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High-tide roost choice by coastal waders

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At high tide, most waders that feed in the intertidal zone are forced to sites known as roosts. Here I discuss the factors that influence roost choice: they include predation risk and disturbance rates, as well as the energetic costs of remaining thermoneutral at the roost, and flying to the roost from the feeding grounds. The relative importance of these factors is poorly known. I identify some fundamental gaps in our knowledge of roost choice mechanisms. I suggest that it is feasible to construct roost choice models that will be valuable in the management of threatened shorebird sites.

INTRODUCTION

Many of the world's waders are coastal and feed in the intertidal zone. At high tide, they are forced from their low-water feeding grounds. The sites to which they move are traditionally called roosts, whether or not the waders actually sleep while they are there.

Roost site choice is important for waders. A good roost should be safe from predation and involve low energy costs, as every kilojoule spent roosting is lost from such vital activities as maintenance metabolism, moult and migratory fuelling. Waders typically avoid predators by energy-expensive flight, so the objectives of low predation risk and low energy costs are potentially contradictory. In practice it may be difficult for waders to find suitable roosts, a point perhaps most strikingly demonstrated by observations that waders, such as Dunlins *Calidris alpina* and Western Sandpipers *C. mauri*, are sometimes forced to spend the entire high tide on the wing (Dekker 1998,Hötker 2000, Buehler 2002). Piersma *et al.* (2002) also report an incident where waders were unable to find a roost site in thick fog.

Studies and management plans directed towards the conservation of coastal waders typically emphasize the intertidal feeding areas (e.g. Goss-Custard 1984, 1985). They are indeed crucial, but the best feeding areas may be of no use to waders if they are not associated with adequate roosting habitat. This is a situation that is already occurring where roost sites are lost to human use as, for example, at Panama City (Buehler 2002). Intertidal flats are costly and difficult to convert for human purposes, so coastal development tends to occur on the shore where waders often roost. The importance of protecting roost sites is widely recognised (e.g. Rehfisch *et al.* 1996) and this has even led to the costly creation of artificial ones (e.g. Burton *et al.* 1996). However, there is surprisingly little literature on how waders select roost sites. As a result, little advice is available to wildlife managers on the conservation or creation of these habitats. In this article I discuss some of the factors that may influence where waders choose to roost, the methods available for measuring them and potential directions for future research.

BEHAVIOUR AT HIGH TIDE

Most wader species roost communally in flocks ranging from tens to thousands of birds. The most likely explanation for communal roosting is that it reduces the individual's risk of predation (Cresswell 1994a). It has also been suggested that communal roosting allows information to be exchanged on potential feeding sites and may play a role in birds synchronizing their annual cycles (Piersma 1983).

When suitable habitat is available, waders may sometimes feed at high tide (e.g. Velasquez & Hockey 1996, Luís *et al.* 2001). This does not always apply though. Many high tide roosts are in situations where there are no feeding opportunities (e.g. Piersma *et al.* 1993, Burton *et al.* 1996). Even when suitable habitat is available waders often loaf or sleep at roosts in preference to feeding (Handel & Gill 1992).

Waders spend a large proportion of their time at high tide roosts apparently sleeping (pers. obs.); for example 77% of the roosting Dunlins in Alaska studied by Handel & Gill (1996) had their bills tucked into their scapulars in a sleeping posture. It has been suggested that the basic function of sleep is to allow the brain to activate and reinforce memory circuits during a period when there is no interference from urgently needed sensory inputs (Kavanau 2001). This view is not universally held (Siegel 2001), but there appears to be wide acceptance that there is a physiological necessity for sleep (e.g. Rattenborg *et al.* 1999, Schwilch *et al.* 2002), a condition which birds should be more ready to assume at some times of day (or night) than others and in which they will show prolonged immobility, raised thresholds to arousal and specific postures (Amlaner & Ball 1983).

