

Estimating the population size of an endangered shorebird, the Madagascar plover, using a habitat suitability model

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Abstract

The Madagascar plover *Charadrius thoracicus* is a shorebird endemic to western Madagascar, currently classified as globally vulnerable. It is restricted to specialized wetland habitats that are increasingly threatened by humans. To inform future conservation measures for this poorly known species, we develop a predictive habitat suitability map and use this map to estimate the size of the Madagascar plover population. We integrate spatially referenced presence-only observations of Madagascar plovers with Landsat data, elevation data and measures of distance to settlements and the coast to produce a habitat suitability model using ecological niche factor analysis. Validation of this model using a receiver operating characteristic plot suggests that it is at least 84% accurate in predicting suitable sites. We then use our estimate of total area of suitable habitat above a critical suitability threshold and data on Madagascar plover density in suitable sites to estimate the total population size to derive a total population estimate of 3100 ± 396 standard error individuals. Finally, we explore the conservation applications of our model.

Introduction

The Madagascar plover *Charadrius thoracicus* is a threatened endemic shorebird currently classified as vulnerable [VU C2a(i); D1; BirdLife, 2004]. This species occurs mainly along the west coast of Madagascar between Bombetoka bay in the North and Taolagnaro in the South. This plover uses the edge of lagoons, coastal grassland and mud, and is dependent upon saltmarsh for breeding. The global population size was estimated to be 750–6000 individuals (Birdlife, 2004).

Wetlands are among the most diverse ecosystems in Madagascar and they provide vital ecosystem services to people. Unfortunately, they are increasingly threatened by siltation from deforestation in their catchments, conversion of wetlands to rice paddies and by the expansion of fisheries and shrimp farming (Durbin, Bernard & Fenn, 2003).

In order to better understand species–habitat relationships and distributions, a number of techniques for predictive modelling based on species observations and environmental data have been developed (for reviews, see Guisan & Zimmermann, 2000; Gottschalk, Huettmann & Ehlers, 2005). However, there have been few studies of large-scale habitat suitability for shorebirds (sandpipers, plovers and allies; Avery & Haines-Young, 1990; Gratto-Trevor, 1996), although 16 species are globally threatened (BirdLife, 2004) and 56% of shorebird populations are declining (Wetlands International, 2006).

Predictive habitat models based on the requirements of a species over large geographical areas have a wide range of uses in landscape ecology, conservation biology and wildlife management (Akçakaya & Atwood, 1997; Dettmers & Bart, 1999). Predicted distributions based on habitat associations can provide a higher level of resolution than the fragmentary distribution data that exist for most species in Madagascar (Scott *et al.*, 1993). Such models may also inform further ecological research (Garshelis, 2000) and aid reserve selection both at a small scale and in the wider landscape (Araújo, Williams & Fuller, 2002; Bani *et al.*, 2002). Habitat suitability models have also been used to estimate the effect of climate change (Austin *et al.*, 1996; Buckland, Elston & Beaney, 1996). Finally, because birds are important indicators of ecosystem health (Furness & Greenwood, 1993), habitat suitability models may guide monitoring programmes.

Here we use a geographic information system to determine whether readily available spatial data can successfully describe Madagascar plover distribution and produce a predictive spatial model. In order for this to be possible, the species must be sufficiently habitat specific to show a significant relationship with remotely sensed environmental data (Dembinski, Kindscher & Jakubauskas, 1999). We then use the habitat suitability model to estimate population size on the basis of the predicted area of suitable habitat and the known density of Madagascar plovers in suitable sites. This approach is particularly relevant in countries such as

Madagascar where the road system is poor, so that many wetland birds have never been surveyed thoroughly.

Methods

In the field, we only collected presence data, because the logistical difficulty of repeatedly visiting sites to verify absence made it impossible to collect a reliable absence dataset. Some authors have suggested that when true absence data have not been collected, distribution models may be produced based on presence data and randomly generated pseudo-absences (Osborne, Alonso & Bryant, 2001; Stockwell & Peterson, 2002); however, Boyce *et al.* (2002) suggest that this approach may result in bias in the absence data if the species has a wide range or there are relatively few presence points. Instead, we use ecological niche factor analysis (ENFA), which only requires a set of presence points. Brotons *et al.* (2004) caution that the lack of absence data prevents suitable areas being restricted by the species' environmental limitations, although Zaniwski, Lehmann & McOverton (2002) argue that presence-only methods generate distributions that best reflect the species' fundamental niche.

The niche concept, defined by Hutchinson (1957), considers a species' ecological niche to be a hypervolume in the multidimensional space defined by information about environmental variables, within which the species can persist. ENFA has been developed to analyse the position of the niche of a species in the wider ecological space of the environment (Hirzel *et al.*, 2002). In ENFA, the niche of a species relative to the environment is described by extracting an axis of marginality (a vector from the average of available habitat characteristics to the average of used habitat characteristics). The analysis then extracts successive uncorrelated orthogonal axes maximizing the specialization of the species. Having described the niche of a species, it is then possible to predict the probability that each unit of the landscape, with associated habitat characteristics, is suitable habitat for the focal species.

