Article

Exceptionally high apparent adult survival in three tropical species of plovers in Madagascar

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Adult survival is a key component of population dynamics, and understanding variation in and the drivers of adult survival rates and longevity is critical for ecological and evolutionary studies, as well as for conservation biology and practice. Tropical species of landbirds are often selected to have higher adult survival due to high nest predation rates, but it is unclear if the same patterns occur in other avian lineages with different life history strategies. Here, we investigate adult survival of three sympatrically breeding species of shorebirds in south-west Madagascar: the endemic and endangered Madagascar plover *Charadrius thoracicus* and two more widely distributed African species: the white-fronted plover *C. marginatus* and the Kittlitz's plover *C. pecuarius*. Using mark–recapture data from 1843 individuals breeding at an intensely monitored saltmarsh over a 13-year period, we estimated annual rates of apparent survival (φ) corrected for encounter probability. Adult apparent survival rates were high for all three species (mean ± SE): Madagascar ($\varphi = 0.899 \pm 0.010$) and white-fronted plovers ($\varphi = 0.923 \pm 0.008$). Kittlitz's plovers showed a difference between the first ($\varphi^1 = 0.719 \pm 0.026$) and subsequent transitions ($\varphi^{2+} = 0.892 \pm 0.014$), suggesting that transient breeders are common in this species. For birds first captured as adults, these survival estimates translate to life expectancies of 9.72 (±1.11) years in Kittlitz's plovers, 9.36 (±0.98) years in Madagascar plovers and 12.48 (±1.32) in white-fronted plovers. We hypothesise that a long lifespan could be an adaptation arising from the unique climatic pressures on the island of Madagascar that would otherwise lead to reduced fitness. However, long lifespans may not sufficiently compensate for a reduction in breeding opportunities due to possible climatic disruption in the future. Consequently, at least two of these plover species seem vulnerable to ongoing habitat destruction and changing climate cycles.

Keywords: demography, life history, lifespan, mark–recapture, shorebird

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Introduction

Adult survival is an essential component in understanding population dynamics and has major implications for evolutionary ecology and conservation biology (Perlut et al. 2008, Székely et al. 2014, Eberhart-Phillips et al. 2018). Studies of terrestrial landbirds often reveal a tendency towards higher survival among tropical species than north temperate species (Martin 1996, Peach et al. 2001, Harris 2011, Wolfe et al. 2014, Muñoz et al. 2018). However, most previous studies have focused on forest-dwelling species, particularly passerines, and thus, it is unexplored whether survival rates in other lineages of birds follow similar patterns. Differences might be expected, since nest predation pressures for open habitat species are significantly different from woodland or scrubland species (Söderström et al. 1998, Willson et al. 2001). Shorebirds provide an excellent system in which to study inter- and intraspecific patterns of survival and longevity and how demographic variation is linked to broader ecological and evolutionary phenomena (Piersma and Wiersma 1996, Colwell and Haig 2019, Székely 2019).

Madagascar is recognised for its high level of endemism and the critical status of many of its unique ecosystems. However, the wetlands of Madagascar are an often overlooked yet highly threatened hotspot of endemism (Benstead et al. 2003, Bamford et al. 2017). Coastal wetlands are under increasing pressure from intensifying human activities such as shellfish farming and salt and mineral extraction (Harris 2011, Scales et al. 2017). Madagascar is an island that experiences strongly cyclical climatic conditions that often involve prolonged droughts (Ropelewski and Halpert 1987), and many of the organisms that inhabit Madagascar have evolved demographic and behavioural mechanisms to cope with variation in environmental conditions (Dewar and Richard 2007). However, it has been predicted that the cyclical nature of Madagascar's climate will be exacerbated in the face of global climatic change, which may lead to droughts at higher frequencies and increased duration (Hannah et al. 2008). Increasingly, other parts of the world are experiencing high levels of climatic stochasticity inherent to Madagascar; therefore, the population patterns and processes that are occurring now may be used to inform conservation priorities in other areas such as Australia (Hughes 2003) or the Americas (De La Maza et al. 2009, Falk and Millar 2017).

