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Research article

Climatic variation influences annual survival of an island-breeding tropical shorebird

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Global biodiversity loss is a major environmental concern. The wildlife on islands are particularly vulnerable to threats posed by alien predators, habitat loss and overexploitation. Effective conservation management of vulnerable species requires reliable information on vital population rates for all life stages and an understanding of key environmental drivers. However, demographic data are often not available for island populations before they decline or are extirpated. Here, we use Cormack–Jolly–Seber (CJS) models and 15 years of data for 1370 juveniles and 687 adults to estimate apparent survival for a genetically distinct resident population of Kentish plovers *Charadrius alexandrinus* on the island of Maio, Cabo Verde. We report two main findings. First, environmental conditions have a large effect on demographic performance since chicks that hatch during dry years experience a tenfold reduction in first-year survival compared to chicks that hatch during wet years. Second, female and male plovers in Maio are expected to live for 7.41 ± 0.69 (mean $\pm$ SE) years and 6.75 ± 0.64 years, respectively, due to relatively high annual survival among comparable-sized shorebirds. High adult survival thus could buffer the population against low reproductive success that this population has experienced over the last decade. Cabo Verde is typical of tropical islands with increased development that can impact native breeders and/or will accelerate habitat loss. Thus, more frequent droughts associated with climate change may exacerbate the prospects of native wildlife on many islands.

Keywords: apparent survival, demography, island conservation, Kentish plover, Macaronesia, wader

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Introduction

Tropical islands are biodiversity hotspots because they usually support exceptionally high numbers of endemic species (Veron et al. 2019). However, island species have restricted ranges and have often lost behavioural adaptations to predation or competition that makes them vulnerable to human-induced changes in the environment such as habitat loss, the introduction of alien species, or climate change (Lazrus 2012, Kueffer and Kinney 2017, Whittaker et al. 2017, Kelley et al. 2019). Anthropogenic activities often cause changes in the environment at faster rates than species can adapt (Guttery et al. 2013). The impact of rapidly changing environments might be particularly severe for island species due to lower genetic diversity and often smaller population sizes (Macinnis-Ng et al. 2021). A key step to understand how island populations cope with increased pressure is to quantify vital rates and the drivers of their variability across all life stages (Guttery et al. 2013). Nest survival and age-specific adult survival are key demographic indicators to understand population dynamics and have a major significance for evolutionary biology and conservation biology (Sandercock et al. 2000, Székely et al. 2014). In long-lived vertebrates, population growth rates are often most sensitive to variation in adult survival (Sandercock 2003, 2005). Adult survival tends to be higher in island populations compared to mainland populations, possibly due to milder climate on islands that are buffered by oceanic conditions and fewer parasites or predators (Beauchamp 2021). In addition, life history theory predicts that in tropical regions smaller clutch sizes are balanced with higher adult survival compared to the north temperate populations that have larger clutch sizes and lower adult survival (Martin 1996, Ghalambor and Martin 2001, Muñoz et al. 2018, Jones et al. 2022).

Climatic variation has a strong effect on the demographic rates of birds (Sæther et al. 2004, Grosbois et al. 2008), and tropical birds are often adapted to a 'hygric niche' with the best demographic performance under suitable conditions but reduced performance in either extremely dry or wet years (Boyle et al. 2020). Bird populations have been studied on several tropical islands with semi-arid conditions, and reproductive success and survival are often higher during years with above-average precipitation (Gibbs and Grant 1987, Curry and Grant 1989, Rivera-Milán and Schaffner 2002, Brooke et al. 2012).

Cabo Verde is a tropical island country that is internationally recognised for its terrestrial and marine biodiversity (Merino 2006, Pena 2017). Cabo Verde's biodiversity is under threat from two main sources. First, the archipelago has become a desirable tourist destination with a fivefold increase in the numbers of tourists over the past 20 years, which is likely to increase in the future (López-Guzmán et al. 2013, Bernardo 2022, González-Gómez 2022). Second, Cabo Verde is vulnerable to climate change due to its tropical location, small area and susceptibility to natural hazards such as coastal flooding or droughts (Varela et al. 2020, 2022). The archipelago is of volcanic origin in the Sahel sub-region and is generally defined by a dry tropical climate with two distinctive climatic seasons: a long dry season during the winter followed by a short season of concentrated rainfall during the summer (Ferreira Costa 2020). Historically, Cabo Verde has undergone cyclic patterns of climatic conditions that involved prolonged periods of droughts. Global climate change might aggravate the cyclical nature of Cabo Verde's climate, with droughts projected to occur at higher frequencies and with an increased duration (Dabanli 2018, Veron 2019), which could negatively affect island biodiversity.

