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RESEARCH ARTICLE

# Interplay between physical and predator landscapes affects transferability of shorebird distribution models

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**Abstract** Coastal landscapes with extensive intertidal mudflats provide non-breeding habitat for Arctic shorebirds. Few attempts have been made to develop and test landscape-level models predicting the intertidal distribution of these birds. We modelled the distribution of a Holarctic species, Dunlin (*Calidris alpina*), at a hemispherically important non-breeding site, the Fraser River Delta, British Columbia, Canada, in seasons with different predator landscapes. We trained the models during a season when nocturnal predators were common and tested temporal transferability of the models on independent datasets when nocturnal predators were absent. Snowy Owls (*Nyctea scandiaca*) influenced Dunlin distribution and thus model transferability. After accounting for their presence, models displayed good to excellent discrimination, i.e. prediction of the instantaneous and cumulative (over low tide period) probability of mudflat use by Dunlin, in fore- and backcasting applications. Model calibration was good or else, where over-prediction was observed, the reason for the bias was identified. The distribution models may predict mudflat use by Dunlin and possibly related species given relevant data describing the intertidal landscape. The models are amenable to GIS application, describe the amount of use per hectare of the intertidal zone and can be used to determine and visualise relative and absolute suitability of intertidal areas.

**Keywords** AUC · Calibration · Distribution model · Dunlin · Intertidal landscape · Non-breeding shorebird · Transferability

## Introduction

Estuaries with extensive intertidal mudflats are globally threatened biomes due to coastal development and sea-level rise (Piersma and Lindstrom 2004; Kirwan and Murray 2008). In the boreal winter, these environments provide critical foraging habitat for

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Artic-breeding shorebirds, which are globally declining long-distance migrants (Brown et al. 2001). Evaluation of landscape-specific effects of coastal changes on non-breeding shorebirds requires both an understanding of how physical and biological landscape properties shape shorebird distribution (Taft and Haig 2006; Gillings et al. 2005; Beauchamp 2007a) and the use of temporally and spatially robust distribution models (Hirzel and Le Lay 2008). Such models allow assessment and visualisation of how anthropogenic and natural changes in intertidal landscapes affect shorebirds and the potential outcomes of mitigation measures (Durell et al. 2005; Vanreusel et al. 2007).

While theoretical and empirical advances in distribution modeling have been made, uncertainties in model derivation, interpretation and application remain (Vaughan and Ormerod 2005; Barry and Elith 2006). Among the most pressing issues is spatial, temporal and methodological model transferability, i.e. models' ability to perform outside their training environments. Three issues undermine model transferability. (*i*) Models may reflect local spatio-temporal ecological phenomena (Boyce et al. 2002; Betts et al. 2006). (*ii*) Models may be overfitted, they may capture only a restricted range of the organism's response curve to a particular predictor, or be missing important and/or including "useless" variables (Guthery et al. 2005; Barry and Elith 2006; McAlpine et al. 2008). (*iii*) Predictors may be too coarse and have uncertain links to ecological processes driving distribution (Vanreusel et al. 2007). Although persistent ecological idiosyncrasies may necessitate development of site- or time-specific models, overall, distribution models are more likely to transfer well when the training sample is large, the sampling frame captures the range of conditions under which the model will be applied, the relationship between the response and predictors is based on explicit direct or mitigated ecological links, the models represent ecologically plausible hypotheses, and conditions under which the models perform poorly have been reported (Vaughan and Ormerod 2005; Hirzel and Le Lay 2008).

Here we develop models to predict and visualise distribution, expressed as the probability of use, for a shorebird, Dunlin (*Calidris alpina*), across the full spatial (intertidal range) and temporal (diel, non-breeding season) extents of an intertidal landscape at an important non-breeding site. We assessed the likely decrease in model performance due to overfitting, tested model fore- and backcasting transferability at the original training site using independent data, and explored the relationship between the predicted probability and the actual amount of use. While the physical environment during our study remained annually constant, the predator landscape changed, presenting an opportunity to investigate the effect of nocturnal predators on both shorebird distribution (Beauchamp 2007a) and model transferability. We expected that the birds would modulate their distribution to maximise feeding opportunities while minimising exposure to both diurnal (falcons, Whitfield 2003; Dekker and Ydenberg 2004) and nocturnal (owls, Brown et al. 1988; Mouritsen 1992) predators.

## Methods

### Predictor variables

In intertidal environments shorebirds distribute themselves, often in a density-dependent manner, to optimise a fitness function driven jointly by intake rate (Gill et al. 2001; Goss-Custard et al. 2006) and predation danger (Whitfield 2003; Pomeroy 2006). Unfortunately, these two factors do not easily lend themselves to spatially explicit high-resolution mapping.

We chose a priori eight digitally map-able physical predictors that correlate with food abundance and availability, and predation danger, grouping them into three general factors. Sediment organic content (*Org*, to 0.001%) (Yates et al. 1993), proportion of fine sediment (*FineSed*, to 0.01%) (Yates et al. 1993; Sewell 1996), proximity to tidal channel (*DistChan*, to 0.01 km) (Lourenço et al. 2005) and tidal elevation (*Elev*, to 0.1 m relative to zero-water level) (Pomeroy 2006) were assumed to describe *food abundance*. Percent of sediment surface covered by water >0.1 cm (*Water*, to 1%), surface water depth (*Depth*, to 0.1 cm) and distance to tide-line (*DistTide*, to 0.1 m) were designated as describing *food availability* (Zwarts and Wanink 1993; Taft and Haig 2006). Distance to cover used by avian predators (saltmarsh, dike, vegetation; *DistCover*, 0.01 km) was considered as a proxy for *predation danger* (Mouritsen 1992; Whitfield 2003; Dekker and Ydenberg 2004). Additionally, we included the *temporal* factor comprised of three variables that can interact with food and predators to influence shorebird distribution. Julian date (*Julian*, 1 December = 1) and position of the tide-line relative to zero-water level (*Tide*, to 0.1 m) at the time of observation accounted for seasonal or intra-tidal trends in distribution and possible density-dependent effects (Whitfield 2003). The period of emersion of a given location (*Time*, to 1 min) reflected local depletion and vertical movements of prey (Yates et al. 2000). Some variables likely contribute to more than one factor, and assigning them to a factor was a matter of convenience.

## Study landscape

The study was carried out in the southern arm of the Fraser River Estuary, British Columbia, Canada (Fig. 1a; 49°03′ N, 123°09′ W) during the non-breeding seasons 1995–1996, 1997–1998, 2005–2006, and 2006–2007. Over 2 million shorebirds use the estuary annually, including internationally important numbers of Dunlin (100,000) and Western Sandpipers (*Calidris mauri*, 2 million), making the estuary a key site in the Western Hemispheric Shorebird Reserve Network (Shepherd and Lank 2004). The immediate study area, Roberts Bank, represented a distinct, 7.5 × 4.8 km, intertidal mudflat (tidal range 0.0–3.8 m) separated from agricultural fields by dikes. The mudflat supported ca. 8,000 Dunlin in December–February, and by early April the population rose to ca. 24,000 due to an influx of migrants. The mudflat is partitioned by two causeways supporting a ferry terminal and a port facility. Up-shore sections of the mudflat are fringed with saltmarsh and bushes; sediments range from soft mud to sand. Eelgrass, *Zostera marina*, occupies parts of the lower intertidal zone. In December 2005–March 2006 eight Snowy Owls (*Nyctea scandiaca*) resided in the study area and hunted over the intertidal at night. Snowy Owls “invade” the area every 5–10 years and were absent in the other three winters (pers. obs). Peregrine and Merlin (*Falco peregrinus* and *F. columbarius*) have been winter residents in the area since early 1990s (Dekker and Ydenberg 2004).

