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# Roost availability may constrain shorebird distribution: Exploring the energetic costs of roosting and disturbance around a tropical bay

Danny I. Rogers<sup>a,\*</sup>, Theunis Piersma<sup>b,c</sup>, Chris J. Hassell<sup>d</sup>

<sup>a</sup>Johnstone Centre, Charles Sturt University, P.O. Box 789, Albury, NSW 2640, Australia

<sup>b</sup>Department of Marine Ecology and Evolution, Royal Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands

<sup>c</sup>Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 45, 9750 AA Haren, The Netherlands

<sup>d</sup>Turnstone Nature Discovery, P.O. Box 3089, Broome, WA 6725, Australia

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## ABSTRACT

High tides force shorebirds from their intertidal feeding areas to refuges known as roosts. This paper explores the energetic costs of roost disturbance of great knot (*Calidris tenuirostris*) and red knot (*C. canutus*) at Roebuck Bay, North-western Australia, assessing disturbance levels at different roost sites through direct observation and automatic radio-telemetry, and applying physiological equations and predictive roost choice models to estimate energetic costs of disturbance through a complete tidal cycle. The study area had a variety of roosts, but use of each was constrained by conditions of tide and time. The roost most suitable for shorebirds on daytime high tides of intermediate height experienced high levels of disturbance from both natural sources (birds of prey) and humans. Flight costs caused by disturbance at this site exceeded the costs of flying to and roosting at the nearest alternative roost, 25 km away. However, shorebirds did not roost at the alternate site, possibly because of the risk of heat stress in a prolonged flight in tropical conditions. Increases in disturbance levels at just one of the roost sites of Roebuck Bay would increase energetic costs substantially, and could easily reach the point at which feeding areas accessed from this roost cannot be used without incurring a net energy deficit. Roost availability can therefore limit access to feeding areas and hence limit population size. Adequate provision and management of roost sites is accordingly an important consideration in conservation of sites used by coastal shorebirds.

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## 1. Introduction

The distribution of animals is usually thought to be restricted by the occurrence of good feeding areas, with predators and disease organisms determining the quality of such areas in

addition to resource abundance (Newton, 1998). However, many animals use feeding areas for only part of the day and at other times rely on alternative areas to roost and loaf. In tidal areas shorebirds have to leave their intertidal feeding areas for high tide roosts. Shorebirds are particular in their

\* Corresponding author. Permanent address: 340 Nink's Road, St Andrews, Victoria 3761, Australia.

E-mail addresses: [drogers@melbpc.org.au](mailto:drogers@melbpc.org.au) (D.I. Rogers), [theunis@nioz.nl](mailto:theunis@nioz.nl) (T. Piersma), [turnstone@wn.com.au](mailto:turnstone@wn.com.au) (C.J. Hassell).

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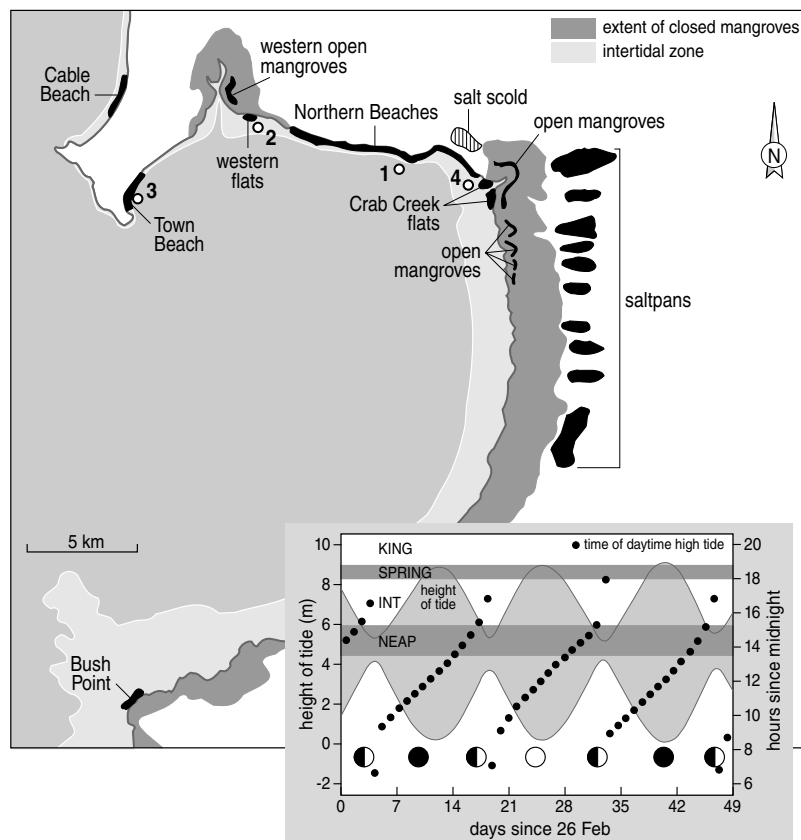
choice of such roosts (Piersma et al., 1993; Luís et al., 2001; Rogers, 2003), preferring accessible sites where birds are safe and not thermally stressed. Accessibility is a function of the distance from the feeding grounds. Safety is a function of the risk of predator attack, perhaps in combination with human disturbance (Rosa et al., 2006). Thermal stress, either because of wind and cold induced rises in maintenance costs (Wiersma and Piersma, 1994) or excessive heat load (Battley et al., 2003), is a function of the geomorphological features of a place, and may also be influenced by human disturbance.

