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The costs of using night roosts for migrating whimbrels

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Migrant shorebirds operate within a series of landscapes and must adjust their daily activities to achieve seasonal time and energy objectives. Night roosts are essential landscape elements that provide safety from predators for many shorebird species. What costs migrants incur to use night roosts and how these costs vary across staging sites are poorly understood. We tracked 42 adult whimbrels *Numenius phaeopus* with satellite transmitters and used night locations to delineate 39 night roosts during spring and fall migration. We used daytime locations to measure round-trip commuting distances between night roosts and foraging areas and estimated daily commuting costs including distance, time and metabolic energy expenditure. We identified night roosts on offshore islands (n = 20) and onshore locations including along habitat edges (n = 13) and on topographic highs within extensive marshes (n = 6). Mean daily commuting costs varied between roosts. Whimbrels took 3.9–52.1 min (median = 15.2) to fly 3.1–42.2 km (median = 12.3) which costs 6.1–82.4 kj (median = 22.3) in lean mass energy expenditure and 8.1–109.2 kj (median = 31.5) in leaving mass energy. Birds using offshore roosts had twice the commuting distance and associated costs compared to those using onshore roosts. The contribution of commuting costs to the premigratory energy budget ranged from 1.5 to 18.8% with costs for nearly 30% of roosts exceeding 10%. Commuting costs to and from night roosts appear to be biologically relevant within some staging sites and should be considered among other constraints faced by migrants during stopover periods when food or time is limiting.

Keywords: flight costs, migration, night roosts, *Numenius phaeopus*, satellite tracking, Western Atlantic Flyway, whimbrel

Communal roosts are essential landscape features for most shorebirds within migratory staging sites (Rogers 2003, Colwell 2010). The daily, alternating pattern of individuals congregating within communal areas to rest and then dispersing throughout the surrounding landscape to forage is common across a wide range of species

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(Burger et al. 1977, Handel and Gill 1992, van Gills et al. 2006). Characteristics of acceptable roosting locations include proximity to profitable feeding patches (Rehfisch et al. 1996, Rosa et al. 2006, van Gills et al. 2006) and reduced risk of predation (Luis et al. 2001, Sprague et al. 2008, Adams 2011). The need to balance decisions between these two habitat dimensions often makes acceptable roost sites uncommon on the landscape leading to the suggestions that 1) roost availability may constrain economic access to rich foraging sites (Dias et al. 2006, Rogers et al. 2006a) and 2) that the loss of roost sites may have significant conservation implications (Burton et al. 1996, Rehfisch et al. 1996, Buehler 2002, Kim and Yoo 2004, Milton and Harding 2011).

Shorebirds staging along the coast use both high-tide and night roosts (Rogers 2003). High-tide roosts are used when tide stage covers intertidal food patches, are often interspersed with feeding areas (Furness 1973, Rehfisch et al. 1996, Rosa et al. 2006, Andres et al. 2007), may exhibit inconsistent use patterns (Colwell et al. 2003, Rehfisch et al. 2003, Peters and Otis 2007, Sprague et al. 2008) and have been widely reported and studied (Rogers 2003, Peters and Otis 2007, Lilleyman et al. 2016). By contrast, night roosts are often used independent of tide stage (Hockey 1985, Handel and Gill 1992), are used within nontidal settings (Swinebroad 1964, Myers 1984), are typically more distant from foraging patches (Handel and Gill 1992, Dickens 1993, Piersma et al. 2006, Rogers et al. 2006b), have high consistency of use (Conklin and Colwell 2007) and are poorly studied. In comparison to high-tide roosts, selection of night roosts appears to give more weight to the predation and/or weather environment rather than proximity to feeding sites (Sitters et al. 2001, Rogers 2003, Sanders et al. 2013).

Long-distance migrants must maintain a positive energy balance while adjusting their activities to a series of landscapes that vary in the availability and distribution of essential resources. What costs these migrants incur to use night roosts and how these costs vary across staging sites are poorly understood. We used satellite transmitters to delineate night roosts used by whimbrels *Numenius phaeopus* during spring and fall migrations throughout the Western Atlantic Flyway, evaluated the spatial relationship between night roosts and foraging areas and quantified the costs of these relationships in terms of commuting distance, time expenditure and the energetic costs of commuting flights. Understanding the characteristics of night roosts used by whimbrels during migration will improve our ability to manage potential sites. Understanding the time and energy costs associated with roost use will help us to better understand the constraints faced by whimbrels within migratory staging areas.

Methods

Field methods

We captured 42 whimbrels between 2008 and 2016 on migration staging sites along the lower Delmarva Peninsula in Virginia, USA (n = 15) (37.3982°N, 75.8655°W), along the coast of Georgia, USA (n = 8) (31.1447°N, 81.3787°W), along the Acadian Peninsula in New Brunswick, Canada (n = 6) (47.9733°N, 64.5089°W), as well as on the nesting grounds in the Mackenzie River Delta, Northwest Territories, Canada (n = 13) (69.3725°N, 134.8938°W). Birds were captured using rocket nets (n = 17), noose lines (n = 12) and nest traps (n = 13). All birds were aged as adults by plumage (Prater et al. 1977, Pyle 2008) and were banded with United States Geological Survey tarsal bands and coded leg flags. Gender of captured birds was not determined.

