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Importance of matrix permeability and quantity of core habitat for persistence of a threatened saltmarsh bird

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Species habitat preferences can be obscured when individuals have been recorded in non-core habitats because of dispersal, spillover effects or spatial errors in observation locations. Disentangling the direct effects of the habitats species are observed in from the effects of proximity to other nearby habitats is especially challenging in fragmented landscapes, as many fragmentation metrics are correlated and it is difficult to prove independent effects. In this paper we addressed this issue by comparing a number of models based on predefined ecological theories. We compared models based on quantity of core habitat surrounding observations, proximity to core habitat, or a combination of the two to explain the observed distribution of the saltmarsh inhabiting white-fronted chat (*Epthianura albifrons*) in coastal New South Wales, Australia. Proximity to core habitat was considered as either Euclidean distance or cost distance, and models were assessed using Akaike's information criterion and the area under the receiver operator characteristic curve on 10 random subsets of the data. We found that all models performed similarly, with the combination of cost distance and the quantity of saltmarsh performing better, but not significantly so. We compared the advantages and disadvantages of different models and also present a model averaged result. Our models suggested that the majority of saltmarshes in New South Wales were too small to have a large effect on probability of occurrence. As climate change is expected to further reduce the amount of available saltmarsh through continued mangrove incursion, coastal populations of the white-fronted chat are expected to come under increasing threat. The conversion of grasslands to urban areas may also increase the effective distance between different populations of the species and reduce gene flow and rescue effects.

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**The importance of matrix permeability and quantity of core habitat for persistence of a
threatened saltmarsh bird**

Running title: Landscape ecology of a saltmarsh bird

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Abstract

Species habitat preferences can be obscured when individuals have been recorded in non-core habitats due to dispersal, spillover effects, or spatial errors in observation locations. Disentangling the direct effect of the habitats the species is observed in from the effect of proximity to other nearby habitats is especially challenging in fragmented landscapes, as many fragmentation metrics are correlated and it is difficult to prove independent effects. In this paper we addressed this issue by comparing a number of models based on predefined ecological theories. We compared models based on quantity of core habitat surrounding observations, proximity to core habitat, or a combination of the two to explain the observed distribution of the saltmarsh inhabiting white-fronted chat (*Epthianura albifrons*) in coastal New South Wales (NSW), Australia. Proximity to core habitat was considered as either Euclidean distance or cost-distance, and models were assessed using Akaike's information criterion and the area under the receiver operator characteristic curve on ten random subsets of the data. We found that all models performed similarly, with the combination of cost-distance and the quantity of saltmarsh performing better, but not significantly so. We compared the advantages and disadvantages of different models and also present a model averaged result. Our models suggested that the majority of saltmarshes in NSW were too small to have a large effect on probability of occurrence. As climate change is expected to further reduce the amount of available saltmarsh through continued mangrove incursion, coastal populations of the white-fronted chat are expected to come under increasing threat. The conversion of grasslands to urban areas may also increase the effective distance between different populations of the species and reduce gene flow and rescue effects.

Key words: dispersal, *Epthianura albifrons*, fragmentation, habitat loss, home range, landscape configuration, least-cost distance, urban ecology

INTRODUCTION

A fundamental goal of ecology is to understand the distributions and habitat preferences of species. This is especially important for threatened species and communities, as we need this information to develop management and species recovery plans (e.g. Gibson *et al.* 2004; Rainho & Palmeirim 2011). However, quantifying habitat preferences is not always straight forward. Some species may require more than one type of habitat for different portions of their life cycle (Fahrig 2003) and proximity of these habitats in space may be more important than presence of any one habitat type (Rainho & Palmeirim 2011). Species may also avoid otherwise favourable habitat due to the presence of edge effects (Murcia 1995; Koper *et al.* 2009) or be found in adjacent habitats due to dispersal, spillover or spatial errors in species observations (Chardon *et al.* 2003; Betts *et al.* 2007; Wiser & Buxton 2008). Disentangling the roles of habitat and proximity can be challenging (e.g. Conner *et al.* 2005; Dussault *et al.* 2005), especially as there are many metrics to quantify habitat fragmentation in a landscape, and many of these are highly correlated (Cushman *et al.* 2008; Smith *et al.* 2009).