This study examines the importance of having a range of roosting options available for differing conditions of tide, time of day and season. Using a tropical system, Roebuck Bay in north-western Australia, we build on an analysis of the choices made by two species of shorebird (Rogers et al., in press). Our interest in these roosting options is twofold. First, we would like to examine whether the options available to shorebirds in this particular setting are secure in the face of increasing levels of human disturbance. Secondly, we would like to know if roost availability can limit access to feeding grounds, an issue that has received little attention in shorebirds despite the finding that foraging itineraries of red knot *Calidris canutus* and dunlin *C. alpina* are influenced by the proximity of roosts (Van Gils et al., 2006; Dias et al., 2006).

Several studies have shown that foraging success, and hence potentially the survival, of shorebirds can be limited by interference (Triplet et al., 1999; Van Gils and Piersma, 2004) or excessive depletion of their prey (O'Connor and Brown, 1977; Van Gils et al., 2003; Zharikov and Skilleter, 2003). Roost-constrained access to feeding grounds could therefore interact with density-dependent limits on food availability to regulate shorebird numbers even if the food supply is widespread, a mechanism termed “focal point regulation” by Newton (1998).

The two study species, red knot and great knot *Calidris tenuirostris*, are large migratory sandpipers that breed in Arctic tundra. In the non-breeding season both species occur in large flocks, and are restricted to coastal habitats, where they specialise in hunting buried molluscs in intertidal mud- and sandflats (Tulp and De Goeij, 1994; Van Gils et al., 2003). At high tide they characteristically roost in flocks on the ground in open habitats, taking to the air if threatened by potential predators. Both species are lean for most of their non-breeding period in Australia, but mass increases to about 150% in Feb.–Apr as they accumulate the stores required to fuel northwards migration (Battley et al., 2004; Piersma et al., 2005).

Roebuck Bay (18° S, 122° E; Fig. 1), on the north-west coast of Australia, has large intertidal flats that provide feeding



**Fig. 1** – Map of the Roebuck Bay study site, adapted from aerial photographs. Feeding sites considered in this study are denoted with white-centred dots and numbered; from left to right: Town Beach, Dampier Flats, Fall Point and Crab Creek. Roosting habitats are marked in black and labeled. Inset: Amplitude of tides in the bay (plotted against the left-hand y-axis) through the study period, 26 Feb. to 15 April. Times of the peak daytime high tides are plotted against the right-hand y-axis. Grey shading depicts high tides classified as springs (8.3–8.95 m) and neaps (>6.0 m); intermediate and king tides are also shown. Lunar phases are shown at the bottom of the graph.

areas for internationally significant numbers of 20 migratory shorebird species (Rogers et al., 2003). It has a hot tropical climate, and extensive mangroves surround much of the bay (Fig. 1). Mangroves are usually too densely vegetated to be suitable roosts for coastal shorebirds (Zwarts, 1988). As a result, shorebird roosts of Roebuck Bay are restricted to a few discrete sites (Fig. 1): small mangrove clearings about 100 m in diameter (Open Mangroves and Western Open Mangroves); supratidal claypans east of the bay (Saltpans); raised mudflats only exposed on high tides during neaps (Western Flats, Crab Creek Flats); and beaches (Bush Point, Cable Beach and the Northern Beaches). Sparsely vegetated white dunes back Cable Beach and Bush Point. The Northern Beaches are narrower, are backed by vegetated dunes and low laterite cliffs and have a few small adjacent sea-stacks sometimes used by roosting shorebirds; they are internationally renowned as a shorebird-viewing site (Rogers et al., 2003). The adjacent town of Broome has a thriving tourist industry and is growing rapidly, increasing the risk of shorebird disturbance on the Northern Beaches.

**2. Methods**

**2.1. Temporal variation in the roosting option set**

Rogers et al. (in press) used a radio-telemetry study at Roebuck Bay to calibrate simple bounds-based models of local roost choice in great and red knots. These models were applied in this paper to assess whether roosts were potentially suitable. The models assume that knots roost at the closest site to their low-tide feeding area, provided that at these roosts, threshold values for certain environmental attributes (Table 1) are met. By day, environmental thresholds were: (1) a wet substrate, as sites with dry substrates had too warm a microclimate for roosting shorebirds; (2) nearest tall cover that should be at least 10–59 m from the roost (predictive success of models on non-neap tides, 63.5% for Great Knot, 70.0% for Red Knot; predictive success of models on neap tides, 90.6% for Great Knot, 80.3% for Red Knot). At night, microclimate did not affect the bounds models (it was cool at all sites in the absence of direct solar radiation); thresholds were that the nearest tall cover should be at least 10–59 m from the

roost and that the background colour at the roost should not be dark (predictive success of models on non-neap tides, 59.9% for great knot, 64.6% for red knot; predictive success of models on neap tides, 92.3% for great knot, 80.1% for red knot).

**2.2. Disturbance**

The frequency of disturbance was measured directly at five sites (final column of Table 2) in October 1997, March and August 1998, and October 2000, by watching roosting flocks from concealed positions. Each time a flock or part of flock took to the air, the time and number of flying shorebirds was noted. Flights were classified as alarm flights if birds towered and gave alarm calls. The cause of observed disturbances was recorded if identified. The percentage of shorebirds that were airborne was recorded at regular 5-min or 10-min intervals throughout the observation periods, and pooled data from these observations were used to estimate the percentage of the high tide period that was spent airborne due to disturbance. At the Northern Beaches a multiple linear regression showed the proportion of shorebirds in alarm flights per half-hour of observation to be significantly related to both tide height ( $P = 0.0028$ ) and a categorical variable describing whether the tide was rising or falling ( $P = 0.0029$ ;  $R^2 = 0.641$ ,  $n = 17$ ), with birds being more likely to be disturbed on a rising tide. In estimating the number of disturbances and amount of time spent in flight due to disturbance throughout a high tide period at this site, it was therefore necessary to account for the number of observations made on rising and falling tides. At other roost sites estimates of the number of alarm flights per hour were based on study days in which disturbance was recorded systematically throughout a high tide period; the number of observations made on rising and falling tides was therefore equal and no correction was needed.