Assuming that waders do need to sleep, how much do they need, when do they need to do it and what are the implications for the selection of roost sites? Frustratingly, very little is known about how much sleep waders get, let alone how much they need. Birds are capable of sleeping with one eye open and one hemisphere of the brain awake, and Mallards *Anas platyrhynchos* can increase their use of this unihemispheric sleep in circumstances of increased predation risk (Rattenborg *et al.* 1999). Presumably this ability also

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occurs in waders; if so, it increases the complexity of recording sleep systematically in free-living individuals. Nevertheless a good deal could be learned about this very fundamental aspect of wader biology simply by the systematic recording of sleep posture (Amlaner & Ball 1983) and by assuming that there is a direct relationship between the amount of time a roosting bird spends with its eyes closed and the amount of time that it is actually asleep (Amlaner & McFarland 1981).

Amlaner & McFarland (1981) demonstrated that sleep cycles in Herring Gulls *Larus argentatus* are influenced by tidal cycles, with sleep more likely to occur at high tide. One would expect a similar tidal rhythm to occur in coastal waders, given their need to feed in the intertidal zone. A more common scenario in birds is that sunset or sunrise is associated with sleeping and waking (Amlaner & Ball 1983). Could this consideration also influence the sleep cycles of waders? At my study site in Roebuck Bay, NW Australia, Great Knots are forced from the intertidal flats for about 6 hours by each high tide. On daytime high tides, the average Great Knot appears to sleep for only 50 minutes (standing still with eyes closed or with bill tucked into the scapulars). On night-time high tides, however, the average Great Knot sleeps for about five hours (unpubl. data). I suggest this may be typical of coastal waders, and that the circadian cycle is likely to favour high-tide sleeping mostly at night, as by day there are greater advantages to remaining vigilant (see discussion of predation below). Accordingly waders may need safer high-tide roosts at night than they do by day.

PREDATION RISK

Waders are often vulnerable to predation by birds of prey. Sometimes this can be severe; for example, at Bolinas Lagoon in California, it was estimated that at least 21% of the wintering population of Dunlins were taken by Merlins *Falco columbarius* (Page & Whitacre 1974). Even where the risk of depredation is low, the need to avoid predators may have a strong effect on wader behaviour. Birds of prey have been shown to target those individuals that show the least adept predator-avoidance behaviour, either through inexperience or poor condition (e.g. Whitfield 1985, Bijlsma 1990, Cresswell 1994b). When a predator approaches a wader flock, it is clearly in the interests of each wader to be faster and more alert than at least one of its flockmates!

What are the predator-avoidance behaviours that waders employ? The most conspicuous and well known are flocking and flight. Benefits of flocking include the "dilution effect" (for an individual the probability of becoming a victim is lower in a large flock because other birds in the flock may be taken instead) and increased vigilance, with more sets of eyes looking for potential danger (Cresswell 1994a). Every wader-watcher is familiar with the sight of a flock of disturbed waders flying off at high speed, banking and turning in such accomplished unison that the entire flock can appear to change colour in a fraction of a second. This behaviour is thought to create a "confusion effect" with the presence of nearby birds making it difficult for a predator to follow any individual (Cresswell 1994a). Bijlsma (1990) reported that large falcons hunting waders at the Banc d'Arguin, W Africa, typically attempted to capture birds by surprise, using available cover to fly as close as possible before detection. In circumstances where they could not take waders before or during take-off, they tried to isolate single waders from the flying flock and pursued those, abandoning the chase if they could not single out an individual. This corresponds well with other published accounts of diurnal raptor predation on waders and my own field experiences in Roebuck Bay. It suggests that waders that detect predators early and can keep up with an airborne flock are reasonably safe.

The other strategy waders often use to avoid predators is concealment. When approaching predators pose a potential but not imminent threat, waders will often crouch or freeze, presumably in the hope that they will not be detected. Most shorebird species have dorsal plumage that is cryptically patterned in the right habitat: a motionless *Charadrius* plover on a sandy beach, or a Curlew *Numenius* sp. on grassland, can be very difficult to see. The roosting sites preferred by a wader species could therefore be strongly influenced by their plumage pattern, and there are certainly species-specific idiosyncrasies in habitat preferences at high tide.