As part of a long-term monitoring study to understand Malagasy shorebirds' ecology and behaviour (D'Urban Jackson et al. 2021, Zefania and Székely 2021), here we report sex-specific adult survival estimates for three tropical species of plover: Madagascar plover *Charadrius thoracicus,* white-fronted plover *C. marginatus* and Kittlitz's plover *C. pecuarius*, breeding sympatrically at a coastal wetland site in south-western Madagascar. The endemic Madagascar plover is restricted to coastal and saltwater marshes on the west coast of the island and is listed as globally vulnerable, with a total estimated population of <3500 individuals and is declined partly because of anthropogenic habitat degradation (Zefania et al. 2008). The white-fronted plover is a widespread but declining species that breeds in coastal and riverine habitats across sub-Saharan Africa (Zefania and Székely 2013). While currently classified as least concern, the subspecies that occur in Madagascar, *C. m. tenellus*, is genetically and morphologically distinct from mainland African populations and should be treated as a separate conservation unit to mainland populations (Dos Remedios et al. 2020). It is also subject to the same threats as the Madagascar plover. The Kittlitz's plover is widespread across most of the African continent and has less strict habitat requirements than the other two species, breeding in a wide range of wetland and grassland habitats (Zefania and Székely 2013).

Breeding conditions in Madagascar are highly dependent on seasonal rainfall, and the plovers regularly skip breeding in years of drought (Zefania et al. 2008). Madagascar and white-fronted plovers are strictly monogamous and engage in biparental care of their offspring, whereas Kittlitz's plovers have weak pair-bonds and exhibit uniparental care of young (Parra et al. 2014, Maher et al. 2017, Eberhart-Phillips et al. 2018). Clutch sizes tend to be smaller than those of plover species breeding in more northerly latitudes, ranging from two to three eggs in white-fronted plovers, two eggs in Madagascar plovers and one to two eggs in Kittlitz's plovers (Colwell and Haig 2019).

We aimed to determine whether apparent survival differed among the three sympatric species and whether males and females exhibit different apparent survival rates that are linked to population ecology or sex role variation. First, we predicted that Malagasy plovers might have high adult apparent survival when compared with other plover species, due to their tropical range, island habitats and slow life histories characterised by small clutch sizes. Secondly, we predicted that Madagascar plovers would have lower apparent survival rates than the other two species, based on their population declines and rarity. Finally, based on species' differences in mating systems and patterns of parental care, we predicted greater sex differences in apparent survival and encounter probability for Kittlitz's plovers than the other two species with social monogamy and biparental care.

Methods

Fieldwork

The three plover species have been studied intensively at Andavadoaka (S°22.02, E°43.39) in the south-western Madagascar – an area expanded by approximately 8 km² and characterised by a complex system of sandy beaches and ephemeral, saltwater lagoons that are encompassed by dry, spiny forest (Parra et al. 2014). Protection of the area is complex, although the bulk of the saltmarsh habitat is covered by the Velondriake marine reserve (Andriamalala and Gardner 2010, Harris 2011), while to the east, the area is protected by the buffer zone for the Mikea forest (Seddon et al. 2000). Breeding occurs following seasonal periods of heavy rainfall, and nesting begins as early as December and January

and ceases by the beginning of June, when the floodwaters have mostly evaporated. As many as 170 pairs of Madagascar plovers, 150 pairs of white-fronted plovers and 450 pairs of Kittlitz's plovers can breed in the vicinity (Zefania, pers. obs.).