These quantified observations were not made at all roost sites in Roebuck Bay, many of which were not readily accessible to human observers or were otherwise unsuitable for systematic disturbance observations. An ordinal *a priori* assessment of disturbance levels at other sites (Table 2) was made for all Roebuck Bay roosts on the basis of unquantified observations made while birdwatching regularly in the region

**Table 1 – Attributes of roost sites of Roebuck Bay**

Tide height (m)	Back-ground colour	Distance to tall cover; daytime substrate temperature			
		All	Neap (<6 m)	Intermediate (6.0–8.2 m)	Low Spring (8.3–8.9 m)
Northern beaches	Int.	60–199 m; cool	10–59 m; cool	1–10 m; cool	1–10 m; int.
Crab creek flats	Pale	>200 m; cool	<1 m; flooded	<1 m; flooded	<1 m; flooded
Cable beach	Pale	>200 m; cool	60–199 m; cool	10–59 m; cool	10–59 m; cool
Bush point	Pale	>200 m; cool	>200 m; cool	60–199 m; cool	60–199 m; cool
Western flats	Int.	1–10 m; cool	<1 m; flooded	<1 m; flooded	<1 m; flooded
Western open mangroves	Dark	10–59 m; hot	10–59 m; hot	10–59 m; int.	10–59 m; cool
Open mangroves	Dark	10–59 m; hot	10–59 m; hot	10–59 m; cool	1–10 m; int.
Saltpans	Pale	>200 m; hot	>200 m; hot	>200 m; cool	>200 m; cool
Town beach	Int.	60–199 m; cool	10–59 m; cool	10–59 m; cool	10–59 m; cool

Background colour was scored as pale, intermediate (Int.) or dark. Substrate temperature was scored as wet, intermediate (in situations where it was drying out or the wet area was small) or dry; sites scored as flooded were too deeply immersed for shorebirds to roost.

**Table 2 – Parameters and formulae used in models**

Site	Disturbance level (a priori classification)	% of radio-signals interrupted	No. of radio records	Alarm flights per hour, time spent in alarm flights per tide
Cable beach – day	Very high		0	
Town beach – day	High	89.5%	143	
Northern beaches – day	High	81.2%	617	3.36 (29 h obs.), 30.1 mins
Open mangroves – night	Moderate	66.7%	9	
Northern beaches – night	Moderate	63.6%	165	
Open mangroves – day	Moderate	58.3%	115	0.90 (10 h obs.), 7.8 mins
Town beach- night	Moderate		0	
Western flats -day	Moderate	50%	2	
Western flats -night	Moderate	50%	2	
Western open mangroves – night	Moderate	50.0%	4	
Western open mangroves – day	Moderate	46.4%	69	
Bush Point – day	Low	43.5%	23	0 (9 h obs.)
Bush Point – night	Low	30.0%	70	
Crab Creek Flats – day	Low	29.7%	118	
Crab Creek Flats – night	Low	25.9%	139	
Salt pans – day	Low	9.0%	89	0 (5 h obs.)
Cable Beach – night	Low	5.2%	677	0 (10 h obs.)
Salt pans – night	Low	3.1%	159	

over several years (DIR, CJH, unpubl. data). These classifications were compared with data obtained in a radio-telemetry study carried out from Feb. to Apr. 2000, reported in detail by Battley et al. (2004) and Rogers et al. (in press). The study involved 25 great and 23 red knots with a 1.8 g Holohil BD2 radio-transmitter superglued to their rumps. Their local movements were monitored with an array of 14 continuously operating automatic radio-tracking stations sited at the key roost sites of Roebuck Bay. The stations had a short radio-reception range (0.7–1.0 km) and individuals were treated as being present at a station if the signal strength was  $\geq 1.4$  times the background noise. In constructing disturbance indices for this paper, a bird at a specific roost was considered to have been disturbed if its radio-signal was interrupted during within an hour of high water (i.e. if it moved to another roost during high tide, or if its signal stopped and later resumed at the same site). Sites with the highest percentage of interrupted radio-signals were assumed to be the most heavily disturbed.

### 2.3. Disturbance costs

Roost choice costs were simulated for great and red knots from four feeding sites in northern Roebuck Bay (Fig. 1), all of which are regularly used by one or both knot species (Rogers, 1999, unpubl. data). In theory a roost site would be unsuitable if the energetic costs of roosting there exceeded energy intake minus maintenance requirements. However, energy deficits incurred while roosting on a specific tide might be offset by surpluses made on other tides. The roost choice models (summarised above) were therefore used to predict where great and red knots from the four selected feeding sites would roost on high tide, through a complete cycle of 28 low and 28 high tides. It was assumed that during non-neap tides, individuals would be faithful to only one feeding area, and that on neap tides they would move to the Crab Creek Flats in the east of the bay (Fig. 1); this movement pattern was followed regularly by the knots radio-tracked by Rogers et al. (in press). The average number of neap (<6 m), intermediate

(6–8.2 m), spring (8.3–9 m) and king (>9 m) high tides per cycle was calculated from a year (2000) of tide-height data (National Tidal Centre, Australian Bureau of Meteorology). The landward edge of the intertidal flats of Roebuck Bay corresponds well with mean sea level (pers. obs.), so low and high tide periods were treated as being of equal duration, 370.1 min. Suitability of some roost sites in Roebuck Bay is influenced by heavy rainfall; for the simulations herein it was assumed the tidal cycle occurred in a rainless period (typical of Roebuck Bay, except in the wet season from about December to April).