Previous studies analysing demographic aspects of tropical island populations have mainly focused on comparisons among tree-dwelling land birds (Faaborg and Arendt 1995, Johnston et al. 1997, Sandvig et al. 2017). Shorebirds are an interesting study system to investigate patterns of survival and how demographic variation might be linked to wider ecological and evolutionary processes (Colwell and Haig 2019, Székely 2019). Here, we report on a demographic study of the largest breeding population of Kentish plover *Charadrius alexandrinus* in the Macaronesian archipelagos on the tropical island of Maio, Cabo Verde (15.15°N, 23.22°W). The island population in Maio is resident and genetically distinct from mainland populations of Kentish plovers, which increases its importance as a unique target of conservation that is under threat from anthropogenic pressures (AlmalkI et al. 2016). The island environment is xeric, and the Kentish plover population depends on the seasonal rainfall for breeding, thus climate change may disrupt demographic processes (Kubelka et al. 2018). Nest survival and breeding densities of this population have been decreasing over the past decade (Engel et al. 2023a). Continuing trends for low productivity are a concern and thus we investigated apparent adult survival rates of this population. High adult survival could offset the reproductive losses associated with poor nest survival, which could be an adaptive strategy of tropical island dwellers to maintain long-term population viability. We used 15 years of capture–recapture data to estimate juvenile and adult survival of individuals ringed as chicks or as male and female adult Kentish plovers (Tico 2011, Carmona 2016, Engel et al. 2020, McDonald et al. 2020). *Charadrius* plovers are well-studied model systems in population ecology (Colwell and Haig 2019, Székely 2019) so that here we can compare the Maio demographic parameters with other *Charadrius* plovers that breed on other islands or on mainland (Stenzel et al. 1994, Sandercock et al. 2005, Mullin et al. 2010, Windsor 2020, Jones et al. 2022, Tejera et al. 2022).

Here, we report the annual survival of Kentish plovers for two specific objectives: 1) to obtain estimates of age- and sex-specific apparent survival for a resident population of Kentish plovers on a tropical island, and 2) to understand the implications of weather conditions on annual variation of apparent survival rates of juvenile and adult Kentish plovers.

Material and methods

Fieldwork

Fieldwork was conducted during the 15-year period of 2007–2022 on the island of Maio, Cabo Verde (15.15°N,

23.22°W). The study area was the Salinas do Porto Inglês (Fig. 1), which is the largest wetland in Maio and a protected area supporting important biodiversity that was designated as a Ramsar Site in 2013 (ca 535 ha) (Oliveira 2013, Pereira Neves 2016). The local population of Kentish plovers is resident year-round and includes between 200 and 400 individuals that breed in the Salinas do Porto Inglês. This population depends on the yearly rainfalls during the summer months (July–October) to start breeding. During this time, the Salinas do Porto Inglês fill up with a mixture of sea water and rainwater, which leads to increased insect reproduction (Engel et al. 2023a). The resulting increased food availability provides the necessary resources to breed and the Kentish plovers produce between 50 and 150 clutches each year (Carmona-Isunza 2015, Engel et al. 2023a). Data collection followed a standard protocol developed to monitor the breeding ecology of plovers (Székely et al. 2008). When a Kentish plover nest was first found, the attending parents were captured at the nest with a funnel trap, and each bird was marked with a unique metal-colour ring combination. To minimise the risk of some breeders abandoning the nest upon capture, we only captured individuals on nests that had been incubated for at least five days. At some nests where the parents of the nest were already ringed, the metal-colour ring combination was read with binoculars or a spotting scope. The sex of adults was visually determined by sexual differences in plumage where females are drab brown, and males have black streaks on their forehead, eye stripe and around their neck. Chicks were ringed with one metal ring either at the nest at hatching or if encountered as a mobile juvenile after departing the nest. Some adults were also ringed or resighted while tending chicks. If juveniles survived and were recaptured as adults at a nest in a later year, they were marked with a full combination of colour-rings.