Many birds are central-place foragers (Kacelnik 1984; Rainho & Palmeirim 2011) and therefore we might expect them to be found in various habitats around some core habitat type that is important for breeding or feeding resources. Models that attempt to explain the distribution of these species in terms of habitat alone may be poor if there are many observations in proximal non-core habitats (Rosenberg & McKelvey 1999). In these cases landscape scale analysis may yield better results, especially if there is *a priori* knowledge on the core habitat for a species (e.g. Betts *et al.* 2007). In these circumstances we can use metrics such as the amount of core habitat in the area surrounding observations (e.g. Betts *et al.* 2007) or the distance to core habitat (e.g. Rainho & Palmeirim 2011) to model species distributions, as these have the potential to explain observed presences in proximal non-core habitat.

The amount of core habitat in a landscape is predicted to have a large effect on the suitability for a species, as reducing the amount of habitat has been consistently shown to have large, negative effects on species (Bender *et al.* 1998; Fahrig 2003). The population size may decline linearly with the amount of habitat available (proportional area hypothesis) or may decline rapidly once the amount of habitat drops below a threshold (extinction threshold hypothesis; Fahrig 2003). Thresholds may exist for some species but not others (e.g. Villard *et al.* 1999; Betts *et al.* 2007), which means that it is crucial to examine the shape of the relationship between suitability and habitat area so that we can estimate the level of risk associated with a given amount of habitat (Wilhere 2007).

Approaches based on distance to core habitat types have been promoted because the use of a habitat by a species is unlikely to be independent of the surrounding habitat types (Conner *et al.* 2005). Although the Euclidean (straight line) distance may be adequate for some species, many species can move more easily through some habitat types than others, and hence distances may be better calculated using an effective-distance, least-cost or cost-distance approach (Adriaensen *et al.* 2003; Chardon *et al.* 2003; Zhu *et al.* 2010). The resistance values for different habitat types are typically estimated by expert opinion, but different combinations of costs can be tested to determine which is best (e.g. Richard & Armstrong 2010; Cushman *et al.* 2006). The main shortcoming of purely distance-based approaches is that they ignore the size of the patch from which they are calculating the distance. However, this shortcoming can be overcome by only measuring distances to patches larger than a certain threshold size (e.g. Chardon *et al.* 2003), and this approach combines both habitat quantity and distance if an appropriate threshold exists.

In this study we examined these different ecological models to determine which, if any, was better at explaining the distribution of the white-fronted chat (*Epthianura albifrons*) in coastal New South Wales (NSW), Australia. The particular methods we examined were: 1)

an approach based on the amount of core-habitat in the area surrounding observations; 2) a distance to core-habitat approach using both Euclidean and cost-distances; and, 3) a combination of habitat quantity and distance-based approaches. The aim was to compare these different models to investigate the relative importance of distance and habitat quantity. As alternative models of species distributions can often perform similarly, comparing a limited number of models based on established ecological knowledge can provide greater insights into the importance of different habitat factors than simply selecting one model that may only perform marginally statistically better than the alternatives (Mac Nally 2000, 2002; Bahn & McGill 2007; Ashcroft *et al.* 2011).

METHODS

Study species and study area

The white-fronted chat (*Epthianura albifrons*) is an Australian passerine weighing about 13 g and belonging to the honeyeater family (Meliphagidae) (Driskell & Christidis 2004). Unlike other honeyeaters, white-fronted chats do not feed on nectar, but are exclusively insectivorous, feeding on the ground (Major 1991a). They frequently forage in flocks of 10–20 individuals and even in the breeding season, individuals will join feeding flocks away from their nest sites, rather than defending all-purpose territories (Major 1991b). White-fronted chats roost communally and have been recorded foraging up to 3 km from their roost sites, with foraging sites changing periodically in response to temporary outbreaks of insects (Major 1991a).

