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Humans alter habitat selection of birds on ocean-exposed sandy beaches

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ABSTRACT

Aim Resource-selection functions (RSFs) can quantify and predict the density of animal populations across heterogeneous landscapes and are important conservation tools in areas subject to human disturbance. Sandy beach ecosystems have comparatively low habitat heterogeneity and structural relief in the intertidal zone, but intense human use. We aimed to develop predictive RSFs for birds on ocean-exposed sandy beaches at two spatial scales, 25 ha (local scale) and 250 ha (landscape scale), and to test whether habitat selection of birds that commonly use the surf–beach–dune interface is influenced by the rates of human activities.

Location Moreton and North Stradbroke Island, eastern Australia.

Methods Avifauna and human activities were mapped on three sandy beaches covering 79 km of coastline for 15 months. Habitat characteristics of the surf–beach–dune interface were derived from remote sensing and ground surveys. RSFs were developed for 12 species of birds at two spatial scales: 25 ha (local scale) and 250 ha (landscape scale).

Results At local (25 ha) and landscape scales (250 ha), dune dimensions and the extent and type of vegetation structure were important predictors of bird density. Adding the frequency of human activities improved the predictive power of RSFs, suggesting that habitat selection of birds on beaches is modified by human use of these environments. Human activities occurred mostly in the mid- to lower intertidal zone of the beach, overlapping closely with the preferred habitats of Silver Gulls (*Larus novaehollandiae*), Pied Oystercatchers (*Haematopus longirostris*), Red-capped Plovers (*Charadrius ruficapillus*) and endangered Little Terns (*Sternula albifrons*).

Main conclusions In addition to demonstrating the appropriateness of RSFs to the surf–beach–dune interface, our results stress the need for systematic conservation planning for these ecosystems, where ecological values have traditionally been subsidiary to the maintenance of sand budgets and erosion control.

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Keywords

Conservation, habitat selection, human impacts, shorebirds, spatial scale.

INTRODUCTION

Habitat selection can be influenced by human activity because many animals perceive humans as predators (Frid & Dill, 2002; Blumstein *et al.*, 2005). Human disturbance can result in population-level declines in species if critical habitats are frequently disturbed across large areas at intensities high enough to limit habitat use (Mallord *et al.*, 2007). Quantifying and predicting the impacts of human disturbance across large spatial scales can be challenging, and knowledge of the physiological and behavioural responses of species to disturbance is often limited.

Resource-selection functions (RSFs) are emerging as an important quantitative tool to relate the distribution and abundance of animals to the availability of habitats (Hebblewhite & Merrill, 2008; McLoughlin *et al.*, 2010), such

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that restoration and conservation measures can target appropriate areas (Boyce & McDonald, 1999; Harju *et al.*, 2011). Although RSFs are often used for areas that require management interventions because of human impacts, few RSFs explicitly account for human disturbance (Harju *et al.*, 2011). Consideration of how human activities modify habitat selection is likely to improve the success of management and conservation actions (Pfister *et al.*, 1992; Boyce & McDonald, 1999; Harju *et al.*, 2011).

Scale is a fundamental component of RSFs (Boyce *et al.*, 2003; Boyce, 2006; McLoughlin *et al.*, 2010) and conservation management (Whittingham *et al.*, 2005). While animals usually feed and choose habitats at local scales, their home ranges are often determined by features at landscape scales (Hutto, 1985; Addicott *et al.*, 1987; Ciarniello *et al.*, 2007; McLoughlin *et al.*, 2010). Similarly, the influence of human activities on habitat selection by wildlife can be scale-dependent because animals may tolerate certain activities only at specific scales (Thompson & McGarigal, 2002). Bald Eagles, *Haliaeetus leucocephalus*, for example, avoid humans at local scales, but not at landscape scales (Thompson & McGarigal, 2002). The proximity of humans has a strong influence on behavioural responses of individuals, whereas impacts on animal populations are determined by the distribution and intensity of human activity across entire landscapes (Hill *et al.*, 1997; Colwell & Sundeen, 2000; Mallord *et al.*, 2007; Hebblewhite & Merrill, 2008).

Much of the work on RSFs has been in heterogeneous landscapes such as forests and mountainous terrain, where habitat features are easily mapped across a range of scales using remote sensing or other techniques (Johnson *et al.*, 2004; Hebblewhite & Merrill, 2008; Estes *et al.*, 2011). It is less clear whether RSFs also work in more homogenous habitats that lack a diversity of prominent topographic features or substrata, and where vegetation structure is simple, ephemeral or mostly absent. These are the typical landscape and habitat properties on areas seawards of dunes on high-energy sandy shores. Here, structural relief is comparatively homogeneous, and vegetation is absent (in the intertidal zone) or relatively simple in terms of composition and complexity (on low embryonic dunes or foredunes) (Defeo & McLachlan, 2005; Schlacher *et al.*, 2008).

Human activities are predicted to have a particularly strong influence on habitat selection in such habitats, because humans are visible to wildlife from large distances (Stalmaster & Newman, 1978; Knight & Gutzwiller, 1995) and the long and narrow shape of beaches spatially concentrates human–wildlife interactions (Knight & Gutzwiller, 1995). Furthermore, beaches are popular sites for human recreation and hence likely to be the sites of frequent human–wildlife interactions (Schlacher *et al.*, 2007a,b).

Ocean-exposed sandy beaches are important nesting, foraging and roosting habitats for birds, including numerous species that are in decline or endangered (Hubbard & Dugan, 2003; Weston & Elgar, 2005; Lafferty *et al.*, 2006). Declines of many shorebird species (Piersma, 2007; Nebel *et al.*, 2008; Wilson *et al.*, 2011) combined with numerous human threats to sandy beach ecosystems (Schlacher *et al.*, 2007a,b; Defeo *et al.*, 2009) have highlighted the need for a better understanding of habitat selection by birds on ocean beaches. Shorebirds on beaches are known to be sensitive to indirect and direct disturbances from popular recreational activities that include hiking, driving of off-road vehicles (ORVs), walking domestic dogs, harvesting bait and angling (Burger & Gochfeld, 1991; Burger, 1994; Lafferty, 2001; Defeo *et al.*, 2009). However, restrictions on beach access or recreational activities can be costly in terms of diminished recreational opportunities and social acceptance and hence need to be based on quantitative models at a spatial resolution appropriate for management (Knight & Gutzwiller, 1995).

In the present study, we develop predictive RSFs for birds on ocean-exposed sandy beaches at two spatial scales: 25 ha (local scale) and 250 ha (landscape scale). We test whether habitat selection of birds that commonly use the surf–beach–dune interface is influenced by the rates of human activities. Our models are based on a 15-month series of quantitative bird surveys from three sandy beaches covering 79 km of coastline on two barrier islands off eastern Australia. We focus on species that are common residents on dunes, beaches and the surf zone throughout the year (Table 1).

METHODS

Study area

The study was conducted on the ocean-exposed beaches of two barrier islands (Moreton and North Stradbroke Island) in southern Queensland, Australia (Fig. 1). These islands form the eastern rim of the Moreton Bay 'Ramsar' protected area (Ramsar Convention of Wetlands, 1971, http://www.ramsar.org) and constitute the largest sandy beach habitat for birds within this area. The exposed beaches of Moreton and North Stradbroke Island are foraging, nesting, roosting or resting sites for an estimated 57 species of birds (T. Nielsen & T.A. Schlacher, unpublished data). A recent study of 30 waterbird species in the Moreton Bay area showed declines in the abundance of seven migrant species and an increase in the abundance of only one species (Wilson *et al.*, 2011). Habitat loss and degradation and the proximity of a rapidly growing population centre (the greater urban area of Brisbane) are thought to be the main threats to the avifauna of Moreton Bay (Environment Australia, 2011).

The Eastern Beaches of the islands are popular sites for recreation, open to ORVs, camping in the dunes, bait collection, angling and boating (Schlacher *et al.*, 2011). The primary and secondary dunes of the Eastern Beach on Moreton Island are located within a national park, while Flinders and Main Beach on North Stradbroke Island are administered by the local authority. Domestic dogs are not allowed on Moreton Island, but are common on the beaches of North Stradbroke Island. On Eastern Beach, a 4-km section of the beach at the northern end and a 1-km section at the southern end are designated 'Conservation Park Zones', where angling and bait collecting are forbidden. Local laws prohibit vehicles and dogs

Table 1 Summary of key biological traits of bird species included in the resource-selection functions. Also shown is the overall number of 25-ha grid cells in which they occurred (*n*, max. 139) and the total number of individuals recorded. Conservation status (in Queensland): S, secure: E, endangered.