Statistical analyses

Juvenile survival

To estimate apparent annual survival of juveniles, we used live recapture information on 1370 juveniles from between 2007 and 2022, excluding juveniles newly ringed during the last year. Our analysis included all individuals that were ringed as chicks and at a later stage recaptured or resighted
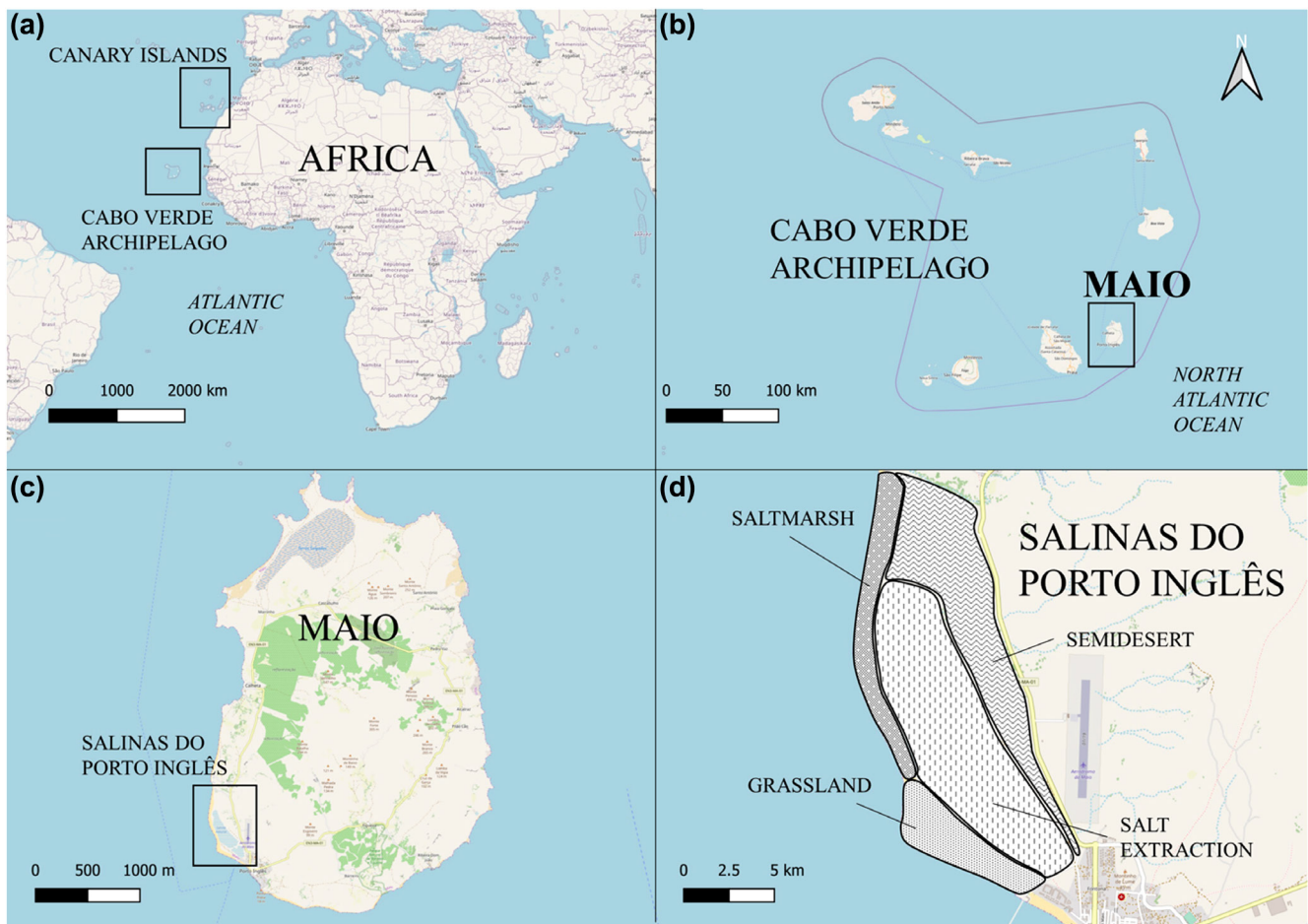

Figure 1. Location of the study area in the archipelago of Cabo Verde in West Africa. Panels show: (a) the archipelago of Cabo Verde, (b) the location of the island of Maio in Cabo Verde, (c) the study area Salinas do Porto Inglês in Maio and (d) the four different habitats of the Salinas do Porto Inglês. Maps developed with OpenStreetMaps (©OpenStreetMap contributors).