White-fronted chats occur in damp open habitats in southern Australia, particularly in wetlands bordered by grassland or samphire, and they are only occasionally seen in habitats with trees or dense understorey vegetation (Higgins *et al.* 2001). They have been recorded as resident in many coastal locations, particularly in coastal saltmarsh (Higgins *et al.* 2001), but they are considered to be nomadic in some inland regions (Keast 1958). This study focuses

on coastal populations in New South Wales (within 20 km of the Pacific Ocean) which are separated from inland populations by the forest cover of the Great Dividing Range.

The white-fronted chat was listed as a vulnerable species in New South Wales in 2010, due to it having undergone a moderate reduction in population size (NSWSC 2010a). The decline has been particularly marked in coastal areas and has been linked to the loss of coastal saltmarsh (Jenner *et al.* 2011), which itself is listed as an endangered ecological community. The decline of the species in the Sydney region has been so severe that the “White-fronted Chat *Epthianura albifrons* (Jardine & Selby, 1828) population in the Sydney Metropolitan Catchment Management Authority area” has been listed as an endangered population (NSWSC 2010b). In order to manage potential habitat in a way that promotes the recovery of the species it is important to understand the extent to which it is associated with saltmarsh vegetation, particularly given that in some parts of its range it is thought to have benefited from clearance of woodland for agriculture (Saunders & Ingram 1993).

Data

We obtained a polygon shapefile of saltmarsh estuarine habitat from NSW Department of Primary Industries. This map was very detailed, with patches as small as 1 m² identified, and individual mangrove canopies excluded. However, the cost-distance functionality of ArcMap (ESRI) operates using raster datasets, and hence we converted the shapefile to a 25 m resolution raster dataset. This resulted in some loss of detail, but was the finest resolution manageable at a state scale. Fine-resolution layers of other habitats were not available at the state scale for use in cost-distance analysis, so we used the statewide vegetation data (Keith 2002) from the NSW Office of Environment and Heritage, which was available as a 200 m resolution raster. The Office of Environment and Heritage also provided the “Land Use: New

South Wales (version 1)” shapefile, which provided details on the use of each polygon, but did not always distinguish between different land covers within each polygon.

We developed a 100 m resolution cost raster layer based on the combined land use and land cover as determined using the above layers. As the saltmarsh layer had the highest resolution, we assigned ‘saltmarsh’ to all areas that were identified in that layer. Many polygons in the land use layer were found to be heterogeneous in terms of land cover, and so we used the 200 m resolution land cover layer as the next highest priority to identify areas of ‘forest’, ‘woodland’, ‘shrubland’, ‘water’ and ‘grassland’. The land use layer was only used where the land cover layer suggested the land was cleared, and was used to distinguish between ‘urban’, ‘grasslands’ and ‘roads’. Costs were assigned based on expectations derived from more than 10 years studying the habitat preferences and flight behaviour of this species across its geographical range (Major 1991a, b; Jenner *et al.* 2011; Major & Sladek 2012), with a cost of 1 for grassland and saltmarsh, 2 for shrubland, 5 for water, 10 for forest and woodland, and 20 for roads and urban. The species has a reputation for being timid (Gould 1865; Jenner *et al.* 2011), and these costs reflect behavioural avoidance of urban areas as much as a physical barrier to movement. We also tried a second set of costs (20 for urban/roads and 1 for everything else), but results presented similar trends, albeit with slightly poorer relationships, and so we only present the results for the first set of costs.

Data on the distribution of bird sightings (individuals or flocks) were obtained from Birds Australia’s Atlas database (see Barrett *et al.* 2003) for the period between 1998 and 2002. We restricted our analysis to surveys within 20 km of the NSW coast that were obtained using a 2-ha 20-min area search or the <500-m radius 20-min area search (Barrett *et al.* 2003). That is, we excluded incidental records or those that were taken over larger areas and may have had less spatial accuracy. This dataset had 110 recorded locations for white-fronted chats and 7122 survey locations where the species was not detected. The data were

analysed as a presence-absence dataset. As observations reflect a given point in time (not necessarily the long term habitat usage), our models will predict probability of observing the species with the effort given above, and reflect occurrence at a given location, not necessarily long-term usage.