Plovers were caught and resighted or recaptured in the years 2009–2020 inclusive (2008–2020 for the Madagascar plover). Most plovers were trapped on their nest using funnel traps. Each individual was fitted with a unique combination of Darvic colour rings and an alphanumeric SAFRING metal ring. Lost rings were replaced on recaptured birds wherever possible. Colour ring loss over time can be a minor issue, making subsequent apparent survival estimates up to 1.2% more conservative (Allen et al. 2019). In addition to standard measurements, we also collected blood samples from 63.5% to 76.9% of captured birds for genetic sexing. Blood samples (25–50 µl) were collected by brachial venepuncture and stored in Queen's lysis buffer (Seutin et al. 1991). As all three species are sexually monomorphic (Zefania et al. 2010), therefore individuals were sex-typed using established molecular methods developed for *Charadrius* species (Küpper et al. 2006, Parra et al. 2014). A subset of 270 individuals was sexed multiple times to gauge the accuracy of the molecular sexing. Repeatability was high with only 22 individuals (6.2% Madagascar plovers, 7.6% white-fronted plovers and 11.2% Kittlitz's plovers) being mis-sexed. The latter individuals were included in the survival analyses as being of unknown sex, together with individuals that were not sex-typed because blood sample was not collected. Birds were then resighted over subsequent years either at the nest, or opportunistically in the field, or more rarely during standardised point and transect counts.

Statistical analysis

We used a time-specific Cormack–Jolly–Seber modelling framework to estimate constant and annual probabilities of apparent survival (φ) and encounter probability (p). Apparent survival was defined as the probability of a marked individual surviving and returning to the study site between consecutive years. Yearly encounter histories for all individuals were constructed, where $0 =$ undetected and $1 =$ recaptured or resighted at the study site during the breeding season. A small number of individuals were first trapped and ringed as hatch-year juveniles that had subsequently returned to the study area as adults. These individuals were included in the apparent survival models, but the information from their natal year was censored from their encounter history. Conditioning upon first capture as an adult is a standard analytical practice in mark–recapture modelling because natal year survival is often much lower than adult survival and is governed by different factors (Sandercock et al. 2005, Eberhart-Phillips et al. 2018). Sex covariates were set as '1' for males and '0' for females, while unsexed individuals were coded as the mean of the known-sexed individuals (Kittlitz's plover: 0.52, Madagascar plover: 0.49 and white-fronted plover: 0.50) so that unsexed individuals would contribute to species-level survival estimates but not the sex-specific survival estimates.

This method assumes that the sex ratio of known-sex individuals did not deviate from the sex ratio of the unknown population. Deviation from this would make sex-specific estimates less reliable; however, while there are some biases in adult sex ratios in Malagasy plovers (Eberhart-Phillips et al. 2018), these are relatively minor and are unlikely to skew the results significantly.

Mark–recapture analyses were implemented in Program MARK (White and Burnham 1999). In preliminary analyses, we ran 20 models for each species to test for the annual variation of a sex effect in survival estimates for each species (Table 1). For all three species, models with full time dependence for apparent survival had low Akaike information criterion (AIC) scores but the parameter estimates had CIs that were often at the boundaries of zero or one – a pattern that is diagnostic of sparse data for some annual transitions. Consequently, we opted to discard models with time dependence in φ. We kept models with time dependence in (p) due to the highly stochastic climatic variation, leading to strong variation in breeding effort and potentially detection, as well as variation in observer effort. Time-since-marking models, where apparent survival in the interval following capture (φ^1) was separated from subsequent encounters (φ^{2+}), produced widely bounded survival estimates for Madagascar and white-fronted plovers and so they were also discarded for these species. Thus, our global model for each species included effects of sex in apparent survival and a model for sex and year in the probability of encounter: φ(sex) p(sex × year). Model fit for the global model was assessed using the parametric

Table 1. The 20 models run separately for each species. $\varphi =$ apparent survival, p $=$ encounter rate and c $=$ constant (males and females combined). Models with a year covariate were tested preliminarily but excluded due to data sparsity in some years. The time-since-marking model 'φ^1 (.)/φ^{2+} (.) p(year)' and 'φ^1 (sex)/φ^{2+} (sex) p(year)', which separates first-year survival from subsequent transitions, was similarly discarded for Madagascar and white-fronted plover model comparisons due to sparsity of data.