Parameters and formulae used to calculate costs of maintenance and roost flights are summarised in Table 3. Body mass and Basal Metabolic Rate have been measured in great knot in Roebuck Bay, as has body mass of red knot; Basal Metabolic Rate of red knot in the bay was calculated by scaling down from the great knot estimates using an interspecific mass exponent of 0.71. Remaining parameters and formulae were obtained from published studies in laboratories or extra-limital sites. Thermoneutrality was assumed at all times, as operative temperatures of knots in the study area are typically in the thermoneutral zone (Wiersma and Piersma, 1994; Piersma et al., 1995), except in hot conditions when knots avoid overheating by seeking roosts with cool microclimates (Rogers et al., in press), a preference accounted for by the roost choice models. However, a correction was included for heat loss to ingested cold water during foraging, modifying the equation of Piersma et al. (2003a). The original equation included heat loss of 0.58 W in water of 15 °C, and this was corrected by a factor of 0.792, acting on the assumptions that all such heat loss was conductive, and that average surface- and pore water temperature in Roebuck Bay mudflats was 28 °C (unpubl. data). As the birds in the study site were living under thermoneutral conditions, we additionally assumed that all cost factors were additive (Van Gils et al., 2006).

Durations of commuting flights from the four selected feeding sites to the different roosts of Roebuck Bay were calculated assuming direct flights that were regarded as occur-



**Table 3 – Site-specific likelihood of disturbance at the roosts of Roebuck Bay, ordered approximately from most to least highly disturbed, with night roosts shaded grey**

Parameter	Assumptions and calculations	Source
Mass ( $M_b$ )	Great knot lean mass = 147.7 g Great knot departure mass = 240 g Red knot lean mass = 105 g Red knot departure mass = 165 g	Higgins and Davies (1996) Higgins and Davies (1996) Piersma et al. (2005) Piersma et al. (2005)
Flight speed	54 km h <sup>-1</sup>	Kvist et al. (2001)
Power input ( $P_{in}$ ) in flight	Long flights: $P_{in} = 0.38 + 0.35 \log_{10} M_b$ Short flights: $P_{in} = 250.05 M_b^{0.8741}$	Kvist et al. (2001) Nudds and Bryant (2000)
Basal metabolic rate (BMR, in W)	$-2.57 + 1.24(\log_{10} M_b)$	Battley et al. (2001)
Cost of sleeping (KJ)	BMR × time spent sleeping (in seconds)	Piersma et al. (2003a)
Cost of active rest (KJ)	BMR × 1.659	Piersma et al. (2003a)
Cost of foraging (KJ)	$[(BMR \times 1.659) + (BMR \times 0.613)] \times$ time spent foraging (in seconds)	Piersma et al. (2003a)
Cost of digestion (KJ)	$(BMR \times 1.105) \times$ time spent foraging (in seconds) × 0.792	Piersma et al. (2003a)

ring during the high tide period. Alarm flights, in which both species of knot take off rapidly and climb to considerable height (often >100 m, pers. obs.) were assumed to be more costly than steady flight (Hambly et al., 2004). Their costs were calculated using the allometric equation for short flights of Nudds and Bryant (2000), which predicted the short-flight costs of our study species to be 3.03 times greater than steady-state flight in lean red knots, 3.58 times greater than steady-state flight in lean great knots. This equation has not been calibrated on birds >150 g, so may not be perfectly suitable for red and great knots approaching departure mass. The alarm flights of knots include bursts of high speed, rapid changes in direction and substantial height gain, so our suspicion is that their costs are more likely to exceed than to fall short of the costs predicted by the equation. In another respect the assessment of disturbance costs was also conservative; disturbance may cause increased heartbeat rate and metabolic costs without actually forcing birds to take flight (Giese,

1998), and our models did not attempt any correction for this effect.

The amount of time spent sleeping, in active rest (e.g. standing, walking or preening) or foraging was estimated through activity scans made at feeding and roosting habitats in Roebuck Bay.

### 3. Results

#### 3.1. Temporal variation in the roosting option set

The suitability of individual roost sites used by the great and red knots of northern Roebuck Bay (Fig. 1) varied according to whether it was day or night, and with tide and climate conditions (Rogers et al., in press). In general usage of roosts corresponded well with that predicted by the bounds models (Table 4). The Northern Beaches were used more than expected on spring and king tides because some knots roosted on a few

**Table 4 – Suitability of roost sites, Feb.–Apr. 2000, in different conditions of tide, climate and time**

Conditions and no. of records	Crab creek flats	Western flats	Northern beaches	Town beach	Cable beach	Bush point	Western open mangroves	Open mangroves	Salt pans
<i>Day (dry)</i>									
Neap (112)	90.2%	1.8%	7.1%	0.9%	0%	0%	0%	0%	0%
Intermediate (254)	0%	0%	85.0%	5.1%	0%	0%	0.4%	4.3%	5.1%
Spring (193)	0%	0%	65.3%	5.2%	0%	0%	11.9%	16.1%	1.6%
King (0)	–	–	–	–	–	–	–	–	–
<i>Day (wet)</i>									
Neap (75)	81.3%	2.7%	16.0%	0%	0%	0%	0%	0%	0%
Intermediate (225)	0%	0%	45.3%	7.1%	0%	0%	11.6%	3.1%	32.9%
Spring (118)	0%	0%	40.7%	5.9%	0%	0%	16.1%	18.6%	18.6%
King (111)	0%	0%	33.3%	20.7%	0%	0%	27.9%	0%	18.0%
<i>Night</i>									
Neap (153)	86.3%	0.7%	3.9%	0%	8.5%	0.7%	0%	0%	0%
Intermediate (464)	0%	0%	11.0%	0.2%	58.6%	1.1%	1.3%	0%	27.8%
Spring (88)	0%	0%	27.3%	0%	26.1%	4.5%	2.3%	0%	39.8%
King (0)	–	–	–	–	–	–	–	–	–