As spatial autocorrelation could have inflated the perceived performance of models if many records were obtained from a limited number of saltmarshes, we divided the area into a 5 km grid and randomly selected 10 records from each grid cell while maintaining the spatial accuracy of the records. We repeated this process ten times to obtain ten replicate datasets, each containing an average of 49.7 presences (s.d. = 4.2) and 4698.3 absences (s.d. = 4.2). This process addressed the trade-off between spatial autocorrelation and having sufficient data for modelling, with 10 records in a 5km grid selected as it reduced the influence of grid cells with the most records, while still maintaining the recommended 50 presences for modelling species distributions (Stockwell & Peterson 2002; Coudun & Gégout 2006). Each of the 10 datasets was divided into 3324 (70%) records for model training and 1424 (30%) records for testing.

Models based on habitat quantity

The amount of habitat in the surrounding landscape was incorporated into models using the Focal Statistics tool in ArcMap. We used a circular moving window to calculate the amount of saltmarsh, and examined different radii of between 1 km and 8 km in 1 km increments. For each radius we produced a Generalised Additive Model (Hastie & Tibshirani 1990; gam package in R), with the amount of saltmarsh predictor included as a spline with 2 degrees of freedom. This allowed for non-linear response shapes, but did not provide enough freedom for complex responses which may have led to overfitting. Models were assessed by calculating the average Akaike's Information Criteria (AIC function in R) on the ten training datasets and the average area under the receiver operator characteristic curve (AUC of ROC;

catools package for R) for the ten test datasets. Average specificity and sensitivity (proportion of correct absences and presences respectively) for the ten test datasets were determined using the caret package in R and a threshold that ensured that specificity and sensitivity were equal. Response curves (and 95% confidence limits) were determined as the mean (± 2 s.d.) of the ten replicate models.

Models based on distance

The distance from a survey location to the nearest patch of saltmarsh was determined using both the Euclidean Distance and Cost Distance tools in ArcMap. These were separately included in Generalised Additive Models as splines with two degrees of freedom and validated as for the models based on habitat quantity.

Models based on distance and habitat quantity

Two sets of models were produced that considered both distance and habitat quantity. The first set of models consisted of multivariate models that included both the habitat quantity and distance predictors from the previous two sections as individual predictors. The inclusion of an extra predictor will increase the ability to explain the training data, but may or may not lead to improved performance in the test data set depending on whether the additional predictors lead to overfitting.

The second set of models modified the distance-based models to only calculate distance from patches that exceeded a certain threshold size. As small patches in close proximity may have an effective area larger than the area of individual fragments, we applied a 100 m buffer to patches and combined the area of all patches that overlapped. We tested threshold sizes of 10, 20, 40, 80, 120 and 160 ha. We also calculated areas using a 500 m buffer, but results were similar so we only present results using the 100 m buffer.

As all models were produced using the same ten replicate datasets, we tested for significant differences between different models using a two factor ANOVA, with model and

dataset as the two factors (aov function in R). If results were significant, we used the TukeyHSD function to simultaneously test all pairwise combinations for differences. The models included in the ANOVA were a Euclidean distance model, cost difference model, the Euclidean and cost differences models with the best habitat threshold, a habitat quantity model using the best neighbourhood radius, and the combination of the best habitat quantity model with Euclidean and cost distances. A model averaging approach was used to average the outputs from different models that performed similarly in terms of AUC and AIC, with outputs from different models displayed in ArcMap to determine how predictions varied spatially.

RESULTS

Of the 110 records of the white-fronted chat, only 11 (10%) were within saltmarsh. However, this reflected the rarity of observations within this community as a whole (68 observations; 0.9%), with the proportion of presences higher within saltmarsh (11 of 68; 16.2%) than other nearby locations (Fig. 1). The white-fronted chat was more often observed between 100 m and 3 km from saltmarsh, although this reflected greater sampling effort, and the proportion of presences declined monotonically as the distance from saltmarsh increased (Fig. 1).

