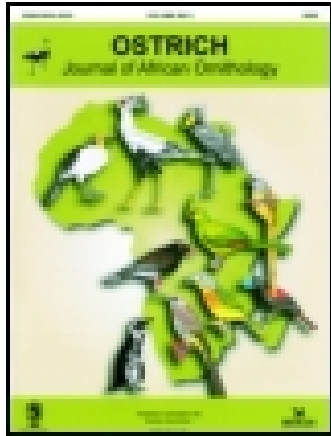


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Breeding distribution and ecology of the threatened Madagascar Plover *Charadrius thoracicus*

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The Madagascar Plover *Charadrius thoracicus* is a threatened wader endemic to Madagascar. We report the first detailed study of its distribution and breeding ecology. Madagascar Plovers breed on the west coast of Madagascar between the Mahavavy delta in the north and Fort-Dauphin in the south-east. Between 2002 and 2005, we found a total of 149 nests concentrated at two sites: Lake Tsimanampetsotsa (108 nests), an alkaline inland lake in the south, and Marambitsy Bay (24 nests) on the north-west. Nesting was observed between August and May, with peak activity between December and April. We followed the success of 74 nests from egg-laying to chick fledging. Hatching and fledging success were both low (22.9% and 41.4%, respectively, using the Mayfield method). Overall breeding success was also low and only 9.5% of nests produced fledged chicks. The effects of this low breeding success are compounded by the specific habitat requirements of the plover and its limited dispersal. Using these data, we constructed three population projections, all of which predict rapid population decline. The Madagascar Plover is currently classified as Vulnerable by the IUCN but, given its low breeding success and bleak population trajectories, a review of this status may soon be necessary.

Introduction

Wetland birds, including waders, are declining alarmingly. A recent global survey showed that 54% of 237 wader populations with known population trends are declining or already extinct, and only 9% are increasing (Delany and Scott 2006). These data, however, represent only half of the global wader populations, since for the rest of the populations no data (or qualitative expert opinion) exist on population trends. In addition, much data on their basic demography, ecology and behaviour remains to be documented, which hampers conservation actions.

There are two fundamental reasons for gathering data on the distribution and ecology of endangered waders. Firstly, we need baseline data to evaluate the distribution and long-term sustainability of threatened populations. Whilst waders feature prominently in studies of evolutionary ecology including migration, foraging ecology and breeding systems (see reviews by del Hoyo *et al.* 1996, Kam *et al.* 2004, Thomas *et al.* 2007), collecting data on their demography is difficult, due to their low breeding densities in transient habitats, the nomadic nature of breeding adults, and the high mobility of their young (but see McCulloch 1992, Sandercock 2003, Watson *et al.* 2006, Lloyd 2007). Secondly, waders exhibit an unusual diversity in their behaviour, ecology and life histories, with sophisticated phylogenetic relationships between these traits (Bókony *et al.* 2003, Székely *et al.* 2004a, Thomas and Székely 2005, Thomas *et al.* 2007). A common limitation of such comparative studies, however, is that life-history and ecological data are lacking from tropical regions and the southern hemisphere, where many waders breed. Further,

gathering data in the field is particularly challenging in biodiversity hotspots such as Madagascar, where the road infrastructure is poor and research facilities basic.

We collected ecological and behavioural data from the Madagascar Plover *Charadrius thoracicus*, a small plover (adult body mass of c. 37 g) endemic and resident breeder in Madagascar, in three years (2002–2005). The IUCN classifies the Madagascar Plover as ‘vulnerable’ (IUCN 2007), based on a small population that is inferred to be decreasing owing to pressures on its wetland habitats, and estimates the global population size at 750–6 000 individuals (BirdLife 2004). In contrast, our surveys combined with GIS analysis suggest a global population estimate of only $3\ 100 \pm 396$ (SE) individuals (Long *et al.* in press). Thus the Madagascar Plover, along with two small African plovers, the St Helena Plover *Charadrius sanctaehelenae* and Chestnut-banded Plover *Charadrius pallidus* (Simmons *et al.* 2007, N McCulloch pers. comm.), may all have a more threatened conservation status than currently acknowledged.

Our project had three main objectives. Firstly, to describe the distribution of breeding Madagascar Plovers along the west coast of Madagascar. Secondly, to document basic life-history traits and breeding ecology, including nest success and brood survival. We also measured chick developmental rates, because they influence the duration of a chicks’ exposure to terrestrial predators. Thirdly, using our estimated productivity, we constructed population trajectories to predict future changes in population size of the Madagascar Plover.

To achieve these objectives, we carried out surveys on the western coast of Madagascar and then chose two sites with a high density of nesting plovers, Marambitsy Bay in the north and Lake Tsimanampetsotsa in the south, for more detailed study. This paper is the first comprehensive report on the breeding ecology of the Madagascar Plover encompassing 383 d of fieldwork; the only previous publications we are aware of were by Milon (1950) and Appert (1971), which were sporadic records on its distribution, nest or young (see Discussion).