## Bird sampling

Bird occurrence was sampled at 242 random points $\geq$200 m apart and 100–4,500 m seaward from the shore/saltmarsh edge, spanning the tidal elevation of 0.5–3.6 m (Fig. 1a). Areas below 0.5 m relative to the zero-water level were rarely exposed; land above 3.6 m was occupied by saltmarsh and dikes. Waterlogged patches ($\geq$15 cm depth) were excluded as inaccessible to Dunlin. Each point was marked with a small surveyor’s flag. Between 2 December 2005 and 4 April 2006, 2–6 randomly selected points per low tide, located $\geq$400 m apart, were accessed on foot, using a GPS (Garmin eTrex$^{\text{TM}}$, accuracy ±4 m). Points were sampled within ±2.5 h relative to the lowest water, and when the predicted tidal height was $\leq$2.0 m (range 0.3–2.0 m), i.e. $\geq$40% (1,250 ha) of the maximum available intertidal area (2,950 ha) was exposed. Points were accessed day and night during the natural occurrence of low tides (in December all tides $\leq$2.0 m occurred at night), except when $\geq$15 mm of rainfall and winds $\geq$50 km h$^{-1}$ were forecast for the field session. Day was defined as 30 min before sunrise to 30 min past sunset.

All birds within 100 m of a flag were counted during a 20-min observation. By day 8 × 30 binoculars were used from a point 200 m from a flag. At night, a monocular night vision scope (ITT$^{\text{TM}}$ generation III pocketscope, with StarTron$^{\text{TM}}$ catadioptic 4.5× lens) was used from 120 m. Dunlin evaded a stationary or slowly moving observer at $\leq$100 m by day and $\leq$25 m by night. Given the openness of the landscape, perfect detection probability was assumed, although some individuals may have been missed at night. Tidal channels, when present, were walked following an observation to flush any shorebirds that may have been screened from view. Following observations, a dropping count was made within a 16 m$^2$ quadrat at the flag to provide an index of cumulative habitat use (McCurdy et al. 1997; McAlpine et al. 2008). Droppings of Black-bellied Plover (*Pluvialis squatarola*), the only other common shorebird in the study area, could be easily distinguished from Dunlin’s (cf. 25 and 5 cent Canadian coins, respectively). At each point air temperature (0.1°C), wind-speed (0.1 m s$^{-1}$), wind-chill (0.1°C), air pressure (1 kPa), and illumination (0.01 Lux; night only) were recorded using a Kestrel$^{\text{TM}}$ 4000 portable weather-metre and Extech Instruments Datalogging Lightmeter (Model 401036), respectively. After model-fitting (see below), the residuals were regressed against (*i*) the environmental variables to

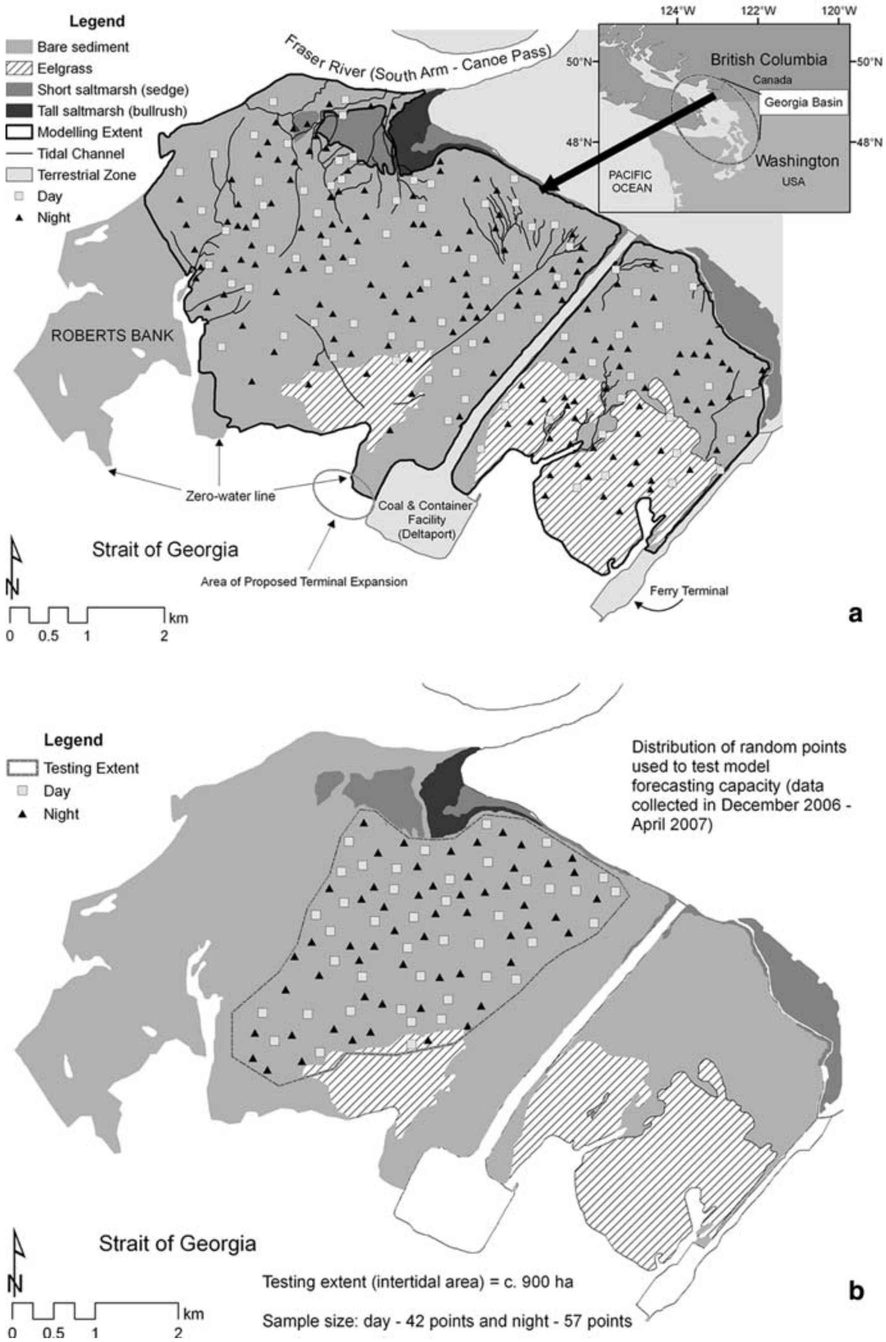


**Fig. 1** Roberts Bank and distribution of sampling points used to train Dunlin distribution models (**a**) and test their forecasting (**b**) and backcasting (**c**) performance

test for deviations in distribution due to weather (Kuwae 2007) and (*ii*) illumination at night to test the hypothesis that darkness contributes to predation danger and affects distribution (Brown et al. 1988). Residuals were also tested for autocorrelation (Moran's *I*; CrimeStat 3.0, The National Institute of Justice, Washington, DC).