We fitted all birds with a satellite transmitter called platform transmitter terminal (PTT) using a modification of the leg-loop harness (Rappole and Tipton 1991, Sanzenbacher et al. 2000). Instead of elastic cord, we used Teflon® ribbon (Bally Ribbon Mills, Bally, Pennsylvania, USA) that was fastened with brass rivets or crimps (Watts et al. 2008). We glued transmitters to a larger square of neoprene to elevate it above the body and prevent the bird from preening feathers over the solar panels. The PTTs used in this study were 9.5 g PTT-100 (n = 21) or 5.0 g PTT-100 (n = 12) solar-powered units produced by Microwave Telemetry, Inc. (Columbia, Maryland, USA). The transmitter package was below 3% of body mass (measured at the time of deployment) for all individuals tracked in this study.

Tracking data

Birds were located using satellites of the National Oceanic and Atmospheric Administration and the European Organization for the Exploitation of Meteorological Satellites with onboard tracking equipment operated by Collecte Localisation Satellites (CLS America, Inc., Largo, Maryland, USA; Fancy et al. 1988). Transmitters were programmed to operate with a duty cycle of 24 h off and 5 h on (n = 15) or 48 h off and 10 h on (n = 18). Locations in latitude and longitude decimal degrees, date, time and location error were received from CLS America within 24 h of satellite contact with PTTs. Locations were estimated by the Advanced Research and Global Observation Satellite (ARGOS) system (<www.Argos-system.org>), which uses a Doppler shift in signal frequency and calculates a probability distribution within which the estimate lies for each point. The standard deviation of this distribution gives an estimate of the location accuracy and assigns it to a 'location class' (LC): LC3 ≤ 150 m, LC2 = 150–350 m, LC1 = 350–1000 m, LC0 > 1000 m, LCA = location based on three messages and has no accuracy estimate, LCB = location based on two messages and has no accuracy estimate and LCZ = location process failed. We used LC classes 1–3 to track whimbrel locations.

Night roosts

We used night locations (n = 2716) collected within migratory staging areas from 16 April 2008 to 29 August 2019 to delineate night roosts used by whimbrels during migration. Number of nights per bird before filtering out roosts ranged from 3 to 259 (75.5 ± 10.96; mean ± SE). We define periods of spring and fall migration for adults as 12 April through 2 June and 13 July through 29 August, respectively (Watts et al. 2019). Roosts were identified as clusters of night locations that met minimum criteria including 1) a single individual for 14 consecutive nights, 2) more than one individual and/or 3) more than one migration season. Although these thresholds for inclusion were arbitrary, they were chosen to insure adequate information to characterize commuting distances. We delineated the boundaries of roosting clusters using minimum convex polygons (MCP). We calculated centroids within polygons and overlaid centroids on aerial photographs to identify landscape features supporting roosts. Although some of the roosts were previously known, most were previously unknown. The majority of roosts are within remote locations and it was not feasible to ground truth previously unknown sites to determine the number of roosting whimbrels during the migration seasons.

Diurnal activity

We assessed the spatial extent of diurnal activity associated with night roosts using daytime locations ($n = 3684$). To isolate activity associated with a specific roost, we selected closed days where the day began and ended with the bird using the same night roost. We associated all daytime locations for that day with the specific roost and included them in the spatial analyses. We consider diurnal activity to be the spatial distribution of diurnal transmitter locations associated with birds using a night roost. Similar to central place foraging in some nesting birds (Orians and Pearson 1979), whimbrels that use a communal roost during the night move out into the surrounding landscape during the day and then return to the communal roost for the following night. Their activity during the day reflects space use emanating from a specific communal roost. In order to evaluate the spatial association between daytime activity and roosts, we measured the distance between day locations and associated night roosts.

We characterized daytime feeding areas associated with each roost as either tidal or nontidal by overlaying daytime locations on aerial photographs. Foraging areas were classified as tidal if they occurred on substrates (e.g. saltmarsh, mudflats) subject to tidal inundation. Foraging areas were classified as nontidal if they were inland and beyond the reach of tides.