The distance based models for white-fronted chats (Euclidean distance or cost distance) were the worst performing models in terms of both the AIC on the training data and AUC on the test data (Fig. 2). Implementing a threshold of 10 ha resulted in a small improvement in performance, but results declined markedly if the threshold was increased further (Fig. 3). A predictor based on the amount of saltmarsh in the area surrounding observations was significantly better than all distance-based models in terms of AIC, and generally performed better in terms of AUC, but not significantly so (Fig. 2). The optimal radius for the neighbourhood was 6 km in most models, although there was little difference between different radii and 8km performed best in some instances (Fig. 3). We used models

with 6 km radius for consistency in further analysis. The models that combined the amount of habitat with distance to saltmarsh performed best, although not significantly better than the models based only on the amount of habitat (Fig. 2).

There was a high variation in both AIC and AUC for the 10 replicate datasets we used (Fig. 2), indicating that the models were sensitive to the sparsity of observations near saltmarshes, and the ‘luck’ of how these points were randomly selected into training and test datasets. Indeed, the highest uncertainties in the models were generally close to the saltmarsh (low distances) or where there was a large amount of saltmarsh in the surrounding area (Fig. 4). The ANOVA for the seven different models suggested that both model ($F = 33.1$, d.f. = 6, 54, $P < 0.001$) and dataset ($F = 117.1$, d.f. = 9, 54, $P < 0.001$) had significant effects on the AICs, although the effects were less pronounced in terms of AUC (model $F = 3.1$, d.f. = 6, 54, $P < 0.05$; dataset $F = 12.5$, d.f. = 9, 54, $P < 0.001$). The difference between the worst (Euclidean distance) and best (habitat amount + cost distance) models was 0.801 to 0.853 in terms of AUC and 352.9 to 327.1 in terms of AIC. Using a threshold that ensured that specificity was equal to sensitivity, the proportion of correctly predicted absences/presences varied from 0.712 (Euclidean distance) to 0.770 (habitat amount + cost distance).

All models agreed there was a higher chance of observing this species nearer to saltmarsh, or where there was more saltmarsh in the surrounding area (Fig. 4, 5). The purely distance-based models predicted higher favourability near all saltmarsh patches (Fig. 5a), which resulted in predictions of many small patches of favourability. Applying a threshold restricted model outputs only to the larger patches of saltmarsh (Fig. 5b), which matched the observed presences better (Fig. 6). However, the predicted probability of presence was still identical within or adjacent to these larger saltmarshes. The models based on the amount of saltmarsh in the surrounding area resulted in larger differences between saltmarshes of different sizes (Fig. 5c), and this is probably the reason for the better performance of these

models (Fig. 2). Combining the amount of habitat with cost distance resulted in similar spatial predictions (Fig. 5d), although the differences may be important in areas such as Sydney where urban area is more common. A model averaging approach resulted in predictions that also reflected both habitat amount and distance based models, with uncertainty amongst the seven models highest in the areas with the most saltmarsh present (Fig. 6).

The similarity in the performance of the different models could not be explained simply by collinearity between different predictors. The correlations between different distance-based predictors varied widely (r^2 of 0.13 to 0.54), but all were poorly correlated with the amount of habitat in the surrounding 6 km (r^2 of 0.07 to 0.22). The lack of significant differences between models was instead attributed to the sparsity of observations near saltmarshes and the associated variability of the 10 datasets detailed above.

When we projected the model averaged output onto the coastal region between the Shoalhaven and Port Stephens (Fig. 6), the model successfully explained the populations in the Newcastle, Towra Point, Illawarra and Shoalhaven regions, but it predicted the population at Homebush in Sydney was in marginal habitat, and there was a general lack of observations in the Hawkesbury and Port Stephens areas where the model predicted there was suitable habitat.