Model
φ(.) p(.)
φ(.) p(sex)
φ(.) p(sex × year)
φ(.) p(sex + year)
φ(.) p(year)
φ^1(.)/φ^{2+} (.) p(year)
φ(sex) p(.)
φ(sex) p(sex)
φ(sex) p(sex × year)
φ(sex) p(sex + year)
φ(sex) p(year)
φ^1(sex)/φ^{2+} (sex) p(year)
φ(sex × year) p(.)
φ(sex × year) p(sex)
φ(sex × year) p(sex × year)
φ(sex × year) p(year)
φ(year) p(.)
φ(year) p(sex)
φ(year) p(sex × year)
φ(year) p(year)

bootstrapping and median-ĉ procedures in MARK. To rank the candidate models, we used the quasi-Akaike information criterion corrected for small sample sizes (QAICc). Models with the strongest support were identified as those with normalised Akaike weights (wi) ≥ 0.15 or ΔQAICc values ≤ 2 differences between QAICc of the model with the lowest QAICc and the model under consideration (Burnham et al. 2011). All φ and p statistics are presented with ± SE to 3 decimal places unless otherwise stated. Estimates of the variance inflation factor (ĉ) for all three species did not suggest the presence of overdispersion (Madagascar plover = 1.03, white-fronted plover = 0.99 and Kittlitz's plover = 1.25). Species-specific estimates of apparent lifespan (Ê) were calculated using the formula $\hat{E} = \dfrac{-1}{\ln(\hat{\phi})}$ where $\hat{\phi}$ = the estimate of apparent survival estimate from the model φ(.) p(year), respectively (Brownie et al. 1985). An extra year was added to the apparent lifespan, and estimates were taken from the φ^{2+} transition for Kittlitz's plover as those individuals had already returned in the φ^{1} transition. SEs were calculated using the delta method, which approximates sampling variance when the desired demographic parameter is a function of at least one other demographic parameter (Powell 2007).

Results

Survival and encounter probability estimates of Malagasy plovers

In total, we recorded 12 248 capture and resighting events for 1843 adults across the three species in the 13-year period of 2008–2020 inclusive (Table 2). The percentage of individuals that were resighted more than once was generally high in Madagascar (74.0%) and white-fronted plovers (76.4%), with Kittlitz's plovers being somewhat lower (53.0%). The lowest AIC model for Madagascar and white-fronted plovers was an intercept-only model for apparent survival φ(.) p(year), whereas the model with the lowest AIC for Kittlitz's plover was a time-since-marking model, φ(c/c) p(year) (Table 3). Madagascar plovers (φ = 0.899 ± 0.010) and white-fronted plovers (φ = 0.923 ± 0.008) had

Table 2. Number of individuals of three Malagasy plover species included in this study. Data were collected between 2008 and 2020 for Madagascar plovers and between 2009 and 2020 for both white-fronted and Kittlitz's plovers.

Species	Total	Sex	Total (%)
Kittlitz's plover *Charadrius pecuarius*	1071	Male	435 (40.6)
		Female	389 (36.3)
		Unsexed	247 (23.1)
Madagascar plover *C. thoracicus*	373	Male	116 (31.1)
		Female	121 (32.4)
		Unsexed	136 (36.5)
White-fronted plover *C. marginatus*	399	Male	126 (31.6)
		Female	128 (32.1)
		Unsexed	145 (36.3)

Table 3. Model selection results examining apparent survival of (a) Madagascar plovers, (b) white-fronted plovers and (c) Kittlitz's plovers at Andavadoaka, south-western Madagascar 2008–2020, as a function of sex and year. Model fit is described by the number of parameters (K), the devience (QDeviance) and the difference in quasi-Akaike's information criterion from the best-fit model (ΔQAICc). QAICc values were calculated using a median-ĉ of 1.03 for Madagascar plover, 0.99 for white-fronted plover and 1.25 for Kittlitz's plover. Note that as the asymptotic value of ĉ = 1, the estimate for white-fronted plover was set to 1, and therefore, AICc was used instead of QAICc.