Commuting costs

We estimated the costs of commuting between night roosts and daytime foraging areas using three parameters including commuting distance (km), commuting time (min) and the power input (kj) required for commuting flights. We calculated commuting costs for individuals whimbrels across the roosts they used and for individual roosts using all of the birds that used them. To determine whether roost location or whimbrel identity better predicted the distance traveled between roosting and foraging locations, we constructed generalized linear models with gamma distributions to account for zero-truncated positive skew. We evaluated the fit of the model using Akaike information criterion (AIC). We then used a likelihood ratio test to compare goodness of fit between a model that included roost location as the only fixed effect and a model that included whimbrel identity as the only fixed effect. We calculated the mean commuting distance for each roost using days as samples. We measured the distance between all daytime locations and night roosts and considered the daily commute as the farthest distance recorded for an individual bird during a given day. We defined the daily commuting distance as the length of a direct round-trip flight between the night roost and the farthest point recorded for each day. We acknowledge that location error may potentially skew commuting distance, particularly over short distances. However, low quality locations (LC1) represented only 2.5% of the total locations used to estimate commuting distance. We estimated average commuting time for each roost by multiplying the average commuting distance by a flight speed of $13.8\ \text{m s}^{-1}$. This flight speed ($\bar{x} = 13.8 \pm 0.38\ \text{m s}^{-1}$, $n = 97$) represents the mean of flight segments recorded during migration. Due to the duty cycle of transmitters used here we do not have an adequate sample of local flight speeds but the few ($n < 10$) samples available were within the range of the migration samples. We estimated the power input (metabolic expense) of commuting flights using the interspecific allometric relationship ($P_{met} = 57.3M^{0.73}$) from Norberg (1996) relating mass and the power required for flight where mass (M) is recorded in kg and power (P_{met}) is estimated in Watts (W). Because mass and associated flight costs vary during a stopover event as birds build reserves, we bounded the energetic costs by using estimates for lean and leaving masses. We derived lean mass in grams (384.2 ± 3.03 SE) from birds captured as incubating adults after 15 June since this is a period when most shorebirds approach lean mass (Morrison and Hobson 2004). Because whimbrels migrating through the Western Atlantic Flyway represent two source populations, we used mass data from both Hudson Bay ($n = 77$, Mallory unpubl.) and Mackenzie Delta ($n = 29$, Rousch and Woodard, unpubl.) breeding populations. Mackenzie Delta birds are larger than Hudson Bay. However, due to the sexual size dimorphism there is considerable overlap between Hudson Bay females and Mackenzie Delta males. We derived leaving mass (543.7 ± 12.61) from birds ($n = 27$) captured during the last week of stopover along the coast of Virginia during spring migration (Watts et al. unpubl.). The difference between lean and leaving mass (42%) used here is consistent with that reported for whimbrels preparing for migration elsewhere (Zwarts and Dirksen 1990).

Compensation

We estimated the contribution of commuting costs to the overall seasonal energy requirements to reach leaving mass for individuals in each roost. We stratified daily energy requirements into basal metabolic rate (BMR), energy needed for mass gain and commuting cost. We assumed that birds arrived with a lean mass of 384.2 g and left with a mass of 543.7 g. We used a generalized staging duration of 24 days (Johnson et al. 2016, data from this tracking study – 24.2 ± 1.47 d, n = 51) and interpolated costs on a daily basis between these endpoints. We estimated lean (217.5 kj d^{-1}) and leaving (280.2 kj d^{-1}) BMR using the allometric relationship between BMR and mass for shorebirds ($BMR = 5.06M^{0.73}$) from Kersten and Piersma (1987). We acknowledge that the use of BMR alone underestimates daily maintenance costs with the result of overestimating the contribution of commuting costs to daily budgets. However, estimates of field metabolic rates (Nagy 1987) incorporate commuting costs so their use would result in redundancy. We estimated mass gain (leaving mass–lean mass) as 159.5 g resulting in an average daily mass gain (mass gain/duration) of 6.6 g d^{-1}. This value is comparable to the 7.0 g d^{-1} mass gains recorded during the spring in Virginia (Watts et al. unpubl.). We assumed that fat was the primary tissue accounting for weight gain and that the energy density of fat was 39 kj g^{-1} (Schmidt-Nielson 1975).

Results

Night roosts

Tagged whimbrels used 39 night roosts that met the criteria for inclusion in these analyses (Fig. 1). This set does not represent an exhaustive list of night roosts throughout the flyway. We are aware of additional roosts that did not meet the criteria for inclusion. Roosts were identified within Atlantic Canada (n = 7) including the provinces of New Brunswick, Nova Scotia, Prince Edward Island, Newfoundland and Quebec, along the U.S. South Atlantic Coast (n = 10) including the states of Virginia, South Carolina and Georgia, along the Gulf of Mexico (n = 8) including Tamaulipas Mexico and Texas and Louisiana in U.S., within the Caribbean (n = 3) and along the northern coast of South America (n = 11). Individual roosts were used during the spring (n = 12), fall (n = 24) or both seasons (n = 3). Roosts within Atlantic Canada and along the coast of South America were only used during fall migration and roosts along the Gulf of Mexico were only used during spring migration (Fig. 1). Roosts along the U.S. South Atlantic Coast were used during both spring and fall and although most of these are likely used during both seasons, we lack the coverage in tracking data to evaluate this possibility.

Whimbrels used relatively few landscape features for night roosting. Roosts occurred in both offshore and onshore settings. Offshore roosts were located on offshore islands (n = 16) surrounded by water or on barrier islands (n = 4) that were isolated from mainlands but attached to tidal marshes. Onshore roosts were located along habitat edges (n = 13) or on topographic highs within extensive marshes (n = 6). Whimbrels adjusted their roost selection to regional landscapes. Rocky, offshore islands supported all but two (those in the southern portion of the region) of the roosts in Atlantic Canada. Offshore islands supporting roosts in other regions were sandy, delta islands. Nearly all of the roosts delineated along the coast of South America were positioned along mangrove edges adjacent to extensive intertidal mud flats (habitat discontinuities). Roosts on habitat discontinuities within other regions were along the edges of isolated marshes adjacent to water. Few roosts were on sandy barrier islands or sand spits. These roosts tended to be near the end of extensive sand spits. Roosts along the U.S. South Atlantic or Gulf Coasts also occurred on sand ridges or shrub patches within extensive marshes. Roosts positioned on topographic highs within marshes or along habitat edges were embedded within or close to potential foraging habitats.