Common name	Species	Diet	Beach nesting	Status	Grid cells (*n*)	Total Ind.
Crested Tern	*Sterna bergii*	Pisc		S	79	11,759
Silver Gull*	*Larus novaehollandiae*	Opp		S	91	6323
Pied Oystercatcher	*Haematopus longirostris*	Inve	+	S	116	1122
Welcome Swallow	*Hirundo neoxena*	Inve		S	44	785
Torresian Crow*	*Corvus orru*	Opp		S	75	485
Masked Lapwing	*Vanellus miles*	Inve		S	82	397
Brahminy Kite	*Haliastur indus*	Pred		S	72	194
Whistling Kite	*Haliastur sphenurus*	Pred		S	62	182
Red-capped Plover	*Charadrius ruficapillus*	Inve	+	S	38	179
White-bellied Sea Eagle	*Haliaeetus leucogaster*	Pred		S	60	167
Pied Cormorant	*Phalacrocorax varius*	Pisc		S	35	128
Little Tern	*Sternula albifrons*	Pisc	+	E	20	928

*Human commensal. Diet: Pisc., piscivore; Opp., opportunistic; Inve: benthic invertebrates or insects; Pred., predators and scavengers.

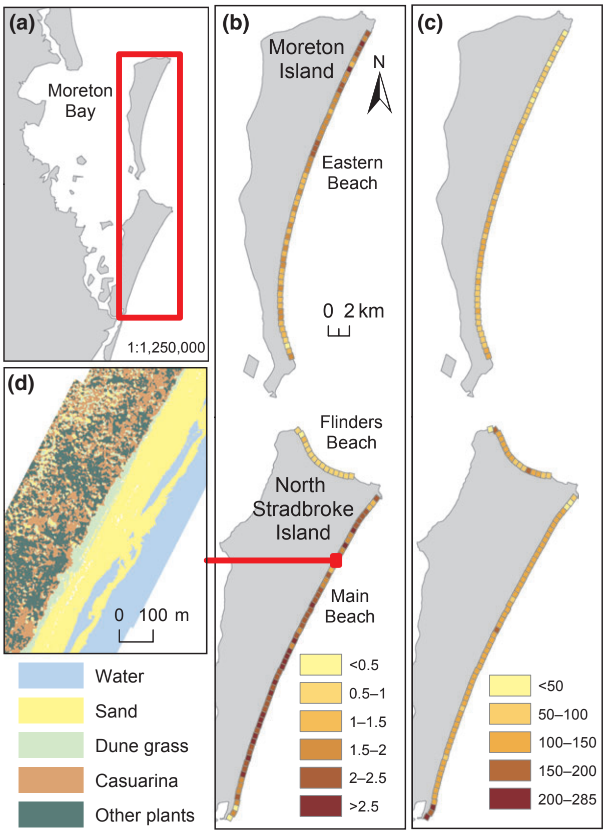

Figure 1 (a) Location of the study area within Moreton Bay (27°13′S,153°12′E) in eastern Australia, (b) primary dune height (m), (c) beach width (m) and (d) an example of classified habitats.

from the northernmost 1 km of Main Beach. Flinders Beach has a township close to the beach at both ends, and a small residential community located near its centre (Schlacher *et al.*, 2011).

Physical beach attributes

Satellite imagery and ground surveys were used to map vegetation and physical attributes along the full length of exposed beaches and coastal dunes on both islands. High-resolution (pixel size: 2.44–2.88 m) satellite images of the coastline were taken during 2009 (QuickBird; DigitalGlobe, Longmont, CO, USA) at four spectral bands (blue: 450–520 nm; green: 520–600 nm; red: 630–690 nm; and near-infrared: 760–900 nm). The images were then analysed using the Normalised Difference Vegetation Index (NDVI, ERDAS-Imagine v. 9.3; Atlanta, GA, USA), which uses the ratio of near-infrared to red spectra to classify the vegetation (Kerr & Ostrovsky, 2003; Lee & Yeh, 2009). This index consistently distinguished between bare sand, water and several classes of dune vegetation. To derive robust vegetation classes, we compared the vegetation classified from remote sensing with vegetation identified *in situ* in a complementary study (Schlacher *et al.*, 2011), for two plots (*c.* 0.5 × 0.5 km) in the centre of Flinders and Main Beach. This resulted in four habitat classes representing the dominant feature in a patch: (1) bare sand, (2) dune grass (*Spinifex hirsutus*), (3) casuarina trees and low shrubs (mainly *Casuarina equisetifolia*) and (4) coastal woodland (mostly eucalypts and trees of the Banksia genus).

The classified images were then transferred to a geographical information system (GIS, ArcGIS version 10; Esri, Redlands, USA) and assigned to a shoreline grid comprised of 25-ha square cells (500 × 500 m) along the entire length of each beach (Fig. 1). The centre of each grid cell was aligned to the axis of the primary dune, extending 250 m inland and 250 m seaward to include the full extent of the surf–beach–dune interface. Grid cells were numbered from 1 on the northern section of Moreton Island's Eastern Beach to 139 for the southernmost section of North Stradbroke Island's Main Beach.

The area covered by each habitat class was then calculated for each of the 139 grid cells. Habitat predictors for the landscape scale (250 ha) were derived by summing the areal coverage of 10 adjacent 25-ha grid cells. 'Local' scale, as used in this paper, corresponded to a 500-m stretch of beach, whereas 'landscape scale' describes a 5-km stretch. The width of grid cells across the dune–beach–surf interface was the same for each scale (500 m).

Beach width was measured in the centre of each grid cell using the Esri World Imagery satellite image layer in ArcGIS (following Harris *et al.*, 2011). In the centre of each 25-ha grid cell, we measured the angle of the primary dune using an inclinometer and the heights of the primary and secondary dunes using digital images of a calibrated theodolite staff placed vertically at the foot of the foredune.

Avifauna and human activities

Avifauna surveys were conducted monthly from February 2009 to May 2010 on North Stradbroke Island and from April 2009 to April 2010 on Moreton Island. Additional surveys were conducted per month during peak holiday periods on North Stradbroke Island, when human–bird interactions were predicted to be the most intense (up to seven additional surveys per month). In total, we mapped 24,742 birds and 7676 instances of human activities in 135 surveys: 11 along Moreton Island's Eastern Beach (34 km of shoreline), 63 surveys along North Stradbroke Island's Flinders Beach (8 km) and 61 surveys along North Stradbroke Island's Main Beach (34 km). During each survey, at least two observers identified, counted and mapped the linear (along-shore) position of all birds sighted between the outer boundary of the surf zone and the tree line at the back of the foredunes (following Hubbard & Dugan, 2003): locations were recorded using a hand-held GPS (Garmin Fortrex 2.1; Garmin Ltd, Kansas City, USA). The position of birds across the shore was also recorded as one of the following: 'dune', 'upper beach' (seaward edge of dune to drift line), 'middle beach' (drift line to effluent line), 'lower beach' (saturated sand below effluent line and swash) or 'surf zone' (seawards of swash zone). Counts on Main Beach and Eastern Beaches were made in a vehicle driven slowly (max. speed 40 km h^{-1}) along the beach, while two observers (T. Nielsen & T.A. Schlacher) walked Flinders Beach. All surveys were conducted within an hour of low tide during the day on each beach, and care was taken to avoid double-counting (observers monitored each flock of shorebirds as they took to flight) or disturbing the birds. Geodetic coordinates of all birds were then transferred to a GIS and binned to grid cells at each spatial scale (local: 25 ha and landscape: 250 ha).

Human activities were mapped during the avifaunal surveys using the same procedure, and activities were recorded as one of the six mutually exclusive categories: (1) ORV, (2) collecting bait (polychaetes or bivalves), (3) recreational angling, (4) water craft (jetski or boat), (5) domestic dog (leased or unleashed) or (6) any other activity (mostly sunbathing, picnicking and short walks from parked cars or campsites).

At the start of each survey, percentage cloud cover was recorded, and temperature, wind strength and direction were measured using a hand-held wind meter (Speedtech Windmate 200; WeatherHawk, Logan, UT, USA). Daily weather data were obtained from the Australian Bureau of Meteorology (Cape Moreton Lighthouse and Point Lookout North Stradbroke weather stations).

Data analysis

We developed RSFs for each of the 12 focal species (Table 1) as a function of (1) habitat attributes (Habitat Model), (2) human activity (Human Activity Model) and (3) habitat attributes + human activity (Habitat + Human Activity Model). All models were developed at two spatial scales ('local', 25 ha; 'landscape': 250 ha) using generalized mixed-effect models (GLMM). GLMM generates conditional parameter estimates of the probable number of birds at each site and during each month with respect to the independent predictor variables (Agresti, 2002). To avoid overfitting GLMMs, we only modelled the most abundant species that were widespread on at least two beaches and that were present for the duration of the 15-month study. All 12 focal species were common residents of beach ecosystems and included shorebirds, seabirds and raptors (Table 1). Three other species were abundant (i.e. $n > 150$), but were not modelled because they were highly aggregated spatially (Australian Gannet, *Morus serrator* and the Common Tern, *Sterna hirundo*) or only seasonally present (Red-necked Stints, *Calidris ruficollis*).