on nests as adults. For each year of the study period in the encounter history, each individual was scored either as 1 = the bird was captured or resighted on a nest or as 0 = the bird was not encountered in that particular year. We conducted mark–recapture analyses in program MARK (ver. 9.0) and used the package 'RMark' (Laake 2013) following methodologies outlined in Cooch and White (2014). We used Cormack–Jolly–Seber mark–recapture models for live encounter data to estimate annual apparent survival (Φ) corrected for the probability of encounter (p). Apparent annual survival (Φ) was the probability of an individual bird surviving from one breeding season to the next one and the probability of encounter (p) was the probability of recapturing/re-sighting an individual bird given it is alive. We created a set of candidate models based on a priori factors to investigate ecological effects that might influence juvenile survival. We expected that survival for juveniles might be different for the first transition compared to all other transitions, so we used time-since-marking (TSM) models, where survival is estimated separately for newly marked birds of age0 versus previously marked birds that were age1+. Since survival might vary among years, we created models looking at annual variation and also testing for a linear trend in survival across years. In addition, we created a model where survival was kept constant. Since probability of encounter could vary among the years, we also tested for annual variation in recaptures, for a linear trend in recaptures and also looked at constant recaptures. Last, to investigate the effects of climate on survival and recapture estimates, we included an annual covariate for precipitation to test whether dry or wet conditions influenced the probabilities of apparent survival or recapture. Maio is an equatorial site with annual variation in rainfall, and we opted to classify each study year as either wet or dry. Classification of years was based on a combination of personal observations and numbers of nests produced each year. We controlled for the effort of fieldwork by calculating the number of nests found per day of fieldwork each year. We tested for a difference between years categorized as dry and wet and found that there was a significant difference in mean numbers of nests found (t = 5.27, p < 0.01, Supporting information), so we used the number of nests as a proxy to code the climate variable. Wet years included 2009, 2010, 2012–2016 and 2020–2022 (range in number of nests: 57–157) whereas dry years were 2007–2008, 2011, 2017–2019 (range in number of nests: 10–36). To test how weather during the natal year affected survival, we scored the natal year of juveniles as either wet or dry in our model. Sample sizes of juveniles surviving past one year were low, thus we pooled all individuals surviving in subsequent years into one age-class (age1+). Based on different combinations of age, annual variation, trends, and climatic effects, we built 18 candidate models (Supporting information). We tested GOF to a CJS model including time-since-marking: $\Phi_{TSM*TIME}$, $p_{SEX*TIME}$ and calculated the overdispersion factor (ĉ) using the Fletcher ĉ procedure to deal with tests of standard CJS assumptions about lack of trap dependency on previous capture and homogeneity of re-encounter probabilities (Cooch and White 2014). The Fletcher ĉ procedure

is thought to be the most robust procedure for CJS models (Fletcher 2011). Our data fit the models well with a Fletcher estimate of ĉ = 1. Thus, we set ĉ to be 1.00 and we conducted model selection based on ranking of AICc values.

Apparent adult survival

We used a combination of live recapture data and re-sightings of parents at the nest to estimate annual variation in apparent survival between 2007 and 2022 for adult male (n = 329) and female (n = 358) Kentish plovers. The sample sizes excluded individuals that were first captured and marked during 2022. Here, we also used Cormack–Jolly–Seber mark-recapture models for live encounter data and we created a set of candidate models based on a priori factors to investigate the potential effects of different ecological factors on apparent annual survival. First, we included the effects of time and sex in our models because we expected annual variation in survival and that males and females might differ in survival (Sandercock 2003, Mullin et al. 2010). Second, we included time-since-marking (TSM) models, where newly marked birds of age1+ were treated separately from previously marked birds age2+ (Sandercock 2020). The age classes of age1+ referred to the first time an individual adult was marked on the nest and age2+ referred to all captures/re-sightings on nests in later years after marking. Our study site is open, and we expected birds to enter and leave the population such that individuals might not be re-caught in all years they were alive. Furthermore, the number of nests monitored in a given year might influence the probability of encounter for attending parents, and therefore we included the number of nests per year as a covariate in our models. We used the ANODEV procedure in Program MARK to compare nested models and to calculate how much of the variation observed in the encounter rates could be explained by the number of nests per year. Records for philopatric individuals that were first marked on the nest as chicks were conditioned upon the year that they were first captured as an adult and records from the natal year were excluded from the analyses of adult survival. Different combinations of time, sex, TSM and covariates of climate, and the number of nests per year resulted in 70 candidate models. We tested GOF to a CJS model including time-since marking: $\Phi_{SEX*TSM*TIME}$, $p_{SEX*TIME}$. We used the Fletcher ĉ estimate to test goodness-of-fit. Our estimate of ĉ was 0.99, so we set ĉ in our models to 1 and proceeded with model selection based on AICc values.

To estimate the apparent lifespan Ê of Kentish plovers in Maio, we used the following formula:

$$\hat{E} = \frac{-1}{\ln(\hat{\phi})} + 1,$$

where $\hat{\phi}$ is the apparent survival estimate from the Φ^{2+} transition from the time-since-marking model. An extra year was added to the apparent lifespan estimates taken from the Φ^{2+} transitions because individuals had already returned from the Φ^1 transition. Standard errors for apparent lifespan were

calculated using the delta method, which approximates sampling variance when the desired demographic parameter is a function of one or more demographic parameters (Powell 2007, Sandercock et al. 2022). To examine whether male or female breeding dispersal might explain sex differences in survival, we recorded locations of nests with portable GPS units and then calculated the linear distances between consecutive nests of the same individuals in different years within the Salinas do Porto Inglês.

All statistical analyses were performed in programme R ver. 4.1.2 (2021-11-01) (www.r-project.org), and data were visualised with the 'ggplot' 2 3.3.6 package (Wickham 2016). Estimates ± SE are reported.