Unshaded cells depict potentially suitable roost sites. Cells shaded dark grey depict flooded sites where roosting was impossible. Cells shaded light grey depict other cases where climate, distance from tall cover or background colour were outside the thresholds of bounds models (Rogers et al., in press). Percentages of radio-tagged birds found at specific roosts in different tide conditions are shown, with the number of total cases given in parentheses in the first column.

small adjacent sea-stacks; only a small proportion of the knots present could fit onto these sites, so their habitat attributes were not included in the roost choice models. Roosts on mudbanks on the intertidal flats of Roebuck Bay were frequently used during neaps, but were submerged and never used by shorebirds on tides >6 m. At night, knots avoided sites that had nearby tall cover or had a dark background colour, one or both of these considerations making them avoid roosts in mangrove clearings, Town Beach and the Northern Beaches. As a result, distances flown from feeding areas to roosts were significantly greater at night than by day, on both non-neaps (at night  $6.69 \pm 4.61$  km,  $n = 655$ ; by day  $1.72$  km  $\pm 1.59$ ,  $n = 734$ ,  $z = 26.313$ , Dunn-Sidak adjusted  $P < 0.01$ ) and on neaps (at night  $2.66 \pm 3.46$  km,  $n = 136$ ; by day  $1.89$  km  $\pm 2.87$ ,  $n = 175$ ,  $z = 2.095$ , Dunn-Sidak adjusted  $P < 0.05$ ).

Microclimate was similar at all sites at night. By day when exposed to direct solar radiation, shorebirds were at risk of heat stress, and only used roost sites with wet substrates or shallow water, where counter-current exchange mechanisms could be used to lower body temperature (Battley et al., 2003). Suitably cool microclimates could be found along the wave-washed sand of beaches in all tide conditions by day. However, Cable Beach is next to a tourist resort and is often unsuitable by day because of continuous human disturbance; the Northern Beaches became unsuitable on the highest tides, when the water-edge was too close to tall cover. In such tide conditions, however, roosting options became available in habitats that were otherwise too hot. Spring tides extended far into the mangroves to form shallow lakes within some large mangrove clearings. King tides flooded these clearings so deeply that they became unsuitable for shorebirds, but in these conditions the tide extended completely through the mangroves to flood extensive lakes on the claypan systems beyond. The claypans and mangrove clearings are also suitable for shorebirds when flooded by heavy rain.

### 3.2. Disturbance

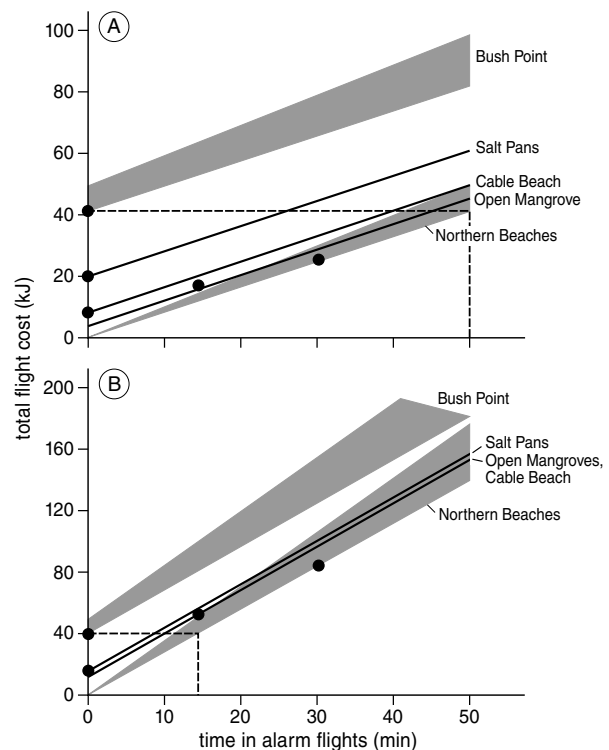
Classifications of roost disturbance levels made through opportunistic observations corresponded well with more rigorous data obtained through radio-telemetry or systematic observation (Table 2), suggesting our assessment of relative disturbance levels of the roosts is adequate. The most heavily disturbed daytime roosts were beaches that are also the roosts most easily and often visited by humans (pers. obs.). In particular, Cable Beach (the most frequently used roost at night) is a popular tourist resort and the lack of radio-records from the site by day may have been due to near-continuous human disturbance.

Of 105 cases of disturbance observed along the Northern Beaches by day, most (24.8%) were caused by birds of prey: Brahminy kite (*Haliastur indus*), whistling kite (*H. sphenurus*), black kite (*Milvus migrans*), white-bellied sea-eagle (*Haliaeetus leucogaster*), spotted harrier (*Circus assimilis*), nankeen kestrel (*Falco cenchroides*) and Australian hobby (*Falco longipennis*). Raptors used a concealed approach when attacking shorebird roosts, flying towards them behind the cover of dunes, cliffs or trees. Attacks were abandoned if a shorebird flock became airborne before any birds could be taken from the ground.

Roosting shorebirds were wary on the Northern Beaches and often (21.9% of cases) took off in response to false alarms, such as ospreys (*Pandion haliaeetus*), Caspian terns (*Sterna caspia*) or silver gulls (*Larus novaehollandiae*) flying low over roosts. Ospreys were never seen attacking shorebirds and were generally ignored by them, so instances in which they flushed waders were treated as false alarms. Many disturbances (20.9%) were caused by humans, their dogs or their vehicles. This measure probably underestimated the effect of human disturbance, for unlike birds of prey, humans often remained on beaches for some time after disturbing shorebirds, potentially preventing them from resettling. In 32.6% of cases we could not identify the cause of disturbance.