Based on autocorrelation plots, residual diagnostics and Akaike's Information Criterion (AIC) of different mixed models (following Zuur *et al.*, 2009), the optimal GLMM variance structure for our data was given by the following equation:

$$y_{st} = e^{\mu_0+\beta_1 x_{1st}+\cdots+\beta_k x_{kst}+b_s+b_t+\varepsilon_{st}} \quad (1)$$

where y_{st} is the number of birds at site s, during month t, as a function of the continuous predictors ($x_1 \ldots x_k$). $\beta_1 \ldots \beta_k$ are the selection coefficients estimated from the data. Other terms in the model are the general intercept (μ_0), random intercepts for each site (b_s) and month (b_t) and unexplained error, ε_{st}, which is normally distributed with a mean of 0 and a variance of σ^2_ε. Equation 1 was fitted with the 'glmer' function of lme4 v. 0.999375-35 of the R package (v. 2.13.1; R Development Core Team, 2011), using Laplace approximation. The response variable was the count of birds in each grid cell and was therefore modelled with a log-link function and Poisson error (Faraway, 2006).

The full set of predictor variables was first screened for variables that (1) had low collinearity with other predictors (i.e. $|r| < 0.4$ and variance inflation factor <2, Faraway, 2005; see Table S3 in Supporting Information) and (2) were most likely to influence the distribution of birds based on the literature (e.g. Colwell & Sundeen, 2000; Yasue, 2006; Neuman *et al.*, 2008; Zharikov & Milton, 2009) (Table 2). Amongst the human activity categories, bait collection and driving of water

Table 2 Potential predictors of habitat selection measured in this study. (1) Habitat attributes were measured once in each of the 139 grid cells, (2) human activities were measured in each grid cell during each survey and (3) weather data were collected at the start of each survey.

Category	Variable	Source of measurement
(1) Habitat attributes	Primary dune height (m)*	Ground truthing
	Secondary dune height (m)	Ground truthing
	Primary dune angle (°)	Ground truthing
	Beach width (m)	Satellite photographs
	Water (% cover)	QuickBird multispectral images
	Bare sand (% cover)*	QuickBird multispectral images
	Dune grass (spinifex, % cover)*	QuickBird multispectral images
	Casuarina trees and shrubs (% cover)*	QuickBird multispectral images
	Coastal woodland (% cover)	QuickBird multispectral images
(2) Human activities	Off-road vehicles (number per grid)*	Field surveys
	Domestic dogs (number/grid)*	Field surveys
	Recreational angling (number/grid)*	Field surveys
	Collecting bait (number/grid)	Field surveys
	Water craft (number/grid)	Field surveys
	Other (walking, sunbathing, swimming and picnicking) (number/grid)	Field surveys
(3) Weather	Wind speed (ms^{-1})* and direction (°)	Field surveys (1 per survey)
	Temperature (°C)	Field surveys (1 per survey)
	Cloud cover (%)	Field surveys (1 per survey)
	Rainfall (mm)	Aust. Bureau of Meteorology

*Non-collinear predictors included in the resource-selection functions (see Table S3 in Supporting Information).

craft were too sparse and infrequent to be included as predictors. Wind speed is known to strongly influence the behaviour and habitat selection of shorebirds (Pienkowski, 1983; McGowan *et al.*, 2002; McConkey & Bell, 2005; Peters & Otis, 2007) and was therefore treated as a covariate in the RSFs. Initial Habitat Models included wind speed, primary dune height, bare sand cover (%), dune grass cover (%) and casuarina tree and shrub cover (%). Habitat cover predictors were standardized to *z* scores (Quinn & Keough, 2002). Human Activity Models included wind speed, ORVs, domestic dogs and recreational angling, and Habitat + Human Activity Models included all eight predictor variables (Table 2). To identify and make inferences from the most parsimonious model, each saturated model including all predictor variables was simplified using nested log-likelihood ratios (G^2) (Faraway, 2005).

We determined the best RSF model from the three candidate models (Habitat, Human Activities and Habitat + Human Activities) using Akaike weights (w_i) based on second-order, bias-corrected Akaike's information criterion (AIC_c) (full equations in Burnham & Anderson, 2002). In all cases, there was a clear best model, i.e. evidence ratios exceeded 7 (Burnham & Anderson, 2002). Where data were too sparse for models that included human activities, only the Habitat Model was fitted. The same general modelling procedure was used at both the local (25 ha) and landscape (250 ha) spatial scales, but Flinders Beach was excluded from the landscape scale because there was only one spatial replicate at that scale (i.e. the exposed beach is only 8 km in length).

Model averaging was not required for RSF prediction because there were clear best models in all instances, and marginal (population) coefficients were estimated from GLMM coefficients following Agresti (2002). Spatial cross-validation was used to evaluate the model predictive performance (Guisan & Zimmermann, 2000; Boyce *et al.*, 2002). A random subset of 21 grid cells on Main Beach was used as the evaluation set, and models were calibrated with data from the remaining 118 grid cells. Cross-validation was not performed at the landscape scale because there were too few spatial replicates at this scale (i.e. 14 landscape grid cells in total).

Habitat preference of each species across the dune–beach–surf gradient was examined with mixed-effect log-linear models, using the same random-effects structure and 'glmer' function as in the RSFs (equation 1). The number of birds in each zone (Dunes, Upper, Mid, Low or Surf) was the multinomial response variable. Log-likelihood ratio tests were used to test whether habitat choice differed from random and selection of each habitat was compared using the Wald test [$Pr(>|z|)$, Agresti, 2002]. The same analysis was applied to the most frequent human activities (ORVs, anglers, domestic dogs and other activities) to examine whether human activities were location-dependent.

RESULTS

Physical beach attributes and human activity

In general, frontal dunes were highest on Main Beach (mean ± SD: 2.25 ± 0.66 m) and lowest on Flinders Beach (0.75 ± 0.32 m) (Fig. 1b). Average beach width was 108 ± 35 m and was the narrowest on the northern ends of Eastern and Main Beach and widest on the southern end of Main Beach (Fig. 1c). The size and configuration of dunal vegetation patches was variable within sites (see Fig. 1d for an example), and no vegetation was present in the intertidal zone.

At each of the three beaches, 'other activities' (mostly sunbathing, picnicking and short walks) was the most frequent category of human activity (mean linear density ± SD: 1.5 ± 6.2 km^{-1}, Fig. 2c), followed by driving of ORVs

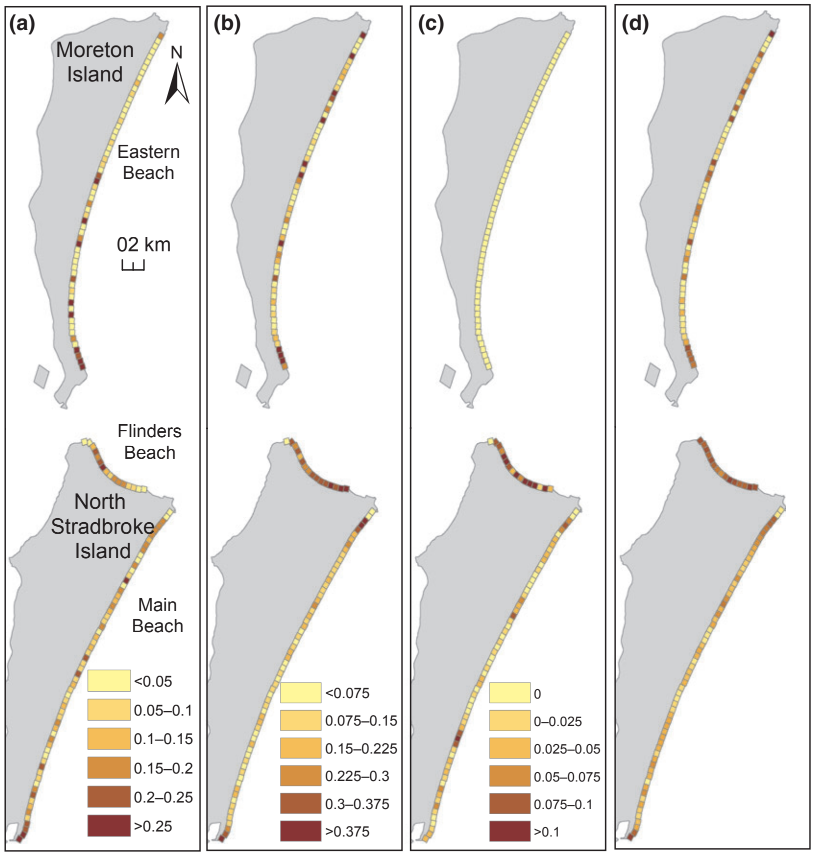

Figure 2 Mean number of human activities per 0.5 km: (a) anglers, (b) off-road vehicles, (c) domestic dogs and (d) overall recreational-use intensity (anglers + vehicles + dogs, classified by Jenk's optimization): darker areas are used more intensively.