Materials and methods

Study area

Surveys were carried out between December 2002 and April 2004 on the west coast of Madagascar, from Mahavavy Delta (15°50.55' S, 45°47.08' E) in the north to Fort-Dauphin (24°53.71' S, 47°07.21' E) in the south-east (Figure 1). Fieldwork covered sites where suitable habitat for Madagascar Plovers was available and included sites where they have been observed previously (Milon 1950, Appert 1971, Hayman *et al.* 1986). During surveys plovers were counted in each location and signs of breeding activity (including nests and broods) noted. Subsequently, detailed data on plover breeding ecology were collected at Marambitsy Bay (15°51' S, 45°38' E) between May and November 2004, and at Lake Tsimanampetsotsa (24°04' S, 43°44' E) between December 2004 and May 2005.

Data collection

At Lake Tsimanampetsotsa fieldwork was carried out using a mobile hide to improve the efficiency of nest searching, trapping and brood observations (Székely *et al.* 2004b). Once a nest was found, its location was recorded using a hand-held GPS receiver (Garmin e-trex); the sizes of eggs (length [*L*] and breadth [*B*] in mm), clutch size and the habitat immediately around the nest were also recorded. Egg volume (*V*) was estimated using the equation

$$V = L \times B^2 \times K_v \quad (1)$$

where $K_v = 0.486$ of the Kentish Plover *Charadrius alexandrinus* (Székely *et al.* 1994) was deemed sufficiently close to that of the Madagascar Plover. We used a floating chart that was developed for the Kentish Plover to estimate hatching date (O Pinneau unpubl. data), although we modified this chart to take into account the prolonged incubation of the Madagascar Plover (see Results). Nests were checked every 4–6 d, and daily around the expected date of hatching. Adults were trapped at their nest using a funnel trap and were ringed using a South African Bird Ringing Unit (SAFRING) metal ring and an individual combination of three colour rings. Males and females have monomorphic plumage; sexing of these adults using molecular markers is in progress.

The incubation period was calculated for three clutches that were found during egg-laying and that survived until both chicks hatched. We calculated nest success of 74 nests at Lake Tsimanampetsotsa. These nests were followed from the completion of egg-laying until the eggs hatched or

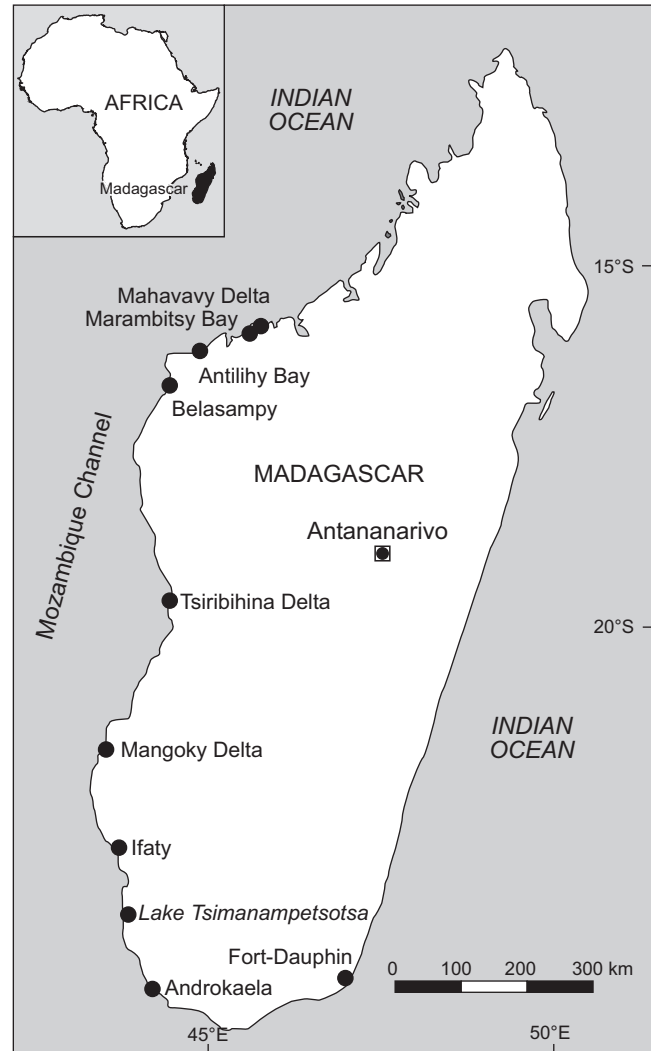


Figure 1: Distribution of Madagascar Plover breeding sites

failed. The daily mortality of nests was calculated following Mayfield (1975), and hatching success was estimated for the duration of 27 d of incubation as $(1 - \text{daily mortality of nests})^{27}$. We lacked data on egg-laying periods so egg-laying periods were not included in calculating the exposure. Note that this makes our nest survival estimate more conservative. Twenty out of 74 nests hatched (see Results), and we calculated fledging success from following these chicks until they fledged or failed, as the Mayfield probability of brood survival from hatching until fledging at 31 d of age $(1 - \text{daily mortality of broods})^{31}$. To estimate overall breeding success of nests and broods together, we multiplied hatching success with fledging success (see Mayfield 1975).