DISCUSSION

The relative contributions of habitat quantity and distance to habitat

It is inherently difficult to isolate the effects of different habitat fragmentation metrics, because many predictors are correlated, and are potentially competing to explain the same portion of model variance (Mac Nally 2000, 2002; Cushman *et al.* 2008; Smith *et al.* 2009). In our study, the different predictors were generally poorly correlated, but the habitat quantity models and the distance-based models still performed similarly. Although there were many

differences between models in terms of the AIC on the training data, there were few significant pairwise differences in AUC on the test data (Fig. 2). However, pairwise differences based on training AIC suggested that habitat quantity was more important than distance, and this was also supported by non-significant improvements in AUC (Fig. 2).

The lack of significant differences was largely attributed to the sparsity of observations near saltmarsh, and dividing our data into ten randomly selected training and test datasets highlighted how much uncertainty this sparsity of observations introduced. The highest uncertainties in response curves (Fig. 4) and spatial predictions (Fig. 5, 6) were in the vicinity of saltmarsh, and a higher density of observations would be needed in these locations to definitively separate the effects of habitat quantity and distance to core-habitat. Nevertheless, there were large differences in model performance between those based on Euclidean distance (AUC = 0.801; sensitivity = specificity = 0.712) and models based on cost distance and habitat quantity within 6 km (AUC = 0.853; sensitivity = specificity = 0.770), and we tentatively suggest both habitat quantity and cost-distance to core habitat are important (see also issues with other models discussed below). If the uncertainty is dealt with using a model averaging approach (e.g. Fig. 6), then this implicitly includes both cost-distance and habitat quantity anyway, as it combines models based on both factors. Indeed all models produce similar spatial distributions (Fig. 5), but the model averaged output is most similar to the models based on both distance and habitat quantity.

Habitat loss has large negative effects on biodiversity, although it is not clear if a threshold exists or if declines are linear (Villard *et al.* 1999; Fahrig 2003; Betts *et al.* 2007). Our models based on cost distance and the amount of saltmarsh within 6 km suggested the effect was continually increasing, with the probability of occurrence increasing from maximum of 1.0% when there was no saltmarsh within 6 km, to 3.2% with 125 ha (~ amount at Towra point), to 6.1% with 250 ha, to 13.2% with 470 ha (~ amount at Newcastle; Fig. 6).

Given that there are few locations along the NSW coast where large patches (> 125 ha) of saltmarsh are found (Fig. 6), the majority of saltmarshes are too small to have a large effect on the probability of occurrence. Populations in the smaller saltmarshes may face increased threats if the amount of saltmarsh continues to decrease (Saintilan & Hashimoto 1999; Saintilan & Williams 1999, 2000), as is expected in response to climate change and mangrove invasion (Saintilan *et al.* 2009).

Distance to habitat patches above a certain threshold size also has the potential to explain threshold effects of habitat quantity (e.g. Chardon *et al.* 2003), but we found that this type of model performed relatively poorly in our study (Fig. 2). We suggest this is because these models ignore the continual increases in landscape suitability as habitat area increases (Fig. 4), and instead treat habitat area as a hard threshold. For example, a threshold of 20 ha means a 19.9 ha patch is treated the same as no habitat at all, while a 20.1 ha patch is treated the same as a 400 ha patch. Models based on distance from patches exceeding a threshold size did not work well where presences located near small habitat patches had to be explained by a larger distance to a large patch of saltmarsh. For example, the saltmarsh at Homebush is less than 10 ha, and the distance-based models had to explain these presences in terms of proximity to the Towra Point saltmarsh. This led to an upward inflection in the response curves at large distances, especially with cost-distance (Fig. 4). As the threshold was increased further, these effects became more prominent and there was a large drop in model performance (Fig. 3). Habitat quantity effects were better captured using habitat quantity as a separate predictor, and this also allows potential threshold effects to be separated from distance effects.