## Sediment sampling and processing

Sediment was sampled in April–May 2006, 2.5 h around the lowest water. For organic content and grain size data, at each original random point two 5 cm-deep sediment cores located 1 m apart were collected using a 60 cc syringe with a cut off top and pooled in a

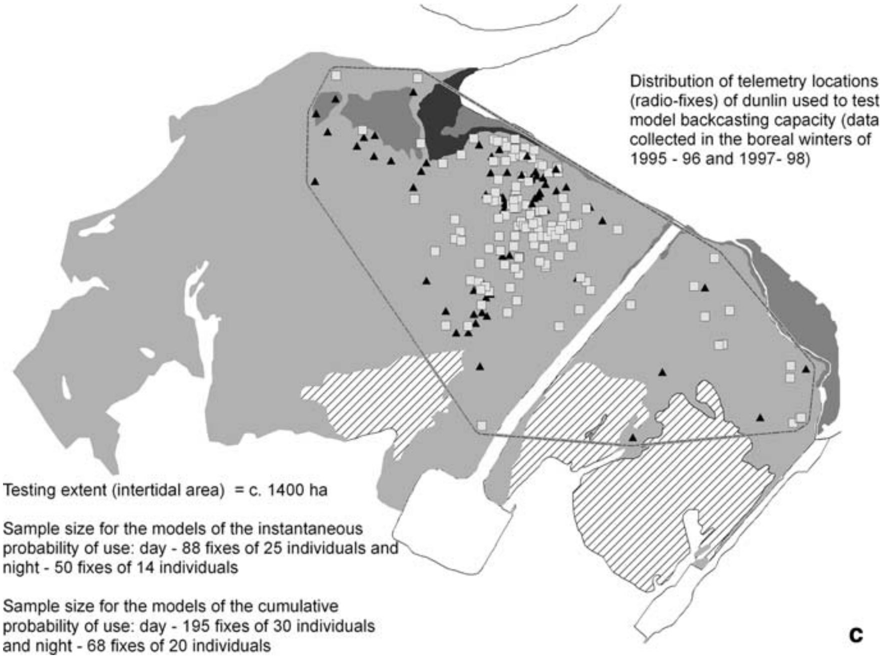


**Fig. 1** continued

zip-lock bag. Sediment organic content was determined using the standard loss-on-ignition approach: dried homogenised sub-samples (85°C, 45–60 h; dry mass ca. 25 g) were combusted in a muffle furnace for 5 h at 550–600°C. Proportion of fine sediment (% dry mass of particles with diameter <0.125 mm) was determined by wet-sieving samples across a stack of sieves with mesh diameters of 0.5, 0.25 and 0.125 mm. Surface water depth was measured using a ruler at two points 1 m apart, and the mean depth was used in subsequent analyses. A 4 $m^2$ quadrat was photographed using a digital camera and subsequently scored on-screen using a 100-cell grid for percent water cover (0–100%). Some points fell in eelgrass (Fig. 1a). Distance to eelgrass and eelgrass density were not used in modelling since they were strongly correlated with surface water depth and regionally, many sites used by Dunlin have no eelgrass.

## Generation of landscape variables

To permit digital distribution mapping, the original physical point-data were interpolated over the entire study area (Supplementary Table 1). Given the prevalence of smooth and continuous environmental gradients in the intertidal zone, kriging was the interpolation method used (Herman et al. 2001). The interpolated values were used in modelling. Tidal channels (≥2 m wide) and shoreline were digitized from aerial photographs taken in 2003 provided by the Vancouver Port Corporation. Distances (*DistChan* and *DistCover*) were derived from continuous surfaces generated in ArcGIS 9 Spatial Analyst. Tidal elevation (*Elev*) was obtained from a LiDAR tidal elevation model provided by the Geological Survey of Canada. All spatial data were resolved at 100 m. Distance to tide-line (*DistTide*) represented the difference between tidal elevation of a focal point and position of the tide measured at the nearby Tsawwassen tidal gauge (http://tbone.biol.sc.edu/tide/) at the time of observation.

## Model selection, testing and implementation in GIS

Dunlin distribution was modelled using logistic regression. Data were coded as presence/absence (1/0) due to pronounced aggregative tendencies in foraging shorebirds (Yates et al. 2000; Granadeiro et al. 2004) and thus strong non-independence among count units. The probability of use by Dunlin of a ca. 3 ha habitat unit during 20 min reflected the instantaneous probability of use. The probability of dropping deposition in a 16 m$^2$ quadrat between the emersion of the intertidal location and the end of a 20-min observation captured the cumulative probability of use (McCurdy et al. 1997) of a location by Dunlin throughout a receding and mid-low/rising tide. Day and night data were analysed separately because the distribution of shorebirds may change considerably between day and night (Gillings et al. 2005; Beauchamp 2007a).

Thirteen a priori models (Table 1) represented alternative hypotheses describing Dunlin distribution. Initially, predictors were explored to remove intercorrelated ($r_p > 0.7$) or potentially useless variables (Guthery et al. 2005) within the four factors (i.e. *food abundance*, *availability*, *predation danger* and *temporal*). At least one variable per factor was kept to distinguish among different hypotheses. Importance of quadratic terms, standardised by the mean, was tested for all predictors (Granadeiro et al. 2004). Interactions between *Julian* date, *Tide*, *Time* and *DistCover* and each of the other predictors were tested to address possible changes in habitat selection along the temporal and predation danger gradients. Only those quadratic and interaction terms suggesting a consistent effect on the response were included in the final candidate models, which were ranked based on their AIC$_c$ and Akaike weights ($\omega$) (Burnham and Anderson 2002). To qualitatively assess the effect of model complexity on overfitting, we selected two models for further evaluation from each candidate confidence set (AIC$_c$ $\leq$ 4): the structurally simplest model and the model with the highest discriminatory capacity (see below). Importance of predictors was assessed by summing up respective model weights across the entire set.

**Table 1** Candidate models of intertidal distribution of Dunlin with the number of independent predictors and hypothesis tested

| | Models | Predictors[a] | Hypothesis[b] |
|---|---|---|---|
| 1 | Food abundance | 4 | Distribution is driven by food abundance |
| 2 | Food availability | 3 | Distribution is driven by food availability |
| 3 | Food abundance + Food availability | 7 | Food abundance and availability drive distribution in an additive manner |
| 4 | Predation | 1 | Birds always select safer sites[c] |
| 5 | Food abundance + Food availability + Predation | 8 | Birds trade-off richer sites for safer sites or vice versa depending on individual condition |
| 6 | Food abundance + Predation | 6 | Distribution is described in terms of a trade-off between food abundance and predation danger |
| 7 | Food availability + Predation | 4 | Distribution is described in terms of a trade-off between food availability and predation danger |
| 8 | Food abundance + Temporal + Predation | 9 | Trade-off between food abundance and predation danger has a temporal (or density-dependent) component |
| 9 | Food availability + Temporal + Predation | 7 | Trade-off between food availability and predation danger has a temporal (or density-dependent) component |
| 10 | Food abundance + Food availability + Temporal | 10 | Food abundance and availability drive distribution in an additive manner but the pattern changes with season and/or population density |
| 11 | Food abundance + Food availability + Temporal + Predation | 11 | All four factors collectively shape distribution |
| 12 | Temporal | 3 | Bird distribution depends on tide movement and total population |
| 13 | Null | 1 | Distribution co-varies with no predictors |