Direct measurement of predation rates on waders is difficult, and has only been done a few times. Even by day, many hours of observation are needed to see a single incident of predation. Therefore obtaining a representative data set could easily take weeks; at night, the task is even more difficult. However, measurement of some variables likely to be related to predation risk is more straightforward. Abundance and type of predators near the roost site is likely to be correlated with predation risk and this can be easily quantified by counts. The difficulty that waders experience in detecting predators is related to the distance between the roost site and the nearest landforms or vegetation that can be used as cover by approaching predators. This too is easily measured. Conspicuousness of potential predators will probably also be affected by the background against which they are seen. Another roost attribute of potential importance is the background colour of the roost (which influences how conspicuous waders will be to predators). As yet nobody appears to have developed a method for quantifying the last two attributes, though both can be classified subjectively using categorical variables (Luís *et al.* 2001).

DISTURBANCE

The disadvantage of flying to avoid predation is the high energetic cost (Davidson & Rothwell 1993). Therefore waders should only take flight when absolutely necessary. Nevertheless they generally adopt risk-averse behaviour and often take flight in response to what turns out to be a false alarm (e.g. Handel & Gill 1992, Burton *et al.* 1996). Remaining crouched when flight would be the best option may have fatal consequences. Accordingly, waders should seek roost sites where disturbance rates are low.

In many wetlands, a major source of disturbance to roosting waders is humans, their vehicles and pets (Davidson & Rothwell 1993). Although the energetic costs of human and natural disturbance are difficult to evaluate, it is reasonably straightforward to measure the frequency with which disturbance occurs and thus to make comparisons between sites (Davidson & Rothwell 1993). This measurement is not necessarily a direct correlate of energy costs, as the type of disturbance, and the proximity of alternative roosting sites, will also influence the energetic costs of disturbance. Nevertheless, within a wetland complex it should help to identify the most favourable roost sites. The distance at which waders will take alarm in response to different threats can also be measured systematically (Davidson & Rothwell 1993). Disturbance levels differ between sites, not only because the

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number of predators varies, but also because waders learn to be tolerant of disturbance that is frequent and not particularly dangerous (Smit & Visser 1993). For this reason, in assessing the rate of disturbance at a specific site it is preferable to make measurements at that site rather than drawing upon literature from elsewhere.

ENERGY CONSERVATION – AT THE ROOST SITE

Energy expenditure at roosts will be lowest when waders are effectively thermoneutral, not needing to spend energy to keep their body temperature above or below critical limits. All birds have a core temperature of 40–41°C (Wiersma & Piersma 1994), but the effective temperatures at which they will be thermoneutral differ markedly from species to species. In general, large species should be more tolerant of cold temperatures than small ones. However, there is also a great deal of interspecific variation arising from differences in the insulation capabilities of the plumage, the amount of heat lost through bare parts and many other factors (e.g. Piersma 1994). Even within species, there may be much variation in thermoregulatory capacity. Breeding plumages, for example, tend to be heavier (and presumably warmer) than non-breeding plumages in waders, and the temporal changes that migratory waders undergo in organ size and strategic fat stores (e.g. Battley *et al.* 2000) are also likely to influence thermoregulatory capacity.

Despite all this variation, physiological studies now enable us to make reasonably good estimates of the energy costs of thermoregulation in different conditions. Wiersma & Piersma (1994) carried out a series of measurements of the heat loss of taxidermic mounts of Red Knots *Calidris canutus* in different field situations, and were able to construct a regression model to predict operative body temperature from three critical weather variables: air temperature, wind speed and solar radiation. In principle, if these are measured at specific roost sites it will be possible to calculate the maintenance metabolic costs that Red Knots will experience there. Portable climate stations that can measure these variables (and download them to a computer) are widely used for agricultural purposes, so the necessary equipment is readily available. Modifications to Piersma & Wiersma's model by Cartar & Morrison (1997) make it easy to estimate these maintenance metabolic costs for other shorebird species. Cartar & Morrison (1997) also demonstrated that ambient temperature (more easily measured than operative temperature) is an acceptable substitute for operative temperature in arctic situations where solar radiation levels are low.

