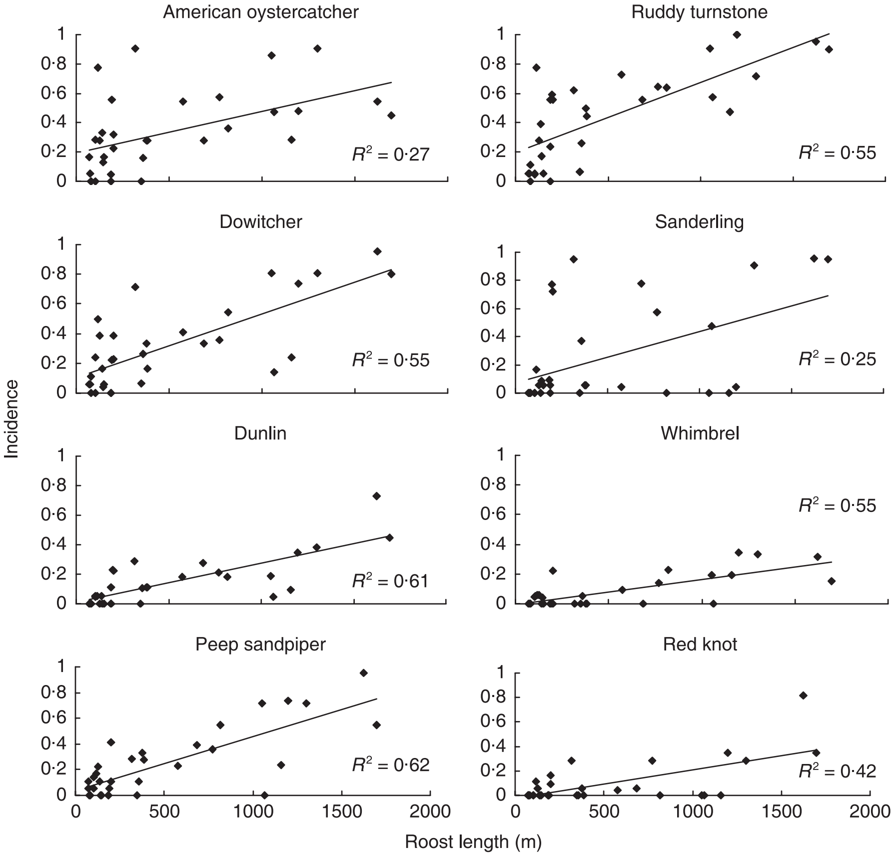

Fig. 1. Relationship between roost length (m) and incidence ratings for select species on Cape Romain National Wildlife Refuge, South Carolina, USA, 1999–2002. Incidence reflects the proportion of samples for which a species was present at the roost. Regression equations and *P*-values for each species were as follows: American oystercatcher, $y = 0·0003x + 0·1933$, $P = 0·003$; ruddy turnstone, $y = 0·0005x + 0·1978$, $P < 0·0001$; dowitcher, $y = 0·0004x + 0·1035$, $P < 0·0001$; sanderling, $y = 0·0004x + 0·0738$, $P = 0·004$; dunlin, $y = 0·0003x + 0·0086$, $P < 0·0001$; whimbrel, $y = 0·0002x - 0·0042$, $P < 0·0001$; peep sandpiper, $y = 0·0004x + 0·0367$, $P < 0·0001$; red knot, $y = 0·0002x - 0·0229$, $P < 0·0001$.

likely to be occupied (Table 5). American oystercatcher, dowitcher, red knot and sanderling flocks were also significantly affected by region, with oystercatcher, dowitcher and red knot tending to occur in larger flocks on outer beaches in the northern region of the refuge, while sanderling selectively roosted at the Marsh Island region. Oystercatcher, dowitcher, whimbrel and peep sandpiper also appeared to select roosts with shell substrates, whereas sanderling strongly preferred a sand substrate (Table 5). Dowitcher, sanderling and peep sandpiper were more likely to be found on more level than highly graded roosts. Red knot, whimbrel, ruddy turnstone and peep sandpiper were found primarily on roosts that did not provide a north-facing slope (Table 5). Ruddy turnstone and peep sandpiper selected roosts with an east-facing slope, and American oystercatcher, dowitcher, whimbrel and ruddy turnstone were more likely to use roosts that faced west. The only species that showed notable avoidance of roosts with high average boat activity was red knot, which responded to boat activity within 1000 m (Table 5). Conversely, sanderling tended to have a greater probability of use of roosts that had high boat activity, on average, within 100 m (Table 5).