(0.57 ± 2.19 km^{-1}) and angling (0.35 ± 1.62 km^{-1}). Domestic dogs were also common (0.12 ± 0.7 km^{-1}, Fig. 2c), while bait collecting and driving of water craft were uncommon (i.e. mean linear density <0.02 km^{-1}). The vast majority of domestic dogs were unleashed (i.e. only three of 351 dogs observed were leashed). Human use of beaches was most intense on Flinders Beach compared with the other two sites (Fig. 2a–d). For example, the mean density (± SD) of people on Flinders Beach (0.19 ± 0.19 ind. km^{-1}) was an order of magnitude higher than on Main Beach (0.01 ± 0.03 ind. km^{-1}), or Moreton Island's Eastern Beach (0.02 ± 0.12 ind. km^{-1}).

Resource-selection functions

Seven of the 12 species were sufficiently abundant and widespread to fit all three models (Habitat, Human Activity and Habitat + Human Activity) at the local scale, and there were enough data for five species to fit all three models at the landscape scale (Table 3). The RSFs that included both habitat and human activity predictors were the best models in six of seven species at the local scale and were the best models for all five species at the landscape scale (Table 3).

In all of the 12 species modelled, at least one habitat attribute had a significant influence on bird abundance (Table 3). Primary dune height was included in the RSFs for eight of the 12 species (Table 3). On average, areas abutted by higher primary dunes supported higher densities of Pied Oystercatchers, Whistling Kites and White-bellied Sea Eagles. Conversely, Silver Gulls, Brahminy Kites, Red-capped Plovers, Pied Cormorants and Little Terns were more abundant in areas abutted by lower dunes (Table 3). Of the vegetation attributes, casuarina cover was included in final RSFs for seven of the 12 species, and dune grass cover was included in six of the 12 species. More individuals of Welcome Swallows, Masked Lapwings, Brahminy and Whistling Kites, and Pied Cormorants were predicted to occur in grid cells with higher vegetation cover (either dune grass or casuarinas), whereas Silver Gulls, Crested Terns and Torresian Crows were negatively associated with vegetation cover (Table 3). Little Terns were negatively associated with both casuarina and bare sand cover, and Red-capped Plovers were negatively associated with casuarina cover but positively associated with dune grass cover. A weak negative response to wind speed was found in five species (Table 3).

Human activities featured in RSFs at either one or both scales for all seven species that could be modelled and were included in all five species for which landscape models were fitted (Table 3). The best model was the same at both scales for all species, with the exception of Crested Terns (Table 3). Crested Terns were negatively associated with domestic dogs ($\beta = -0.42$, $P < 0.001$) at the landscape scale, but were not influenced by human activities at the local scale.

Welcome Swallows and Torresian Crows were negatively associated with the number of ORVs and anglers. Silver Gulls

Table 3 Resource-selection functions (RSFs) at local (25 ha) and landscape (250 ha) scales (Hab, habitat; HA, human activities), coefficients for each predictor (DnGs, dune grass; PDH, primary dune height; Cas.; casuarina; Ang., anglers; ORVs, off-road vehicles) and cross-validation of predictions against an independent data set (r, ***$P \leq 0.001$, **$P < 0.01$, *$0.01 < P < 0.05$, $n = 118$). The final column gives the habitat preferred by each species across the dune–beach–surf gradient (D, dunes; U, upper; M, mid; L, low and S, surf).

Species	Local	Landscape	RSF Coefficients (β)	*r*	Across shore
Crested Tern	Hab.	Hab. + HA	DnGs (−0.35)	0.10	M,L
Silver Gull	Hab. + HA	Hab. + HA	Wind (−0.01), PDH (−0.57), Cas (−0.19), Sand (0.09), DnGs (−0.16), Anglers (0.14), ORV (0.09), Dogs (0.18)	0.67**	M,L
Pied Oystercatcher	Hab. + HA	Hab. + HA	Wind (−0.02), PDH (0.47), Dogs (0.28)	0.62**	M,L
Welcome Swallow	Hab. + HA	Hab. + HA	DnGs (0.15), Anglers (−0.64), ORV (−0.98)	0.17	D
Torresian Crow	Hab. + HA	–	Sand (0.16), DnGs (−0.20), Anglers (−0.32),ORV (−0.53)	0.23	D
Masked Lapwing	Hab.†	–	Cas (0.12)	0.04	M,L
Brahaminy Kite	Hab.†	–	Wind (−0.05), PDH (−0.17), Cas (0.27)	0.44*	D
Whistling Kite	Hab.†	–	Wind (−0.03), PDH (0.36), Cas (0.16)	0.36	D
Red-capped Plover	Hab. + HA	Hab. + HA	PDH (−0.40), Cas (−0.44), DnGs (0.39), Anglers (−0.48), ORV (0.17), Dogs (−0.52)	0.83***	U,M,L
White-bellied Sea Eagle	Hab.†	–	Wind (−0.03), PDH (0.33)	0.15	D
Pied Cormorant	Hab. + HA	–	PDH (−1.18), Cas (0.59), Sand (−0.37), DnGs (0.24), ORV (0.09)	0.01	S
Little Tern	Hab.†	–	PDH (−1.00), Cas (−1.35), Sand (−0.33)	–	M,L,S

†Only the habitat model was fitted. $P < 0.05$ for all coefficients in the RSFs and across-shore generalized mixed-effect models.

were positively associated with ORVs, domestic dogs and anglers. Red-capped Plovers were negatively associated with anglers and dogs, but were positively associated with ORVs. The densities of Pied Oystercatchers and dogs were also positively correlated (Table 3).

Cross-validation against an independent subset on Main Beach indicated that model performance was high (i.e. $r > 0.6$) for the RSFs for Silver Gulls, Pied Oystercatchers and Red-capped Plovers, and there was also a significant correlation between observed and predicted values for Brahminy Kites (Table 3).

The Red-capped Plover RSF had the best overall performance ($r = 0.83$) and was therefore used to model the average densities of Red-capped Plovers on Main Beach in response to three possible scenarios: (1) a 20% reduction in dune grass cover, (2) a 20% reduction in primary dune height and (3) excluding domestic dogs from beaches and dunes. Scenario 1 (i.e. less dune grass) did not greatly influence predicted plover densities (0.9% fewer plovers overall, Fig. 3b). Scenario 2 (lower dunes) resulted in 15% more predicted Red-capped Plovers overall, an increase that was pronounced along Main Beach (Fig. 3c), where the original primary dunes were high (Fig. 1b). Scenario 3 (dog exclusion) resulted in a 1.3% increase in predicted overall densities of Red-capped Plovers, but had little influence on densities on Main Beach (Fig. 3d), where domestic dogs were already infrequent (Fig. 2c).

Across-shore distribution of birds and human activities

Human activities were not distributed randomly across the shore ($G^2 > 816$, $P < 0.001$) (Fig. 4). Anglers were significantly more likely to occur in the mid- ($\beta = 1.52$, $P < 0.001$) and low-intertidal areas ($\beta = 0.76$, $P < 0.001$), than elsewhere on the shore (Fig. 4). This was also true for ORVs (mid: $\beta = 1.63$, $P < 0.001$; low: $\beta = 0.86$, $P < 0.001$) and other activities (mid: $\beta = 4.47$, $P < 0.001$; low: $\beta = 3.22$, $P < 0.001$). Domestic dogs were significantly more likely to occur in the mid-intertidal than elsewhere on the beach ($\beta = 0.97$, $P < 0.001$, Fig. 4).

None of the 12 bird species were distributed randomly across the shore ($G^2 > 28.9$, $P < 0.001$) (Fig. 4). The mid- to low-intertidal areas where human activities were concentrated were also the preferred habitats of Silver Gulls, Pied Oystercatchers, Crested Terns, Masked Lapwings, Red-capped Plovers and Little Terns (Table 3, Fig. 4). Red-capped Plovers and Little Terns were also frequent in the upper shore and surf zone, respectively (Table 3 and Fig. 4). Pied Cormorants preferred the surf zone, and Welcome Swallows and the raptors (White-bellied Sea Eagle, and Brahminy and Whistling Kites) preferred the dunes (Table 3 and Fig. 4).