Fieldwork and data collection

The historical range of the Madagascar plover is from the Mahavavy delta in the north to Fort Dauphin in the south-east (Milon, 1950; Appert, 1971; Hayman, Marchant & Prater, 1986). Despite extensive surveys, Madagascar plover have never been sighted along the limestone coastline north of the Mahavavy delta (S. Goodman, pers. comm.). We collected data on the distribution and abundance of Madagascar plover during 8 months of fieldwork over 3 years between March 2003 and May 2005 throughout this historical range. Thirty-five wetland sites representing the range of wetland habitats present in western Madagascar across the whole range of the Madagascar plover were selected using 1:500 000 Foiben-Taosarintanin'i Madagaskara topographic maps. In some cases, site selection was constrained by logistical limitations, in particular the poor

condition of most roads in the region. All data were collected in the field by S. Z.

At each site, Madagascar plovers were counted, and the exact location where each bird was sighted was recorded with a GPS receiver (Garmin e-Trex, Olathe, KS, USA). Of 35 sites surveyed, 21 contained Madagascar plovers, and we collected the co-ordinates of 162 presence points. The area of habitat homogenous with the points at which Madagascar plover were sighted was estimated at each study site by considering each habitat patch in each site as a rectangle, estimating the lengths and widths (in m) in the field, and then calculating the area of each rectangular patch and summing all patches in each site.

All presence points were plotted in the UTM 38S reference system using the WGS1984 datum. This point shapefile was converted to a raster grid with the same dimensions as the environmental datasets. We then created 100 m buffers around these points to describe the environment in the birds' immediate vicinity, generating a set of cells that are used by Madagascar plovers. These were then made into a Boolean raster in which the presence cells were coded as 1 and all other cells received a value of 0.

Ecogeographical variable (EGV) maps

Owing to the large size of our study area, and our aim of modelling habitat selection by Madagascar plovers at the finest possible scale, we selected Landsat 7 data because they have a relatively high spatial and good spectral resolution and are readily available for our study area. We used 17 Landsat 7 scenes acquired in summer 2000, 2001 and 2002 (Table 1). The source for this dataset was the Global Landcover Facility (<http://www.landcover.org>). These images were selected because all were collected during the dry season and all have negligible cloud cover. Owing to our large study area, it was not possible to find a set of images collected in the same year that were free of cloud cover.

Bands 1, 2, 3, 4, 5 and 7 were mosaiced separately and the mosaics were then clipped to within the west coast of Madagascar to produce six coverages of our study area, a total area of 242 445 km² (Fig. 1). All image processing work used Idrisi Kilimanjaro (Eastman, 2003).

The tasseled cap transformation (Kauth & Thomas, 1976) is a robust vegetation index that may be used with six bands of Landsat Enhanced thematic mapper plus (ETM+) data (Crist & Cicone, 1984). This method exploits correlations between the bands in a multispectral Landsat image and allows the principal axes in hyperdimensional band space to be visualized easily. We used a tasseled cap transformation using coefficients for the Landsat ETM+ sensor (Huang *et al.*, 1998) to reduce the number dimensions of reflectance data and extract biologically meaningful environmental indices. This produced three rasters: tasseled cap greenness shows the amount of green vegetation, tasseled cap moistness describes the amount of water and tasseled cap brightness summarizes soil characteristics (Fig. 2). Finally, all three transformed images were rescaled such that pixels took digital number values from 0 to 255.

Table 1 Landsat scenes used in this study

Path/row (WRS #)	Date	Sensor	Landsat #	ID
p158r077 (WRS 2)	13 September 2001	ETM+	Landsat 7	L7CPF20010701_20010930_05
p159r078 (WRS 2)	11 July 2001	ETM+	Landsat 7	L7CPF20011001_20011231_05
p159r077 (WRS 2)	28 May 2000	ETM+	Landsat 7	L7CPF20000401_20000630_09
p160r071 (WRS 2)	24 September 2000	ETM+	Landsat 7	L7CPF20000719_20000930_10
p160r072 (WRS 2)	23 April 2002	ETM+	Landsat 7	L7CPF20020401_20020630_03
p160r073 (WRS 2)	4 April 2001	ETM+	Landsat 7	L7CPF20010401_20010630_06
p160r074 (WRS 2)	23 April 2002	ETM+	Landsat 7	L7CPF20020401_20020630_03
p160r075 (WRS 2)	4 April 2001	ETM+	Landsat 7	L7CPF20010401_20010630_06
p160r076 (WRS 2)	1 April 2000	ETM+	Landsat 7	L7CPF20000401_20000630_09
p160r077 (WRS 2)	6 May 2001	ETM+	Landsat 7	L7CPF20010401_20010630_06
p161r071 (WRS 2)	8 April 2000	ETM+	Landsat 7	L7CPF20000401_20000630_09
p161r072 (WRS 2)	27 June 2000	ETM+	Landsat 7	L72161072_07220000627_B80
p161r073 (WRS 2)	4 February 2000	ETM+	Landsat 7	L72161073_07320000204_B80
p161r074 (WRS 2)	27 June 2000	ETM+	Landsat 7	L7CPF20000401_20000630_09
p161r075 (WRS 2)	23 March 2000	ETM+	Landsat 7	L7CPF20000101_20000331_11
p161r076 (WRS 2)	27 June 2000	ETM+	Landsat 7	L72161076_07620000627_B80
p161r077 (WRS 2)	30 April 2002	ETM+	Landsat 7	L7CPF20020401_20020630_03