DAILY ROOST SELECTION

The best predictor models for roost use on a daily scale also varied among species (Table 4), with model fit for the full models ranging from poor to fair (American oystercatcher, $R^2 = 0·20$; dowitcher $R^2 = 0·12$; dunlin, $R^2 = 0·36$; peep sandpiper, $R^2 = 0·05$; red knot, $R^2 = 0·12$; ruddy turnstone, $R^2 = 0·06$; sanderling, $R^2 = 0·14$; whimbrel, $R^2 = 0·48$). Convergence criteria were met for all models. Daily roost use for several species, including dowitcher, whimbrel and sanderling, was best predicted by models including environmental conditions as well as number of boats within 100 m (Table 4). Roost use by American oystercatcher and red knot was best predicted by a model including environmental conditions and boat activity at a larger scale (1000 m). The best models for predicting red knot, dunlin and ruddy turnstone roost use incorporated only environmental parameters, and the best model for predicting roost use by peep sandpiper included only year and stratification by roost (Table 4). Whimbrel and dowitcher were the only species for which good model support suggested a relationship between boat presence (within 100 m) and roost-site selection (i.e. ≥ 2·0 AIC point difference between competing models).

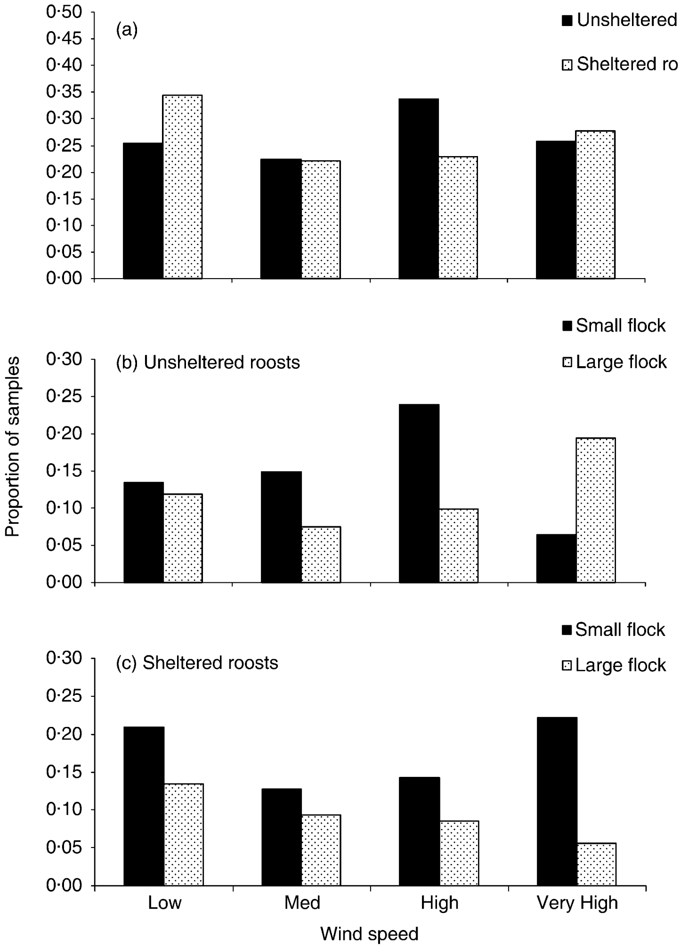

Fig. 2. (a) Interaction among roost sheltering effect, wind speed (low, 0–8; medium, 9–17; high, 18–24; very high, 24 km h^{-1}) and peep sandpiper flock presence. (b) Probability of encountering large flocks (> 10 individuals) increased and of encountering small flocks (≤ 10 individuals) decreased on unsheltered roosts during very high winds, whereas (c) the likelihood of encountering small flocks increased at sheltered sites during very high winds.