DISCUSSION

Human use of beaches measurably influenced habitat selection by birds, which responded to physical features of the beach–dune interface and coastal dunes at both the local (25 ha) and landscape (250 ha) scales. Including human activities as predictors significantly improved the predictive power of RSFs at both scales, for six of the seven species for which all models were tested, and for all five species at the landscape scale. This supports the growing body of evidence indicating the importance of including human activities when mapping habitat suitability for wildlife in disturbed landscapes or in habitats where humans are present

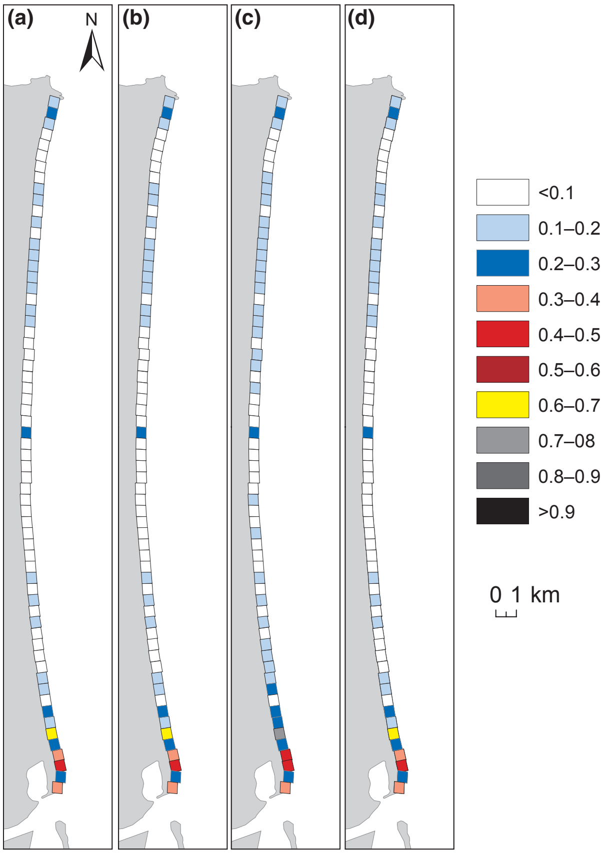

Figure 3 Monthly average density (per 10 km of linear beach) of Red-capped Plovers predicted on North Stradbroke Island's Main Beach under various possible scenarios: (a) actual habitat attributes and human activity levels (i.e. fitted resource-selection function), (b) 20% less dune grass cover, (c) 20% reduction in primary dune height and (d) domestic dogs excluded from beach.

(Mladenoff *et al.*, 1995; Hebblewhite & Merrill, 2008; Harju *et al.*, 2011).

In our study, human recreational activities influenced habitat selection by birds, with ORVs having the strongest influence (Table 3). As expected, the density of Silver Gulls (a human commensal, Smith & Carlile, 1993) responded positively to human activity (i.e. anglers, ORVs and domestic dogs), whereas negative responses were evident in other species such as Welcome Swallows and Red-capped Plovers. Another human commensal, the Torresian Crow, responded negatively to anglers and ORVs. The difference in the response of crows and gulls to instances of human activity probably reflects the nature of their association with humans, or their level of tolerance to the presence of humans. Silver Gulls feed opportunistically (Smith & Carlile, 1993) and are likely to attain food from human angling and bait collecting, whereas crows may benefit more indirectly from habitat disturbance (Marzluff & Neatherlin, 2006) and urbanization (Chace & Walsh, 2006).

It has been suggested previously that human activities that are individually benign can be collectively detrimental for bird populations (Knight & Gutzwiller, 1995). In our study, habitat selection was influenced by more than one type of human activity in four of the six bird species examined with the Habitat + Human Activity Model. Synergistic and interactive effects of human activities on beach avifauna should be the focus of future work, particularly given that some activities such as bait collecting and vehicles can also influence food resources (Skilleter *et al.*, 2005; Schlacher & Thompson, 2007; Schlacher *et al.*, 2007a,b).

Theory and empirical data suggest that human disturbance acts on habitat selection of birds at both local and landscape spatial scales (Thompson & McGarigal, 2002), as was the case in our study. While local human–bird encounters influence flushing behaviour and decisions such as where to forage and when to abandon nests (Burger, 1994; Hill *et al.*, 1997; Lafferty, 2001), birds are likely to avoid habitats at the landscape level if human activities are sustained over an area (Stalmaster & Newman, 1978; McGarigal *et al.*, 1991; Pfister *et al.*, 1992; Mallord *et al.*, 2007). The spatial configuration of habitats within landscapes, such as the size of habitat patches and the proximity of alternative habitats, can also modify the responses of birds to human disturbance (McGarigal *et al.*, 1991; reviewed by Knight & Gutzwiller, 1995).

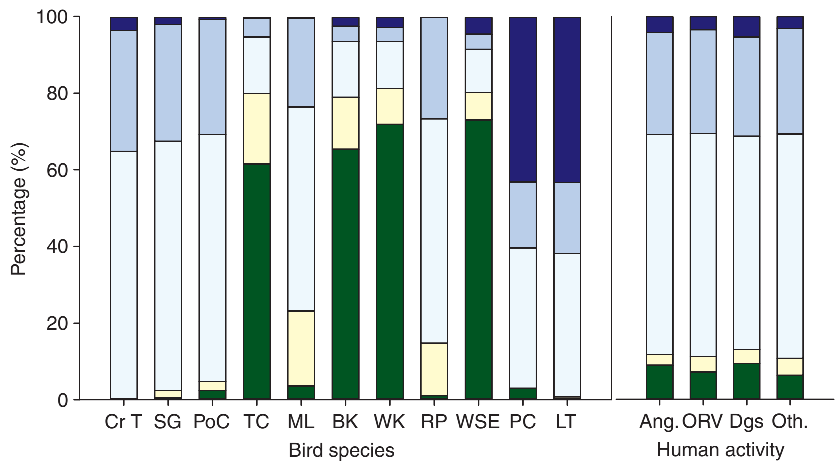

Figure 4 Distribution of birds and human activities across the shore (% of total observations). Crt, Crested Tern; SG, Silver Gull; PoC, Pied Oystercatcher; TC, Torresian Crow; ML, Masked Lapwing; BK, Brahminy Kite; WK, Whistling Kite; RP, Red-capped Plover; WSE, White-bellied Sea Eagle; PC, Pied Cormorant; LT, Little Tern; Ang., anglers, ORV, off-road vehicles; Dgs, dogs; Oth., other activities.

At the finer spatial scale, the lower intertidal and swash zone was the preferred habitat not only for foraging shorebirds and resting seabirds, but also for people. Domestic dogs and activities such as angling and harvesting bait were popular on this area of the beach, and it was here that most vehicle traffic was also concentrated. Interactions between humans and birds on the middle to lower beach were the most likely for Silver Gulls, Pied Oystercatchers, Red-capped Plovers and Little Terns. Other species, such as Welcome Swallows, Brahminy Kites, Whistling Kite, Torresian Crows and White-bellied Sea Eagles, occurred mostly on the dunes where humans were rarely present (except in areas where dune camping is allowed). In the case of two of these species, Welcome Swallows and Torresian Crows, angling and ORVs still had a negative influence in the RSFs (Table 3). This suggests that they may be sensitive to human activities at relatively coarse spatial scales (i.e. within 0.5 km) – even if direct encounters with humans were comparatively infrequent.

Are resource-selection functions suitable for ocean-exposed sandy beaches and dunes?

The sparse vegetation structure and often unstable morphology of ocean-exposed sandy beaches (Feagin *et al.*, 2005; Schlacher *et al.*, 2008; Dugan & Hubbard, 2010) suggest correspondingly high variability in habitat properties and in the distribution of resources. Resources that are unpredictable in space and time are predicted to result in considerable population-level variation in the distribution of animals and are not expected to facilitate the development of strong-site fidelity (Mueller & Fagan, 2008). Yet, we show that the distribution of birds was clearly associated with habitat features, such as the physical dimensions (i.e. primary dune height), and the type and structure of vegetation cover on coastal foredunes. These associations were evident across three different sites and throughout the 15-month study for 12 species of birds that covered a broad spectrum of life histories, trophic levels and ecological niches. Birds also responded to physical features of the beach–dune interface and coastal dunes at both local (25 ha) and landscape (250 ha) scales.

Most species and individuals were counted in the intertidal zone between the swash and the base of the foredunes. The habitat attributes that were the most important in our models, however, were related mainly to the frontal dune itself (i.e. height) and areas up to 250 m landwards (i.e. vegetation cover and characteristics). There are three possible (but complementary) explanations for this: (1) species counted on the unvegetated beach face also roost, perch, nest or forage in the dunes (e.g. Pied Oystercatchers and Little Terns), (2) dune characteristics were correlated with aspects of the beach face (e.g. sand cover covaried with beach width) and (3) bird usage of the dune increased at night, when they were not counted and mapped. Irrespective of the reasons for the association, these results suggest that birds may be dependent on the entire littoral active zone of sandy beaches, rather than on individual components such as the surf zone, beach or dunes in themselves. In support of this, species that were counted mainly in the dunes or at the dune–beach interface (i.e. raptors and crows) often forage on the unvegetated beach seawards of the dunes (Smith, 1985; Hendricks & Hendricks, 2011).

In general, habitat features associated with higher densities of birds were related to either roosting/resting requirements or foraging habitat. For example, the abundances of all three raptor species in our study were strongly associated with either primary dune height or the cover of casuarina trees and shrubs (Table 2). Raptors often roost on high trees near hunting grounds (Marchant & Higgins, 1993; Clancy, 2005), and we often observed raptors roosting on casuarina trees on the primary dunes during our surveys. Conversely, the densities of species that prefer to rest on bare sand, such as Silver Gulls and Crested Terns (Marchant & Higgins, 1993), were negatively influenced by vegetation cover and primary dune height. Both species were also more abundant on wider sections of beaches.