(a) Model	K	QDeviance	QAICc	ΔQAICc
φ(.) p(year)	13	794.14	2289.72	0.00
φ(.) p(sex + year)	14	794.02	2291.65	1.94
φ(sex) p(year)	14	794.12	2291.76	2.04
φ(sex) p(sex + year)	15	793.97	2293.66	3.94
φ(.) p(sex × year)	25	789.64	2310.15	20.43
φ(sex) p(sex × year)	26	789.64	2312.25	22.53
φ(.) p(.)	2	1009.75	2482.99	193.28
φ(.) p(sex)	3	1009.34	2484.59	194.87
φ(sex) p(.)	3	1009.71	2484.96	195.25
φ(sex) p(sex)	4	1009.16	2486.43	196.71

(b) Model	K	Deviance	AICc	ΔAICc
φ(.) p(year)	12	927.94	2749.12	0
φ(sex) p(year)	13	927.69	2750.92	1.8
φ(.) p(sex + year)	13	927.87	2751.10	1.98
φ(sex) p(sex + year)	14	927.67	2752.95	3.83
φ(.) p(sex × year)	23	925.73	2769.64	20.52
φ(sex) p(sex × year)	24	925.52	2771.51	22.39
φ(.) p(.)	2	1132.61	2933.52	184.4
φ(sex) p(.)	3	1132.33	2935.26	186.14
φ(.) p(sex)	3	1132.59	2935.52	186.4
φ(sex) p(sex)	4	1132.33	2937.27	188.15

(c) Model	K	QDeviance	QAICc	ΔQAICc
φ(c/c) p(year)	13	838.78	4283.92	0.00
φ(sex/sex) p(year)	15	838.07	4287.27	3.35
φ(.) p(sex + year)	13	859.41	4304.55	20.63
φ(sex) p(sex + year)	14	858.14	4305.30	21.38
φ(.) p(year)	12	863.08	4306.19	22.27
φ(sex) p(year)	13	863.07	4308.21	24.29
φ(.) p(sex × year)	23	853.06	4318.57	34.65
φ(sex) p(sex × year)	24	852.39	4319.94	36.02
φ(.) p(sex)	3	1027.99	4452.96	169.04
φ(sex) p(sex)	4	1026.82	4453.80	169.88
φ(.) p(.)	2	1031.62	4454.58	170.66
φ(sex) p(.)	3	1031.62	4456.59	172.67

high annual apparent survival rates (Fig. 1), while Kittlitz's plovers had lower apparent survival in the first interval after capture (φ^{1} = 0.721 ± 0.026), with survival estimates closer to the other two species in subsequent years (φ^{2+} = 0.892 ± 0.013, Fig. 1). Encounter probabilities followed a similar pattern (Fig. 2), with high encounter rates for Madagascar (male p = 0.54 ± 0.02 versus female p = 0.51 ± 0.02) and white-fronted (male and female p = 0.50 ± 0.02) plovers and lower encounter rates for Kittlitz's plover (male, p = 0.35 ± 0.02 vs female, p = 0.31 ± 0.02). These apparent survival estimates generated rather long average apparent lifespans for individuals caught as adults for each species: 9.72 ± 1.11 years in
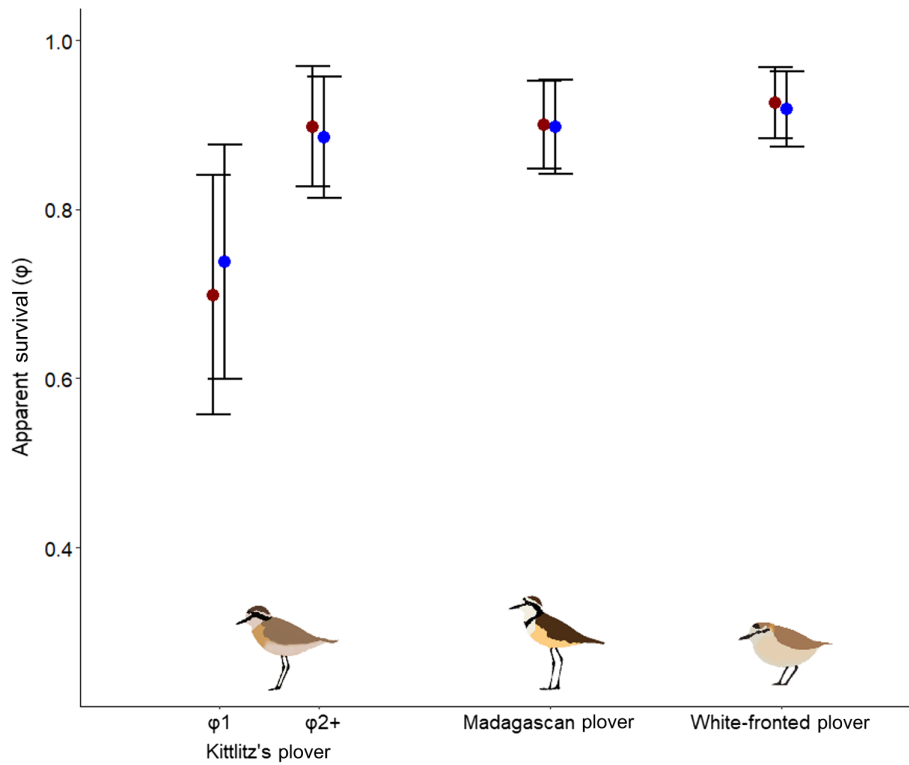
Figure 1. Annual sex-specific survival estimates for Kittlitz's, Madagascar and white-fronted plovers, with 95% CI in Madagascar (females in red, males in blue). For Kittlitz's plover, we show the apparent survival estimates from the time-since-marking model, showing lower apparent survival estimates in the capture year. For sample sizes see Table 2.