All species showed strong selection for specific roosts, as depicted by large AIC scorethat did not incorporate a roost strata and those that did (Table 6). Occupied roosts for whimbrel differed across years but for other species remained relatively constant (Table 6). Probability of roost use changed significantly within seasons according to Julian date, with oystercatcher, dowitcher and whimbrel flocks decreasing in occurrence over the season, and dunlin and sanderling flocks increasing (Table 6). Whimbrel and sanderling roost use was related to shelter characteristics; both were more likely to use a roost when it provided shelter from the wind that day (Table 6). A wind speed–shelter interaction was detected for roost selection by peep sandpiper, wherein during high winds (18–24 km h^{-1}) we were more likely to encounter a flock at unsheltered roosts but during very high winds (> 24 km h^{-1}) the probability of detecting a flock at these roosts decreased (Fig. 2a). Closer inspection of the data revealed that during very high winds at unsheltered roosts the probability of observing small flocks (≤ 10 individuals) decreased

Table 5. Parameter estimates (LCI, lower confidence intervals; UCI, upper confidence intervals) and odds ratios (OR) for factors related to mean annual shorebird occupancy of roosts. Estimates are derived from the lowest AIC scoring logistic regression models displayed in Table 4

	American oystercatcher				Dowitcher				Red knot				Whimbrel				Dunlin				Sanderling				Ruddy turnstone				Peep sandpiper			
	P	LCI	UCI	OR	*P*	LCI	UCI	OR	*P*	LCI	UCI	OR	*P*	LCI	UCI	OR	*P*	LCI	UCI	OR	*P*	LCI	UCI	OR	*P*	LCI	UCI	OR	*P*	LCI	UCI	OR
Substrate*																																
Sand only vs. shell only	**0·003**	–1·42	–0·37	0·37	**0·02**	–1·10	–0·07	0·51	0·45	–0·70	1·58		**0·04**	–2·64	–0·06	0·26	0·51	–0·57	1·12		**< 0·0001**	1·91	3·95	18·73	0·33	–0·27	0·79		**0·02**	–1·51	–0·14	0·44
Both vs. shell only	0·09	–0·04	0·75		0·48	–0·53	0·28		0·53	–1·24	0·64		0·15	–0·25	1·55		0·92	–0·64	0·56		**0·03**	–1·58	–0·06	0·44	0·84	–0·63	0·59		0·87	–0·50	0·53	
Slope (degrees)	0·38	–0·15	0·37		**0·04**	–0·53	0·00	0·74	0·27	–0·86	0·24		0·20	–0·64	0·14		0·12	–0·73	0·10		**0·04**	–1·80	–0·04		0·30	–0·43	0·12		**0·001**	–0·83	–0·20	0·59
Slope aspect†																																
North	0·32	–0·11	0·35		0·15	–0·41	0·07		**0·01**	–1·47	–0·21	0·43	**0·01**	–2·01	0·29	0·32	0·51	–0·62	0·31		0·60	–0·68	0·38		**0·01**	–0·59	–0·08	0·72	**0·02**	–0·75	–0·05	0·67
East	0·47	–0·31	–0·15		0·65	–0·17	0·27		0·59	–0·78	0·44		0·60	–0·48	0·82		0·17	–0·15	0·80		0·25	–0·24	0·90		**0·02**	0·05	0·52	1·32	**0·02**	0·04	0·71	1·48
South	0·77	–0·20	0·28		0·33	–0·37	0·14		0·02	–1·66	–0·14		0·07	–1·63	0·05		0·53	–0·63	0·32		0·83	–0·63	0·51		0·20	–0·41	–0·10		0·18	–0·59	0·10	
West	**0·002**	0·12	0·63	1·54	**0·03**	0·01	0·53	1·38	0·75	–0·61	0·85		**0·04**	0·06	1·90	2·66	0·80	–0·47	0·37		**0·04**	–0·96	0·02	0·61	**0·02**	0·03	0·55	1·35	0·35	–0·16	0·49	
Length (m)	**< 0·001**	0·48	1·05	2·39	**< 0·0001**	0·65	1·38	3·29	**< 0·001**	0·78	2·26	4·57	**< 0·0001**	0·67	1·93	3·67	**< 0·0001**	0·51	1·28	2·48	**0·0004**	0·48	1·70	2·97	**< 0·0001**	0·86	1·38	3·10	**< 0·0001**	1·14	1·81	4·26
Region	**< 0·001**				**0·0002**				**0·01**				0·17				0·39				**< 0·0001**				0·10				0·11			
Average boats 100																	0·71	–0·20	0·30		0·02	0·05	0·63	1·40	0·89	–0·17	0·19		0·92	–0·21	0·23	
Average boats 500	0·20	–0·36	0·08		0·35	–0·36	0·12										0·72	–0·42	0·28						0·25	–0·32	0·08		0·35	–0·40	0·14	
Average boats 1000	0·09	–0·40	0·04		0·14	–0·41	0·07		**0·04**	–1·23	–0·01	0·54	0·09	–0·95	0·07		0·53	–0·47	–0·47						0·19	–0·33	–0·33		0·17	–0·46	–0·46	