Results

Model results

Apparent juvenile survival

Chick return rates in Maio were high compared to other plover populations with 9.27% of all individuals ringed as chicks returned and were recaptured as adults. The model that fit the data best and had the greatest explanatory power included climate effects of the natal year and pooled individuals surviving past the natal year for survival and annual variation for the probability of recapture $\Phi^0_{CLIMATE} \Phi^{1+}_C p_{TIME}$ (Table 1). This model revealed strong climatic effects on the first-year survival of juveniles (± 1 SE), where first year survival was almost ten times higher during wet years $\Phi^0_{WET} = 0.293 \pm 0.032$ than during dry years $\Phi^0_{DRY} = 0.035 \pm 0.012$ (Fig. 2). Survival of philopatric young in all subsequent years following a wet or a dry natal year was $\Phi^{1+} = 0.827 \pm 0.020$. The second-best supported model without climate effects $\Phi_{TSM} p_{TIME}$ has low model weight but showed that the overall probability of surviving the first year tended to be low: birds marked as chicks had low survival with $\Phi^0 = 0.201 \pm 0.024$ compared to subsequent years $\Phi^{1+} = 0.838 \pm 0.021$ (Table 1).

Apparent adult survival

We captured and re-sighted 730 adult Kentish plovers on nests or with chicks between 2007 and 2022. After excluding

Table 1. Model selection results for apparent survival for juvenile Kentish plovers at Salinas do Porto Inglês in Maio, Cabo Verde between 2007 and 2022, ĉ = 1.00. The top five models are shown from 18 candidate models (Supporting information for full details).

	Model structure[b]		Model statistics[a]			
			K	AIC$_c$	ΔAIC$_c$	w_i
1	$\Phi^0_{CLIMATE} \Phi^{1+}_C$	p_{TIME}	17	1638.47	0.00	1.00
2	Φ_{TSM}	p_{TIME}	17	1649.53	11.06	0.00
3	Φ_{TIME}	p_{TIME}	30	1692.15	53.68	0.00
4	Φ_C	p_{TIME}	16	1737.60	99.13	0.00
5	$\Phi^0_{CLIMATE} \Phi^{1+}_C$	p_C	17	1738.05	99.59	0.00

[a]Model statistics. Model fit was assessed by the number of parameters K, AIC$_c$, the difference of AIC$_c$ from the best fit model and Akaike weight w_i. [b]Model structure. Φ = apparent annual survival probability, p = recapture probability, CLIMATE = climate on natal year, TIME = annual variation, TSM = time-since-marking, C = constant.
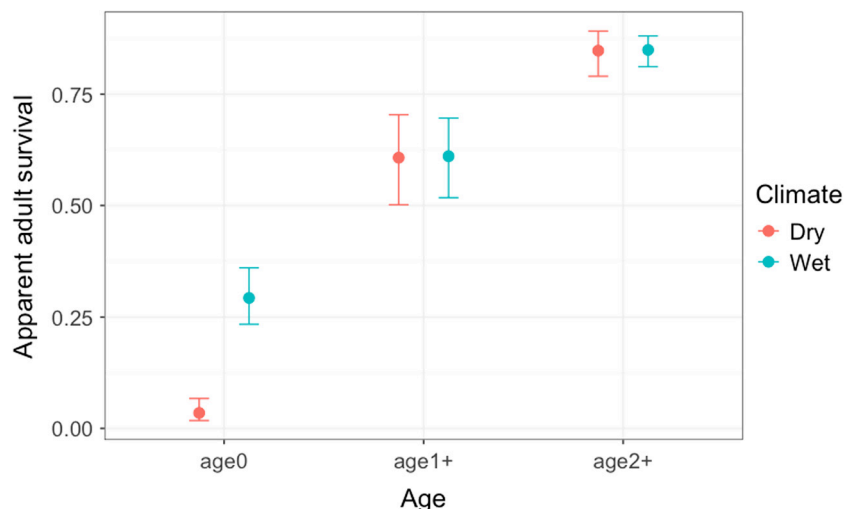
individuals ringed on the last occasion, our models were based on encounter histories for 687 individuals including 329 males and 358 females. The best supported model included an effect for time-since marking on apparent survival and annual variation in the probability of encounter $\Phi_{TSM} p_{TIME}$ (Table 2). Apparent survival (± 1 SE) was lower during the transition after first capture compared to all subsequent years ($\Phi^1 = 0.609 \pm 0.038$, $\Phi^{2+} = 0.849 \pm 0.013$, Fig. 2). The second-best supported model also included sex effects on apparent survival $\Phi_{TSM+SEX} p_{TIME}$, showing that females tended to have higher apparent survival than males, especially during the first transition ($\Phi^1_{Males} = 0.594 \pm 0.041$, $\Phi^1_{Females} = 0.622 \pm 0.040$, $\Phi^{2+}_{Males} = 0.840 \pm 0.016$, $\Phi^{2+}_{Females} = 0.856 \pm 0.014$, Table 2). Lower apparent survival among males could have included losses to permanent emigration. However, when we estimated breeding dispersal distances for males and females as the distance in metres between consecutive nests of the same individual, we found the opposite pattern that the dispersal distance of females (mean = 473.45 ± 56.06 metres, n = 224) were actually greater than males (mean = 310.43 ± 41.16 metres, n = 163). Based on estimates of apparent survival from the time-since-marking model, the average apparent lifespan of Kentish plovers in Maio was estimated to be 7.10 ± 0.57 SE years for all adults, 7.41 ± 0.69 SE years for females and 6.75 ± 0.64 SE years for males. From the third-best supported model $\Phi_{TSM+CLIMATE} p_{TIME}$, we found that survival of adult plovers tended to be slightly lower during dry years compared to wet years although the difference seems to be minimal when considering the ± SE ($\Phi^1_{WET} = 0.611 \pm 0.046$, $\Phi^1_{DRY} = 0.607 \pm 0.052$, $\Phi^{2+}_{WET} = 0.850 \pm 0.018$, $\Phi^{2+}_{DRY} = 0.848 \pm 0.026$, Table 2, Fig. 2). Although the trend model $\Phi_{TREND} p_{TIME}$ had low support, we found that adult survival tended to increase over time (> 2 AICc from the best model, intercept: 0.771 ± 0.186 and $\Phi_{TREND} = 0.113 \pm 0.031$, Supporting information). Probability of encounter (p) varied among years and overall 24.9% of the variation was explained by the number of nests (ANODEV: F(2, 15) = 2.48, p = 0.117).