Kittlitz's plovers, 9.36 ± 1.35 years in Madagascar plovers and 12.48 ± 1.35 years in white-fronted plovers. Male and female apparent survival estimates were not significantly different in any of the three species (Fig. 1).

Discussion

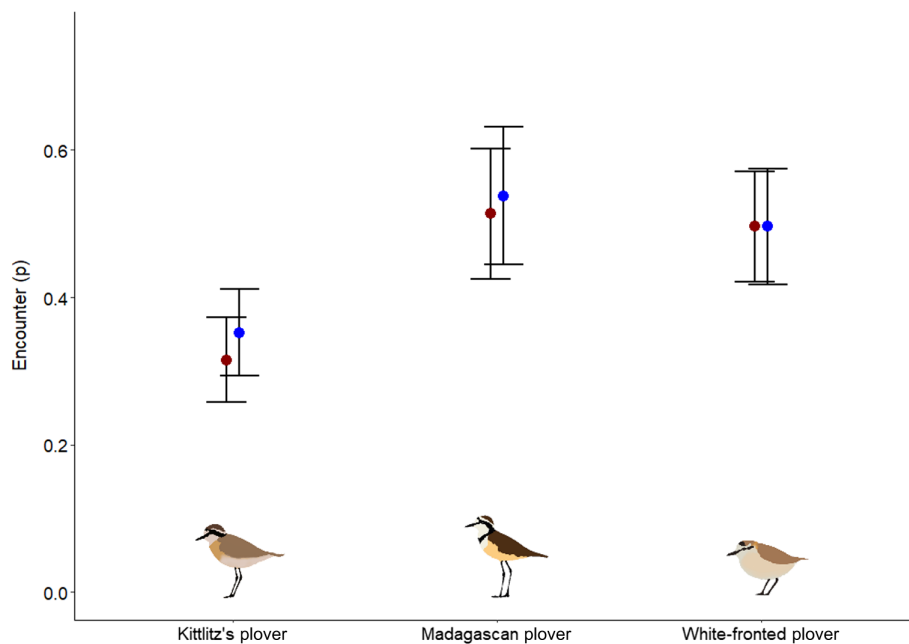Our long-term study of plovers in south-west Madagascar yielded some of the highest apparent survival

Figure 2. Annual sex-specific encounter estimates for Kittlitz's, Madagascar and white-fronted plovers, with 95% CI in Madagascar (females in red, males in blue).