We attempted to capture each brood whilst the chicks were still in the nest. Chicks were measured (tarsus length [mm] and body mass [g]) and ringed with a SAFRING metal ring. Sixteen chicks ($n = 12$ broods) were captured on the day of hatching. Note that the Pesola balance we used only allowed us to measure mass to 1 g precision. Broods were

checked three to five times from hatching until the chicks were able to fly (or perished). We also calculated the percentage of hatched chicks that fledged. Most broods stayed in the vicinity of nests until the chicks fledged. Thus, we believe that those broods that we did not find again had probably died and were classified as deceased.

We explored three growth equations to estimate chick development: logistic, Gompertz and von Bertalanffy (see equations in Osorno and Székely 2004). Since both body mass and tarsal length reached their asymptotic values beyond the chick ages in our sample (maximum chick age = 37 d), we used the body mass and tarsus length of adults as asymptotic values (mass 37.40 ± 2.70 (SE) g; tarsus length: 32.9 ± 1.06 mm; $n = 124$ adults). We provide the equations that gave the best fit as measured by the Pearson correlation coefficient (r). Statistical analyses were carried out using SPSS 12.0 and growth curves were fitted by CurveExpert 1.3. We report the mean \pm SD unless otherwise stated. All statistical tests were two-tailed.

We projected population size (N) for $t = 20$ years using annual productivity and adult survival (Hunter 2002):

$$N_{t+1} = (N_t \times S_{ad}) + (N_t \times B \times S_{im}) \quad (2)$$

where S_{ad} and S_{im} are the probability that an adult or fledged young, respectively, survive to next year, and B is productivity. We took a population size estimate of 3 100 individuals (PL unpubl. data) and used our study at Lake Tsimanampetsotsa (see below) to estimate productivity per individual (B). Thus the average number of eggs produced by an individual is half of the mean clutch size (0.905 egg; see Results) multiplied by the frequency of re-nesting (1.072) and by the probability that an egg produces a fledged chick (0.112). We estimated the apparent survival of adults and juveniles by running our re-sighting dataset 2004–2007 in program MARK (White and Burnham 1999). Using MARK we estimated an average adult survival of 0.8 ($n = 142$) and juvenile survival of 0.36 ($n = 126$, SZ unpubl. data), and we used these values in population trajectories. These estimates seem reasonable, since juvenile survival is close to that of Snowy Plover *Charadrius alexandrinus nivosus* (body mass 40–42 g, $S_{im} = 0.39$), whereas adult survival appears somewhat higher than in the Snowy Plover ($S_{ad} = 0.69$), which is consistent with the expectation for a tropical bird (Sandercock 2003).

Results

Breeding distribution

We visited 35 sites on the western coast of Madagascar and found nests (or broods) at ten of these sites (see Figure 1 and Table 1). Of these ten sites, the two with the highest numbers of nesting Madagascar Plovers were Lake Tsimanampetsotsa and Marambitsy Bay, where we found 108 families (that included 87 nests and 21 broods) and 24 families (19 nests and 5 broods), respectively. These data were consistent with the number of adults we counted at these sites: the largest numbers were recorded at Lake Tsimanampetsotsa and Marambitsy Bay (Table 1). Although subsequent fieldwork concentrated on the latter two sites,

we believe that the frequencies of nests and broods realistically reflected the breeding activities across all sites.

Breeding period

The breeding period of the Madagascar Plover was between August and May with the peak egg-laying period between December and April (Table 1). This is also seen from the distribution of nests at Lake Tsimanampetsotsa (Figure 2); we found no new nests in June and July, and few nests from August to November across all sites. The lack of breeding activity in June and July was apparent at Marambitsy Bay; we spent 128 d in the field between June and October, and despite intense searching we found no nest or brood (Figure 2). Some breeding may take place from August to November at Lake Tsimanampetsotsa, although this is probably less intense from December onwards.

Nesting habitat

Madagascar Plovers bred in open grasslands and dry mud flats around mangroves and alkaline lakes. We only found one nest in sandy soil among railroad vine *Ipomoea pes-caprae* in Besalampy. Nests were often found beside living vegetation, which may be varied according to the type of habitat. Representative plant species of grassland in salt pans of Marambitsy Bay were *Eriocaulon* sp. (Eriocaulaceae), *Bulbostylis cinnamomea* (Cyperaceae), *Arthrocnemum indicum* (Chenopodiaceae), *Panicum* sp. (Poaceae), and *Kalanchoe* sp. (Crassulaceae). The following plants were collected in a Madagascar Plover breeding habitat at Fort-Dauphin: *Stenotaphrum dimidiatum* (Poaceae), *Mollugo decandra* (Aizoaceae), *Cyperus* sp. (Poaceae), *Panicum* sp. (Poaceae), *Senecio* sp. (Asteraceae), *Kalanchoe* sp. (Crassulaceae), *Euphorbia* sp. (Euphorbiaceae), *Phyllohydrax madagascariensis* (Rubiaceae), *Fimbristylis* sp. (Cyperaceae) and *Launea bellidifolia* (Asteraceae).

