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Long-term decline in nest survival of a ground-nesting shorebird on a tropical island

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ABSTRACT

Tropical islands harbour a disproportionally high number of endemic species, which face increasing threats due to habitat loss, disturbance and introduced alien predators. Long-term demographic studies are needed to understand how such threats may impact on population productivity. We report an investigation of a key demographic parameter, nest survival, over a 13-year period in a small ground-nesting shorebird on the island of Maio (Cabo Verde). Similar to many tropical islands, Maio is expected to face increased tourism, disturbance, and potential loss of nesting habitats. We monitored over 700 nests of the largest, year-round resident breeding population of Kentish plover in the Atlantic Ocean archipelago. Our work produced three important findings. First, we show that nest survival differed among the major habitats of the main breeding site, the Salinas do Porto Inglês, because nests in the salt-extraction area had higher daily survival rates DSR = 0.9654 ± 0.0076 SE than nests in grasslands DSR = 0.9557 ± 0.0038 SE. The salt-extraction is a dynamic habitat that is naturally regulated by rainfall and sea water inflow and managed with traditional methods for salt-extraction. Kentish plovers breed on small islets surrounded by salty water where mammalian predators may have restricted access. Second, we found that breeding densities of plovers decreased from 0.11 nests/ha to 0.03 nests/ha over 13 years. Last, we show that nest survival declined from 0.9784 ± 0.0107 in 2007 to 0.8967 ± 0.0401 in 2019. We suggest that the declining breeding density and nest survival may be driven by a combination of ecological factors including predation by native and introduced species, and by increased human disturbance. To help maintain sustainable levels of nest survival and to ensure long-term persistence of this Kentish plover population, we propose to incorporate traditional Salinas management into direct conservation actions, to reduce human disturbance and manage nest predators to help nest survival on tropical islands.

1. Introduction

Tropical islands are the powerhouses of evolutionary adaptation and offer great opportunities to understand patterns of diversity,

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species diversification, and trait evolution within and among archipelagos (Whittaker et al., 2017). Islands are often biodiversity hotspots which harbour high levels of endemism and of unique species and subspecies (Pruett et al., 2010; Veron et al., 2019). However, islands are also among the most endangered systems in the world and island populations are particularly threatened due to human-induced processes (Kueffer and Kealohanuiopuna 2017, Whittaker et al., 2017, Kelley et al., 2019). Human activity is disrupting natural ecosystems globally through unsustainable practices, and oceanic islands display one of the highest levels of human-driven biodiversity loss (Novacek and Cleland 2001, Waldron et al., 2017). Tourism is often the largest and fastest-growing economic sector on islands, and construction of urban structures such as hotel resorts or other tourism-related infrastructure can lead to habitat loss and fragmentation threatening island biodiversity (Brooks et al., 2002; Otto et al., 2017; Steibl et al., 2021). In addition, human activity can threaten island populations by the introduction of alien species of competitors or predators (Russel et al., 2017), which can contribute to accelerated rates of extinction of native and endemic island populations (Kiehn et al., 2000, Gaston et al., 2003, Clavero and García-Berthou, 2005). Introduction of mammalian predators to oceanic islands has had particularly detrimental consequences on the native avifauna by increased rates of nest and adult predation, and therefore causing the extinction of multiple bird species (Blackburn et al., 2004; Hilton and Cuthbert, 2010, Trevino et al., 2007).

To understand how extant populations on tropical islands are influenced by anthropogenic threats and to identify the ecological pressures influencing reproductive success of wild populations, it is crucial to understand spatial and temporal patterns of demographic variation (Que et al., 2014, Specht et al., 2020). Many species of tropical birds are buffered against environmental variability with high and invariant adult survival, and variation in productivity and juvenile survival can have a greater effect on population dynamics (Reed et al., 2015; Hilde et al., 2020; Jones et al., 2022). Here, we focus on nest survival, which is a key component of productivity that can influence individual fitness and population growth because most demographic losses occur at early life-stage and most nest failures are due to predation (Sæther and Bakke, 2000). Information on variation in nest survival and its underlying drivers can be used to assess the status of populations and inform conservation strategies (Doherty et al., 2014, Que et al., 2014). Nest survival is a key vital rate with implications for population growth (Allen et al., 2022) that can be used as a tool to assess population status and evaluate threats to population persistence. Understanding how environmental factors drive the persistence of avian populations requires long-term information on breeding and nesting success to reveal the links between demography and the ecological drivers of long-term demographic trends (Maxson et al., 2007, Wilson et al., 2007, Smith and Wilson, 2010, Crombie and