Most of these models have been developed to calculate of metabolic costs in cold situations. Yet many of the world's shorebirds spend the non-breeding season in tropical or warm temperate places where the challenge is to avoid overheating. In such situations, these models do not work well: for example at many of the roost sites around Roebuck Bay, when operative temperatures exceed body temperature, the models predict negative maintenance metabolism costs. Further research would be needed to assess the energy costs of remaining cool in hot conditions, and it may not be worthwhile. Increased energy costs are not the only drawbacks to overheating and perhaps not as important to waders as the risk of tissue damage or death from hyperthermia (Marder *et al.* 1989).

Another caveat in using microclimate data to calculate operative temperatures is that waders can use behavioural ploys to avoid temperature extremes. Wiersma & Piersma (1994) demonstrated that in cold conditions Red Knots can reduce heat loss and make a substantial energy saving by flocking and facing into the wind. Bruinzeel & Piersma (1998) have shown that Red Knots in low temperatures can make a large compensation for thermoregulation costs by using the heat generated as a by-product of walking or running; presumably flight would have a similar or stronger effect.

In hot conditions other ploys are open to waders; raising of back feathers ("ptiloerection") can be used to dissipate body heat (Battley *et al.* 2002), as can evaporative cooling through panting. Probably the most efficient way for waders to remain cool is to stand in water or on a moist substrate, so that heat can be lost from the legs either by evaporation or thermal conductance; waders can increase the blood flow to their legs in hot conditions so that more blood is cooled and then returned to the core of the body (Piersma 1994, L. Bruinzeel & T. Piersma in prep.). This behavioural ploy raises an interesting question: although they rarely do so, most waders can swim quite capably (Minton 2000), so, in hot conditions, why do they not simply spend high tide afloat? I suspect the answer is that they are unable to take-off from water as quickly as more specialized swimming species with webbed feet, and are therefore more vulnerable to predation. However this possibility has never been investigated.

ENERGY CONSERVATION – ON THE WAY TO THE ROOST SITE

In principle, roost sites should be close to the feeding grounds, to minimise energy consumed flying from one to the other. But are flights between roosting and feeding areas sufficiently long for this to be important to waders that are capable flying thousands of kilometers non-stop on migration? Fig. 1 shows the distances flown from feeding to roosting sites by radio-tracked Great Knots *C. tenuirostris* and Red Knots in Roebuck Bay. Median one-way flights were 1–3 km by day and 6–8 km at night, with some individuals flying as far as 10 km by day and 18 km at night. These birds almost invariably returned to the original feeding site after high water, and as there were two high tides per day, individual birds typically commuted 30 km per day, with some travelling over 60 km. The scale of these movements is comparable to those reported for Red Knots in the Dutch Wadden Sea (Piersma *et al.* 1993), where it was calculated that roost flights cost about 10% of daily energy expenditure. In these cases therefore, commuting to roost sites would appear to involve a substantial investment of energy. The distances recorded are probably not exceptional. Similar flights have been found for Western Sandpipers in San Francisco Bay, California, (Warnock & Takekawa 1995), waders in the Wash, E England (Rehfisch *et al.* 1996) and in Moray Firth, Scotland (Rehfisch *et al.* in press). The maximum distances that waders are prepared to fly from feeding sites to roosts on a regular basis are unknown, but are likely to vary according to the factors that influence the energetic costs of flight: body size, wing moult and fuel load. Nevertheless, the scale of such movements is probably large enough to mean that minimizing distance is a significant factor in the daily energy budget. It was noted earlier that Dunlins and other species may spend the entire high water period on the wing (Dekker 1998, Hötker 2000, Buehler 2002). Even in cold temperate regions this seems to be a rarely used last resort (Hötker