Proximity to water appears to be important, because during incubation the parents feed frequently along the water's edge or bathe in the water. The nests were usually located 2–50 m from the water's edge. Nests that were too close to water (within 10 m from edge) were often flooded due to either an unusually high tide (April–May, Marambitsy Bay) or strong wind that flooded lake water over the nests during cyclones that regularly hit south-west Madagascar (January–February, Lake Tsimanampetsotsa).

The nest is a small scrape lined with debris of dry or fresh plant material; sometimes the nest is also lined with small stones or pieces of shell (Figure 3). Both parents excavate the scrape and then throw nest material from around the nest into the scrape. Both parents defend the vicinity of nest against other plovers including Kittlitz's Plover *Charadrius pecuarius* and White-fronted Plover *Charadrius marginatus*.

Eggs, clutches and incubation period

The volume of Madagascar Plover eggs was 8.87 ± 0.52 cm³ ($n = 104$ clutches). Eggs at Lake Tsimanampetsotsa tended to be larger 8.91 ± 0.51 cm³ ($n = 85$ clutches) than at Marambitsy Bay 8.67 ± 0.52 cm³ ($n = 19$ clutches, two-sample t test, $t = 1.894$, $p = 0.061$). Egg volumes were not different between months either at Lake Tsimanampetsotsa

Table 1: Number of nests (including broods) at breeding sites of Madagascar Plover visited between December 2002 and May 2005, and the number of adult Madagascar Plovers that were observed. Effort is the number of days spent at each site. For the location of sites see Figure 1

Site	Location	Jan	Feb	Mar	Apr	May	Aug	Sep	Oct	Nov	Dec	Total number	Effort	Number of adults
Androkaela	25°02.484' S, 44°04.830' E	0	3	0	0	0	0	0	0	0	0	3	2	29
Antihy Bay	16°12.552' S, 44°58.704' E	0	0	0	0	0	0	1	0	0	0	1	8	14
Besalampy	16°41.001' S, 44°25.927' E	0	0	0	0	0	0	1	0	0	0	1	3	19
Fort-Dauphin	24°53.710' S, 47°07.214' E	0	0	2	0	0	0	0	0	0	0	2	15	11
Ifaty	23°09.443' S, 43°36.999' E	0	0	0	0	0	0	0	1	0	4	5	6	9
Mahavavy Delta	15°50.499' S, 45°47.111' E	0	0	0	0	0	1	1	0	0	0	2	45	8
Mangoky Delta	21°39.785' S, 43°26.198' E	0	0	0	0	0	0	0	2	0	0	2	4	6
Marambitsy Bay	15°55.006' S, 45°39.649' E	0	0	0	9	9	0	0	0	2	4	24	165	86
Lake Tsimanampetsotsa	24°03.817' S, 43°43.913' E	7	39	11	26	2	0	0	0	0	23	108	130	133
Tsiribihina Delta	19°40.592' S, 44°24.745' E	0	0	0	0	0	0	0	1	0	0	1	5	21
Total		7	42	13	35	11	1	3	4	2	31	149	383	336

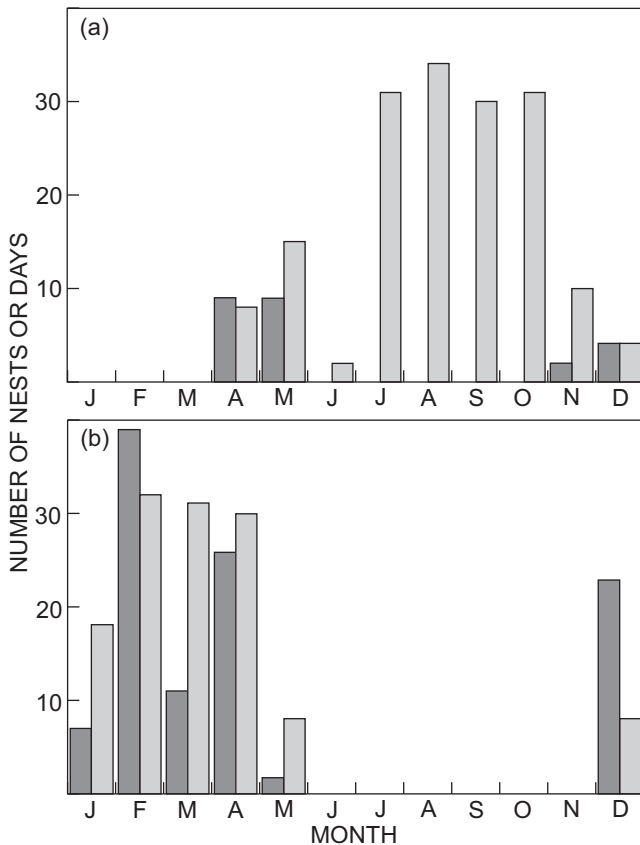


Figure 2: Frequency distribution of nests (dark) and effort, i.e. observation days (pale), at (a) Marambitsy Bay and (b) Lake Tsimanampetsotsa

(one-way ANOVA with month as factor, $F_{5,79} = 1.511$, $p = 0.196$) or at Marambitsy Bay ($F_{3,18} = 0.425$, $p = 0.738$).