Examination of daytime locations revealed that the use of tidal and nontidal habitats varied by region. Nontidal feeding habitats included wild 'blueberry barrens' and commercial blueberry fields within Atlantic Canada and agriculture and rice fields along the Gulf Coast. All feeding habitats along the U.S. South Atlantic and South American Coasts were tidal including salt marshes and intertidal mud or sand flats.

Commuting costs by individual

Commuting costs varied widely between individuals. Average commuting distances traveled between roosts and foraging areas ranged over an order of magnitude from 5.1 to 54.7 km d^{-1} and estimated energy expenditures (lean mass) for commutes ranged from 9.9 to 105.5 kj d^{-1}. However, the commuting costs incurred by individuals conformed to the roosts and landscapes they were using. The fixed-effect model including roost identify (AIC = 3566.2) fit the data better than the fixed effect model including whimbrel identity (AIC = 3797.2) when predicting the distance traveled between roosts and foraging locations. The difference in fit between the two models was significant (likelihood ratio $\chi^2 = 250.98$, df = 10, $p < 0.001$). This result suggests that choices available to staging whimbrels are constrained by the structure of the landscape (relative locations of night roosts and foraging sites). This suggestion is supported by whimbrel no. 105874 that adjusted commuting distances across five different roosts (Fig. 2). Given this result, we present further cost assessments from the roost perspective.

Commuting costs by roost

Collectively, daily commuting distances were highly variable (Fig. 3) ranging from less than 1 km to nearly 150 km (median = 11). Estimated commuting time, based on distance, ranging from 3.9 to 137.8 min (median = 14.1). Estimated commuting costs for lean and leaving masses ranged from 6.1 to 217.8 (median = 24.1) and 8.1 to 288.7 kj (median = 31.9) respectively. Commuting distances were skewed to low values with 45% below 10 km, and 93% below 20 km. Although relatively uncommon, commuting distances between 20 and 60 km were distributed across all regions and most (59%) roosts. Commuting distances above 75 km