*Sand, shell or both.

†1, shore-facing beach or shell-rake present; 0, shore-facing beach or shell-rake absent.

Table 6. Parameter estimates (LCI, lower confidence intervals; UCI, upper confidence intervals) and odds ratios (OR) for factors related to daily shorebird occupancy of roosts. Estimates are derived from the lowest AIC-scoring logistic regression models displayed in Table 4

	American oystercatcher				Dowitcher				Red knot			Whimbrel				Dunlin				Sanderling				Ruddy turnstone			Peep sandpiper		
Estimate	*P*	LCI	UCI	OR	*P*	LCI	UCI	OR	*P*	LCI	UCI	*P*	LCI	UCI	OR	*P*	LCI	UCI	OR	*P*	LCI	UCI	OR	*P*	LCI	UCI	*P*	LCI	UCI
Year	0·93				0·11				0·61			0·05				0·44				0·56				0·91			0·98		
Wind direction*	0·68				0·94				0·11			0·65				0·77				0·85				0·06			0·74		
Days†	**< 0·0001**	−0·89	−0·16	0·47	**0·006**	−0·61	−0·10	0·70	0·46	−0·24	0·62	**0·0003**	−1·25	−0·22	0·39	**< 0·0001**	1·25	2·41	6·17	**0·01**	0·05	0·82	1·82	0·97	−0·22	0·21	0·84	−0·23	0·36
% moon illuminated	0·39	−0·22	0·10		0·18	−0·08	0·39		0·07	0·03	0·76	0·67	−0·38	0·26		0·40	−0·23	0·56		0·82	−0·29	0·22		0·43	−0·30	0·13	0·42	−0·11	0·41
Minutes past sunrise	0·33	−0·27	0·11		0·72	−0·32	0·22		0·72	−0·47	0·37	0·81	−0·38	0·45		0·75	−0·38	0·48		0·86	−0·33	0·31		0·59	−0·27	0·16	0·53	−0·28	0·35
Tidal direction (F vs. R)‡	**0·02**	−0·05	0·38	0·97	0·11	−0·04	0·45		0·43	−0·19	0·52	0·77	−0·32	0·48		0·63	−0·45	0·28		0·55	−0·39	0·60		0·68	−0·29	0·19	0·62	−0·24	0·30
Tide (cm)	0·75	−0·19	0·14		0·63	−0·30	0·18		0·19	−0·63	0·13	0·09	−0·67	0·07		0·93	−0·36	0·37		0·90	−0·31	0·22		0·06	−0·38	0·01	0·91	−0·13	0·42
Wind speed (km h^{-1})	0·27	0·42	−0·68		0·18	0·60	−0·84		0·25	1·34	−0·59	0·50	0·95	−0·70		0·44	1·48	−0·45		0·44	0·79	−0·26		0·53	1·01	−0·87	0·11		
Wind speed–shelter	0·88	−0·37	0·23		0·35	−0·13	0·37		0·45	−0·19	0·46	0·86	−0·30	0·36		0·80	−0·30	0·38		**0·05**	−0·03	0·57		0·21	−0·34	0·08	**0·04**	−0·01	0·44
Shelter†	0·07	−0·34	0·45		0·06	−0·02	0·52		0·24	−0·13	0·66	**0·008**	0·08	1·03	2·05	0·65	−0·33	0·50		**0·02**	0·00	0·71	1·60	0·13	−0·06	0·47	0·99	−0·26	0·33
Boats 100 m					**0·03**	−0·53	−0·02	0·76	0·64	−0·50	0·30	0·12	−1·75	0·20		0·39	−0·17	0·42		0·10	−0·60	0·05		0·72	−0·26	0·18	0·28	−0·39	0·11
Boats 500 m									0·38	−0·71	0·00					0·82	−0·37	0·47						0·69	−0·23	0·34	0·26	−0·14	0·52
Boats 1000 m	0·16	−0·51	0·08						0·31	−0·95	0·25	0·08	−1·70	0·10		0·67	−0·39	0·60						0·41	−0·40	0·16	0·46	−0·211	0·4671

