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

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Keywords
wader; species distribution model; geographic information system; remote sensing; ecological niche factor analysis.

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 model 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 silting 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 (Açkakaya & 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 Zaniewski, 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 southeast (Milon, 1950; Appert, 1971; Hayman, Marchant & Prater, 1986). Despite extensive surveys, Madagascar plovers have never been sighted along the limestone coastline north (Milon, 1950; Appert, 1971; Hayman, Marchant & Prater, 1986). Despite extensive surveys, Madagascar plovers 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 plovers 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 Land-cover 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.
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 mosaicked 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.gospat.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 Madagascar plover presence points with respect to the habitat suitability values (0–100%) calculated for every 30 m sample area (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).

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 k index (Monserud & Leemans, 1992), which give the same importance to false positives and false negatives (when unsuitable habitat is

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**Table 1 Landsat scenes used in this study**

<table>
<thead>
<tr>
<th>Path/row (WRS #)</th>
<th>Date</th>
<th>Sensor</th>
<th>Landsat #</th>
<th>ID</th>
</tr>
</thead>
<tbody>
<tr>
<td>p158r077 (WRS 2)</td>
<td>13 September 2001</td>
<td>ETM+</td>
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</tr>
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<td>p159r077 (WRS 2)</td>
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<td>Landsat 7</td>
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</tr>
<tr>
<td>p160r071 (WRS 2)</td>
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<td>ETM+</td>
<td>Landsat 7</td>
<td>L7CPF20000719_20000930_10</td>
</tr>
<tr>
<td>p160r072 (WRS 2)</td>
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<td>ETM+</td>
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</tr>
<tr>
<td>p160r073 (WRS 2)</td>
<td>4 April 2001</td>
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<td>ETM+</td>
<td>Landsat 7</td>
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<tr>
<td>p160r075 (WRS 2)</td>
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<td>ETM+</td>
<td>Landsat 7</td>
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<tr>
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<tr>
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</tr>
<tr>
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<td>ETM+</td>
<td>Landsat 7</td>
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</tr>
<tr>
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<td>27 June 2000</td>
<td>ETM+</td>
<td>Landsat 7</td>
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</tr>
<tr>
<td>p161r073 (WRS 2)</td>
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<td>ETM+</td>
<td>Landsat 7</td>
<td>L72161073_0732000624_B80</td>
</tr>
<tr>
<td>p161r074 (WRS 2)</td>
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<td>ETM+</td>
<td>Landsat 7</td>
<td>L7CPF20000401_20000630_09</td>
</tr>
<tr>
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<td>Landsat 7</td>
<td>L7CPF20000101_20000331_11</td>
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<tr>
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<td>ETM+</td>
<td>Landsat 7</td>
<td>L72161076_0762000627_B80</td>
</tr>
<tr>
<td>p161r077 (WRS 2)</td>
<td>30 April 2002</td>
<td>ETM+</td>
<td>Landsat 7</td>
<td>L7CPF20020401_20020630_03</td>
</tr>
</tbody>
</table>

ETM+, Enhanced thematic mapper plus.

**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 k index (Monserud & Leemans, 1992), which give the same importance to false positives and false negatives (when unsuitable habitat is
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 deter-
mined 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 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.
Figure 2 Six ecogeographical variable maps used to explain Madagascar plover distribution.
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 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).

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

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

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.
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 km² (mean ± se, Fig. 5). The mean density of Madagascar plovers in suitable habitat was 0.13 ± 0.03 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 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...
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 zebus 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 congenic 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 criterion 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 congeners, and using productivity data from the stronghold of Madagascar plover at Lac Tsimanampetsotsa, 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, Antilhy bay, Besalampy, Fort-Dauphin, Ifaty, Mahavavy delta, Mangoky delta, Marambitsy bay, Lake Tsimanampetsotsa and the Tsiribihina delta. Of these, the two most important breeding strongholds are at Lake Tsimanampetsotsa 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 Tsimanampetsotsa 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 Tsimanampetsotsa 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

### Table 3: Density of Madagascar plovers in suitable sites

<table>
<thead>
<tr>
<th>ID</th>
<th>Site</th>
<th>Area of suitable habitat (ha)</th>
<th>Number of Madagascar plovers</th>
<th>Density (ha⁻¹)</th>
</tr>
</thead>
<tbody>
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<td>Mahavavy delta</td>
<td>98</td>
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<td>0.08</td>
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<tr>
<td>2</td>
<td>Bombetoka bay</td>
<td>200</td>
<td>4</td>
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</tr>
<tr>
<td>3</td>
<td>Marambitsy bay</td>
<td>655</td>
<td>86</td>
<td>0.13</td>
</tr>
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Site numbers correspond to the legend in Fig. 1.
direct positive correlation between habitat suitability and density (Elith, Burgmann & Regan, 2002).

Acknowledgements

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