Clutches of two eggs were most common; out of 104 nests found at Lake Tsimanampetsotsa and Marambitsy Bay, 84 nests contained two eggs (80.8%) and 20 nests contained one egg (19.2%). We checked 12 of these one-egg clutches several times between 3 to 30 d after egg-laying and their clutch-size remained unchanged. Thus we believe these one-egg clutches were complete and they were not partially predated before we found them.

Three nests were checked at 1–2 d intervals during both egg-laying and hatching (see Methods). At these three nests incubation lasted for 27.3 ± 0.8 d (minimum: 26 d, maximum 28 d) after the last egg was laid. Some nests, however, were incubated for longer at Lake Tsimanampetsotsa. The longest incubation we recorded was 37 d. At the latter nest the parent(s) only stopped incubation when the eggs broke. Another clutch was incubated for 20 d after the expected hatching date, and then the nest was flooded. At Mahavavy Delta, parent(s) incubated eggs in one nest for 30 d after the expected hatching date. We suspect that at these unusual nests the eggs were either infertile or the embryo died during early development.

Chick growth and fledging period

The tarsus length of freshly hatched chicks was 21.29



Figure 3: Typical nesting habitat of the Madagascar Plover (A), and a typical nest (B)

± 0.61 mm and their body mass was 7 ± 0 g ($n = 16$ chicks). As is common in waders, the chicks lost some weight for a few days shortly after hatching and then gained mass; growth appeared to accelerate after 25 d. Weight gain was 0.53 ± 0.24 g d^{-1} ; tarsus growth was 0.37 ± 0.06 mm d^{-1} ($n = 16$ chicks). The oldest chick in our sample was 37 d old and the time interval between first and last captures was 24.7 ± 9.7 d ($n = 16$ chicks).

For both body mass and tarsus growth, the logistic equation provided the best fit (Figure 4, body mass: $r = 0.961$; tarsus $r = 0.961$). For body mass the best fit was body mass (g) = $37.40 / (1 + 5.781 \times \exp(-0.080 \times \text{age} [\text{in days}]))$, and for tarsus: tarsus (mm) = $32.90 / (1 + 0.600 \times \exp(-0.074 \times \text{age} [\text{in days}]))$. Note that some chicks near fledging had longer tarsi than that of the mean of the adults (Figure 4).

Twelve chicks from nine broods survived until fledging. The maximum age when the chicks were unable to fly ranged between 27 d and 37 d (30.5 ± 2.5 d, $n = 12$ chicks); 1–5 d later these chicks fledged.

Breeding success

We established the fate of 74 nests at Lake Tsimanampetsotsa;

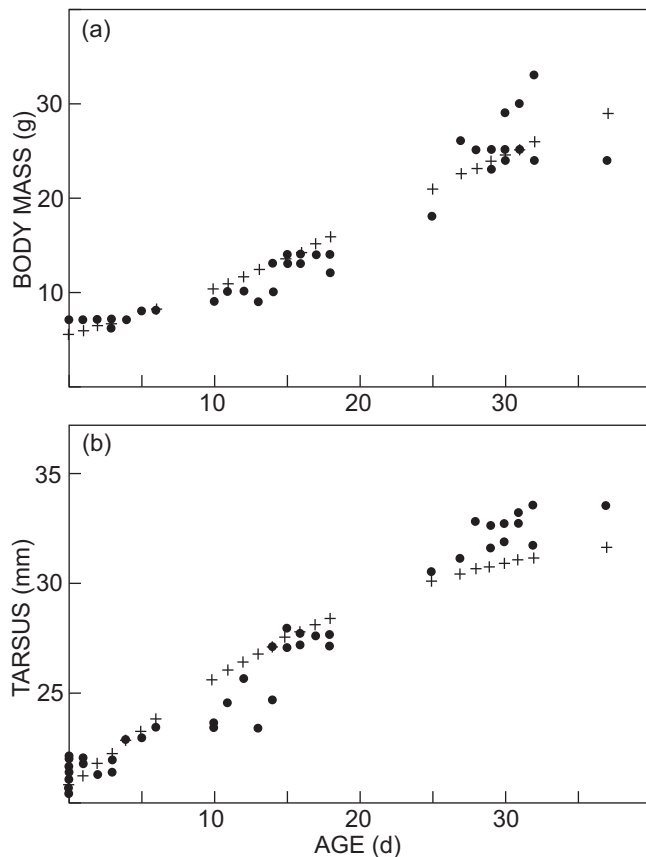


Figure 4: Growth of chicks at Lake Tsimanampetsotsa ($n = 16$ chicks). (a) Body mass (Pearson correlation coefficient, $r = 0.961$), and (b) tarsus length ($r = 0.961$). For both traits the logistic equation provided the best fit (see Methods). The predicted growth curves are indicated by +