### 3.3. Disturbance costs

Total flight costs during a high tide for different roost sites were plotted against the time spent in alarm flights. Results for great knot from Fall Point (Fig. 2) were conceptually similar to those for red knots, and for both species at other feeding sites of northern Roebuck Bay (not presented here). Heavy birds at departure mass incurred higher flight costs than lean



**Fig. 2 – Flight costs (kJ) per high tide of lean great knots flying to different roosts from a feeding area at Fall Point, assuming equal costs  $s^{-1}$  for commuting and alarm flights (Panel A) or that alarm flights are 3.58 times more costly (Panel B). Grey-shaded areas indicate variation in flight costs related to variation in body mass at Bush Point and the Northern Beaches (upper boundary = costs for birds at departure mass). Observed levels of disturbance at each roost are indicated by black dots. Dotted lines indicate the level of disturbance at the Northern Beaches above which flying to Bush Point becomes a more economical option.**

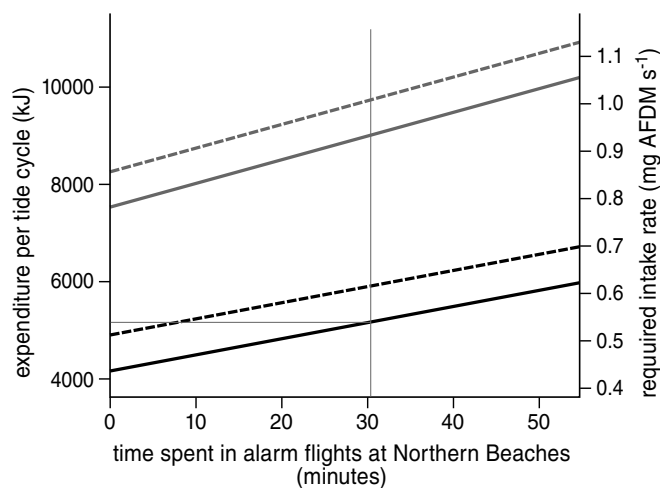
birds, but the difference was relatively small, considerably lower than the difference in costs between roosting at the closest potential roost site or the most distant (Fig. 2). If short alarm flights were assumed to be no more costly per time unit than commuting flights, the Northern Beaches turned out to be the most economical roost, provided the time spent in alarm flights per high tide did not exceed 50 minutes (Fig. 2A). However, the allometric equation of Nudds and Bryant (2000) predicts that costs of short flights in lean great knot will be 3.58 times those of commuting flights, and following this assumption, Bush Point (when undisturbed) turns out to be a more economical roosting option than the Northern Beaches if disturbance levels at the latter exceed 15.79 minutes (Fig. 2B). On average  $30.17 \pm 6.63$  minutes ( $n = 233$  scans) were spent in alarm flights per high tide at the Northern Beaches, making that site a more expensive roost option than an undisturbed Bush Point if short flights were 2.18 or more times more costly than steady-state flight; this threshold factor was 1.84 for red knots at the same feeding site.

The relative amounts of energy allocated to different activities at current levels of disturbance over a complete tidal cycle did not appear to differ greatly between species or between feeding sites within northern Roebuck Bay (Table 5). Foraging and digestion consumed more energy than other activities. However, the additional costs of roosting were also considerable. The combined costs of flying to roosts, and disturbance flights at roosts, ranged from 17.3% to 25.4% of the total energy expenditure of great knot at different feeding sites in northern Roebuck Bay (Table 5), and from 19.4% to 28.7% of the expenditure of the smaller red knot. In both species the cost of roost flights exceeded the amount of energy expended when sleeping or when at active rest (i.e. awake, but carrying out minimal activities such as vigilance or preening), although much more time was invested in these activities.

Estimates of total energy expenditure during a complete high tidal cycle increased with body mass. Energetic costs of great knots at departure mass (of c. 240 g) were almost twice

**Table 5 – Energy budgets of great knots (white background) and red knots (shaded grey) from four different feeding sites (Fig. 1): (1) Fall Point; (2) Dampier Flats; (3) Town Beach; (4) Crab Creek Flats**

	Site 1	Site 2	Site 3	Site 4	Site 1	Site 2	Site 3	Site 4
Relative cost of activity								
Sleeping	10.3%	8.7%	8.6%	10.7%	9.9%	8.2%	8.2%	10.4%
Active rest	11.6%	11.8%	12.4%	12.0%	10.6%	10.7%	11.3%	11.1%
Foraging	35.7%	33.2%	33.5%	36.8%	34.9%	32.1%	32.7%	32.7%
Digesting	22.6%	21.0%	21.2%	23.3%	22.1%	20.3%	20.7%	22.9%
Commuting	5.2%	6.6%	4.5%	2.3%	6.8%	8.5%	5.8%	2.9%
Alarm flights	14.6%	18.7%	19.7%	15.0%	15.8%	20.2%	20.3%	16.4%
Total roost flights	19.8%	25.4%	24.2%	17.3%	22.6%	28.7%	27.1%	19.4%
Average daily energy budget								
Expenditure ( $\text{kJ day}^{-1}$ )	336.2	362.3	358.0	326.7	230.4	250.6	246.2	221.8
Expenditure/BMR	4.53	4.88	4.83	4.40	4.36	4.75	4.66	4.20
Daily requirement for pre-migratory mass gain ( $\text{kJ day}^{-1}$ )	386.2	412.3	408.0	376.7	271.3	291.6	287.2	262.7
Required intake rate to balance expenditure and fuelling								
Intake ( $\text{mg AFDM s}^{-1}$ )	0.58	0.62	0.61	0.56	0.40	0.43	0.42	0.38