ETM+, Enhanced thematic mapper plus.

Elevation data were derived from the Shuttle Radar Topography Mission (SRTM). Tiles of SRTM data corresponding to the 17 WRS-2 scenes of Landsat data used (Table 1) were downloaded from the Global Landcover Facility (<http://www.landcover.org>). These were then mosaiced and clipped in the same way as the satellite images. The resolution of this dataset was 90 m, but in order to overlay all layers of environmental data exactly, we re-sampled the SRTM to 30 m resolution to produce the final elevation map (Fig. 2). Elevation in the study area ranges from 0 to 1625 m.

As a *proxy* measure of human impact, we made a raster in which each cell took as its value the distance (km) to the nearest settlement. A point shapefile containing all settlements in Madagascar was projected to UTM 38S and clipped to the study area plus a 50 km buffer to eliminate edge effects. The source of this data was <http://www.gospacial.com>. This shapefile was then converted to a 30 m raster in which cells containing a settlement were coded 0 and all others were coded 1. The distance (in km) from every cell to the nearest settlement was then calculated and each cell took a value 0–54.9 km. Finally, this raster was clipped to the study area to produce a map that could exactly overlay the other environmental datasets (Fig. 2).

Because the Madagascar plover appears to be dependent on coastal habitats, we created a raster in which each cell took as its value the distance to the coast. To create this, the coastline shapefile used to define the study area was converted to a 30 m raster with the same extent as the other environmental datasets. Coastal cells were coded 1 and all other cells were coded 0. The distance (in km) from every cell to the coast was then calculated and each cell took a value 0–259.6 km. Finally, this raster was clipped to the study area to produce the coast distance map (Fig. 2).

Habitat suitability modelling

The program Biomapper (Hirzel, Hausser & Perrin, 2004) was used for all habitat suitability modelling. We prepared all EGV maps for Biomapper using a Box-Cox transformation to *normalize* the distribution of values in each map (Sokal & Rohlf, 1994).

Following Hirzel & Arlettaz (2003), we then used the distance geometric mean algorithm in Biomapper to predict habitat suitability across the landscape because this algorithm is designed to have high generalization power and it makes no assumption about the frequency distribution of Madagascar plover presence points with respect to the values in each EGV dataset. The resultant habitat suitability maps produced by Biomapper are a spatial representation of habitat suitability values (0–100%) calculated for every 30 m cell in the study area ($n = 384\,833\,342$ cells).

We repeated the habitat suitability modelling process twice. First, we used *k-fold partitioning* with 10 sets to allow model validation using a receiver operating characteristic (ROC) plot and to also estimate the mean frequency and standard error of area of habitat predicted to fall within each suitability class across 10 different runs of the model (Boyce *et al.*, 2002). Data were partitioned by site and then individual presence cells were selected. This procedure minimized the potential for spatial pseudo-replication. Second, we used all available presence data to produce a final habitat suitability model as recommended by Fielding & Bell (1997).

To validate our model, we produced a ROC plot. Because false positives (where suitable habitat is predicted in areas where no presence data have been collected) provide no information about the quality of this model, standard validation estimators such as the κ index (Monserud & Leemans, 1992), which give the same importance to false positives and false negatives (when unsuitable habitat is