[a] Not all initial predictors appeared in final models

[b] All models assume presence of food sufficient to elicit numeric response throughout the study system (Goss-Custard et al. 2006)

[c] The model assumes that food abundance and availability are high enough to no longer affect intake rates and thus aggregation (Gill et al. 2001; Goss-Custard et al. 2006)

### Model discriminatory capacity and overfitting

Models were trained using the full training dataset, i.e. the 242 points collected in 2005–2006. The data-optimised discriminatory capacity of the models was evaluated using the area under the curve (AUC) of the probability threshold-free receiver operating curves. Boot-strapping was employed to assess the amount of overfitting and subsequently obtain a more realistic evaluation of discriminatory capacity (Vaughan and Ormerod 2005). Parameter coefficients of each selected structural model were re-trained on a 50% random subset of the data. The $\mathrm{AUC}_{\mathrm{train}}$ value was calculated, simulating the assessment of the data-optimised discriminatory capacity. The trained model was then applied to the set-aside 50% of the data and the respective $\mathrm{AUC}_{\mathrm{test}}$ value was calculated. This simulated application of the model to independent data under identical conditions. The amount of overfitting in model performance due to data optimisation can be expressed as $\mathrm{AUC}_{\mathrm{train}} - \mathrm{AUC}_{\mathrm{test}}$. The process was repeated 50 times and the mean overfitting estimate was subtracted from the data-optimised AUC values of the respective models developed from the full dataset to obtain a more realistic picture of their performance. Models with AUC = 0.7–0.9 are considered useful in conservation applications (Boyce et al. 2002).

### Temporal transferability—discrimination

For assessing forecasting capacity, scaled-down bird- and dropping-sampling using the same field methods was carried out on Roberts Bank a year later (15 December 2006–5 April 2007, Fig. 1b). Continuous surfaces of predicted probabilities of use by Dunlin were generated in ArcGIS 9 Spatial Analyst via reverse logistic transformation. The respective response- and period- (i.e. day or night) specific models were applied to the previously generated spatial data and temporal variables specific to the day/tidal stage at which the new records were obtained. Agreement between the predicted probability of use and recorded occurrence was assessed using AUC. If the models transferred well, i.e. could adequately predict Dunlin distribution in 2006–2007, the AUC > 0.**7** was expected**.**

To assess backcasting capacity, Dunlin telemetry locations collected on Roberts Bank in the boreal winters of 1995–1996 and 1997–1998 were used (see Shepherd and Lank 2004 for details) (Fig. 1c). Radio-tagged Dunlin were tracked throughout a tidal cycle and their positions were determined to ca. ±100 m. To be conservative about positional accuracy, we used only intertidal locations within 2.5 km of a telemetry station. Because different sample sizes of locations were available per individual (range 1–24), locations were weighted to sum to 1 for each Dunlin (Apps et al. 2004). Model testing was conducted within a minimum convex polygon encompassing all telemetry locations buffered by 200 m (Fig. 1c). Predicted probabilities of use were generated as above. The area within the polygon was reclassified into 10 quantiles—equal-area classes of predicted probability of use. The sum of weights of locations falling within each quantile was tabulated with the expectation that progressively more individuals would occur in higher-ranked quantiles. If the models transferred well, the ranked probability of use would be positively correlated with the sum of weights of individual locations ($r_s > 0.7$) (Boyce et al. 2002; Apps et al. 2004). All selected telemetry locations were used to assess the models of cumulative probability of use, since they reflect intertidal Dunlin distribution during all tidal stages. Only locations detected at tidal height ≤2.4 m were used to test the models of instantaneous probability of use, since they represent Dunlin distribution around mid-low tide.

### Temporal transferability—calibration and amount of use

While AUC and $r_s$ are widely used to assess the performance of distribution models, they measure discrimination, i.e. the capacity of a model to correctly rank sites, but not calibration, i.e. whether the species will be detected eight out of 10 times in an area with predicted probability of 0.8 and whether this is twice as much as for a site with probability of 0.4 (Harrell et al. 1996). Accepting the assumption that modelling output correctly reflects the occurrence on the ground without explicitly testing it, may lead to erroneous conclusions. Model calibration was assessed only for the forecasting data, since both presence and absence locations were available (Barry and Elith 2006). Prevalences (proportions of positive cases) were regressed against probabilities (break values) of the 10 quantiles produced as above. A perfectly calibrated model, where the predicted probability of use corresponds to the proportion of positive observations, would produce a regression with a slope of 1 and intercept of 0 (Vaughan and Ormerod 2005).

Finally, while we did not directly model abundance due to the strong propensity of shorebirds to aggregate, we did explore the relationship between the probability of use and the actual amount of use, to extract more information from the data. The ten quantiles described above were used to assess the relationship. Here the probabilities—quantile break values—were regressed against either the average density of Dunlin or Dunlin droppings (forecasting) or against the sums of weighted telemetry location (backcasting) within a quantile as appropriate. If predicted probabilities match the amount of use, a strong positive relationship between these variables is expected.

## Results

### Dunlin distribution

By day, Dunlin often congregated in a few large mobile flocks (mean ± SD bird density 85 ± 264 $\text{ha}^{-1}$, dropping density 10 ± 17 $\text{quadrat}^{-1}$, $n = 83$), which tracked the tide-line, although some birds consistently remained near the shore. By night, Dunlin foraged in small, broadly dispersed groups (bird density 12 ± 42 $\text{ha}^{-1}$, dropping density 1 ± 4 $\text{quadrat}^{-1}$, $n = 152$).

Day-time instantaneous probability of mudflat use was associated with, in order of importance: lower percent water cover, intermediate distance from cover, higher sediment organic content, and closer distance to tide-line. The best confidence set (2 models, sum of AIC $\omega = 0.95$) also included the position of tide (*Tide*) with a weak positive effect (Table 2; Fig. 2a).

At night (2 models, sum of AIC $\omega = 0.98$), the instantaneous probability of detecting a Dunlin increased with deeper surface water and when the tide was higher up-shore. It also decreased towards the end of season, and increased with proximity to tidal channels and sediment organic content. There was a weak positive effect of distance from cover. The effect of surface water depth was confounded with those of Julian date and tidal height: Dunlin were more likely to use locations with deeper water (<15 cm) later in the season, but shallower (more drained) sites when the tide was higher up-shore (Table 2; Fig. 2b).

Cumulative probability of mudflat use by day (2 models, sum of AIC $\omega = 0.95$), as expressed by dropping occurrence, was associated with intermediate distances from cover; it increased with proportion of fine sediment, lower water cover, greater time since emersion and proximity to tide-line (Table 2; Fig. 2c).

There was much uncertainly about the best night model predicting the cumulative probability of mudflat use (5 models, sum of AIC $\omega = 0.88$). At night droppings were more likely to be found in areas with intermediate surface water cover. Sediment coarseness, time since emersion, and distance to cover were retained but had uncertain effects on the response (Table 2; Fig. 2d).