**Fig. 3 – Energy expenditure (solid lines) and extra requirement for mass gain (dashed lines) of  $1.1 \text{ g day}^{-1}$  in great knot from Fall Point over a full tidal cycle, plotted against the average duration of disturbance per high tide when roosting on the northern beaches. Models for a lean great knot (147.5 g) are shown in black, for a fat great knot (240 g) in grey. The vertical line indicates the disturbance levels found at the Northern Beaches in this study.**



as high as those at the usual non-breeding mass of 147.5 g (Fig. 3). Costs were still higher in periods of pre-migratory mass gain (Fig. 3), assuming mass-gain rates of  $1.1 \text{ g day}^{-1}$  in great knots (linearly scaled up from red knot estimate of  $0.9 \text{ g day}^{-1}$  at Roebuck Bay, Piersma et al., 2005). Energy expenditure per tidal cycle was also sensitive to the amount of disturbance on the Northern Beaches, although this roost was only used on 25.9% of high tides. For example, the half-hour of alarm flight per high tide observed at the Northern Beaches consumes almost as much energy per day as does undertake pre-migratory mass gain at a typical rate (Fig. 3).

## 4. Discussion

### 4.1. Roosting options at night

At night on non-neap tides birds were prepared to pay a high commuting price to roost in ideal conditions, most flying to Cable Beach or the saltpans. Both sites were considerably more distant than the roosts used on corresponding daytime high tides. Use of different roost sites by day and night appears to be common in coastal shorebirds (Hockey, 1985; Handel and Gill, 1992; Smit and Visser, 1993; Sitters et al., 2001), though it is by no means universal (Warnock and Takekawa, 1996; Van Gils and Piersma, 1999; Leyrer et al., 2006).

The roost choice models correctly predicted the observed preferences for Cable Beach and the saltpans on night-time neap high tides because the sites had pale backgrounds and were distant from tall cover (the same applied to Bush Point, but this site was rejected by the models as it was considerably further away). Both attributes would increase the ease of detecting approaching predators. In addition Cable Beach and the saltpans happened to have the lowest levels of disturbance of the night-time roost sites (Table 3), suggesting they were particularly “safe” roosts.

Although this reasoning is plausible, it is not entirely consistent with field observations. Shorebirds at Cable Beach at night spent 87% of the high tide period asleep, and did not appear vigilant enough to detect predators; human observers could walk to within 10 m of them as they slept, provided that they moved quietly without using torchlight (pers. obs.). In addition, Cable Beach is not free of predators; barking owls (*Ninox connivens*) and house cats (*Felis catus*) have been observed hunting shorebirds there at night (pers. obs.).

Sleeping is the most energy-efficient activity possible for shorebirds (Piersma et al., 2003a) and probably a physiological necessity (Rattenborg et al., 1999); recent studies indicate that birds are most predisposed to sleep in darkness (Rattenborg et al., 2005). If there is a physiological requirement to spend much of the night asleep, shorebirds may therefore select night-time roosts perceived to have low levels of “danger” (i.e. the inherent probability of becoming a prey item if no anti-predator measures are taken, Lank and Ydenburg, 2003). This consideration has received little consideration in the disturbance literature (e.g. Davidson and Rothwell, 1993), but may be critical in urban shorebird habitats. Our repeated field experience at Roebuck Bay is that shorebirds avoid roosting at sites where they are exposed to artificial lighting such as streetlights or traffic. Possibly such lighting makes roosting shorebirds too easily detected by predators,

or otherwise makes them perceive night-roosts to be too dangerous for sleeping.

At Roebuck Bay the lack of vehicle access to the remote saltpans should protect night roosts in this habitat for the foreseeable future. Cable Beach is potentially more sensitive, being close to the town of Broome; the roost there has serendipitously been protected from intrusion or illumination at night because the dunes behind it are part of the Minyirr Coastal Park, maintained for its cultural importance to Aboriginal people.

### 4.2. Roosting options by day

Shorebirds at Roebuck Bay are more tolerant of disturbance by day than at night, and on daytime high tides the most commonly used roosts, Northern and Town Beaches, were also among the most heavily disturbed. Much of this disturbance is natural, caused by birds of prey. However, it is now augmented by human activity, and the combined disturbance effects could reach the point at which the roosts become unsuitable. This point may not be far away, given that alternative roosts in mangrove clearings and saltpans are preferred when they become suitable on spring tides, or if flooded by rains. In 2003, unseasonal rainfalls in May flooded large salt-scolds on Roebuck Plains (Fig. 1) and before they dried out in August, they were used in preference to the Northern Beaches in all tide conditions.

Despite the high levels of disturbance at the Northern Beaches, they were the preferred roost on daytime high tides of intermediate height (6.0–8.2 m). Our models indicate that this is because knots roost on wet substrates with a relatively cool microclimate; on tides of intermediate height the only alternative roosts for knots using feeding areas in the North of Roebuck Bay are Cable Beach (frequently unsuitable due to near-continuous human disturbance by day) and Bush Point (about 25 km away). The combined commuting and alarm flight costs of roosting on the frequently-used Northern Beaches exceed the costs of commuting to roost at the undisturbed Bush Point. Surprisingly though, Bush Point was not used by day by any radio-tracked birds from feeding grounds in northern Roebuck Bay (Rogers et al., in press). We suspect this is because an uninterrupted flight of about 25 km in the middle of the day could cause heat stress problems. Captive studies indicate that the water efflux rate of flying knots increases rapidly with temperature, starting to exceed water influx rates somewhere between 15 and 23 °C (Kvist, 2001). Evidence that this critical water efflux rate is readily exceeded in the tropical conditions of Roebuck Bay is provided by observations of panting in great and red knots; this heat loss behaviour occurs regularly for a minute or so after short flights (Battley et al., 2003). In cool climates where the costs of flight are offset by the thermoregulatory advantages of obtaining metabolic heat through locomotion (Bruinzeel and Piersma, 1998), shorebirds can probably undertake longer flights at high tide, an extreme example being a few sites where intertidal shorebirds will spend an entire high tide on the wing (Dekker, 1998; Hötter, 2000).