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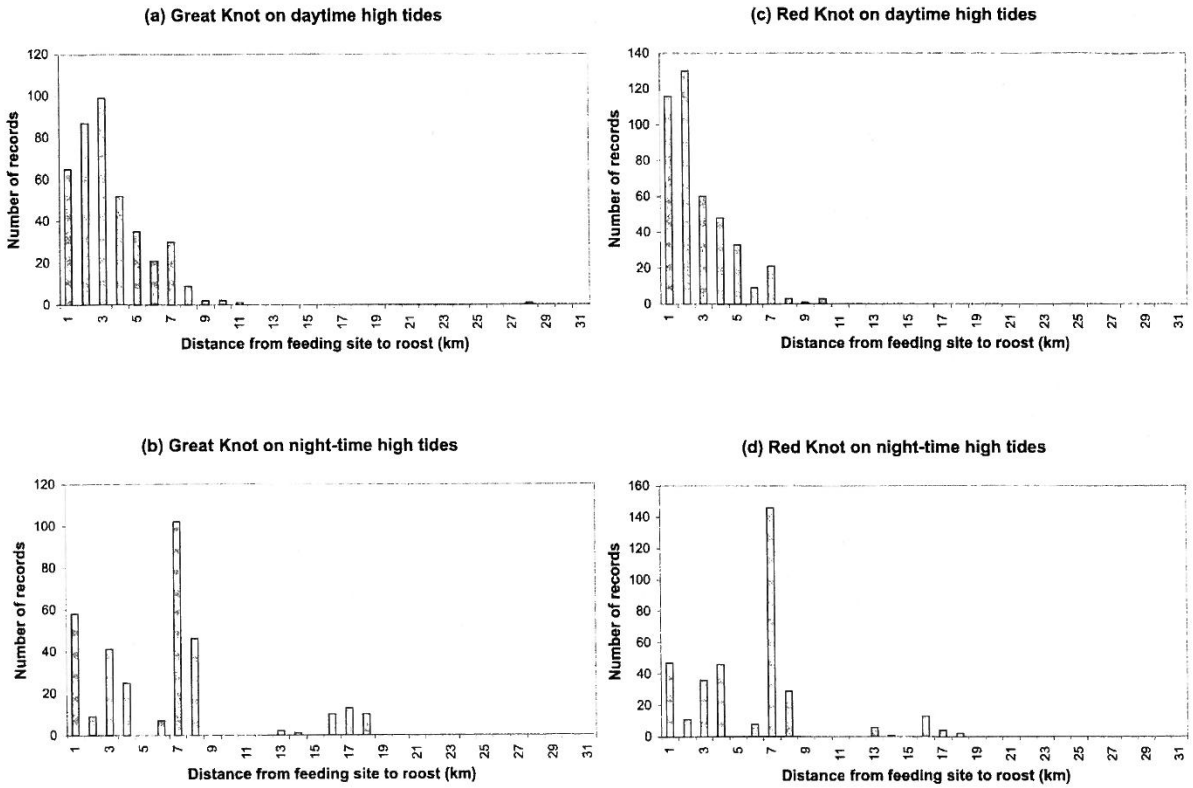


Fig. 1. Distance between day and night feeding and high tide roost sites at Roebuck Bay, Australia, for 25 radio-tagged Great Knots (a & b) and 23 radio-tagged Red Knots (c & d) during March-April 2000 (excluding extreme neap tides).

2000), and it may only be possible on a regular basis because the costs of flight are off-set by the thermoregulatory advantages of obtaining metabolic heat through locomotion (Bruinzeel & Piersma 1998). I suspect that spending all high tide on the wing may not a viable option at all in warm sites where waders must take care to avoid hyperthermia. In Roebuck Bay, waders are only seen panting immediately after a flight, suggesting that this is an activity in which overheating is most likely to occur (Battley *et al.* 2002).