*Northerly, southerly, easterly or westerly.

†Julian date.

‡Positive values represent increased flock sizes during falling tides, negative values represent increased flock sizes during rising tides.

§Positive relationship indicates that flock size increased when the shore-facing aspect of the roost provided shelter from the wind.

while the probability of detecting large flocks increased (Fig. 2b). This pattern did not hold true for sheltered sites, where the probability of detecting a small flock increased during very high winds (Fig. 2c). For sanderling, a wind speed–shelter interaction similarly indicated that large flocks tended to be detected at a greater rate at unsheltered sites during very high winds. Dowitcher appeared to track disturbance on a daily scale, avoiding roosts with high boat activity within 100 m (Table 6), but otherwise no notable effect of disturbance was observed at the daily scale.

Discussion

PATTERNS AND CONSISTENCY OF ROOST USE

In this study we observed differences among shorebird species in roost site distribution, with some species tending to congregate on two or three roosts (red knot) and others more often spreading over several roosts (dowitcher, American oystercatcher, ruddy turnstone; Table 3). It is notable that our species-specific Shannon–Wiener calculations were similar to those reported by Colwell *et al*. (2003) for Humboldt Bay, California, despite the fact that our H' values represented autumn roost use over several years while the Humboldt Bay birds were observed throughout autumn, winter and spring within 1 year, indicating that roosting patterns may be generalizable across species' ranges.

The hypothesis that shorebirds use traditional roosts both within (Rehfisch *et al*. 1996; Warnock & Takekawa 1996; Takekawa *et al*. 2002; Rehfisch, Insley & Swann 2003) and among years (Hale 1980; Rehfisch *et al*. 1996; Pearce-Higgins 2001; Sanders, Murphy & Spinks 2004), is widely accepted, with some roosts occupied so predictably that changes in occupancy have been used to evaluate effects of conservation measures and human disturbance (Burton, Evans & Robinson 1996). However, several studies have shown that even at traditional sites there can be high variability in shorebird presence and abundance (Sitters *et al*. 2001; Colwell *et al*. 2003), indicating that the assumption of consistent predictability in roost use should avoided. We found that most roosts on CRNWR (60%) were used by flocks of the focal species ≤ 50% of the time, although we also noted five traditional roosts that harboured flocks ≥ 80% of the time (Table 2). Colwell *et al*. (2003) similarly showed that most roosts in Humboldt Bay were used infrequently by shorebirds and suggested that roosts can be arranged into a broad spectrum, ranging from a large number of ephemeral sites that are rarely used, to a small number of those that commonly host large flocks of shorebirds.