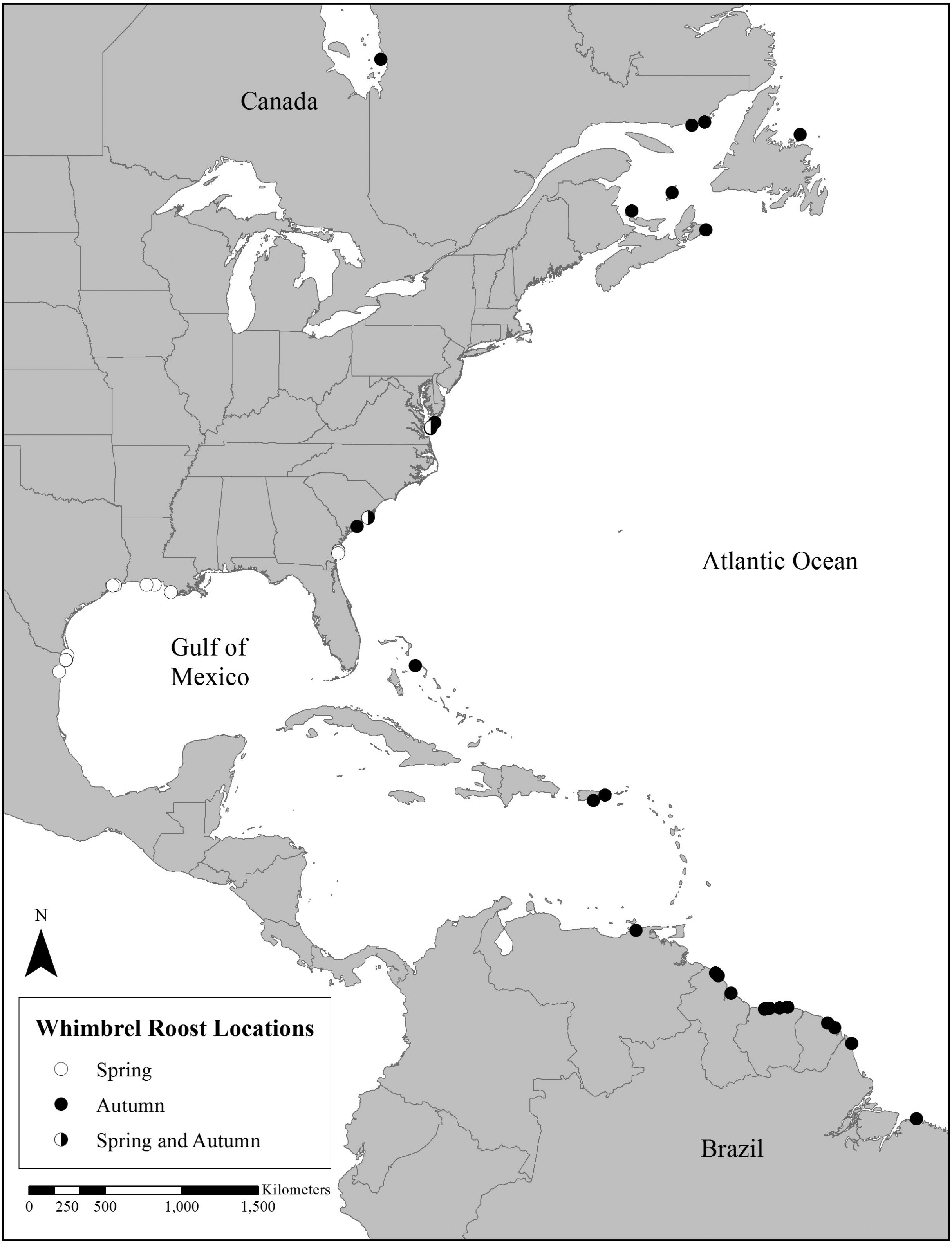

Figure 1. Distribution of night roosts used by whimbrels during migration staging periods (spring and fall) throughout the Western Atlantic Flyway. Roosts were delineated using night fixes from birds fitted with satellite transmitters.

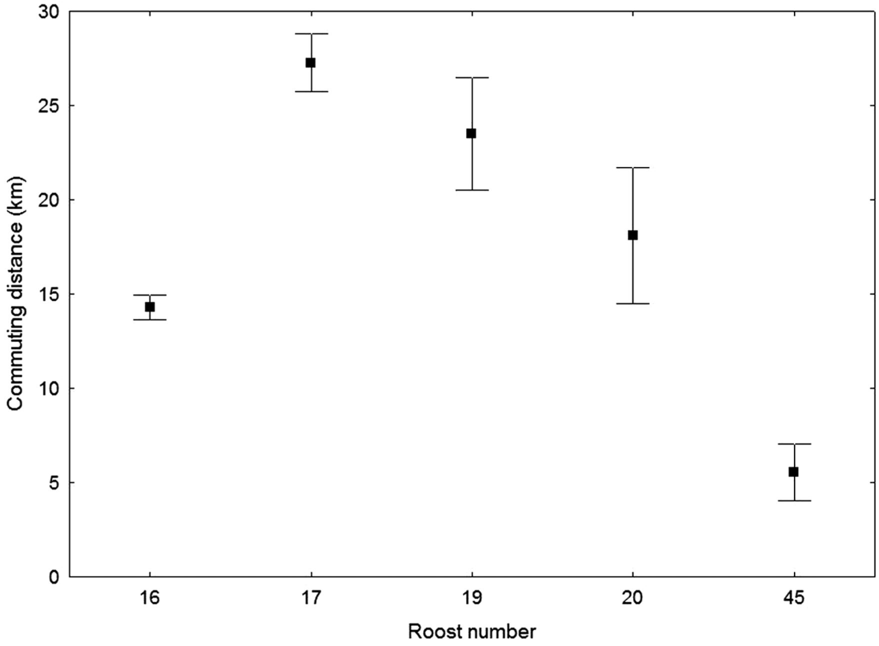

Figure 2. Commuting distances of whimbrel no. 105874 documented while using five different night roosts throughout the Flyway. Values represent means ± SE.

were rare and confined to the Gulf Coast. The most extreme example was a roost along the outer coast of Louisiana supporting birds that consistently flew more than 50 km (one-way) to rice fields. This roost was an outlier exhibiting twice the mean commuting distance and other costs compared to the next highest roost and was not included in analyses below.

Estimated daily commuting costs varied between roosts. Ranges for estimated costs were 3.1–42.2 km (median = 12.3), 3.9–52.1 min (median = 15.2), 6.1–82.4 kj (median = 22.3) and 8.1–109.2 kj (median = 31.5) for distance, time, lean mass energy expenditure and leaving mass energy expenditure, respectively. The increase in daily commuting costs from

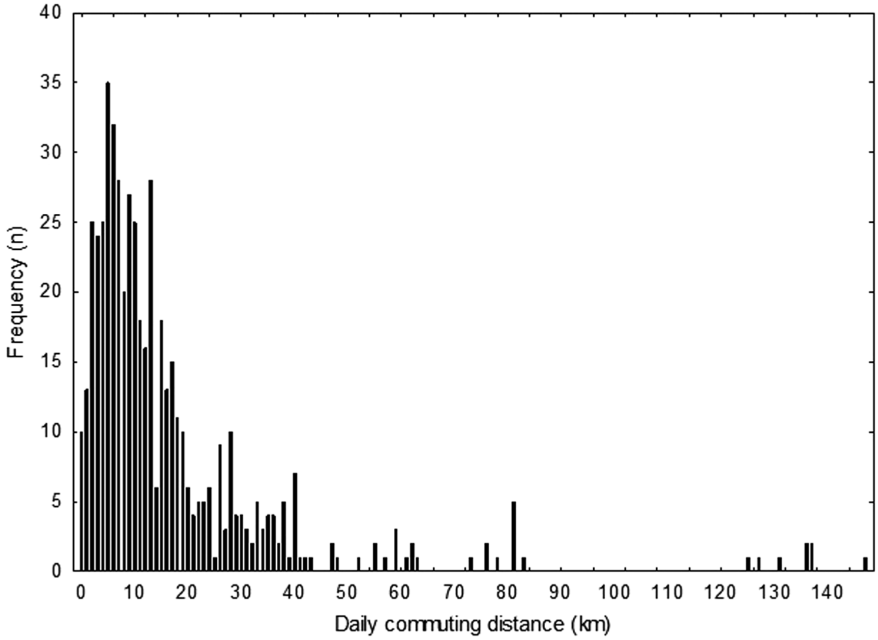

Figure 3. Frequency distribution of daily commuting distances (n = 513) for whimbrels traveling from night roosts to foraging areas. Distances (km) were estimated from day locations to night roosts. Values represent the farthest distance traveled from the roost for each bird during each day.