### Residual tests and overfitting

No model residuals correlated significantly with the environmental variables or illumination ($r_p < 0.1$, $P > 0.20$). Nor was there significant residual autocorrelation (Moran's $I$ −0.041 to 0.010, $P$-values >0.1; lag 400 m, min 20 point-pairs $\text{lag}^{-1}$). Overfitting (range 0.04–0.13 AUC) strongly increased with the number of predictors in the model (Table 3; Fig 3).

### Forecasting discriminatory capacity

After correction for overfitting, only the cumulative night models (*i*) and (*ii*) were not expected to yield acceptable discriminatory capacity. Instantaneous day models predicted that presence locations would receive higher ranking than absences in 76% of cases. When applied to 2006–2007 data, day models produced AUC values <0.7 (Table 3). Night models were expected to correctly classify 71–74% of presence/absence locations, but yielded AUC values of 0.61 (Table 3). Predicted distribution maps suggested that the failure of night models was associated with misclassifying apparently suitable locations, places that were visited by Snowy Owls in 2005–2006, but not in 2006–2007 (Fig. 2b). This implies that night distribution in 2006–2007 was broader and more similar to day than the models (based on 2005–

**Table 2** Candidate models (*i*—structurally simplest; *ii*—highest discriminatory capacity) predicting instantaneous (individual) and cumulative (dropping) probability of intertidal habitat use by Dunlin, including numbers of independent predictors ($\kappa$), prevalence (1/0), internal AUC, and $\chi^2$

| Model[a] | Equation (*logit*=) | $\kappa$ | Prev | AUC |
|---|---|---|---|---|
| Instantaneous, day | (*i*) $0.19(1.72) + 142.57(57.23) * \mathit{Org} - 0.039(0.012) * \mathit{Water} - 1.73(0.74) * \mathit{DistTide} + 1.39(0.72) * \mathit{DistCover} - 3.16(0.98) * \mathit{DistCover}^2$ | 5 | 45/83 | 0.83 |
| | (*ii*) $-0.94(2.30) + 134.32(58.01) * \mathit{Org} - 0.037(0.011) * \mathit{Water} - 1.70(0.75) * \mathit{DistTide} + 0.79(1.05) * \mathit{Tide} + 1.43(0.74) * \mathit{DistCover} - 3.01(0.99) * \mathit{DistCover}^2$ | 6 | 45/83 | 0.84 |
| Instantaneous, night | (*i*) $-2.85(1.09) - 2.40(1.02) * \mathit{DistChan} + 1.46(0.31) * \mathit{Depth} - 0.033(0.010) * \mathit{Julian} + 2.03(0.74) * \mathit{Tide} - 0.015(0.006) * \mathit{Julian} * \mathit{Depth} + 1.12(0.44) * \mathit{Tide} * \mathit{Depth}$ | 6 | 57/152 | 0.79 |
| | (*ii*) $-5.80(1.81) + 80.64(39.62) * \mathit{Org} - 2.48(1.06) * \mathit{DistChan} + 1.58(0.33) * \mathit{Depth} - 0.035(0.011) * \mathit{Julian} + 2.33(0.81) * \mathit{Tide} - 0.015(0.006) * \mathit{Julian} * \mathit{Depth} + 1.26(0.46) * \mathit{Tide} * \mathit{Depth} + 0.72(0.45) * \mathit{DistCover}$ | 8 | 57/152 | 0.82 |
| Cumulative, day | (*i*) $-0.45(0.97) + 4.44(1.51) * \mathit{FineSed} - 0.025(0.010) * \mathit{Water} + 1.91(0.75) * \mathit{DistCover} - 2.59(0.89) * \mathit{DistCover}^2$ | 4 | 48/83 | 0.82 |
| | (*ii*) $0.39(1.25) + 4.63(1.61) * \mathit{FineSed} - 0.043(0.013) * \mathit{Water} - 1.79(0.83) * \mathit{DistTide} + 2.26(0.90) * \mathit{DistCover} - 3.17(1.04) * \mathit{DistCover}^2 + 0.008(0.004) * \mathit{Time}$ | 6 | 48/83 | 0.85 |
| Cumulative, night | (*i*) $-2.13(0.88) - 0.62(0.84) * \mathit{FineSed} + 0.007(0.003) * \mathit{Water} + 0.0007(0.0003) * \mathit{Water}^2$ | 3 | 37/152 | 0.65 |
| | (*ii*) $-2.46(1.16) - 1.02(0.99) * \mathit{FineSed} + 0.006(0.008) * \mathit{Water} + 0.0007(0.0003) * \mathit{Water}^2 + 0.003(0.002) * \mathit{Time} + 0.13(0.43) * \mathit{DistCover}$ | 5 | 37/152 | 0.67 |

Standard errors of coefficients in parentheses

[a] All models statistically highly significant ($P < 0.005$)