In contrast to the comparatively low structural complexity of the unvegetated part of the beach, the abutting dunes have a more complex topography and vegetation structure that can be stable for several years (Hesp, 2002). They therefore resemble other terrestrial habitats where RSF methods have been traditionally applied, and are critical habitats for certain species in their own right (e.g. nesting habitats for Little Terns and oystercatchers, Newman, 1992; Marchant & Higgins, 1993). From this perspective, the intertidal zone on sandy beaches is simply an unvegetated area within a larger heterogeneous landscape matrix, and the principles of RSF apply equally for birds on sandy beaches. Importantly, our results also show that physical and vegetation proxies may be used to predict and map habitat suitability of sandy beaches for wildlife. These surrogates can be obtained relatively quickly and cost-effectively from remote sensing and ground surveys (Wade & Hickey, 2008; Harris *et al.*, 2011).

Model predictive performance

The Silver Gull, Pied Oystercatcher and Red-capped Plover RSFs had high predictive power. This may be because all three species are resident species that forage on beaches, the first opportunistically and the latter two on beach invertebrates. Conversely, the Masked Lapwing RSF had poor predictive performance, indicating that they are not strongly associated with any particular habitat features on beaches. This species is widespread throughout other habitats such as wetlands, parks and crop lands (Marchant & Higgins, 1993; McConkey & Bell, 2005).

The poor performance of the RSFs for Crested Terns and Pied Cormorants can be explained by the gregarious roosting/resting behaviour of these species. Both species feed mainly on fish in the surf zone and beyond, and they roost and rest communally on trees (cormorants) or on bare sand (terns) (Langham & Hulsman, 1986; Marchant & Higgins, 1993). A recent study has indicated that RSFs generally perform poorly for such aggregating species, because they tend to follow each other and occupy only a relatively small proportion of available habitat (Folmer *et al.*, 2010). Further, Crested Terns and Pied Cormorants feed in the surf zone, and hence habitat metrics seawards of the beach are probably more relevant for models than habitat features of intertidal beaches and coastal dunes.

To date, studies of the impact of human disturbance on bird behaviour have mainly focused on behavioural thresholds of birds to disturbance in terms of indicators such as vigilance, flight distance and nest abandonment (reviewed by Hill *et al.*, 1997). However, the impacts of disturbance on populations or over large spatial scales are difficult to predict from such thresholds, because they depend on factors such as the species, behavioural and physiological state of birds that are disturbed, the ecological context of the interaction and the activity and trajectory of the person approaching (Hill *et al.*, 1997; Taylor & Knight, 2003; Yasue, 2005 and other references herein). On the other hand, covariance between factors that determine habitat selection can sometimes make RSFs challenging to interpret. For example, in our study, we suspect that the positive association between Pied Oystercatchers and domestic dogs was because people often take dogs with them when they harvest bait or seafood such as surf clams (which are also important prey for Pied Oystercatchers). However, we cannot be sure without a controlled experimental study of the behavioural responses of Pied Oystercatchers to domestic dogs. The behavioural threshold approach and RSFs are therefore likely to be complementary, because the former can be used to help guide and interpret the latter. Such an integrated approach to RSFs could be a powerful tool in identifying the extent and location of priority areas for management, and to focus field inventory efforts (Mladenoff *et al.*, 1999; Johnson *et al.*, 2004).

Summary

This study shows that (1) human activities modify habitat selection by birds on beaches at both the local (25 ha) and landscape (250 ha) scales and (2) meaningful RSFs can be developed for birds on sandy beaches that are often regarded as comparatively homogeneous landscapes. In many contemporary landscapes, rigorous experimental designs to test the impact of human presence or recreational activities on animal populations, such as before–after control impact studies, are often not possible, and RSFs offer a realistic alternative (Harju *et al.*, 2011). The RSF approach, coupled with habitat characteristics determined from ground surveys and remote sensing, has the potential to inform site selection for conservation and management measures for birds on sandy beaches. This would complement a range of spatial management measures that have already been used on sandy beaches, such as adaptive management of beach access points, vehicle permits and dog 'off-leash' areas (Knight & Gutzwiller, 1995).

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REFERENCES

Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.K., Richardson, J.S. & Soluk, D.A. (1987) Ecological neighborhoods: scaling environmental patterns. *Oikos*, **49**, 340–346.

Agresti, A. (2002) *Categorical data analysis*. Wiley-Interscience, New York.

Blumstein, D.T., Fernandez-Juricic, E., Zollner, P.A. & Garity, S.C. (2005) Inter-specific variation in avian responses to human disturbance. *Journal of Applied Ecology*, **42**, 943–953.

Boyce, M.S. (2006) Scale for resource selection functions. *Diversity and Distributions*, **12**, 269–276.

Boyce, M.S. & McDonald, L.L. (1999) Relating populations to habitats using resource selection functions. *Trends in Ecology and Evolution*, **14**, 268–272.

Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K.A. (2002) Evaluating resource selection functions. *Ecological Modelling*, **157**, 281–300.

Boyce, M.S., Mao, J.S., Merrill, E.H., Fortin, D., Turner, M.G., Fryxell, J. & Turchin, P. (2003) Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience*, **10**, 421–431.

Burger, J. (1994) The effect of human disturbance on foraging behavior and habitat use in piping plover (*Charadrius melodus*). *Estuaries*, **17**, 695–701.

Burger, J. & Gochfeld, M. (1991) Human activity influence and diurnal and nocturnal foraging of sanderlings (*Calidris alba*). *Condor*, **93**, 259–265.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. Springer, New York.

Chace, J.F. & Walsh, J.J. (2006) Urban effects on native avifauna: a review. *Landscape and Urban Planning*, **74**, 46–69.

Ciarniello, L.M., Boyce, M.S., Seip, D.R. & Heard, D.C. (2007) Grizzly bear habitat selection is scale dependent. *Ecological Applications*, **17**, 1424–1440.

Clancy, G.P. (2005) The breeding biology of the Osprey *Pandion haliaetus* on the north coast of New South Wales. *Corella*, **29**, 91–96.

Colwell, M.A. & Sundeen, K.D. (2000) Shorebird distributions on ocean beaches of northern California. *Journal of Field Ornithology*, **71**, 1–15.

Defeo, O. & McLachlan, A. (2005) Patterns, processes and regulatory mechanisms in sandy beach macrofauna: a multi-scale analysis. *Marine Ecology Progress Series*, **295**, 1–20.

Defeo, O., McLachlan, A., Schoeman, D.S., Schlacher, T.A., Dugan, J., Jones, A., Lastra, M. & Scapini, F. (2009) Threats to sandy beach ecosystems: a review. *Estuarine Coastal and Shelf Science*, **81**, 1–12.

Dugan, J.E. & Hubbard, D.M. (2010) Loss of coastal strand habitat in southern California: the role of beach grooming. *Estuaries and Coasts*, **33**, 67–77.

Environment Australia (2011) *Australian Ramsar Wetlands. Australian Wetlands Database*. Department of Sustainability, Environment, Water, Population and Communities, Canberra.

Estes, L.D., Mwangi, A.G., Reillo, P.R. & Shugart, H.H. (2011) Predictive distribution modeling with enhanced remote sensing and multiple validation techniques to support mountain bongo antelope recovery. *Animal Conservation*, **14**, 521–532.

Faraway, J.J. (2005) *Linear models with R*. Chapman & Hall/CRC, Boca Raton.

Faraway, J.J. (2006) *Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models*. Chapman & Hall/CRC, Boca Raton.

Feagin, R.A., Sherman, D.J. & Grant, W.E. (2005) Coastal erosion, global sea-level rise, and the loss of sand dune plant habitats. *Frontiers in Ecology and the Environment*, **3**, 359–364.

Folmer, E.O., Olff, H. & Piersma, T. (2010) How well do food distributions predict spatial distributions of shorebirds with different degrees of self-organization? *Journal of Animal Ecology*, **79**, 747–756.

Frid, A. & Dill, L. (2002) Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, **6**, 16.

Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.

Harju, S.M., Dzialak, M.R., Osborn, R.G., Hayden-Wing, L.D. & Winstead, J.B. (2011) Conservation planning using resource selection models: altered selection in the presence of human activity changes spatial prediction of resource use. *Animal Conservation*, **14**, 502–511.

Harris, L., Nel, R. & Schoeman, D. (2011) Mapping beach morphodynamics remotely: a novel application tested on South African sandy shores. *Estuarine, Coastal and Shelf Science*, **92**, 78–89.

Hebblewhite, M. & Merrill, E. (2008) Modelling wildlife–human relationships for social species with mixed-effects resource selection models. *Journal of Applied Ecology*, **45**, 834–844.

Hendricks, P. & Hendricks, L.M. (2011) Common raven predation on the sand crab. *The Wilson Journal of Ornithology*, **123**, 409–411.