($\varphi = 0.892–0.923$) and life expectancy estimates (9.36–12.48 years) so far reported in plovers and other shorebirds in general (Méndez et al. 2018, Dinsmore 2019). The apparent survival estimates of temperate-breeding *Charadrius* species have been extensively explored such as the piping plover *C. melodus* ($\varphi = 0.66–0.80$) (Roche et al. 2010), the Kentish plover *C. alexandrinus* ($\varphi = 0.59–0.76$) (Boyd 1962, Garcias and Tavecchia 2018) and the snowy plover *C. nivosus* ($\varphi = 0.56–0.76$) (Mullin et al. 2010, Warriner et al. 1986). In all cases, apparent survival estimates are considerably lower than the new estimates that we report from Madagascar. Indeed, the only plover populations with similarly high adult survival estimates were the tropical white-fronted plovers from South Africa ($\varphi = 0.88–0.90$) (Summers and Hockey 1980, Lloyd 2008) and the island-dwelling New Zealand Dotterel, *C. obscurus* ($\varphi = 0.93$) (Marchant and Higgins 1993). Therefore, the high survival estimates that we find may provide evidence that the pattern for higher survival in the tropics extends beyond forest-dwelling, passerine birds. However, adult survival and longevity are likely influenced by a suite of other factors, such as body size, island living or migratory status, so further studies are required from tropical and subtropical populations to confirm this trend.

Another driver of high adult survival in Madagascar could be the unique climatic conditions on the island (Dewar and Richard 2007, Hannah et al. 2008). South-western Madagascar experiences strong interannual climate variation, characterised by frequent droughts (Ropelewski and Halpert 1987). The stochastic conditions may have been selected for longer lifespans in Malagasy plovers, as part of a suite of life history traits to balance intermittent breeding and small clutch sizes (Martin and Mouton 2020). Interesting parallels can be seen with other vertebrates in this region of Madagascar, such as the Verreaux's sifaka *Propithecus verreauxi*, which also has a comparatively high adult survival ($\varphi > 0.89$) and reduced breeding investment in drought years (Richard et al. 2002, Lawler et al. 2009). In addition to climate, living on an island may also increase the annual survival of the Malagasy species, as has been shown in other studies (Beauchamp 2021). Indeed, a remote island species, the Saint Helena plover *C. sanctaehelenae*, a close relative of the Kittlitz's plover, has relatively high rates of adult survival ($\varphi = 0.83$); despite its small body size and in the face of declines due to invasive predators (Burns et al. 2013). However, with an area of 587 041 km² and a diverse guild of native and introduced predators (Madagascar harrier *Circus macroceles*, peregrine falcon *Falco peregrinus*, feral cat *Felis catus* and Dumeril's boa *Acrantophis dumerili*) (Zefania, pers. obs.), it is more appropriate to think of Madagascar as a small continent, rather than an island (de Wit 2003).

For Kittlitz's plovers, we found that the time-since-marking model was the most appropriate. Time-since-marking models control for animals that are never detected after the year of banding, which can be due to a variety of reasons, such as handling effects on apparent survival or site fidelity and dispersal or the presence of transient breeders (Sandercock and Jaramillo 2002). Here, the lower apparent survival in the intervals after the first capture is likely related to the differences in the social systems among our three study species. Kittlitz's plovers have uniparental care, and lower apparent survival in the interval after first capture is likely due to vagility. Estimates of apparent survival in later intervals (φ^{2+}) for Kittlitz's plovers were comparable to overall estimates for Madagascar and white-fronted plovers.

We also found that overall encounter rates (p) were lower in Kittlitz's plover than the other two species (Fig. 2). Encounter rates are a function of site use and true detection rates (Sandercock 2020). Thus, the lower encounter rates for Kittlitz's plovers could also be an indication of higher vagility that leads to temporary emigration where individuals may breed elsewhere but then return to the study area. Both Madagascar and white-fronted plovers in Madagascar (Zefania and Székely 2013) and white-fronted plovers in South Africa (Lloyd 2008) exhibit high site fidelity for shorebirds with maximum recorded adult breeding dispersal distances being 15 km in Madagascar and 0.4 km in South Africa, while average between-season dispersal distances of white-fronted plovers in South Africa were just 0.4 km. Estimates of breeding dispersal distances for tropical plovers are modest compared to other species including Kentish plovers and snowy plovers (Székely and Lessells 1993, Stenzel et al. 1994). There is little current information on dispersal propensity for Kittlitz's plovers, but, anecdotally, the maximum dispersal distance recorded for this species in Madagascar is 113 km (Zefania and Székely 2013) and there appears to be evidence for nomadic behaviour in South Africa (Lipshutz et al. 2011). Signatures of dispersal propensity for all three species have also been detected in their genetic population structure, with Kittlitz's plovers being weakly structured in comparison to the other two Malagasy species (Eberhart-Phillips et al. 2015), indicating support for the idea of gene flow via temporary emigration.