20 nests produced at least one chick (27.0%), 22 nests were predated (29.7%), 20 nests were flooded (27.0%), nine nests were deserted (12.2%), two clutches were probably infertile so the eggs were never hatched (2.7%), and one nest was trampled by livestock (sheep *Ovis aries*, goat *Capra hircus* or zebu *Bos indicus*). Thus, from 134 eggs that were laid, 37 chicks were hatched (27.6%). The daily mortality of nests was 0.053 ($n = 74$ nests), gives 22.9% nest success for 27 d of incubation using the Mayfield method.

Flooding at Lake Tsimanampetsotsa occurred after periods of cyclonic activity and was a common cause of nest failure (see above). We did not observe nest predation, although we noted the alarm behaviour of parents when raptors flew over their nest. A Peregrine Falcon *Falco peregrinus* flushed two parents from the vicinity of their nest on 19 February 2005 and then chased them. This pair subsequently abandoned the nest, probably because the escaping parent kicked one egg out of the nest scrape. We also saw intense responses (crouching or quick departure from the nest) when Sooty Falcon *Falco concolor*, Pied Crow *Corvus albus*, Madagascar Buzzard *Buteo brachypterus* and Yellow-billed Kite *Milvus migrans* flew over plover nests. We saw footprints of carnivores (Granddier's mongoose *Galidictis grandidieri*, an

endemic mongoose to Lake Tsimanampetsotsa, feral cats *Felis catus* and dogs *Canis familiaris*) on the lake edge, but witnessed no predation events.

At Marambitsy Bay, we established the fate of 10 nests of which nine were predated (90%) and one was flooded (10%). Thus no chicks hatched from 18 eggs ($n = 10$ nests), providing zero nest success. The frequency of hatched vs failed nests was significantly lower at Marambitsy Bay than at Lake Tsimanampetsotsa ($\chi^2 = 4.060$, $df = 1$, $p = 0.044$).

Of 20 broods at Lake Tsimanampetsotsa, 11 broods (55.0%) were fledged, six broods (30.0%) disappeared and three broods (15.0%) were flooded. Thus 40.5% of chicks (15 chicks from nine broods) survived until fledging. Therefore 134 eggs that were laid produced 15 fledged chicks at Lake Tsimanampetsotsa (11.2%).

The daily mortality of broods was 0.028 ($n = 20$ broods), and through 31 d of fledging this provides 41.41% fledging success. Taking together the Mayfield estimates of hatching and fledging success at Lake Tsimanampetsotsa, 9.49% of nests were expected to produce fledged chicks.

At Marambitsy Bay one out of 15 colour-ringed adults re-nested between December 2003 and May 2004 (6.67%). At Lake Tsimanampetsotsa six colour-ringed adults (out of 83) of five pairs bred twice between December 2004 and May 2005 (7.23%). Five of the six adults re-nested after their previous nest was flooded (52.2 ± 22.9 d between the date of failure and the first date of their new nest), and another adult had a new nest 27 d after fledging chicks from the first nest. Such a long re-nesting interval after failure appears to be unusual among small plovers (Kentish Plover: 13.9 d, Székely *et al.* 1999; White-fronted Plover: 9 d after failure and 22 d after fledging, Baudains and Lloyd 2007). Two of the five adults with failed nests were the only known pair, which re-nested together. We do not know whether the remaining parents kept the same mate for both of their nests.

Population trend

The population size of the Madagascar Plover is predicted to decline using the demographic parameters we outlined in the Methods (Predicted; Figure 5). We considered two further scenarios. First, we assumed that each individual produced two clutches per year, the maximum number of clutches we observed at Lake Tsimanampetsotsa between 2005–2007 (SZ unpubl. data), and that the probability of producing a fledged chick (0.168) is 50% higher than our field estimate (Optimistic Scenario 1). Second, we assumed two clutches per year and 100% higher probability of producing a fledged chick (0.224; Optimistic Scenario 2). Nevertheless, in all scenarios including the latter two, the population is still predicted to decrease (Figure 5).