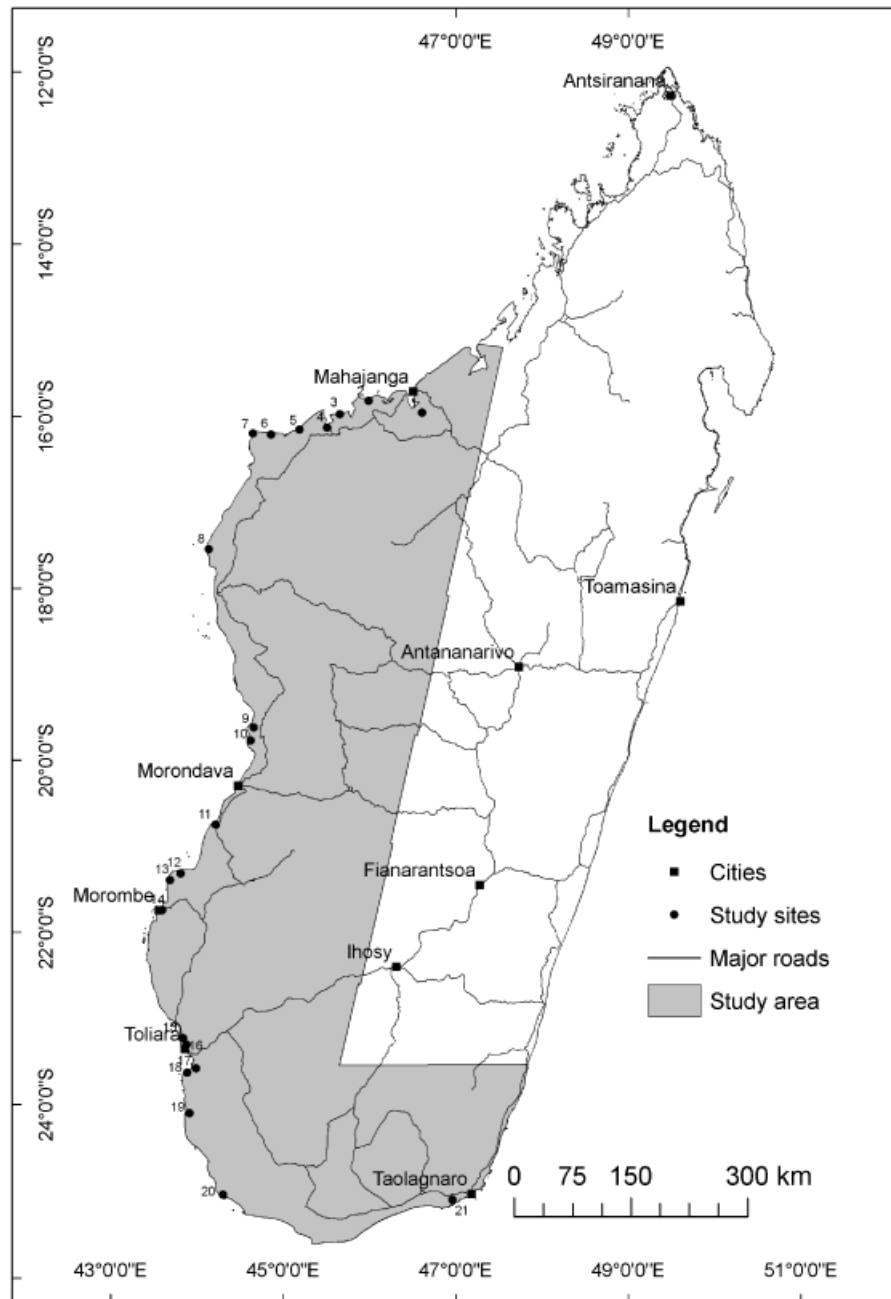


Figure 1 Location map. The shaded area of western Madagascar represents the study region. Study sites are marked by open circles, and major cities by solid circles.

predicted in areas where the species is present), could not be used (Pearce & Ferrier, 2000). The area under the ROC curve (AUC) provides a measure of the overall accuracy of the model that is independent of any particular threshold. The value of AUC ranges between 0.5 and 1.0. A score of 0.5 indicates a model that performs no better than chance, whereas a model scoring 1.0 fits the data perfectly.

Many studies that generate a habitat suitability map pick an arbitrary threshold such as 50 or 70% and state that

all habitats above the threshold are suitable and all habitats below are unsuitable. However, this approach is arbitrary and has no biological justification. Instead, we estimated the success of our model across the full range of possible thresholds using an ROC plot, and determined the most appropriate threshold from a 45° tangent to the ROC curve that assumes an equal risk of false-positive and false-negative predictions (Zweig & Campbell, 1993).