Discussion

To understand how a tropical island-breeding shorebird species is impacted by variable climatic conditions and reacts to recent nest losses (Engel et al. 2023a), we analysed 15 years of data from a genetically distinct resident population of Kentish plovers on the tropical island of Maio, Cabo Verde. Analyses of our long-term field study resulted in three major findings. First, juvenile and adult survival rates of this tropical island plover population were higher than mainland populations but comparable to other island populations of *Charadrius* plovers, which might be a demographic response to reduced reproductive success that lowered stress on breeding adults that resulted in enhanced survival. Second, we found strong evidence for age effects with lower survival during the natal year than among adults. Third, the weather during the natal year had strong effects on first-year apparent survival rates of juveniles but the effects of weather on the survival of adults

Figure 2. Apparent annual survival rates ($\pm$ 95% CI) of juvenile and adult Kentish plovers in Maio, Cabo Verde under different climatic conditions. Estimates for juveniles at age0 taken from the $\Phi^{0}_{\text{CLIMATE}} \Phi^{1+}_{\text{C}} p_{\text{TIME}}$ model and estimates for adults at age1+ and age2+ taken from the $\Phi_{\text{TSM+CLIMATE}} p_{\text{TIME}}$ model.

were weak. Strong effects of climate on survival are of concern because weather conditions may become more unpredictable in the future under climate change.

Although high apparent survival rates on islands might offset recent increases in nest losses, this demographic mechanism alone does not necessarily guarantee population stability. Our results provide demographic estimates that will help conservation authorities to efficiently manage the breeding habitats of Kentish plovers on islands especially in the light of future development and global climate change.

Life-history variation

We predicted that survival rates of our study population might be high because the population is resident year-round and occurs on a tropical island near the equator. Our estimate of apparent annual adult survival of $\Phi^{2+} = 0.849 \pm 0.013$ for Kentish plovers in Maio is relatively high compared to other populations at mainland locations as estimates of apparent adult survival for mainland populations of Kentish and

snowy plover (a close relative of the Kentish plover), range from 0.61 to 0.64 in the Netherlands (Foppen et al. 2006), 0.64 ± 0.01 SE in Turkey (Sandercock et al. 2005), 0.687 ± 0.039 SE in Utah (Paton 1994), 0.756 ± 0.05 SE in Spain (Garcias and Tavecchia 2018), and up to 0.720–0.759 for a population in coastal California (Stenzel et al. 2011). Our estimate was also higher than another population of Kentish plovers in the Canary Islands (0.68, Tejera et al. 2022) but was comparable to survival rates of other tropical island populations of *Charadrius* plovers from Madagascar (0.892–0.923, Jones et al. 2022). High annual survival rates are also a common feature among endemic songbirds elsewhere in the island archipelagos of Macaronesia (Illera and Díaz 2008, Monticelli et al. 2010, Dierickx et al. 2019). Differences between island and mainland survival probabilities might be due to different life-history adaptations. High survival could also be a response that reflects immediate effects of reproductive stress on survival. Tropical island species of birds may have high survival because island climates are more stable or alternatively because they are buffered against environmental variability with high and invariant adult survival (Beauchamp 2021). In addition, site fidelity may be stronger in resident populations on islands whereas breeding dispersal may be more common in mainland populations (Stenzel et al. 1994), which is why apparent survival rates might appear higher due to less losses to permanent emigration. In addition, nest predation rates in the tropics are thought to be higher compared to temperate regions (Martin 1995), which is why low productivity might be counterbalanced with high adult survival.