DAY/NIGHT DIFFERENCES

Humans aside, diurnal birds of prey are probably the only predators capable of taking a heavy toll on non-breeding waders by day. Different considerations are likely to apply at night. In darkness, approaching predators will be harder to detect, and this may be the reason why night roosts are sometimes more distant from terrestrial habitats that might harbour predators (Sitters *et al.* 2001). In addition, performing escape flights in flocks may be more hazardous at night, because flockmates will be harder to see and there may be an increased risk of collision with other waders. Accordingly, shorebirds roosting at night are likely to be more vulnerable to being taken on the ground, an inference consistent with the sparse available data on predators that capture waders at night. These include cats, mustellids and owls (Cramp & Simmons 1983, Sitters *et al.* 2001, pers. obs.).

Roosting at night also poses different thermoregulatory challenges to roosting by day. Even in hot regions, overheating is only likely to be a problem by day when birds are exposed to incoming solar radiation. In cool regions, roosting shorebirds may need more sheltered sites at night. There is also the possibility that waders need to sleep more at night than by day. Given these differences between day and night, we should probably expect the roosts chosen by night and day to differ. This expectation is consistent with most literature in which the sites used by waders by day and night have been reported (e.g. Hockey 1985, Handel & Gill 1992, Smit & Visser 1993, Rohweder 2001, Sitters *et al.* 2001)

PERFECT KNOWLEDGE? THE IMPORTANCE OF MEMORY

Waders may not necessarily evaluate each of the roost characteristics outlined above before every high tide. By day, when they are flying from their feeding grounds at some height, they will be able to see the roost sites long before they land there, and distant views are probably sufficient for them to assess some characteristics: the distance they need to fly, the proximity of potential roost sites to tall cover, the amount of water cover at the site (which probably influences the microclimate, especially in hot conditions). Other roost variables will be harder for waders to predict; for instance, while they may have a general idea of how much disturbance previously used roost sites are exposed to, they cannot know if a specific site will be visited by a bird of prey during a particular high water period. At night, when roost sites may be hard to see in the dark, they will have less information on

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which to draw. It seems plausible therefore that they will rely to some extent on past experience. Indeed a good rule of thumb might be that the roost used on the previous high tide should be suitable if it was relatively undisturbed then. That memory plays a role in roost selection is suggested by the observation that waders often take some time to start making use of newly created roosts (e.g. Burton *et al.* 1996). However, individually marked birds would need to be studied to develop a full understanding of the role that memory plays.

FUTURE DIRECTIONS

To develop an understanding of how waders choose their roost sites I propose the following general course of investigation:

1. Discover the locations of all high tide roosts

The difficulty of this task should not be underestimated. In some wetlands roost choice may be simple, with one roost site serving all needs. In others it may be considerably more complex. For example, Great and Red Knots feeding on the intertidal flats of Roebuck Bay may roost in any one of seven substantially different roosting habitats, depending on the height of the tide and whether it is day or night (Rogers & Taylor 2001). Some of these roosting habitats were relatively well known when we began our studies, but it took a long campaign to discover the roosts used on daytime spring high tides (e.g. Collins *et al.* 2001, Rogers *et al.* 2001) and at night. Locating all of the roost sites in a complex area can require long periods of field observation, and the potential contribution of recreational wader-watchers should not be underestimated. Volunteers who know a site well enough, for example, to carry out thorough high tide counts must necessarily have a reasonable understanding of local roost choice issues. Unfortunately this field lore is rarely set down on paper.

2. Measure roost quality

Once the roost sites at a particular coastal wetland have been located, it is possible to measure the characteristics of each. These can vary with time: for example there are roost sites in Roebuck Bay that are important in some tide conditions, but not others, when, for example they might be completely flooded, too close to tall cover, or too dry. In Table 1, I have summarized those factors that may influence a wader's decision about where to roost and are thus of potential value in describing roost quality. The table is based on two independent studies: one on Great and Red Knots in Roebuck Bay (D. Rogers, P. Battley, T. Piersma, J. van Gils & K.G. Rogers in prep.), and another on Dunlin at the Ria de Aveiro on the west coast of Portugal (Luís *et al.* 2001). These regions differ in important respects: e.g. there were roost sites where the Dunlins of the Ria de Aveiro could feed at high tide while no such options existed for the knots of Roebuck Bay; at Roebuck Bay roosting knots face high temperatures and have to avoid overheating, while in winter in Portugal, any thermoregulation problems are likely to be related to birds becoming too cold. Despite these differences, the independently derived classifications are conceptually similar – an encouraging sign, as it suggests there is consensus about the factors that influence roost quality.