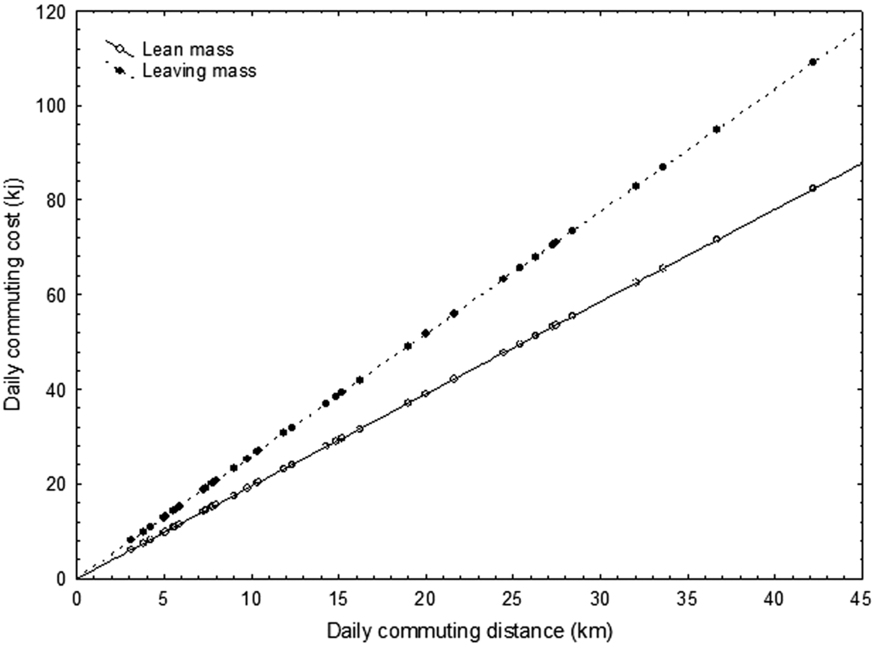

Figure 4. Relationship between mean daily commuting distance (km) between night roosts and foraging areas and the estimated energetic cost (kj) for whimbrels within staging sites. The solid line represents estimated costs for lean-mass birds and the dotted line represent estimated costs for leaving-mass birds. Data points show the distribution of estimated values for individual roosts observed.

lean to leaving masses varied from 2 kj d^{-1} for the lowest commuting distances (< 3 km) to 28 kj d^{-1} for the longest (42 km) (Fig. 4).

Commuting costs were influenced by the setting of roosts (offshore versus onshore) (Table 1) and tidal (tidal versus nontidal) influence on feeding areas. Birds using offshore roosts had twice the commuting distance and associated costs compared to those using onshore roosts (df=36, t-value=3.6, $p < 0.01$) (Table 1). A nearly identical pattern was observed between roosts associated with nontidal versus tidal feeding areas with birds experiencing twice the commuting costs to nontidal feeding areas. However, roost setting and tidal feeding habitats were confounded. Although offshore roosts occurred within all regions, nontidal feeding areas were confined to only Atlantic Canada and the Gulf Coast. The sample of roosts considered here was inadequate to assess the importance of tides on commuting costs independent of roost setting.

Table 1. Influence of roost setting on commuting costs for migrating whimbrels. Offshore samples include 15 individual whimbrels and 27 whimbrel-year combinations. Onshore samples include 19 individuals and 30 whimbrel-year combinations. Values include means ± SE. All t-statistics > 3.6 and p-values < 0.01.

Parameter	Offshore (n=20)	Onshore (n=19)
Commuting distance (km)	20.5 ± 2.12	9.8 ± 2.10
Commuting time (min)	25.3 ± 2.62	12.1 ± 2.54
Lean commuting cost (kj)	39.9 ± 4.14	19.1 ± 4.01
Leaving commuting cost (kj)	52.9 ± 5.49	25.4 ± 5.32

Compensation

The estimated impact of commuting costs on the seasonal premigratory energy budget ranged from 1.5 to 18.8% (Fig. 5). Commuting cost for nearly half of the night roosts accounted for less than 5% of the premigratory budget that was dominated by maintenance and fat accumulation costs. However, commuting costs for nearly 30% of the roosts represented more than 10% of the budget. For the outlier in Louisiana, commuting cost represented just under 50% of the seasonal budget.