We did not find a significant difference in apparent survival between males and females for any of the three species. All three species exhibit female-biased juvenile apparent survival rates, especially in white-fronted and Kittlitz's plovers (Eberhart-Phillips et al. 2018). However, we find virtually no differences in adult sex ratio in white-fronted or Madagascar plovers and a strong male bias in adult sex ratio in Kittlitz's plovers in our study (Table 2). Sex biases in mortality can occur due to a variety of reasons, including differences in reproductive effort (Székely et al. 2014), intrasexual conflict (Clutton-Brock and Isvaran 2007), parasite susceptibility (Poulin 1996) or differential exposure to predators (Lehikoinen et al. 2008). Sex biases in apparent survival may also appear due to biases in dispersal. The latter tends to happen more frequently in metapopulations that are separated by tracts of unsuitable habitat, where replacement of the more dispersive sex is reduced (Broughton and Hinsley 2015). Given that we see no sex bias in Madagascar plovers, the species with the most specialised habitat requirements, but a sex bias in the least specialised and most abundant Kittlitz's plover, sex biases in dispersal are unlikely to be the cause of sex ratio differences in these species. Madagascar and white-fronted

plovers are strictly monogamous, and their mating system may have reduced reproductive costs for both species, while potentially equalising any predation risk that might be experienced during parental care duties. While Kittlitz's plovers exhibit uniparental care and have weak pair bonds, both sexes care for offspring, thereby likely reducing any population-level differences in apparent survival. Therefore, unusually to plovers (Székely et al. 2014), sex-specific adult survival may be less important in determining adult sex ratios in Malagasy plovers (Eberhart-Phillips et al. 2018).

Our estimates of high apparent survival for all three species are encouraging, especially for the Madagascar plover, which is a species of conservation concern. Nevertheless, high annual adult survival rates do not necessarily indicate stable population viability (França and Marini 2010). While the ecosystems surrounding the saltmarshes at Andavadoaka are under a particularly high level of threat (Seddon et al. 2000), threats to plover breeding habitats still require a formal assessment. The three plovers we studied do not use the most threatened, forested parts of the Mikea IBA; but artisanal salt extraction from saline lagoons likely impacts habitat quality (Dahdouh-Guebas et al. 2005, López et al. 2010, Zefania pers. obs.). Furthermore, ongoing climate disruption is predicted to increase the intensity, frequency and duration of droughts in Madagascar (Masih et al. 2014, Abiodun et al. 2019). These two factors could potentially jeopardise the sustainable survival rates of plovers in the future.

Conclusion

We provide the first robust estimates of annual survival for adult Kittlitz's and Madagascar plovers and the Malagasy subspecies of the white-fronted plover and we present some of the highest apparent survival estimates published in shorebirds. Our findings show that, despite differences in breeding systems, adult survival rates were consistently high among these three sympatric species, likely due to the unique mix of climatic stochasticity, site fidelity and predation pressures on the island of Madagascar. Our results demonstrate that adult survival is unlikely to drive population trends in these species. This is particularly important for understanding the causes of population decline in the endemic and vulnerable Madagascar plover. Future work should focus on other life stages, such as nest success and post-fledging survival to pinpoint the source of these declines; as well as parallel studies in other parts of these species' ranges to investigate site-level differences in apparent survival. Yet, we still note that high adult survival rates may not be sufficient to counteract population declines in the face of increased climatic disruption and ongoing habitat destruction in the wetlands of Madagascar.

Author contributions

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Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.8931zcrrv> (Jones et al. 2021).

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