On present knowledge it is not possible to predict how high disturbance levels can get on the Northern Beaches of Roebuck Bay before shorebirds are forced to roost elsewhere

in all tide conditions. The present abundance of shorebirds there suggests that they can cope with the current levels of disturbance. In future management of the site, it would be prudent to ensure that disturbance levels do not increase further.

#### 4.3. Energetic consequences of Roost choice

Our attempt to assess the energetic costs of roosting in Roebuck Bay is the first to use effective roost choice models to predict local movements throughout a tidal cycle, taking into account that shorebirds roost in different places according to tide height and whether it is day or night. The overall energy expenditure of knots in Roebuck Bay over a tidal cycle was estimated to be 4.2–4.9 times as high as basal metabolism. This is a high level of sustained expenditure, approaching the inferred ‘metabolic ceiling’ of 4–5 times Basal Metabolic Rate that was once considered to be found only in hard-working parent birds and growing animals (Weiner, 1992). However, high levels of energy expenditure appear to be typical of shorebirds (Piersma, 2002; Piersma et al., 2003b). Our estimate is similar to the only direct measurements available of field metabolic costs of non-breeding shorebirds (sanderling *Calidris alba*), which ranged from 2.1 to 4.2 times Basal Metabolic Rate according to non-breeding area (Castro et al., 1992). Field metabolic costs of shorebirds are higher in colder climates (Castro et al., 1992; Wiersma and Piersma, 1994), and it has been suggested that an advantage of migrating to warm non-breeding grounds is the energetic saving of spending several months in sites where insulation costs are low (Wiersma and Piersma, 1994). The estimates of energy costs in Roebuck Bay suggest that the tropics are not necessarily “cheaper” non-breeding sites when the costs of activity (including roost movements) are also considered.

The combined costs of flying to roosts, and at roosts because of disturbance, ranged from 17.3% to 28.7% of the total energy budget of red and great knots in Roebuck Bay, a level of expenditure that does not appear to be unusual. Commuting flights accounted for 2.3–8.5% of the total tidal energy expenditure. In studies of red knot elsewhere, estimates of costs of routinely made roost-flights (as a proportion of daily expenditure) were of similar scale: 12.2% at the Dee Estuary (Mitchell et al., 1988) and 5.6% in the Dutch Wadden Sea (Piersma et al., 1993; Rehfisch et al., 1996). The distances between feeding sites and roosts in Roebuck Bay are also consistent with those observed in previous studies, which range from 2.2 km in western sandpipers *Calidris mauri* in San Francisco Bay (Warneck and Takekawa, 1996), to about 20 km or more for red knots at estuaries in western Europe (Mitchell et al., 1988; Van Gils et al., 2006). Comparison of disturbance levels with other shorebird studies is difficult because different workers have used different indices of disturbance. Disturbance levels at the Northern Beaches were high, but the observed frequency of 3.36 alarm flights per hour is not unique. Similar frequencies of disturbance incidents have been recorded on the Dee Estuary (Kirby et al., 1993) and Tagus Estuary (Rosa et al., 2006).

Energy expenditure over a tidal cycle was sensitive to the amount of disturbance. For example, an average 30-min increase per tide in the amount of time spent in alarm flights

at the Northern Beaches (a site used on only 25% of high tides) would increase the total energy expenditure by 13.3% in a lean great knot (Fig. 3). Shorebirds may be able to compensate for these costs to some extent by extending their food intake but the extent to which they can do this will be finite; it will be limited ultimately by digestive capacity or the prey available at a site (Van Gils et al., 2005). Energy expenditure and required intake rates over a tidal cycle increase with body mass (Fig. 3), and would therefore be expected to be highest in the final stages of pre-migratory mass gain. The higher energy demands of heavier birds might be helpful in identifying situations where shorebirds are experiencing difficulty in meeting the energetic costs of roosting, as such individuals may be obliged to select roosts with lower energy costs but presumably higher risk levels. Such scenarios appear to have been observed by Handel and Gill (1992) and by Van Gils and Piersma (1999), who described changes in roosting behaviour of dunlin (*Calidris alpina*) and red knots, respectively, as they approached departure mass.

In one of the few detailed investigations of roost choice in intertidal shorebirds, Rehfisch et al. (2003) remarked that “... any change in roosting conditions is likely to be less detrimental than loss of feeding areas”. While we agree that feeding areas are vital, we do not agree that loss of roosts should not be considered a separate concept; feeding areas are only of use to shorebirds if they are associated with acceptable roosts (Dias et al., 2006). If the energetic costs of roosting should increase expenditure to the point where shorebirds cannot meet their energy requirements for maintenance, moult and pre-migratory fuelling, then diminished survival (Durell et al., 2005) and a loss of feeding areas are inevitable. Our models demonstrate that within the scale of a naturally occurring shorebird site, a relatively small increase in disturbance levels can result in a substantial increase in energy expenditure. The capacity of shorebirds to compensate for such increases will vary according to the feeding and roosting options available at a site, but it is very likely that circumstances can develop where roost costs could drive the energy budget into deficit. The adequacy of roost habitats should therefore be considered carefully in management of coastal shorebird sites.

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