We found that cost-distance usually performed better than Euclidean distance (Fig. 2, 3), which is consistent with previous studies showing that the nature of the matrix can affect species dispersal ability (Chardon *et al.* 2003; Watling *et al.* 2011). For white-fronted chats

cost distance offers the potential to capture their timidity and behavioural avoidance of certain land covers, however, the differences were small and not significant in our study. Although our costs derived by expert knowledge improved results marginally over Euclidean distance, improving the accuracy of the cost layer may lead to better results. For example, costs could be based on radio-tracked observations of species movement, or we could consider the proximity of saltmarsh when determining costs so that many small gaps are easier to pass than one large gap of the same distance (Richard & Armstrong 2010). The fact that cost-distance performed better than Euclidean distance also suggests that land-use change outside the saltmarsh areas could impact on the isolation and survival of white-fronted chats. For example, if the matrix surrounding a saltmarsh was converted from grassland to urban development, our models suggest this would reduce the dispersal distance by 95% (e.g. from 20 km to 1 km), and the birds may no longer be able to disperse to adjacent saltmarshes. This could lead to population declines due to inbreeding, as genetic variability is expected to decrease when there is limited immigration (Sunnucks 2011).

A further drawback of distance-based models is that they are only applicable where distinct habitat patches are present. Where habitats vary in quality and exhibit gradual transitions (e.g. different communities within a continuous forest), it is not possible to determine distance from a hard boundary, but it is still possible to cater for variations in habitat quality when determining neighbourhood averages (Ashcroft *et al.* 2012). The drawback of neighbourhood averages, such as the amount of saltmarsh within 6 km, is that they are not able to differentiate further declines in probability of occurrences at distances exceeding the neighbourhood. Adding distance based predictors allows continuous declines, and the improvement in our multivariate models was probably due to improved predictions at larger distances. Therefore, the combination of distance and habitat quantity has a strong ecological justification, even though results were not significantly better in this instance.

The predicted habitat suitability on the NSW coast

Our model successfully predicted the populations of the white-fronted chat in the Newcastle, Towra Point, Illawarra, and Shoalhaven regions. It predicted low probability of occurrence at Homebush, where the white-fronted chat has been recorded, although this population is in decline and recent surveys (RM unpubl. data from September 2011) have found that there are only four individuals left - and they are all male.

This highlights one shortcoming of landscape scale analyses such as ours, in that they are based on the amount of habitat currently available. Populations that are declining in areas where there was once more habitat available, as is the case at Homebush, may not be in equilibrium with the current environment (Watling *et al.* 2011). Indeed, if there are time lags between habitat loss and population extinctions then our models may be overestimating the suitability of small habitat patches. Therefore, we consider our model conservative, and smaller patches of saltmarsh may actually be less suitable in the long-term than we have predicted.

Our model also predicted that there was suitable habitat at Port Stephens and the mouth of the Hawkesbury River, which was inconsistent with the lack of observations in these areas (Fig. 6). However, while there was only one observation from Port Stephens in our standardised dataset, there were 46 records with less spatial precision in this area and the model prediction appears correct. The absence of white-fronted chats in the Hawkesbury region is more difficult to explain. Indeed, the species was once present in the Hawkesbury Swamps, and its disappearance from this area since the 1950s has been described as a mystery (Hoskin *et al.* 1991). It is possible that mangrove encroachment into saltmarsh habitat (Saintilan & Hashimoto 1999) or another unidentified antagonistic factor led to the extinction of this population, however, it is also possible that it was just a stochastic extinction and the species will eventually recolonise this area should sufficient source

populations persist in the region (Hanski 1994; Donovan *et al.* 1995). This poses two issues. Firstly, increased urban development in the surrounding regions will make this recolonisation more difficult than it would have been historically, as it will increase the effective distance to neighbouring saltmarshes. Secondly, if there is insufficient saltmarsh in the Hawkesbury region to prevent stochastic extinctions, then the populations in the Towra Point, Illawarra and Shoalhaven regions may also be prone to stochastic extinctions, as these now have a similar amount of saltmarsh to the Hawkesbury region.