Age and sex effects

Both juveniles and adults had reduced survival during the first transition after capture and increased survival in subsequent years. For juveniles, first year survival was low with $\Phi^{0} = 0.201 \pm 0.024$ SE compared to survival in subsequent

Table 2. Model selection results for apparent survival of adult Kentish plovers at Salinas do Porto Inglês in Maio, Cabo Verde between 2007 and 2022, ĉ = 1.00. The five top ranked models from the 70 candidate models are shown (Supporting information for full details).

			Model statistics[a]		
Model structure[b]		K	AIC_c	ΔAIC_c	w_i
1 Φ_{TSM}	p_{TIME}	17	2496.81	0.00	0.42
2 $\Phi_{\text{TSM + SEX}}$	p_{TIME}	18	2497.93	1.12	0.24
3 $\Phi_{\text{TSM + CLIMATE}}$	p_{TIME}	18	2498.88	2.07	0.15
4 $\Phi_{\text{TSM} \times \text{SEX}}$	p_{TIME}	19	2499.94	3.13	0.09
5 $\Phi_{\text{TSM} \times \text{CLIMATE}}$	p_{TIME}	19	2500.07	3.26	0.08

[a]Model statistics. Model fit was assessed by the number of parameters K, AIC_c, the difference of AIC_c from the best fit model and Akaike weight w_i. [b]Model structure. Φ = apparent annual survival probability, p = recapture probability, TIME = annual variation, TSM = time-since-marking, C = constant, TREND = linear time trend.

years $\Phi^{1+} = 0.838 \pm 0.021$ SE. Age differences were expected as chick mortality pre-fledging and post-fledging the first year is often high due to predation (Newton 2013). However, the observed chick return rates of almost 10% were higher than the 4% reported for a Kentish plover population in Turkey (Sandercock et al. 2005) and the 7.8% observed in a population on the Canary Islands (Tejera et al. 2022). The high return rates of plovers in Maio might be due to high site-fidelity and low emigration out of their natal area.

Adult survival was also lower during the first transition after capture with 0.61 ± 0.04 SE compared to subsequent years with 0.85 ± 0.01 SE and such losses could be due to various reasons including emigration from the study site, mortality, handling effects on survival or the presence of transient breeders (Sandercock 2020, Jones et al. 2022). Apparent adult survival Φ^{2+} rates were similar to the survival rates of juveniles that survive past year one Φ^{1+}. Thus, once individuals reach one year and more, high survival rates seem to be maintained even at older age as opposed to mallards *Anas platyrhynchos* where yearlings demonstrate higher survival than older adults ($\geq$ 2 years old) (Dufour and Clark 2002).

We did not find large differences in adult survival or breeding dispersal between the sexes, which does not deviate from our expectations as Kentish plovers in Maio are monogamous and share biparental care (Carmona-Isunza 2015). Joint incubation might reduce reproductive costs in both sexes, but it could also equalise predation risk during parental care duties (Jones et al. 2022). Our results agree with previous analyses that found no difference in apparent survival between the sexes but higher encounter rates for males than females in mainland populations of Kentish plovers (Sandercock et al. 2005).

Climate as a driver

Annual variation in the apparent survival of juveniles was strongly affected by the local weather conditions in the natal year, where survival was almost ten times higher during wet years. The same pattern was observed in adults, but the effect was moderate, and survival tended to be slightly increased in wet years compared to dry years. Higher annual survival in wet years is a common feature of tropical birds on arid-zone islands (Gibbs and Grant 1987, Curry and Grant 1989), including the Raso lark *Alauda razae* in Cabo Verde (Brooke et al. 2012). Variation in survival could be explained by the fact that droughts negatively influence body condition of juveniles and adults through low food availability, which reduces survival due to higher mortality linked to poor body condition. Juveniles might not be able to find enough food to survive, but it could also be that the parents are in poor condition and are thus not able to provide adequate parental care leading to higher juvenile mortality. Keller et al. (2002) also showed that two species of finches at the Galápagos islands showed higher levels of inbreeding depression in years of low food availabilities, which were linked to reduced recruitment probability and lower juvenile and adult survival. In addition, in dry conditions, local predators such as the brown-necked raven *Corvus ruficollis* also experience low food availabilities.