Luís *et al.* (2001) used categorical, mainly subjective variables to describe the quality of the roost sites they studied, while in Roebuck Bay we attempted more precise measurements of most variables. The advantage of direct measurements is they are more rigorous and objective, and may help identify the physical characteristics of a good roost site: e.g. distance from tall cover, and the effective body temperature the birds will experience there. On the other hand, measurement of these attributes is time-consuming and expensive, and our Roebuck Bay experience has been that the direct measurements of roost quality we obtained were consistent with the trends we would have expected had we only used subjective categorical classifications.

3. Assess the frequency with which and conditions under which each roost is used

Here the approach will differ from site to site, according to the logistics imposed by geography and the available facilities. Luís *et al.* (2002) used counts to measure the frequency of roost use, an approach also used successfully in a study of Red Knots in the Dutch Wadden Sea (Piersma *et al.* 1993). Rehfisch *et al.* (1996, in press) used recaptures of banded birds at high tide roosts to develop an understanding of site fidelity by individual birds. Where feasible, combined programs of colour-banding and radio-telemetry (e.g. Warnock & Takekawa 1995, van Gils *et al.* 1999) may be the best way of assessing the frequency with which roosts are used. This method can also provide information on where individual birds were feeding during the preceding low tide. Furthermore, radio-telemetry can provide information on where birds roost at night. Large data sets can be obtained through radio-telemetry, especially if automatic radio-tracking stations are used.

4. Use measures of roost quality as independent variables, and frequency of roost use as the dependent variable, to construct and test roost choice models

Nobody has yet published a comprehensive model of roost choice by waders for any site in the world, though the studies of Luís *et al.* (2001) and Rehfisch *et al.* (1996, in press) are steps in that direction. I contend that this aim is achievable, and would be well worth the effort. The modelling process itself would help us to evaluate our understanding of roost choice mechanisms, and the weight that waders apply to each measure of roost quality. Of particular value, it could tell us what thresholds are important to waders – such as the maximum distance they are prepared to fly from a feeding site to a roost. Perhaps most importantly, effective roost choice models could be a valuable management tool, allowing us to make predictions about how waders will respond (and whether they can respond) to the increasing human use and coastal developments that threaten so many important wader refuges.

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Table 1. Schemes for classifying roost quality, developed independently by Rogers *et al.* (in prep.) at Roebuck Bay, North-western Australia, and by Luis *et al.* (2002) at Ria de Aveiro, Portugal.

Category	Attribute	Measurement unit
Rogers *et al.* in prep.		
Predation risk	Distance to tall cover	Metres (direct measurement)
	Visibility	Categorical, subjective
Energetics	Microclimate	Effective body temperature
	Distance from feeding site	Metres
Disturbance	Disturbance	Average number of alarm flights per hour
Luis *et al.* 2001		
Predation risk	Predation (presence of predators)	Categorical, subjective
	Difficulty in spotting predators	Categorical, subjective
	Birds' conspicuousness	Categorical, subjective
Energetics	Distance to the feeding grounds	Categorical, objective
	Difficulty in obtaining food	Categorical, subjective
	Exposure (wind, rain)	Categorical, subjective
Disturbance	Disturbance (presence of people)	Categorical, subjective
	Distance to alternative roosts	Categorical, objective
	Spatial limitation	Categorical, subjective
Other variables worth a try		
Disturbance	Amount of sleep per high tide	% time sleeping
	Time spent in flight	Minutes
	Flight distance from threats	Metres
Information exchange	Proximity and number of nearby feeding sites	Metres; n.

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