Roost-switching has been documented in birds (Rehfisch *et al*. 1996; Rehfisch, Insley & Swann 2003) and bats (Lewis 1995; Kerth, Wagner & Konig 2001) and it has been proposed that variation in roost selection may serve several purposes, such as reducing risk of predation (Lima 1998a) and increasing social interactions (Willis & Brigham 2004). However, the variability in roost use demonstrated in this study and others (Handel & Gill 1992; Colwell *et al*. 2003) also supports the hypothesis that selective factors are operational in determining roost-use patterns. This variability has led to speculation about what factors might influence roost-site selection for different species and at what scale they might influence selection (Colwell *et al*. 2003).

ROOST STRUCTURAL CHARACTERISTICS AND ENVIRONMENTAL CONDITIONS

We found several structural and environmental factors associated with seasonal and daily scales of roost selection. At the broader temporal scale, shorebird presence at roosts was most influenced by roost length (size), region, substrate and aspect (Table 5). Larger roosts were most likely to harbour larger flocks of the focal species, and were also most consistently used (Fig. 1). This finding corresponds with those reported by Pearce-Higgins (2001), who observed that ruddy turnstones were most faithful to the largest roost monitored on the North Wales coast over a 22-year period, and that roost size explained much of the variation in capture rates among roosts. Large roosting areas and the formation of bigger flocks can offer several advantages to survival, including offering a full view of approaching predators (Burton, Evans & Robinson 1996; Rehfisch, Insley & Swann 2003), minimizing thermoregulatory costs (Wiersma & Piersma 1994) and decreasing risk of predation through dilution or detection effects (Roberts 1996; Lima 1998a).

We also noted a strong regional bias in roosting within the refuge for several species, including American oystercatcher, dowitcher, red knot and sanderling, and a suggestion of regional preference in ruddy turnstone and peep sandpiper (Table 5). Other studies have shown regional preferences, although they have also demonstrated extensive movements among roosts within a region (Sanzenbacher & Haig 2002; Rehfisch *et al*. 1996; Rehfisch, Insley & Swann 2003). Roost-site selection is suspected to be related to foraging area (Furness 1973; Swennen 1984) and recent evidence has strengthened this impression (Warnock & Takekawa 1996; Rogers *et al*. 2006; Van Gils *et al*. 2006). Thus it is likely that the regional bias in roost-site selection demonstrated in our study is in part determined by the distribution of available foraging sites on CRNWR.

With respect to daily roost-site selection, the strongest effects apparent in our study were Julian date, shelter from wind and a bias for individual roosts. The effect of Julian date primarily reflected species-specific migration cycles and may also have be related to moult patterns (Handel & Gill 1992). The influence of wind on roost selection has been reported in dunlin (Handel & Gill 1992), ruddy turnstone and common redshank *Tringa tetanus* (Burton, Evans & Robinson 1996) and there is some suggestion that species that tend to form smaller flocks might be more sensitive to wind conditions, while birds that form larger flocks receive shelter from the flock itself (Burton, Evans & Robinson 1996). The species on our site that apparently responded to wind were whimbrel, sanderling and peep sandpiper, but we could not document any obvious pattern between species flock size and reaction to wind speed or shelter. The interaction we observed between shelter and wind speed in peep sandpiper roost use does, however, provide insight into the potential dynamics between flock size and wind conditions observed during the study (Fig. 2). During high winds, small peep sandpiper flocks on unsheltered roosts decreased dramatically while the number of large flocks increased, indicating that larger, more protected flocks were formed at these primarily open-beach sites. Conversely, small flocks increased at sheltered sites, indicating that many of these birds sought out small protected 'nooks' within shell rakes or may have joined the larger flocks at the unprotected sites.

Finally, we observed no effect of tidal height or time of day on occupancy of roosts, although other studies have shown that tides can affect numbers of species such as sandpiper, ruddy turnstone and dunlin (Handel & Gill 1992; Burton, Evans & Robinson 1996) and that roost use can fluctuate significantly by time of day (dunlin; Handel & Gill 1992).