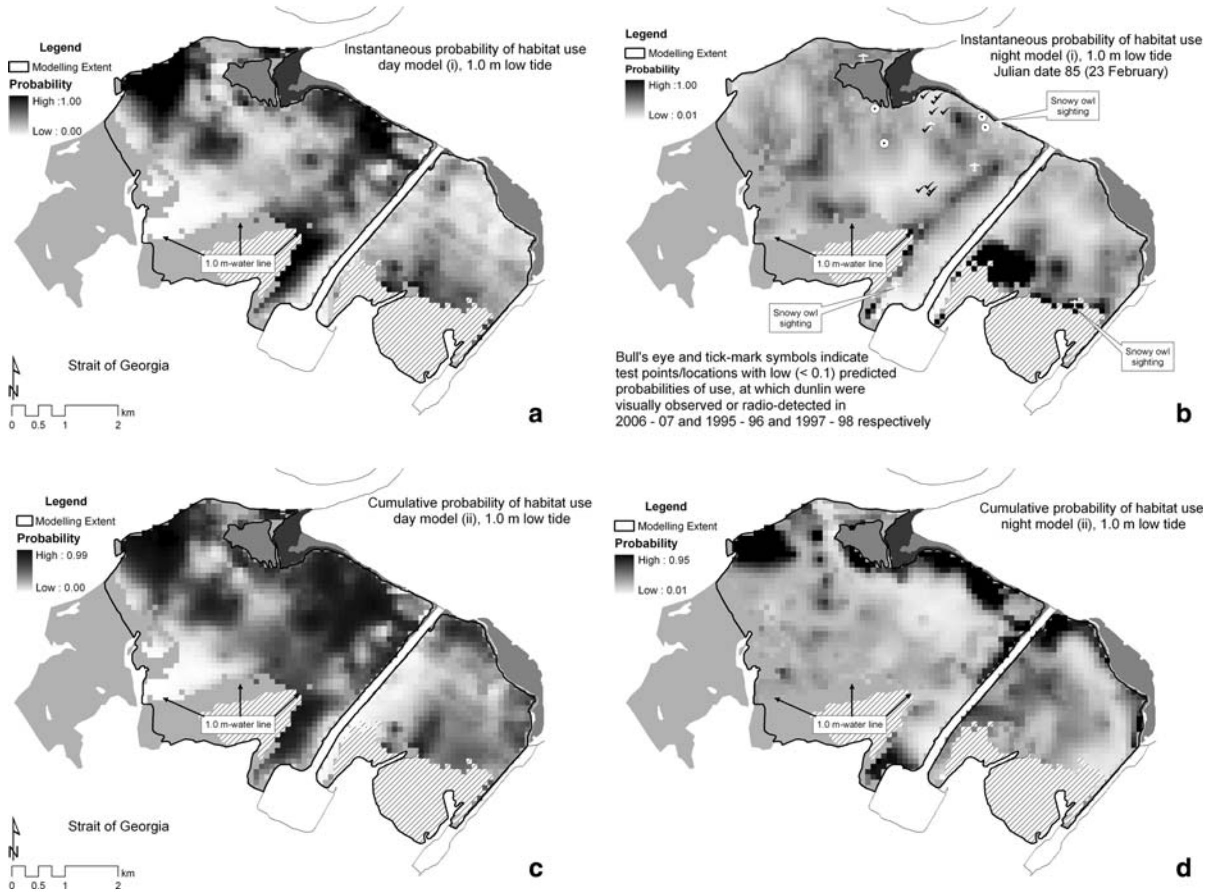


**Fig. 2** Predicted probabilities of habitat use by Dunlin at mid-low tide

**Table 3** Predictive capacity of models of instantaneous and cumulative probability of mudflat use by Dunlin

| Model | Overfitting $AUC_{train} - AUC_{test}$ | Corrected AUC | Forecasting (AUC) | Backcasting ($r_s$) |
|---|---|---|---|---|
| Instantaneous, day, *i* | 0.07 | **0.76** | 0.68/**0.71** | 0.61/**0.72*** |
| Instantaneous, day, *ii* | 0.08 | **0.76** | 0.65/**0.71** | 0.69*/**0.76*** |
| Instantaneous, night, *i* | 0.05 | **0.74** | 0.61/0.57 | 0.41/0.08 |
| Instantaneous, night, *ii* | 0.10 | **0.71** | 0.61/0.52 | 0.65*/0.60 |
| Cumulative, day, *i* | 0.07 | **0.75** | **0.71**/0.68 | **0.79****/**0.88**** |
| Cumulative, day, *ii* | 0.07 | **0.79** | **0.70/0.73** | **0.93*****/**0.94***** |
| Cumulative, night, *i* | 0.05 | 0.60 | 0.59/0.52 | 0.27/−0.22 |
| Cumulative, night, *ii* | 0.13 | 0.54 | 0.67/0.68 | 0.16/−0.27 |

For backcasting predictive capacity Spearman rank correlation coefficients significant at $P < 0.05$, <0.01, and <0.001 given as '*', '**' and '***', respectively. Two forecasting AUC values and $r_s$ indicate results of application of the models to respective (day model to day data) and total (day model to day + night data) datasets. Values in *bold* ≥0.70

2006 data) suggested. To test this hypothesis, day models (*i* and *ii*) were applied to the combined day and night testing data. In both cases, increased AUC values (0.71) were obtained. The reverse was not true: night models performed poorly on the combined dataset (Table 3).

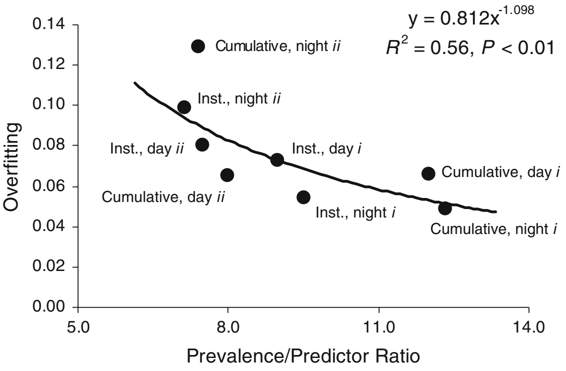


**Fig. 3** Relationship between the ratio of model prevalence to the number of predictors and the amount of overfitting ($AUC_{train} - AUC_{test}$) for eight models describing the probability of Dunlin habitat use

Day models of cumulative probability of use were expected to correctly classify 75–79% of locations. Their application to the test dataset indicated a lower, but still useful discriminatory capacity (Table 3). As expected both night models failed to clear the 0.7 threshold given their low overfitting-corrected AUCs. Similar to the instantaneous probability of use, we applied cumulative day and night models to the combined dataset with a similar outcome: day models produced acceptable AUC values; night models did not (Table 3).

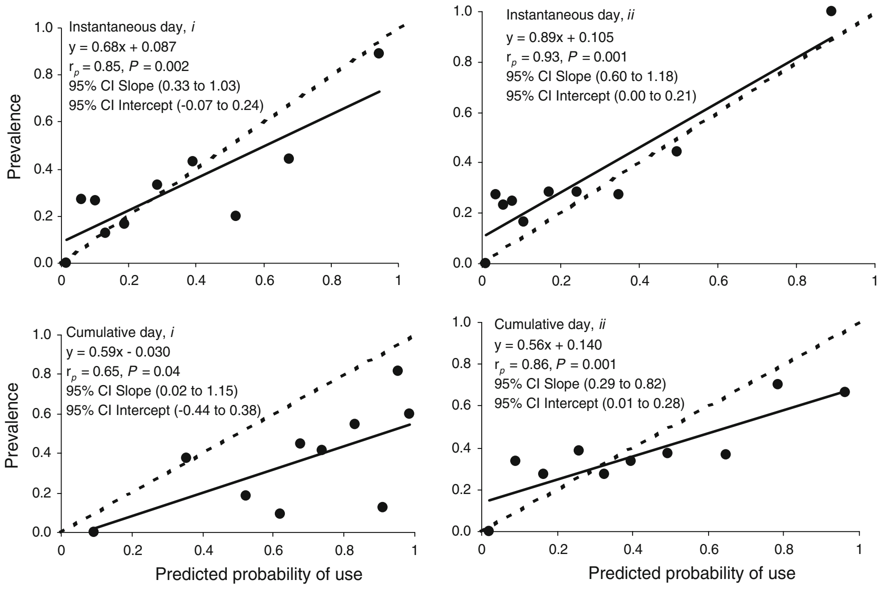
## Backcasting discriminatory capacity

In backcasting application, day and night models of instantaneous probability of use had poor accuracy (Table 3). Examination of the mapped distribution of night locations of radio-tagged Dunlin suggested that the night models under-predicted probability of use (Fig. 2b). Similar to our approach above, the day and night models were tested against the combined dataset of telemetry locations. Day models showed much improved performance on the combined dataset, while night models did not. A similar outcome was obtained for the cumulative probability models (Table 3).

## Model calibration and the relationship between the probability and amount of use

Since only day models performed well in both fore- and backcasting and best on combined datasets, further testing was carried out by applying these models to the combined day/night data. Instantaneous probability of use models displayed good calibration: $r_p > 0.8$, slope and intercept not significantly different from 1 and 0 respectively. The cumulative probability of use models performed worse, suggesting over-prediction (*i*) and over-prediction and overfitting (*ii*, slope <1) (Fig. 4).

**Fig. 4** Relationship between the predicted probability of use ($x$) and prevalence ($y$) within 10 equal-area probability classes (quantiles). *Dashed line* represents ideal model calibration



Asymptotic, exponential, linear, and power relationships between the predicted probability and the actual amount of use were explored (Fig. 5). Asymptotic and exponential regressions produced best fits between the amount of use and instantaneous and cumulative probabilities of use, respectively (Fig. 5a, b).

## Discussion

As far as we know, this work is the first to develop models of shorebird distribution for a non-breeding site that are amenable to GIS applications, capture a near-complete range of environmental conditions across a foraging intertidal landscape, incorporate factors hitherto shown to be important drivers of shorebirds distribution, and have been tested using independent data and display acceptable temporal transferability.