Discussion

Most migratory shorebirds use a diversity of landscapes throughout their annual cycle and regularly adjust to different combinations of predation risk, time constraints and foraging conditions to take advantage of local resources. Whimbrels often selected night roosts in locations that required long commuting flights to feeding areas. This was evident in their use of offshore islands in Atlantic Canada and along the southern U.S. Atlantic Coast and particularly along the Gulf Coast where birds commuted long distances from inland feeding areas to coastal roosts. Offshore islands presumably provide a refuge from ground predators and a potential reduction in risks from nocturnal aerial predators. Commuting distances between foraging and roost sites were more than twice as long for offshore islands compared to onshore locations. Whimbrels appear to willingly incur costs in both time and energy in order to be safer during the night.

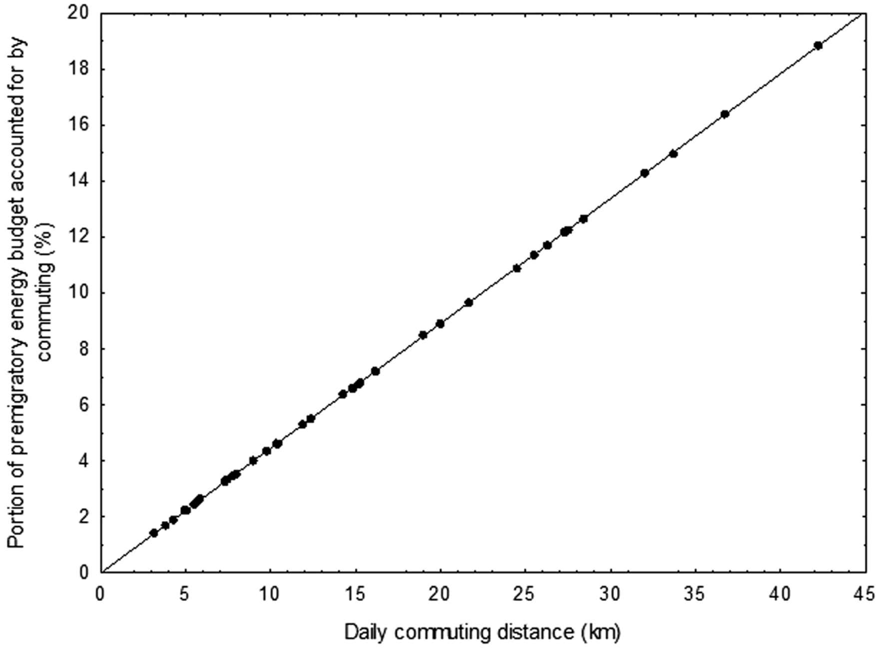

Figure 5. Relationship between mean daily commuting distance (km) between night roosts and foraging areas and the portion of the premigratory energy budget accounted for by commuting costs. Data points show the distribution of estimated values for individual roosts observed.

Johnston-Gonzalez and Abril (2019) quantified characteristics of whimbrel night roosts on mangrove islands during the winter and compared them to other mangrove islands in Sanquianga National Park, Columbia. Mangrove islands used as roosts were surrounded by 30% more mudflat area used by foraging whimbrels compared to mangrove islands that were not used as roosts. This finding is consistent with roosts delineated here along the northern coast of South America that were in mangroves adjacent to expansive intertidal flats. Mangrove islands used as roosts were also more isolated from other mangroves, surrounded by more water during high tide and were more distant from dry land compared to other available islands, a pattern consistent with the notion that roosts were less exposed to potential predators when compared to other mangrove islands. Johnston-Gonzalez and Abril conclude that whimbrels select mangrove islands for night roosts that provide access to foraging areas and that are isolated from potential predators.

The commuting distances between night roosts and foraging areas found here are consistent with general suggestions that night roosts may be selected to reduce the risk of predation (Rogers 2003). Several authors have commented on the disappearance of shorebirds in nearshore habitats with nightfall and have suggested that birds may be moving to more distant roosts with lower predation pressures (Handel and Gill 1992, Sitters et al. 2001, Piersma et al. 2006). However, few studies have identified the locations of night roosts to allow comparisons of commuting distances between roosts and foraging sites. Sanders et al. (2013) found that nocturnal roosts of American oystercatchers *Haematopus palliatus* were more than seven times farther (11.6 versus 1.6 km) from foraging areas than diurnal roosts and positioned on offshore islands in South Carolina. Conklin and Colwell (2007) found that nocturnal roosts of Dunlin *Calidris alpine pacifica* in Humboldt Bay were more than four times farther (1.7 versus 0.4 km) from the Bay than day roosts and were more likely to be inland. Rogers (2003) found that nocturnal roosts were 3–5 times farther from foraging areas compared to high-tide roosts for great *C. tenuirostris* and red knots *C. canutas* in Roebuck Bay, Australia. Due to the difficulty of locating night roosts, most of what we know about the spatial dynamics between roosts and foraging areas has understandably come from high-tide roosts used during the day. Extending studies to night roosts would give a more holistic view of the role that commuting costs play in stopover ecology.