Hesp, P. (2002) Foredunes and blowouts: initiation, geomorphology and dynamics. *Geomorphology*, **48**, 245–268.

Hill, D., Hockin, D., Price, D., Tucker, G., Morris, R. & Treweek, J. (1997) Bird disturbance: improving the quality and utility of disturbance research. *Journal of Applied Ecology*, **34**, 275–288.

Hubbard, D.M. & Dugan, J.E. (2003) Shorebird use of an exposed sandy beach in southern California. *Estuarine Coastal and Shelf Science*, **58**, 41–54.

Hutto, R.L. (1985) Habitat selection by nonbreeding, migratory land birds. *Habitat selection in birds* (ed. by M.L. Cody), pp. 455–476, Academic Press, Orlando.

Johnson, C.J., Seip, D.R. & Boyce, M.S. (2004) A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. *Journal of Applied Ecology*, **41**, 238–251.

Kerr, J.T. & Ostrovsky, M. (2003) From space to species: ecological applications for remote sensing. *Trends in Ecology and Evolution*, **18**, 299–305.

Knight, R.L. & Gutzwiller, K.J. (1995) *Wildlife and recreationists: coexistence through management and research*. Island Press, Washington, DC.

Lafferty, K.D. (2001) Birds at a Southern California beach: seasonality, habitat use and disturbance by human activity. *Biodiversity and Conservation*, **10**, 1949–1962.

Lafferty, K.D., Goodman, D. & Sandoval, C.P. (2006) Restoration of breeding by snowy plovers following protection from disturbance. *Biodiversity and Conservation*, **15**, 2217–2230.

Langham, N.P. & Hulsman, K. (1986) The breeding biology of the Crested Tern *Sterna bergii*. *Emu*, **86**, 23–32.

Lee, T.-M. & Yeh, H.-C. (2009) Applying remote sensing techniques to monitor shifting wetland vegetation: a case study of Danshui River estuary mangrove communities, Taiwan. *Ecological Engineering*, **35**, 487–496.

Mallord, J.W., Dolman, P.M., Brown, A.F. & Sutherland, W.J. (2007) Linking recreational disturbance to population size in a ground-nesting passerine. *Journal of Applied Ecology*, **44**, 185–195.

Marchant, S. & Higgins, P.J. (1993) *The Handbook of Australian, New Zealand and Antarctic Birds. Volume 2: Raptors to Lapwings*. Oxford University Press, Melbourne.

Marzluff, J.M. & Neatherlin, E. (2006) Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation. *Biological Conservation*, **130**, 301–314.

McConkey, K.R. & Bell, B.D. (2005) Activity and habitat use of waders are influenced by tide, time and weather. *Emu*, **105**, 331–340.

McGarigal, K., Anthony, R.G. & Isaacs, F.B. (1991) Interactions of humans and bald eagles on the Columbia River estuary. *Wildlife Monographs*, **115**, 1–47.

McGowan, A., Cresswell, W. & Ruxton, G.D. (2002) The effects of daily weather variation on foraging and responsiveness to disturbance in overwintering Red Knot *Calidris canutus*. *Ardea*, **90**, 229–237.

McLoughlin, P.D., Morris, D.W., Fortin, D., Vander Wal, E. & Contasti, A.L. (2010) Considering ecological dynamics in resource selection functions. *Journal of Animal Ecology*, **79**, 4–12.

Mladenoff, D.J., Sickley, T.A., Haight, R.G. & Wydeven, A.P. (1995) A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great-Lakes region. *Conservation Biology*, **9**, 279–294.

Mladenoff, D.J., Sickley, T.A. & Wydeven, A.P. (1999) Predicting gray wolf landscape recolonization: logistic regression models vs. new field data. *Ecological Applications*, **9**, 37–44.

Mueller, T. & Fagan, W.F. (2008) Search and navigation in dynamic environments – from individual behaviors to population distributions. *Oikos*, **117**, 654–664.

Nebel, S., Porter, J.L. & Kingsford, R.T. (2008) Long-term trends of shorebird populations in eastern Australia and impacts of freshwater extraction. *Biological Conservation*, **141**, 971–980.

Neuman, K.K., Henkel, L.A. & Page, G.W. (2008) Shorebird use of sandy beaches in central California. *Waterbirds*, **31**, 115–121.

Newman, M. (1992) Pied oystercatcher breeding at Mortimer Bay, Tasmania. *Emu*, **92**, 87–92.

Peters, K.A. & Otis, D.L. (2007) Shorebird roost-site selection at two temporal scales: is human disturbance a factor? *Journal of Applied Ecology*, **44**, 196–209.

Pfister, C.A., Harrington, A. & Lavine, M. (1992) The impact of human disturbance on shorebirds at a migration staging area. *Biological Conservation*, **60**, 115–126.

Pienkowski, M.W. (1983) Changes in the foraging pattern of plovers in relation to environmental factors. *Animal Behaviour*, **31**, 244–264.

Piersma, T. (2007) Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. *Journal of Ornithology*, **148**, S45–S59.

Quinn, G.P. & Keough, M.J. (2002) *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge.

R Development Core Team (2011) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org/.

Schlacher, T.A. & Thompson, L.M.C. (2007) Exposure of fauna to off-road vehicle (ORV) traffic on sandy beaches. *Coastal Management*, **35**, 567–583.

Schlacher, T.A., Dugan, J., Schoeman, D.S., Lastra, M., Jones, A., Scapini, F., McLachlan, A. & Defeo, O. (2007a) Sandy beaches at the brink. *Diversity and Distributions*, **13**, 556–560.

Schlacher, T.A., Thompson, L. & Price, S. (2007b) Vehicles versus conservation of invertebrates on sandy beaches: mortalities inflicted by off-road vehicles on ghost crabs. *Marine Ecology – an Evolutionary Perspective*, **28**, 354–367.

Schlacher, T.A., Schoeman, D.S., Dugan, J., Lastra, M., Jones, A., Scapini, F. & McLachlan, A. (2008) Sandy beach ecosystems: key features, sampling issues, management challenges and climate change impacts. *Marine Ecology – an Evolutionary Perspective*, **29**, 70–90.

Schlacher, T.A., de Jager, R. & Nielsen, T. (2011) Vegetation and ghost crabs in coastal dunes as indicators of putative stressors from tourism. *Ecological Indicators*, **11**, 284–294.

Skilleter, G.A., Zharikov, Y., Cameron, B. & McPhee, D.P. (2005) Effects of harvesting callianassid (ghost) shrimps on subtropical benthic communities. *Journal of Experimental Marine Biology and Ecology*, **320**, 133–158.

Smith, G. (1985) An analysis of prey remnants from Osprey *Pandion haliaetus* and White-Bellied Sea Eagle *Haliaeetus leucogaster* feeding roosts. *Emu*, **85**, 198–200.

Smith, G.C. & Carlile, N. (1993) Food and feeding ecology of breeding silver gulls (*Larus novaehollandiae*) in urban australia. *Colonial Waterbirds*, **16**, 9–17.

Stalmaster, M.V. & Newman, J.R. (1978) Behavioral responses of wintering bald eagles to human activity. *The Journal of Wildlife Management*, **42**, 506–513.

Taylor, A.R. & Knight, R.L. (2003) Behavioral responses of wildlife to human activity: terminology and methods. *Wildlife Society Bulletin*, **31**, 1263–1271.

Thompson, C.M. & McGarigal, K. (2002) The influence of research scale on bald eagle habitat selection along the lower Hudson River, New York (USA). *Landscape Ecology*, **17**, 569–586.

Wade, S. & Hickey, R. (2008) Mapping migratory wading bird feeding habitats using satellite imagery and field data, Eighty-Mile Beach, Western Australia. *Journal of Coastal Research*, **24**, 759–770.

Weston, M.A. & Elgar, M.A. (2005) Disturbance to brood-rearing Hooded Plover *Thinornis rubricollis*: responses and consequences. *Bird Conservation International*, **15**, 193–209.

Whittingham, M.J., Swetnam, R.D., Wilson, J.D., Chamberlain, D.E. & Freckleton, R.P. (2005) Habitat selection by yellowhammers *Emberiza citrinella* on lowland farmland at two spatial scales: implications for conservation management. *Journal of Applied Ecology*, **42**, 270–280.

Wilson, H.B., Kendall, B.E., Fuller, R.A., Milton, D.A. & Possingham, H.P. (2011) Analyzing variability and the rate of decline of migratory shorebirds in Moreton Bay, Australia. *Conservation Biology*, **25**, 758–766.

Yasue, M. (2005) The effects of human presence, flock size and prey density on shorebird foraging rates. *Journal of Ethology*, **23**, 199–204.

Yasue, M. (2006) Environmental factors and spatial scale influence shorebirds' responses to human disturbance. *Biological Conservation*, **128**, 47–54.