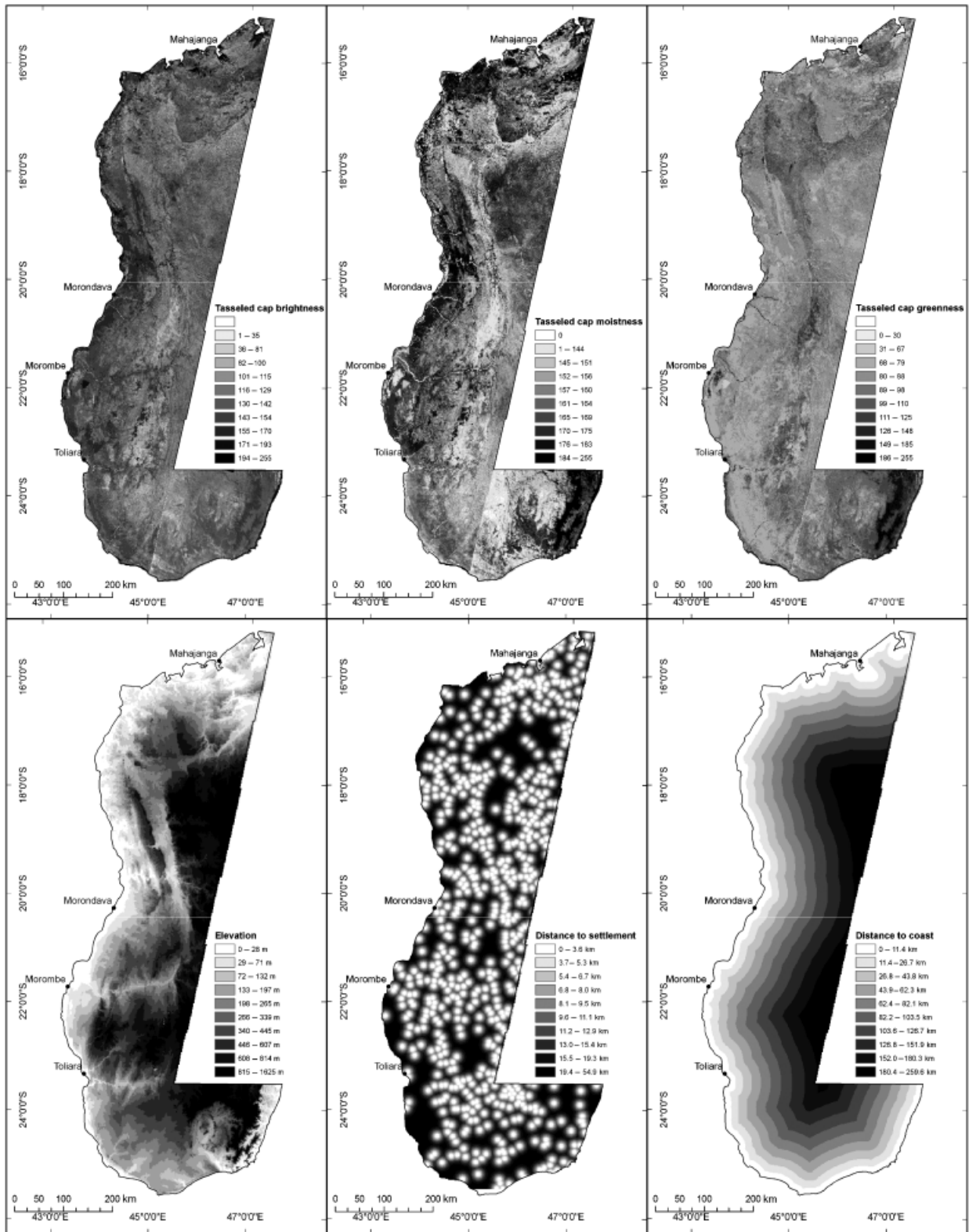


Figure 2 Six ecogeographical variable maps used to explain Madagascar plover distribution.

Table 2 Variance explained by the four marginality and specialization factors calculated by ecological niche factor analysis (ENFA)

EGV	Marginality factor (59%)	EGV	Specialization factor 1 (17%)	EGV	Specialization factor 2 (8%)	EGV	Specialization factor 3 (4%)
Elevation	-0.90	Tasscap moist	0.51	Tasscap bright	0.40	Tasscap green	0.29
Tasscap moist	0.57	Elevation	0.48	Tasscap bright	0.23	Tasscap green	0.16
Tasscap bright	0.35	Tasscap green	0.27	Elevation	0.15	Tasscap moist	0.09
Tasscap green	0.17	Tasscap bright	0.13	Tasscap moist	0.05	Elevation	0.03

A positive marginality coefficient indicates that Madagascar plover presence points have higher values of this EGV than the median of the whole study area, whereas a negative coefficient indicates that Madagascar plovers prefer areas with lower values of the EGV than generally found in the environment. The amount of marginality or specialization accounted for by each factor is given in parentheses. EGV, ecogeographical variable.

Estimating population size from the habitat suitability model

First, we measured the area of suitable habitat for Madagascar plovers by plotting a histogram of the final habitat suitability map, using standard errors (SEs) derived from *k*-fold partitioning to describe the uncertainty in these estimates. Our habitat suitability threshold, the value above which habitat supports Madagascar plovers (determined from the ROC plot), then allowed us to consider only the area of habitat predicted to be more suitable than the threshold.