Dunlin distribution was strongly associated with landscape physical properties known to influence food abundance, availability and predation danger (Model 5—Table 1; Yates et al. 1993; Dekker and Ydenberg 2004; Granadeiro et al. 2004; Lourenço et al. 2005; Taft and Haig 2006; Pomeroy 2006) with a weaker temporal effect. Dunlin distribution differed between day and night when Snowy Owls invaded the area (resident nocturnal owls—Barn Owl (*Tyto alba*) and Great Horned Owl (*Bubo virginianus*)—

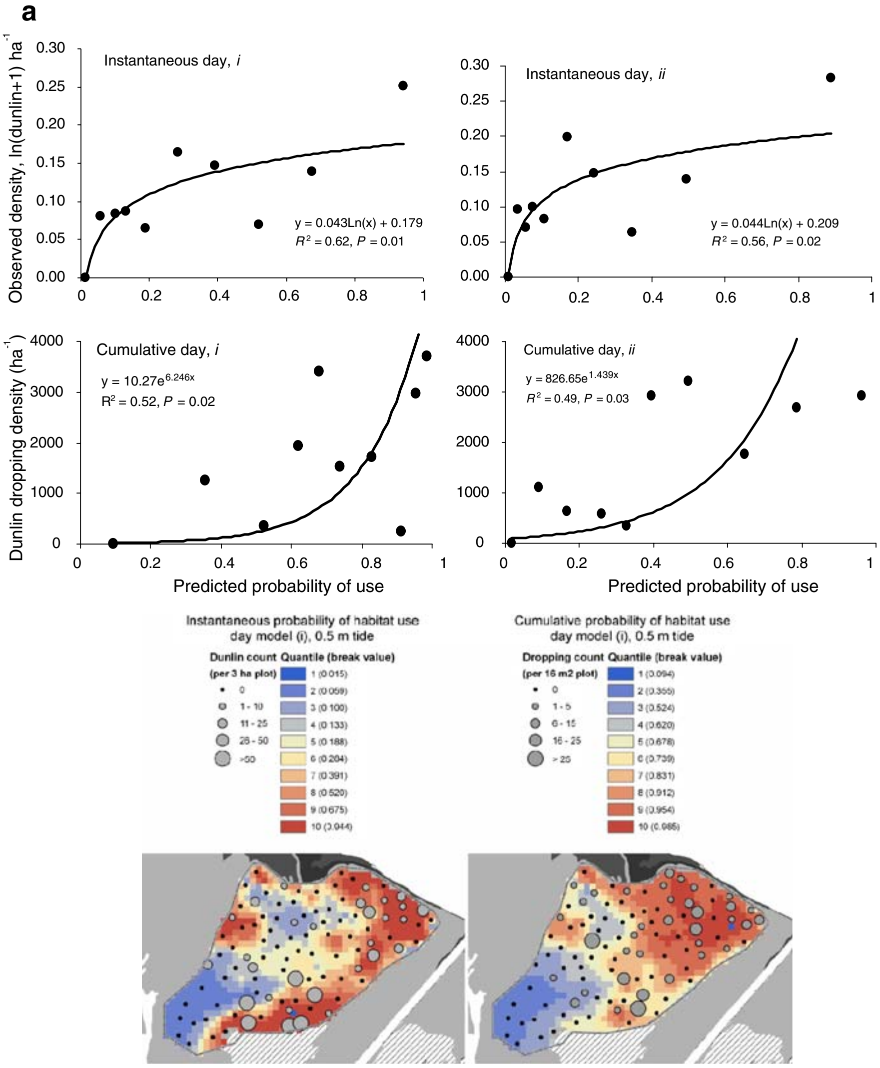
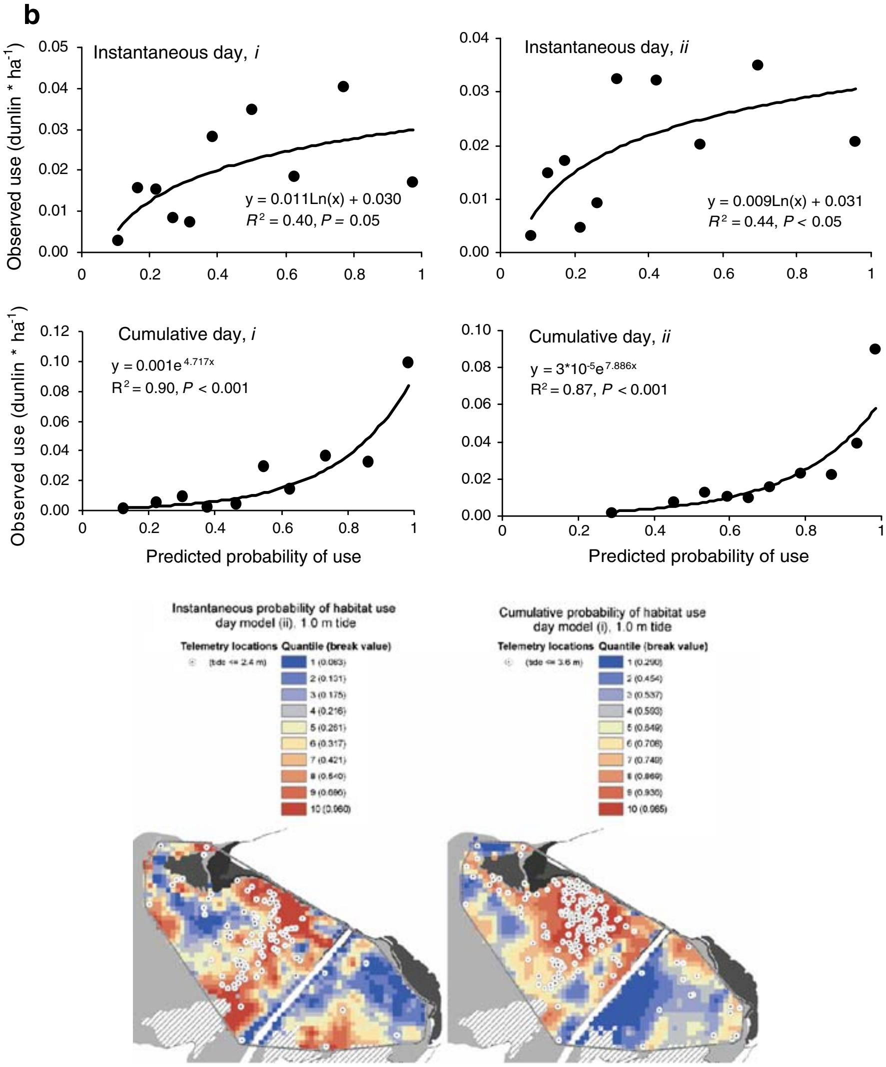


**Fig. 5** Relationship between predicted probability of use by Dunlin (*x*) and amount of use (*y*) as determined by the average density of birds/droppings (**a**) or the weighed sum of telemetry locations (**b**) within 10 equal-area probability classes (quantiles). Insets illustrate spatial distribution of the observed amount of use as expressed by the counts of individuals/droppings (**a**) or telemetry locations (**b**) within the predicted 10 equal-area probability classes (quantiles)