HUMAN DISTURBANCE

We found little evidence for most species that roost-site selection was related to the level of boat disturbance surrounding the roost, at any spatial scale. Furthermore, for species that appeared to respond to disturbance (red knot, dowitcher, whimbrel), we found that responses differed by temporal and spatial scales. On an annual scale, red knot avoided roosts that had high average boat activity within 1000 m. Only dowitcher appeared to track daily disturbance, avoiding prospective roosts when boat activity within 100 m was high. Whimbrel was the only species that exhibited a similar response to disturbance at multiple scales, showing a trend towards avoidance behaviour on both an annual and a daily scale with respect to boat activity within 1000 m and 100 m, respectively. Sanderling was more likely to use roosts that had boat activity within 100 m, a finding that was a consequence of their four most commonly used roosts (i.e. the sandy beaches of Bull Point and Marsh Island) representing sites where people often moored their boats and walked or fished on the shore. Sanderling often exhibit avoidance behaviour in response to pedestrians (Lafferty 2001; Thomas, Kvitek & Bretz 2003) but any such effects would have occurred at a smaller scale than the grain of this study (Webb & Blumstein 2005).

It has been argued that avian responses to disturbance cannot be construed as negative unless an actual impact to fitness can be demonstrated (Nisbet 2000). Shorebirds in particular have evolved in dynamic environments and, as a consequence, may be able to compensate for short-term effects such as lost foraging time and temporary habitat loss (Swennen, Leopold & Brujin 1989; Lafferty 2001; Elner & Seaman 2003). Thus, demonstration of impacts on shorebird fitness as a result of human disturbance is difficult, and it follows that assessment of the efficacy of management tools designed to reduce disturbance can be equally problematic. In general, species that exhibit strong roost fidelity are likely to be most affected by loss of roosting habitat (Rehfisch, Insley & Swann 2003) and movement patterns of the least mobile species should be considered most important in determining the spacing of refuges (Rehfisch *et al*. 1996).

SYNTHESIS AND APPLICATIONS

By taking a multiscale, organism-centred approach (Wiens 1976; Mitchell, Lancia & Gerwin 2001; Thompson & McGarigal 2002), we were able to identify several factors that influence the temporal and spatial dynamics of shorebird high-tide roost site use. Our study and others (Rehfisch *et al*. 1996; Colwell *et al*. 2003) show that shorebirds frequently switch roosts at a local scale, potentially driven by wind or other ambient conditions (McConkey & Bell 2005). Thus future conservation measures should attempt to provide an adequate number of functional roosts for shorebirds. For instance, land acquisition procedures and mitigation projects (Durell *et al*. 2005) should include a wide range of potential roosts that could be used under different wind conditions. The roosts should provide variability in aspect and sheltering capabilities, with open, sandy beaches available for some species such as sanderling. These roosts should also be within reasonable travelling distance of preferred feeding areas (Van Gils *et al*. 2006), which may change within and among years. The same criteria should hold for measures involving the construction of artificial roosts (Burton, Evans & Robinson 1996). Monitoring efforts at roosts should also recognize that use in most cases is highly variable, and caution should be employed when making inferences about changes in habitat use based on roost counts unless surveys have been adequately replicated in space and time. Finally, management tools, such as the use of buffer zones around roosts, have been suggested to reduce effects of human activity (Rehfisch *et al*. 1996; Durell *et al*. 2005). However, before such decisions are made, it is important to determine whether roosting shorebirds are in fact being significantly disturbed or restricted from preferred sites as a result of human activities. Our study demonstrates that, in some cases, birds may react little or not at all to disturbances that might otherwise be construed as harmful.

Acknowledgements

We thank the many technicians who participated in this project for their outstanding fieldwork. Funding and logistical support were provided by the United States Fish and Wildlife Service. Aerial photographs were commissioned by CRNWR and orthorectified by the USFWS office in Georgetown, SC. The South Carolina Cooperative Research Unit is jointly supported by the US Geological Survey, Clemson University, the South Carolina Department of Natural Resources and the Wildlife Management Institute. Michael Reed, Mark Rehfisch and Jan van Gils provided valuable reviews of earlier drafts of this paper.

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Received 16 February 2006; final copy received 13 August 2006
Editor: Jenny Gill