Second, we estimated the density and standard error of Madagascar plovers in each study site (suitable habitats). Having tested for normality, we then estimated the mean density and SE of Madagascar plovers across all sites. Following the logic of Mladenoff & Sickley (1998), we then multiplied this density by the area of suitable habitat to estimate the total population size and its SE.

Results

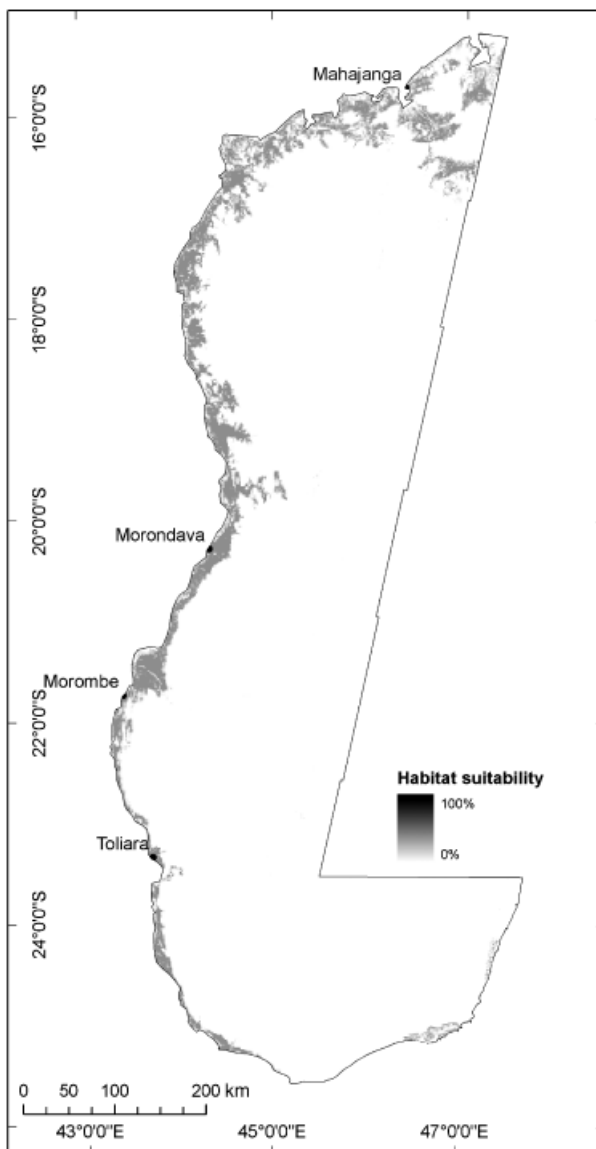
Our surveys found 263 plovers in the dry season (April–November) and 370 individuals in the wet season (December–March) in 21 sites between August 2003 and March 2005 (Fig. 1).

Habitat suitability model

Of six EGVs, two were removed before the final model was produced. Coast distance was removed because it was highly correlated with elevation, and conferred no explanatory power to the model. Settlement distance was also removed because it did not significantly explain variation in Madagascar plover presence.

The four EGVs used to make the final model were tasseled cap brightness, tasseled cap moistness, tasseled cap greenness and elevation (Table 2). Marginality coefficients showed that, relative to the study area as a whole, Madagascar plovers prefer sites with low elevation (elevation = -0.90) and higher moistness (tasseled cap moistness = 0.57), brightness (tasseled cap brightness = 0.35) and greenness (tasseled cap greenness = 0.17).

The final habitat suitability model shows many patches of varying levels of habitat suitability along the west coast of

**Figure 3** Final habitat suitability model.

Madagascar, with smaller suitable areas on the south-east coast. However, the most suitable areas are fragmented from each other by less suitable habitat (Fig. 3).

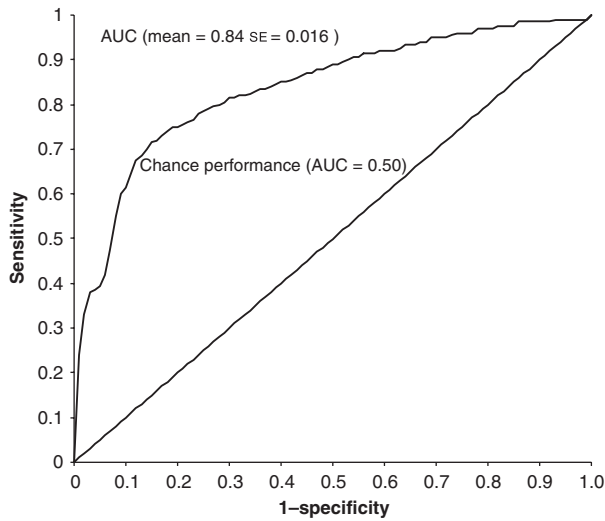


Figure 4 Receiver operating characteristic plot of training and validation data. Sensitivity is the true positive fraction, and 1-specificity is the false-positive fraction for each unique threshold in the data. The diagonal line represents model performance that would be expected by chance alone.