Discussion

The major finding of our study is that the Madagascar Plover is not only restricted to a handful of breeding sites (see below), but also that its population is predicted to decline. As far as we are aware, our study is the first that provides information on both geographic distribution and projected population size out of 120 endemic bird species in Madagascar (Morris and Hawkins 1998). This information

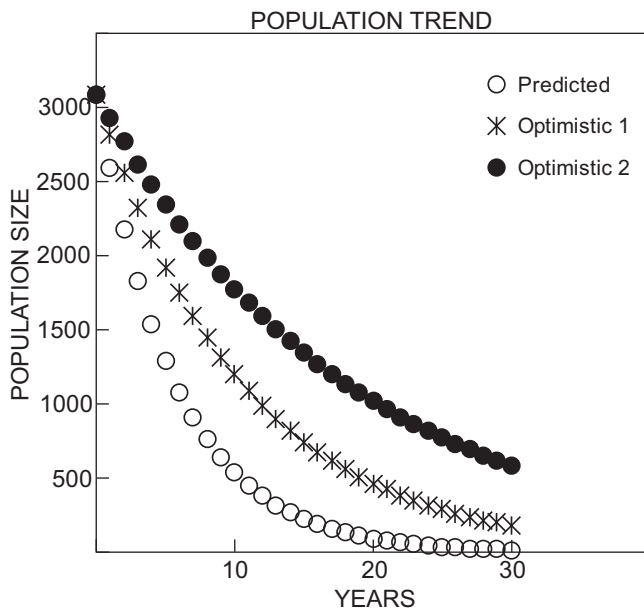


Figure 5: Estimated population size of the Madagascar Plover using three scenarios based upon our productivity estimates from Lake Tsimanampetsotsa (Predicted Scenario), 50% improved productivity (Optimistic Scenario 1), and 100% improved productivity (Optimistic Scenario 2)

is vital given that Madagascar harbours an extremely high frequency of endemism and the country is currently expanding its network of protected areas.

Our population projections, however, have several limitations. Firstly, we did not consider either stochasticity in demographic parameters and the environment, or genetic effects such as bottlenecks or inbreeding (Brook *et al.* 2000, Beissinger and McCullough 2002, Hunter 2002). Secondly, due to the relatively short duration of our study, we are uncertain how robust our demographic estimates are. Perhaps the reproductive success we estimated in three years may be lower than typical for the species and this predicts unrealistically rapid population declines. Alternatively, one may view our 'Predicted' scenario as already optimistic, because we took productivity from the stronghold of Madagascar Plover, Lake Tsimanampetsotsa, and productivity may be poorer elsewhere (see Results). In addition, we assumed the adult sex ratio to be parity, although adult sex ratios may be biased toward males (Sandercock *et al.* 2005, Donald 2007) with a detrimental effect on long-term population trajectories.

The Madagascar Plover has a restricted distribution on the west coast of Madagascar, although historic records suggest occurrence of adults near Antananarivo (Salvan 1971) and on the eastern coast (Richmond 1896). In addition to our records, we are aware of only two previous reports of nests and broods. Milon (1950) found one pair with a two- to three-day-old chick at Toliary airport, and one clutch of two eggs and a pair with two juveniles of about three months of age at Lake Tsimanampetsotsa. Appert (1971) reported a clutch of two eggs at Ambohibe and one unfledged chick at Andavadaoka. In spite of intense search-

ing on the west coast between December 2002 and May 2005, we only found breeding plovers at ten of 35 sites visited. Taken together, these reports suggest that the Madagascar Plover is a localised breeder. We note, however, that potential breeding grounds have not been surveyed beyond Mahajanga in the north and Fort-Dauphin in the south, therefore other breeding sites may remain to be discovered. For example, two new breeding sites were found after May 2005 that we had not included in this paper: one site in Andavadoka (Rf-C and PL pers. obs., December 2005), and another site at Ankazobe, north of Tambohorano (SZ pers. obs., October 2005).

Why do Madagascar Plovers have such a restricted breeding distribution? Firstly, their habitat requirements are restricted to sparse vegetation around alkaline lakes and mudflats. Since these habitats are only found on the west and south coast, this limits the breeding distribution. Thus, there is suitable-looking habitat in the far northwest of Madagascar around Lake Sahaka, but which does not support Madagascar Plover (R Safford pers. comm.). Secondly, we note that a few thousand years ago a vast wetland existed around the current location of Lake Tsimanampetsotsa. This ancestral wetland harboured a rich fauna including three species of hippos and an extinct lapwing (Goodman and Benstead 2003). We speculate that the Madagascar Plover may have historically relied upon this former wetland and that the current range we observe is thus a relict of a potentially much wider distribution in a former wetter period. Further, since the Madagascar Plover is a territorial species with high site fidelity (SZ and TS pers. obs.), they may have limited ability to invade distant locations, thus explaining why some unused habitats seem highly suitable for breeding. Thirdly, the low breeding success of Madagascar Plover is a conservation concern. Even though the endemic birds in Madagascar have evolved to cope with mammalian predators, unlike many other island fauna in the Pacific Ocean and New Zealand, one may argue that the current pressures by introduced predators (cats, dogs and rats) and disturbance by livestock may tip their breeding success below sustainability.