Habitat preferences of the white-fronted chat

This study provides quantitative evidence that the present distribution of white-fronted chats in coastal New South Wales is closely linked to the distribution of saltmarsh. While there are many anecdotal records of white-fronted chats in open agricultural land, our modelling and personal observations suggest that these records are more consistent with the opportunistic exploitation of temporary foraging resources. This habitat may be increasingly important not only for foraging, but also as a low-cost matrix that allows dispersal in a modern landscape in which saltmarsh is highly fragmented. Agricultural landscapes, however, do not appear to be a substitute for core habitat, and preventing the further loss of saltmarsh appears to be fundamental for the conservation of the white-fronted chat in coastal New South Wales, as saltmarsh provides their core nesting and foraging resources.

The models for the distribution of white-fronted chats could potentially be improved with finer characterisation of saltmarsh habitats. While the saltmarsh shapefile we used was at a very fine resolution, it was nevertheless a binary layer (saltmarsh or non-saltmarsh) that did not capture the diversity and complexity of saltmarsh habitats (Saintilan 2009). For example, our personal observations are that white-fronted chats avoid some components of saltmarsh (e.g. extensive patches of *Juncus* spp.), favour shrubby areas for roosting and nesting, and forage in bare areas or low samphire near pools of water. Mapping these specific

saltmarsh elements could lead to better and more ecologically realistic models. It is also possible that one reason why small areas of saltmarsh appeared unsuitable in our models is because small areas may not have the necessary components or diversity of saltmarsh elements needed to support populations of the white-fronted chat.

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Fig. 1 Statistics on the frequency of 7232 observations in the Birds Australia's Atlas

database within saltmarsh and at different distance ranges from saltmarsh. The percentage of the presences of the white-fronted chat is given as a percentage of all observations (presences and absences) within each distance range and as a percentage of the total number of locations where the species was present ($n = 110$).

Fig. 2 The performance of Generalised Additive Models was assessed using the average Akaike Information Criteria (AIC) from ten training datasets and the Area Under the receiver operator characteristic Curve (AUC) from ten data subsets. Models were based on Euclidean distance (Euc. Dist), cost distance (Cost. Dist), distance with a threshold (thresh.), and the amount of saltmarsh habitat within 6km of observations (Hab. Amnt.). Models were compared using an ANOVA with pairwise differences assessed using a Tukey HSD test. Models sharing the same letter are not significantly different.

Fig. 3 The performance of Generalised Additive Models was assessed using the average Akaike Information Criteria (AIC) from ten training datasets and the Area Under the receiver operator characteristic Curve (AUC) from ten data subsets. Distance was considered as either Euclidean distance or cost-distance, with only patches larger than a certain threshold size considered. A threshold of 10 ha resulted in the best models. Habitat quantity was included in models by calculating the amount of saltmarsh within a 1-8 km radius moving window, with a radius of 6 km selected because it usually performed better than other radii.

Fig. 4 Response curves generated for models of the white-fronted chat in coastal New South Wales. Solid lines represent the average of the models with the 10 different datasets, while dashed lines illustrate 95% confidence intervals (mean $\pm$ 2 s.d.). Multivariate models that included both habitat quantity and distance predictors (bottom models) are displayed by holding habitat constant at levels of 0 ha, 125 ha, 250 ha and 470 ha and displaying the relationships with distance (e.g. as suggested by Elith *et al.* 2005).

Fig. 5 The predicted probabilities of occurrence along the NSW coast between Port Stephens and the Shoalhaven based on models with Euclidean distance (a) Euclidean distance to patches larger than 10 ha (b), amount of saltmarsh within 6 km (c) and a multivariate model including cost distance and amount of saltmarsh within 6 km (d). Refer to Fig 6. for place names and locations where white-fronted chats were observed.

Fig. 6 The predicted probabilities of occurrence along the NSW coast between Port Stephens and the Shoalhaven based on the average of the seven models in Fig. 2. Results are displayed with (left) and without (centre) presences of white-fronted chats, with the map on the right displaying the standard deviation of the seven models to convey the areas where there is highest uncertainty.