Model validation

The model performed well in predicting Madagascar plover presence when evaluated with an ROC plot (AUC mean = 0.84, SE = 0.016, Fig. 4). This suggests that in the final model, a cell predicted as suitable habitat, at any threshold of suitability, will be more suitable than a randomly selected cell in the study area at least 84% of the time.

Madagascar plover population estimate

As estimated from the tangent to the ROC curve, the threshold value of habitat suitability (scaled 0–100%; Fig. 3) above which Madagascar plovers use the habitat was 61%. Only cells that predicted a habitat suitability value greater than, or equal to, this threshold were considered to be suitable.

The total area of habitat more suitable than the threshold was $139 \pm 6 \text{ km}^2$ (mean \pm SE, Fig. 5). The mean density of Madagascar plovers in suitable habitat was $0.13 \pm 0.03 \text{ ha}^{-1}$ (Table 3). Integrating the area under the cumulative population size histogram (Fig. 5), we estimate the total population of Madagascar plovers to be 3100 ± 396 individuals.

Discussion

Habitat suitability model

Like other large-scale habitat suitability modelling studies, our choice of EGVs was limited by the available environmental data (Luck, 2002; Gibson *et al.*, 2004). In the trade-off between a model with fine-scaled habitat variables that would predict across a limited area versus a potentially less

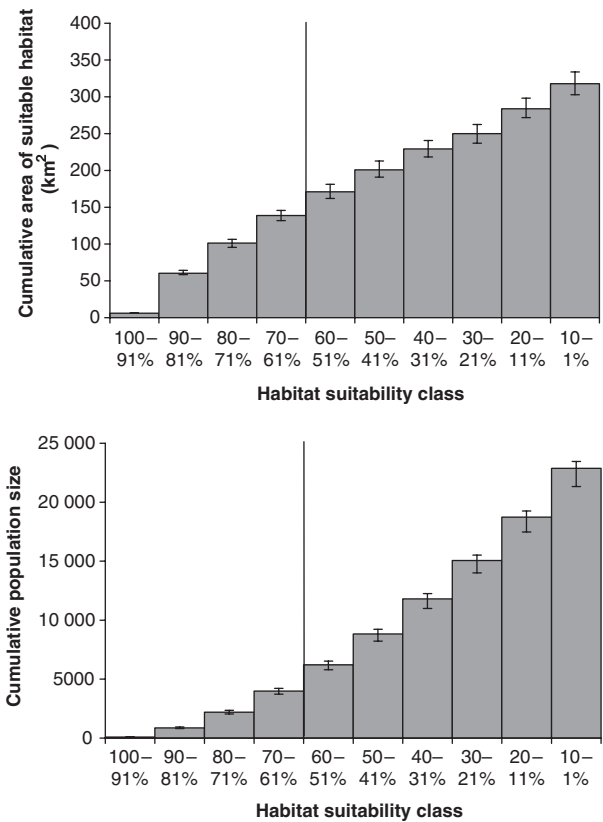


Figure 5 Cumulative area of suitable habitat and cumulative Madagascar plover population estimates in each habitat suitability class. Error bars on the histogram of cumulative area represent standard errors from 10-fold partitioning. The error bars on the histogram of cumulative population represent standard errors in the estimate of area and Madagascar plover density. The vertical bars mark the threshold value (61%) above which habitat is suitable.

accurate model that could be generalized across western Madagascar, we elected for a broad model. There is scope, however, to refine this model by incorporating finer scale data from intensively surveyed sites to better understand the threats to the Madagascar plover.

In this study, it was necessary to validate the model by partitioning the dataset. Ideally, model validation will involve a comparison with independent data, although with rare species such as the Madagascar plover, this is often not available. However, the collection of further data in future studies will allow a fuller assessment of the adequacy of this model.

The habitat suitability model was created using a single snapshot of environmental data. In reality, the coast of western Madagascar is dynamic and sudden changes in habitat conditions may occur after natural events such as cyclones. This would result in individuals being displaced into lower quality habitats (Gates & Donald, 2000). In general, it is reasonable to assume, due to the dispersal ability of birds, that the Madagascar plover is in close equilibrium with the environment, regulated by habitat