Due to the reduced availability of their typical prey items such as insects or small mammals, they might shift their foraging strategy and focus on shorebird nests and juveniles explaining higher juvenile mortalities during these years. Alternatively, it might also be that individuals disperse out of the study area in search of better conditions. Although there might be locations on the island that birds might disperse to, it seems unlikely given the island's small size and therefore we suspect that off-site dispersal is an unlikely explanation. In challenging conditions, such as droughts, individuals often face a trade-off between survival and reproduction (Reznick 1985, Santos and Nakagawa 2012). Some long-lived tropical songbirds can skip a breeding season or reduce their breeding activity as a buffer against droughts (Martin and Mouton 2020). Our evidence for links between juvenile survival and annual variation in weather is an important finding as climate change is expected to increase the frequency, duration, and severity of droughts across the globe (Dai 2012, Cook et al. 2014, Trenberth et al. 2014). Species may be able to cope with adjustments to reproductive activity, but we still do not know the long-term effects of prolonged droughts.

Relevance of high survival rates to population viability

The high adult survival of $\Phi^{2+} = 0.849 \pm 0.013$ SE for Kentish plovers in Maio could help to offset the long-term declines in nest survival that have occurred during the same study period (Engel et al. 2023a). If incubation is costly, then nest losses could reduce parental investment and increase survival if pairs do not renest after nest loss. Indeed, in northern wheatears *Oenanthe oenanthe*, higher parental effort in some habitats was shown to be associated with reduced adult survival compared to habitats where parental effort and thus energy expenditure was lower (Low et al. 2010). Therefore, in Maio, higher adult survival might be a response to reproductive losses this population is facing (Engel et al. 2023a) as to maintain population persistence in a variable tropical island environment. High adult survival is also thought to contribute to improved population viability for endemic songbirds elsewhere in Macaronesia, including the Raso lark in Cabo Verde (Dierickx et al. 2019) and the Azores bullfinch (*Pyrrhula murina*, Monticelli et al. 2010). From a life-history perspective, it is also expected that long-lived species trade-off reproductive invest with higher adult survival because individuals may have multiple opportunities for successful reproduction throughout their lifetime (Charlesworth 1994, Low et al. 2010). Indeed, shorebirds are known to have high longevity (Sandercock 2003) and we found that the expected average lifespan of the Kentish plovers in Maio is roughly seven years. Our new estimates of lifespan for island plovers are higher than available estimates from mainland populations of mountain plover (1.92 ± 0.17 SE years) (Dinsmore et al. 2003) and snowy plovers (3.5 ± 2.1 SE years) (Windsor 2020) but more closely approach island populations of Kittlitz's plover (9.72 ± 1.11 SE years) and Madagascar plover (9.36 ± 1.35 SE years, Jones et al. 2022).

Our results are encouraging for conservation of the genetically distinct Kentish plover on Maio island, but high apparent annual survival rates do not necessarily ensure stable population numbers (França and Marini 2010). Population declines of waders in Europe are thought to be due to poor productivity in agricultural landscapes despite high survival among adults (Roodbergen et al. 2012, Ewing et al. 2023). Therefore, it is important to consider different vital rates at all life stages and carry out a population viability analysis for island populations to predict long-term population trends. In addition, global climate change is expected to lead to more frequent, severe, or prolonged droughts, and the effects might be particularly pronounced on islands. Our study has found that the plover population in Maio might show demographic flexibility by potentially buffering low population productivity with better adult survival, but it is still necessary to develop measures that could help mitigate the effects of climate change. Kentish plovers depend on sufficient seasonal rainfall for successful reproduction (Engel et al. 2023a), and one management measure to improve habitat conditions would be to mechanically pump water into areas of the Salinas do Porto Inglês wetland that typically fill up during the rainy season. Using wind turbine power and large pumps, it would be possible to pump water from the nearby sea into the lagoon and regulate water levels in a controlled manner, especially during years of drought (Poompavai and Kowsalya 2019). Higher water levels should improve insect productivity and thereby increase food availability for breeding pairs of plovers.

Our study highlights that although both juvenile and adult survival for the Kentish plover population are high in the Maio population, but it is unclear if reproductive success is high enough to maintain population viability. We highly suggest that population viability and extinction risk under different environmental conditions should be investigated in a follow-up study. We also encourage conservation authorities in Cabo Verde to test management actions such as flooding that could help to improve productivity and population persistence.

Author contributions

Noémie Engel: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Methodology (equal); Project administration (equal); Writing – original draft (equal). **Brett K. Sandercock:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Methodology (equal); Software (equal); Supervision (equal); Validation (equal); Writing – review and editing (equal). **András Kosztolányi:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Methodology (equal); Software (equal); Supervision (equal); Validation (equal); Writing – review and editing (equal). **Andreia Adrião:** Data curation (equal). **Alex Tavares:** Data curation (equal). **Romy Rice:** Data curation (equal); Writing – review and editing (equal). **Tamás Székely:** Conceptualization (equal); Data curation (equal); Supervision (equal); Validation (equal); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.pvmcvdnsh (Engel et al. 2023b).

Supporting information

The Supporting information associated with this article is available with the online version.

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