Zharikov, Y. & Milton, D.A. (2009) Valuing coastal habitats: predicting high-tide roosts of non-breeding migratory shorebirds from landscape composition. *Emu*, **109**, 107–120.

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009) *Mixed effects models and extensions in ecology with R*. Springer-Verlag, New York.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Mean density (0.5 km^{-1}) of (a) Crested Terns, (b) Silver Gulls, (c) Pied Oystercatchers, (d) Welcome Swallows, (e) Torresian Crows and (f) Masked Lapwings.

Figure S2 Mean density (0.5 km^{-1}) of (a) Brahminy Kites, (b) Whistling Kites, (c) Red-capped Plovers, (d) White-bellied Sea Eagles, (e) Pied Cormorants and (f) Little Terns.

Table S3 Pearson product–moment correlation matrix of predictor variables used in RSFs. Dune hght, dune height (m); ORVs, off-road vehicles (see Table 2 for a full explanation of predictors)

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BIOSKETCHES

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Tara Nielsen is a PhD candidate at USC, with research focusing on threats to shorebirds on ocean-exposed sandy beaches.

Author contributions: TN and TAS collected the survey data. TN, TAS and JJM classified the remote-sensing data. JJM analysed the data and wrote the paper with help from TN and TAS.

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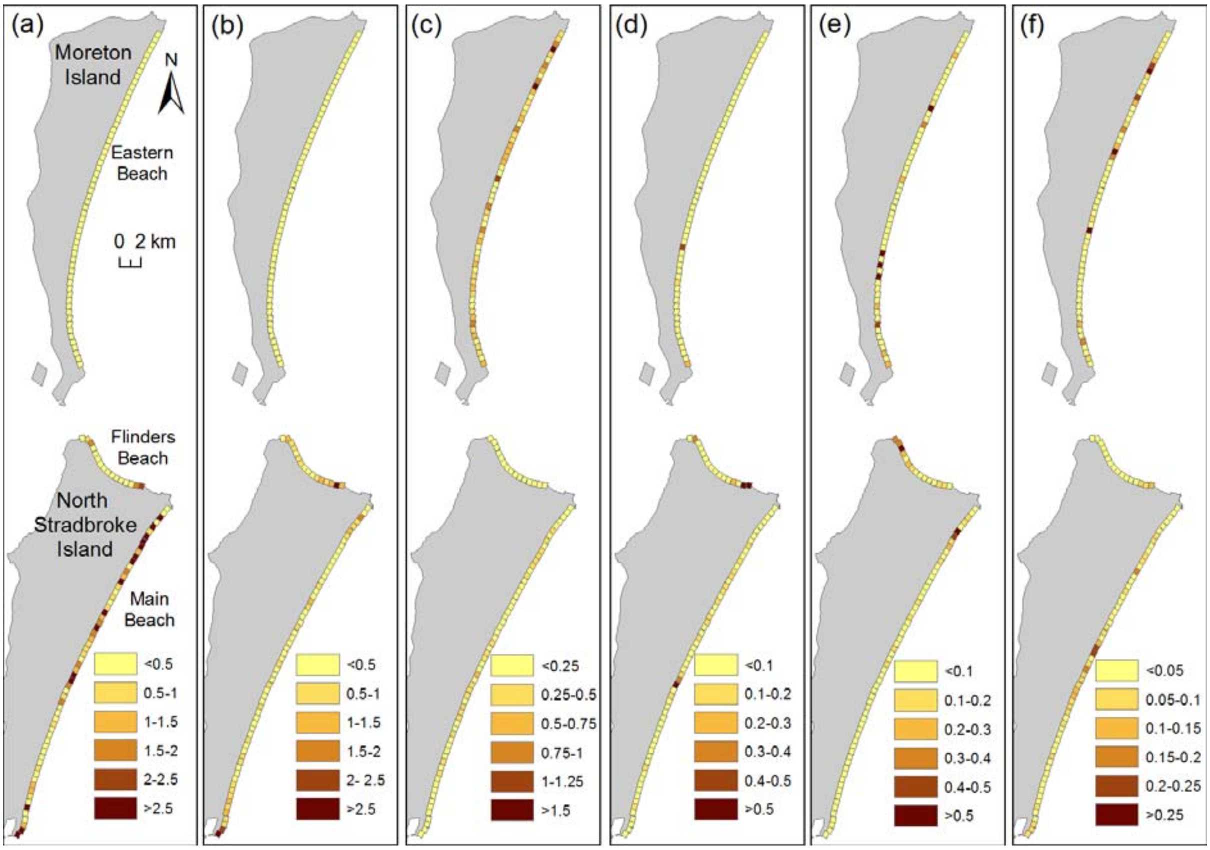

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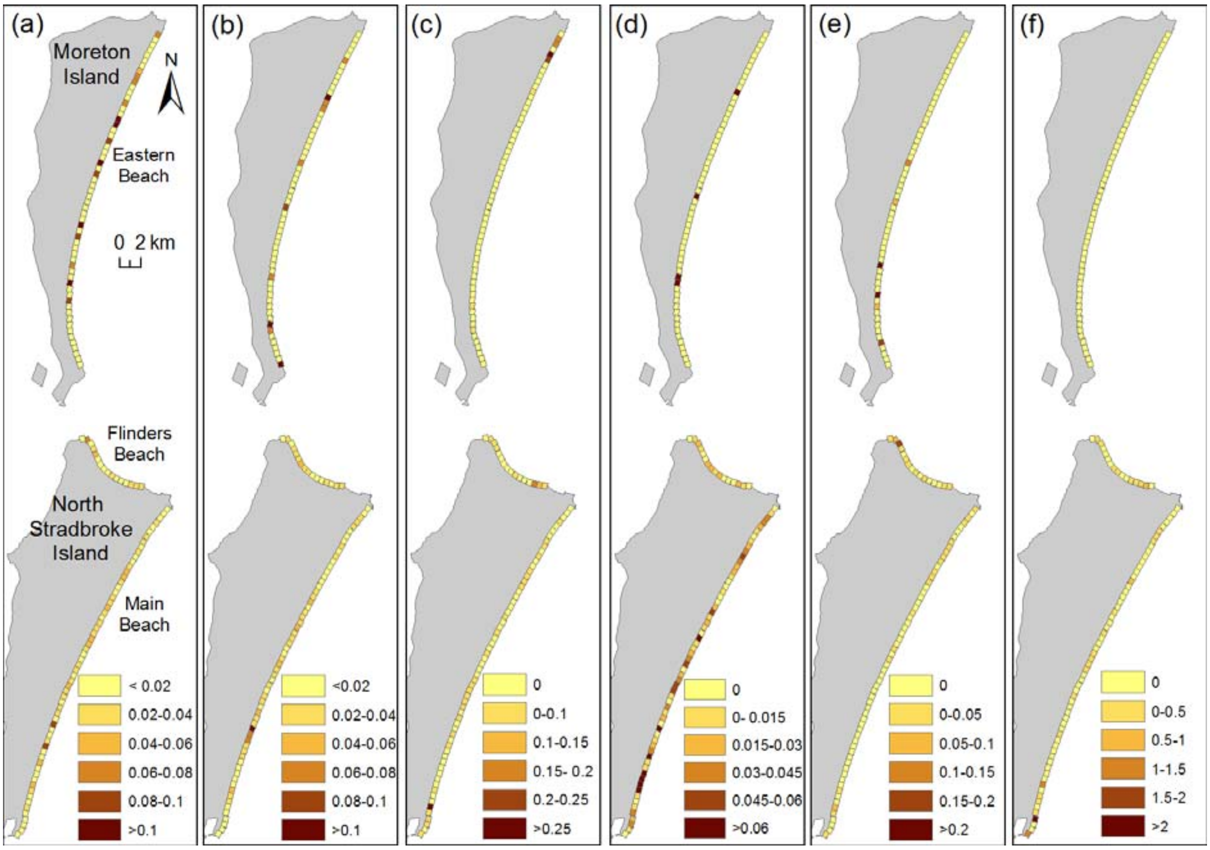

Appendix S3 Pearson product-moment correlation matrix of predictor variables used in resource-selection functions.

	Wind speed	Dune height	Sand	Dune grass	Casuarina	Dogs	Angling	ORVs
Wind speed	1	0.11	0.03	-0.01	0.02	-0.05	-0.08	-0.06
Dune hght	0.11	1	-0.07	-0.05	0.15	-0.12	-0.08	-0.17
Sand	0.03	-0.07	1	0.30	0.28	0.01	0.04	<0.01
Dune grass	-0.01	-0.04	0.30	1	0.05	-0.03	-0.02	-0.04
Casuarina	0.02	0.15	0.28	0.05	1	<0.01	-0.02	-0.03
Dogs	-0.05	-0.12	0.01	-0.03	<0.01	1	0.1	0.35
Angling	-0.08	-0.08	0.04	-0.02	-0.02	0.10	1	0.39
ORVs	-0.06	-0.17	<0.01	-0.04	-0.03	0.35	0.39	1