**Fig. 5** continued



were never observed over mudflats). When the predators were absent the night models developed from the owl-year data biased the probability of habitat use low, suggesting that the shorebirds modulated (shrunk) their distribution in response to increased predation danger (Brown et al. 1988). In 2005–2006, owls attacked Dunlin from the shoreline, which provided cover and vantage points for the predators or when patrolling the mudflats (pers. obs). This pushed Dunlin away from shore into more exposed or otherwise safer areas, a typical food-safety trade-off (Whitfield 2003; Pomeroy 2006). In 1995–1996, 1997–1998 and 2006–2007 Snowy Owls were absent, and nocturnally active Dunlin utilised richer up-shore habitat (Pomeroy 2006), making their distribution pattern more day-like. That Dunlin modulated their distribution pattern with respect to predation danger was also evident from their use of the adjacent agricultural fields. Dunlin were regularly detected at night in fields in the owl-less years of 1995–1996, 1997–1998 and 2006–2007, but few were recorded there in 2005–2006 (Shepherd and Lank 2004; pers. obs.). Illumination explained no additional variance in the night distribution of Dunlin implying that lighting (artificial from the port and natural from the moon) did not alter the food-safety trade-off, as might have been expected if the owls selectively exploited darker areas to hunt for the species with poor night vision (Mouritsen 1992). Unlike falcons (below) owls did not venture far from shore and thus Dunlin avoided the shoreline rather than areas with lower illumination. This pattern is consistent with the behavioural response of many other species, including shorebirds, to night predators (Brown et al. 1988; Mouritsen 1992; Gillings et al. 2005; Beauchamp 2007a).

By day, Dunlin were hunted by falcons over the entire mudflats, although more successfully near the shore. In contrast to night, however, the shorebirds were capable of early visual detection of the predators (Dekker and Ydenberg 2004). This evidently lowered their perception of danger as compared to night, explaining why day-time Dunlin distribution was broader (closer to shore). This component of the predator landscape, to which Dunlin responded by aggregation into larger groups (Beauchamp 2007a), was annually constant and had no bearing on model transferability.

Dunlin did not alter habitat use with changes in forager density. Seasonally, the local population of Dunlin increases three-fold from ca. 8,000 in December to ca. 24,000 in April. The maximum daily available mudflat area varied two-fold (1,250–2,460 ha). These changes could produce six-fold differences in the mudflat-wide Dunlin density. Whitfield (2003) found that at increased population densities more Redshanks (*Tringa totanus*) were forced into habitat suboptimal in terms of safety. We found no positive seasonal and weak positive tidal effects on the probability of habitat use. Thus, in the short-term, as the population increased (or area decreased) Dunlin aggregated at higher densities at preferred sites (Taft and Haig 2006).

Sites more likely to be used by Dunlin also afforded a greater amount of use. The asymptotic relationship with the instantaneous probability of use suggested that density was limited by factors different from those defining occurrence. Such factors could include predators (Beauchamp 2007a) and prey availability (Gill et al. 2001). The exponential relationship between dropping density and cumulative probability of use reflects the slightly sigmoid profile of the mudflat and the first accelerating and then decelerating speed of the ebbing tide. Thus, high-quality areas located up-shore experience disproportionately greater Dunlin densities, and for longer, early at a receding tide. This also occurs at slack-tide when the birds congregate around the tide-line due to greater food availability (Zwarts and Wanink 1993) and safety (Dekker and Ydenberg 2004).

No significant residual autocorrelation was detected, suggesting that the sets of predictors were "sufficient" for model specification and not spurious (Barry and Elith 2006). The wealth of knowledge available on non-breeding shorebirds should allow specification of intertidal distribution models for many species, including, Western Sandpiper: another Calidrid that uses Roberts Bank on migration (Elner et al. 2005; Kuwae et al. 2008).

As did others (Boyce et al. 2002; Betts et al. 2006), we found that data-optimised AUCs overestimate model performance. In distribution modelling, the ratio of $\geq$10:1 presence data points to predictor is thought to be optimal (Barry and Elith 2006). Indeed, this ratio produced the lowest overfitting values. However, the ultimate predictive performance of the models was not related to sample size of presence locations, suggesting that selection of appropriate predictors may be more important than prevalence.

When distribution models are visualised in GIS, predicted probabilities are implied to represent occurrence frequencies. However, model calibration has been rarely tested (Vaughan and Ormerod 2005). Our models of instantaneous probability of use are well-calibrated, but cumulative probability models tend to over-predict the probability of use. The detectability of Dunlin droppings may be an issue. Over the study period on average 6 mm of rain fell on 82% of days and some droppings may have been dissolved. This inflated the level of uncertainty in the models of cumulative probability of use and resulted in over-prediction in the model-testing exercise because in December 2006–April 2007 70 mm more rain fell than in the corresponding period of 2005–2006.

## Conclusions

Physical and topographic properties of a landscape can be utilised to predict shorebird distribution. However, it is important to consider the predator landscape at the time of model development and application (Gillings et al. 2005). Once night predators are taken into account the models display good temporal transferability in this species with broad habitat affinities. The models are temporally robust and are not sensitive to field methodology (visual observations versus radio-telemetry). They can predict areas preferred by Dunlin at mid-low tide, when a broad expanse of habitat is available (instantaneous probability of use) and identify areas where birds aggregate at a receding tide (cumulative probability of use), providing a comprehensive picture of habitat use.

Good retroactive performance of the models implies stable physical conditions in the study area over the past 12 years. A proposed expansion of the port on Roberts Bank could change the physical landscape. Changes such as in mudflat topography, shoreline extent and configuration can be accurately modelled in GIS. The models developed in this study can be adapted to map shorebird areas that could be directly impacted by the development. Further, they could be used to assess and visualise in GIS the indirect impacts of the development on shorebird distribution on the landscape. For example, lateral port terminal expansion (Fig. 1a) would effectively increase the shoreline extent (amount of cover), thus decreasing the mudflat area available to shorebirds due to increased predation danger, even if the physical mudflat extent remained unaltered. According to our models, Dunlin would respond by redistributing to "safer" parts of the mudflat, thus at least initially maintaining local population levels. Whether such habitat alienation could have negative local population consequences would depend on the extent of habitat loss, tolerance of Dunlin to crowding, rates of benthic prey depletion/replenishment (Zharikov and Skilleter 2003; Beauchamp 2007b) and suitability of alternative sites. Answering this question would require behaviour-based modelling (Durell et al. 2005) and such work is forthcoming. For predictors for which only relative change can be assessed (e.g. sediment organic content), a range of scaling factors may be used uniformly over the impacted area, still yielding plausible response scenarios.

In the longer term, Roberts Bank, indeed coastal areas globally, will experience the consequences of rising sea-level, including erosion and migration of the shoreline, sediment coarsening and mudflat area reduction. Some impacts have been modelled at spatial scales compatible with the scale of the study (e.g. salt-marsh erosion, Kirwan and Murray 2008). Other changes, such as relative extent and position of lower (sandy), mid (mud-sand) and upper (muddy) intertidal zones may only allow semi-quantitative predictions (Hill in press). Our models could be used in conjunction with site-level coastal process models to assess and visualise impact of these changes on non-breeding shorebirds, a taxon particularly vulnerable to climate change impacts (Piersma and Lindstrom 2004), providing input for mitigation planning.

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