Commuting costs for some night roosts appear to represent substantial energy investments for whimbrels. In 30% of night roosts individual whimbrels incurred costs that accounted for more than 10% of their premigratory energy budget. Investments on this scale are likely not exceptional. Movements of red knots between roosts and foraging areas in the Dutch Wadden Sea were estimated to account for approximately 10% of the daily energy budget (Piersma et al. 1993). Similarly, Mitchell et al. (1988) estimated that flights from roosts on the Alt Estuary to feed on the Dee Estuary (commuting distance of 40 km) represented 14% of daily energy budgets for knots. Decisions governing time and energy investments for shorebirds have been viewed as a dynamic tradeoff between the risk of predation, the energy intake required to meet specific mass goals under time constraints and the added costs of transporting the increased load (van Gills et al. 2006). Shorebirds within staging sites must fit these tradeoffs to specific landscapes. Birds must operate within particular energetic boundaries, but within these boundaries there is no reason to expect that outcomes should be consistent if underlying constraints vary landscape to landscape. We do not know if 'safer' sites are available to be chosen within stopover landscapes. Within Atlantic Canada, offshore islands used for roosting were typically embedded within a suite of islands and it seems likely that whimbrels could have selected other islands that were more distant from feeding areas. Along the U.S. South Atlantic Coast more distant islands do not exist. If shorebirds confront a risk by distance relationship within this region, risk mitigation is constrained. We do not know the level of predation pressure whimbrels experience across the flyway and so are unable to formulate predictions about specific choices. However, other tradeoffs may constrain risk mitigation within some landscapes. For example, whimbrels are sexually dimorphic in size (Skeel and Mallory 1996) such that commuting costs may be consistently higher for females. Whether or not sexes differ in how they confront energetic tradeoffs is open for investigation.

Whimbrels within staging areas face daily time constraints on foraging and seasonal time limits on achieving leaving weights. Tides impose one of the dominant time constraints on shorebirds staging in coastal landscapes (Burger et al. 1977, van Gills et al. 2006). The regular exclusion of shorebirds from foraging areas by tidal inundation may restrict daily foraging times by as much as 40% depending on the lunar phase and landscape. Whimbrels within other flyways have been documented to conduct some night foraging when preparing for migration (Zwarts and Dirksen 1990, Kuang et al. 2019). We did not see evidence of this behavior within our tracking data. Whimbrels feeding in nontidal habitats were willing to accept nearly twice the commuting costs compared to whimbrels foraging within tidal habitats. Whimbrels foraging within nontidal habitats along the Gulf Coast had the longest commuting distances followed by those in Atlantic Canada. Whimbrels feeding within tidal areas may be time-limited and less able to accommodate high commuting penalties. Roosts identified along the coast of South America were along mangrove edges adjacent to extensive intertidal mudflats where they foraged. Roosts in the Virginia portion of the U.S. South Atlantic Coast were on topographic highs embedded within extensive marshes where the birds foraged. Roosts in South Carolina and Georgia were on sandy offshore islands. These islands were isolated but compared to the nontidal sites, were closer to feeding areas. Presumably, nontidal whimbrels experience less time constraints and may overcome higher commuting penalties by foraging longer throughout the day.

Whimbrel diet may also limit allowable commuting costs. Whimbrels staging in the fall along the coast of South America and during both spring and fall along the U.S. South Atlantic Coast feed primarily on fiddler crabs *Uca* spp. with some contributions from other marine invertebrates (Skeel and Mallory 1996). The chitonous exoskeleton of fiddler crabs places an upper limit on processing and associated metabolic gain. Digestion efficiency of fiddlers by whimbrels is only 65% (Zwarts and Blomert 1990). In addition, the slow digestion rate sets a limit on intake. During periods of high foraging, whimbrels must pause periodically to digest their crab prey (Zwarts and Dirksen 1990). This digestive bottleneck may reduce prey intake rate by more than 50%. Whimbrels attempting to build fat stores within coastal areas where they depend on fiddler crabs may have less flexibility to accommodate high commuting penalties. By comparison, whimbrels staging within Atlantic Canada during fall gorge on soft fruits and consume insects within natural barrens (Skeel and Mallory 1996) or commercial blueberry fields (Nagy-Macarthur 2016). These birds do not experience the same digestive bottlenecks or time limitations imposed by tidal inundation.

The role of human disturbance in roost choice and commuting costs has become an important topic for shorebird research and management (Dias et al. 2006, Rogers et al. 2006a, Rosa et al. 2006). Human disturbance does not appear to be a widespread threat to most night roosts we identified. Most roosts were in locations with low human presence. Night roosts within Atlantic Canada were on rocky, offshore, uninhabited islands with little potential for human visitation. Roosts along the coast of South America were along mangrove edges that were remote from human settlements with very little access. Roosts in Virginia or along the Gulf Coast were either on barrier islands away from population centers or within extensive marshlands with little access. Roosts along the coasts of South Carolina and Georgia appear to have the highest exposure to threats from human disturbance. These roosts are on sandy islands with limited isolation from the mainland and some are readily accessible to population centers. Some if not all of these roosts are used during both spring and fall. Unlike the rocky islands in Atlantic Canada that occur in clusters with alternatives or along the coast of South America where mangrove edges extend for hundreds of kilometers, offshore islands along the U.S. South Atlantic Coast are rare. Roosts within this landscape appear to be the most likely to experience disturbance and the least able to accommodate disturbance in terms of alternatives.

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Data availability statement

Our data is deposited within Movebank, a free online animal tracking database hosted by Max Planck Institute for Ornithology at <https://www.movebank.org/>.

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