About 13% of clutches at Lake Tsimanampetsotsa were infertile or deserted. We suggest two reasons for this. Firstly, small endemic populations such as that of the Madagascar Plover may exhibit reduced viability due to inbreeding depression (Crnokrak and Ruff 1999). The extent and implications of inbreeding depression, however, are highly debated in both evolutionary biology and conservation (Keller and Waller 2002, Briskie and Mackintosh 2004). We have taken an empirical approach to this issue, and we are currently developing microsatellite markers to genotype plovers in order to test whether infertility indeed is driven by inbreeding (Küpper *et al.* 2007). Secondly, nest desertion is a natural feature in many bird species (Székely *et al.* 1996), although many fieldworkers, including us, first suspect human influence (Kania 1992). With this in mind, we took extreme caution working with such an endangered species and designed the least intrusive fieldwork methods that included using a mobile hide whenever possible.

We found that Madagascar Plovers breed seasonally; the majority of nests are initiated between December and April. Interestingly, breeding periods are consistent between sites

in the north (Mahajanga) and in the south (Lake Tsimanampetsotsa). Limited observations suggest that pairs stay in the same territory and lay a replacement clutch if their initial clutch fails. More data are needed to assess the frequencies of re-nesting and, possibly, double brooding.

The Madagascar Plover exhibits several ecological and demographic traits that may explain its vulnerability. Firstly, they breed in a narrow range of habitats. Thus any change in this habitat, for instance drainage, grazing, or conversion to arable land, is likely to drive a decline in their population. Secondly, the Madagascar Plover appears to have longer life histories than comparable plover species. For instance, most plovers lay clutches of four (or three) eggs and incubate them for about 26 d (26.2 ± 1.9 d, $n = 8$ *Charadrius* species; TS and G Thomas unpubl. data). The Madagascar Plover lays two eggs and incubation lasts for 27 or 28 d. Note, that the incubation period of a widespread African species, the Kittlitz's Plover *Charadrius pecuarius*, is much shorter at about 21 d in Madagascar (SZ unpubl. data) at the same breeding site (Lake Tsimanampetsotsa) as the Madagascar Plover. Chick growth also appears to be slow; whereas Kentish Plover chicks gain about 1 g d^{-1} , the chicks of Madagascar Plover grow approximately half as fast. Failed breeders take a long time to start a new nest (c. 52 d, whereas female Kentish Plovers lay a complete clutch of three eggs within only 14 d after nest failure (Székely *et al.* 1999). Thirdly, the reproductive success of Madagascar Plover is very low and only 9.5% of nests produce a fledged chick. Fourthly, the peak period of Madagascar Plover breeding coincided with the wet season, presumably because food abundance increases during this period. The downside of breeding in the wet season, however, was the high risk of nest flooding. Cyclones often fundamentally changed the size and distribution of wetlands. Thus in Madagascar, water levels may increase by half a metre after cyclonic activity. Finally, their rigid breeding system (e.g. high site fidelity, apparent monogamy with obligate biparental care) may reduce the ability of the Madagascar Plover to exploit temporarily available breeding sites. This contrasts with flexible breeding systems of several waders, such as the Mountain Plover *Charadrius montanus*, Kentish Plover and Eurasian Dotterel *Eudromias morinellus*, in which a single parent typically looks after the young and both males and females may have several mates within a breeding season (Oring 1986, Reynolds and Székely 1997, Thomas *et al.* 2007).

Many birds that live on islands face a bleak future because of habitat loss, introduced predators and/or overexploitation. We investigated one island-endemic species, the Madagascar Plover. We found that the low productivity of the Madagascar Plover is likely to lead to a decline in its population. This decline is predicted to be steep even using optimistic estimates of both productivity and adult survival. Catastrophic population declines over short time periods have occurred in several waders including the Eskimo Curlew *Numenius borealis*, Slender-billed Curlew *Numenius tenuirostris*, Sociable Lapwing *Vanellus gregarius* and St Helena Plover (Mowatt 1984, Watson *et al.* 2006, N McCulloch pers. comm.). We conjecture that unless action is taken in the near future, the Madagascar Plover will join this growing list.

Our study has three major implications. Firstly, only one out of 10 breeding sites (Lake Tsimanampetsotsa) are currently protected. It is thus imperative to establish new protected areas to prevent habitat loss due to the current trend of conversion of wetlands to shrimp farms and rice paddies for economic gain. We strongly recommend designating protected status to breeding sites in Marambitsy Bay, Andavadoka and Ankazobe. Secondly, the nests, young and adults should be protected from predators, if necessary by controlling predator numbers. This may pose special challenges if predators are endemic and/endangered species themselves. Such an approach has been taken in North America with Piping Plover *Charadrius melodus* and Snowy Plover (Hunter 2002). Thirdly, further research is essential to establish the predators of nests, young and adults and to estimate survival of fledged chicks and adults. These tasks can be realised, though they remain technically challenging in remote areas, such as many sites in Madagascar. We strongly believe, however, that the results of the collaboration between Malagasy conservation biologists and NGOs, and international research and conservation agencies (some of which funded the current study) are likely to improve the long-term prospects of Malagasy endemics.

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