Table 3 Density of Madagascar plovers in suitable sites

ID	Site	Area of suitable habitat (ha)	Number of Madagascar plovers	Density (ha ⁻¹)
1	Mahavavy delta	98	8	0.08
2	Bombetoka bay	200	4	0.02
3	Marambitsy bay	655	86	0.13
4	Baly bay national park	1980	92	0.05
5	East Antilihay bay	35	14	0.40
6	West Antilihay bay	228	8	0.04
7	Cap Sainte André	703	6	0.01
8	Tambohorano	60	6	0.10
9	Besalampy	160	19	0.12
10	Tsiribihina delta	150	21	0.14
11	Belo sur mer	8000	40	0.01
12	Morombe	314	20	0.06
13	South Mangoky delta	25	6	0.24
14	North Mangoky delta	292	27	0.09
15	Toliara airport	32	10	0.31
16	Mangily/Ifaty	80	9	0.11
17	Soalary	25	1	0.04
18	Mozambika/Manambolo	10	2	0.20
19	Lake Tsimanampetsotse	650	133	0.20
20	Androkaela	175	29	0.17
21	Antamboho	60	14	0.23

Site numbers correspond to the legend in Fig. 1.

selection and population dynamics (Chamberlain & Fuller, 1999). Furthermore, Miller *et al.* (1989) argue that some sacrifice of precision is acceptable in analysis such as this for the sake of the generality and conservation usefulness of the predictions that can be made on the basis of observed species–habitat associations.

It is interesting that distance to settlement had no effect on habitat suitability because human activities likely to affect Madagascar plovers, for instance grazing by zebu *Bos indicus*, help to maintain an appropriate sward height in saltmarshes for plovers to feed and nest. Nonetheless, these impacts could still be harmful if trampling would increase mortality of nests and/or chicks, and the intensity of disturbance increases as a result of increased human migration to the coastal zone.

Madagascar plover population estimate

There are several factors other than modelled habitat suitability that may affect Madagascar plover presence/absence in the areas predicted to be suitable (Flather *et al.*, 1997).

First, historical events such as large-scale colonization and long-term persistence affect whether the species can occur in some areas predicted to be suitable. For example, an isolated patch of suitable habitat may never be colonized (Ricklefs, 2004). Second, metapopulation dynamics may cause some patches of suitable habitat to not support a population of plovers sometimes (Hanski, 1999). The effect of this on the Madagascar plover is difficult to quantify because its dispersal behaviour and seasonal movements are

not known. Third, competitive exclusion (Brown, 1984) by congeneric small plovers such as Kittlitz's plover *Charadrius pecuarius* and white-fronted plover *Charadrius marginatus* could make some areas unsuitable. Note that the latter two species co-occur with Madagascar plover, and all three species breed in several sites (Zefania *et al.*, submitted). Fourth, it is possible that hierarchical habitat selection (Winkler & Leisler, 1985) as a result of human threats, or specific habitat requirements at certain times of the year or parts of the life cycle (e.g. nesting), may further restrict the Madagascar plover within the areas predicted to be suitable by this model. Unfortunately, none of these factors can be measured by remote sensing; instead, models such as the present one must be refined by detailed follow-up fieldwork.

Conservation applications

Currently, the Madagascar plover is classified as vulnerable. Our data suggest that it is close to being endangered using IUCN criteria (IUCN, 2001). The estimated area of occupancy is substantially less than the 500 km² threshold for listing under criteria B2; however, we do not have data on the trends in the extent of occurrence, area of occupancy, habitat quality, number of populations or numbers of mature individuals, which are also necessary to list under this criterion. Our estimated population size is also close to the 2500 mature individuals threshold of criterion C. The productivity of Madagascar plover is extremely low compared with temperate-zone congenics, and using productivity data from the stronghold of Madagascar plover at Lac Tsimanampetsotse, Zefania *et al.* (submitted) predicted rapid decline. Taken together, the specialized habitat requirements, small area of occupancy, low population size and declining population may justify elevating the Madagascar plover status to endangered.

Throughout the range, there are only 10 sites where Madagascar plover are known to breed: Androkaela, Antilihay bay, Besalampy, Fort-Dauphin, Ifaty, Mahavavy delta, Mangoky delta, Marambitsy bay, Lake Tsimanampetsotse and the Tsiribihina delta. Of these, the two most important breeding strongholds are at Lake Tsimanampetsotse and Marambitsy bay (Zefania *et al.*, in press). These sites are, therefore, high priorities for protection and appropriate management.

At present, there are few protected wetlands in the range of the Madagascar plover. These sites are Baly Bay National Park, Lake Tsimanampetsotse National Park and the new Kirindy-Mitea National Park. Additionally, temporary protection has been accorded to the Mahavavy-Kinkony area. These areas include the main breeding stronghold at Lake Tsimanampetsotse and confer some protection on Marambitsy bay. Although Madagascar plover occur in the Kirindy-Mitea area, breeding has not been recorded. Our habitat suitability model allows the areas of greatest importance to Madagascar plover to be identified for use in further protected area planning. In doing this, it is possible to adopt a conservative approach, selecting areas predicted in the highest habitat suitability. This approach assumes a

direct positive correlation between habitat suitability and density (Elith, Burgmann & Regan, 2002).

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