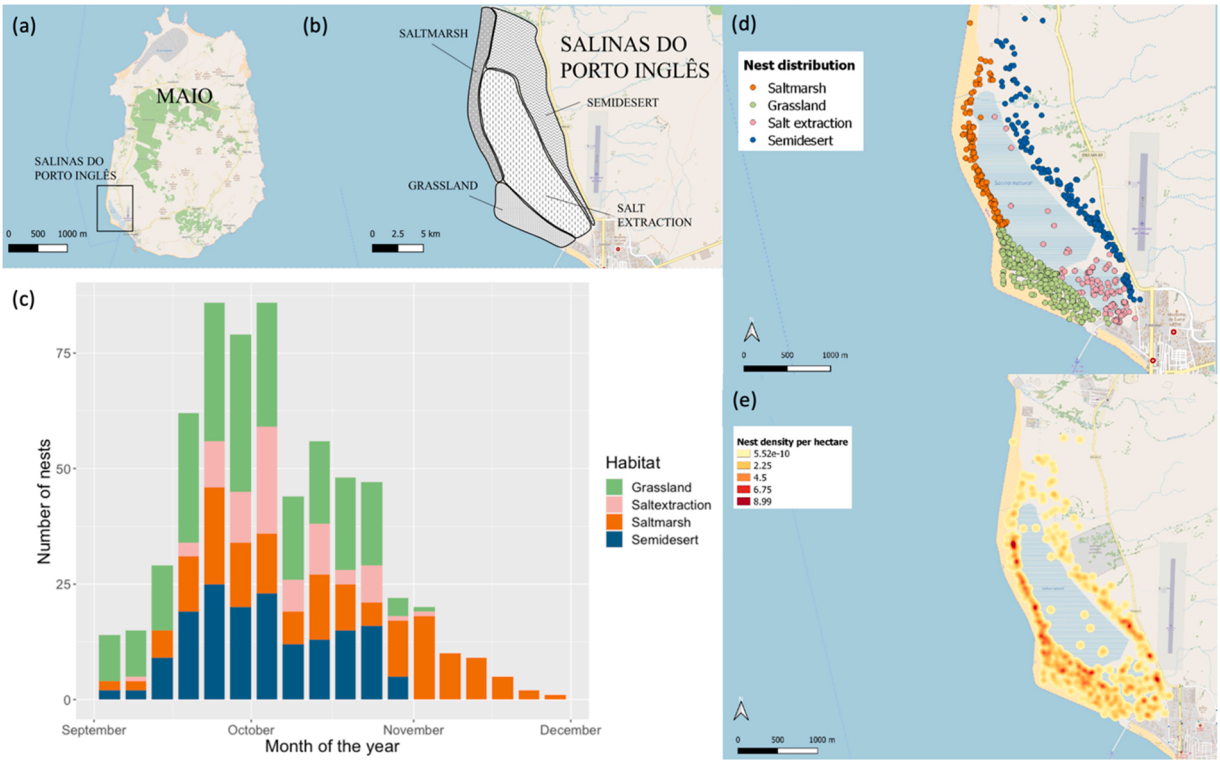

Fig. 1. Spatial and temporal patterns of nesting among Kentish plovers in Maio, Cabo Verde, 2007–2019. (a) Map showing the island of Maio with an inset for the location of our study area at Salinas do Porto Inglês, (b) the main breeding habitats shown by shaded polygons: grassland (60.39 ha), semidesert (199.88 ha), saltmarsh (76.68 ha) and the salt-extraction site (nesting substrate: 35.90–161.90 ha). (c) Number of Kentish plover nests initiated per 5-day window during the 4-month breeding seasons of 2007–2019 (N = 635 nests). (d) Kentish plover nest locations between 2007 and 2019 (N = 765 nests). Point colour indicates the four nesting habitats (grassland, N = 309 nests, semidesert, N = 187 nests, saltmarsh, N = 159 nests, salt-extraction, N = 110 nests). (e) A heatmap with nest densities across the study area at Salinas do Porto Inglês between 2007 and 2019 (N = 765 nests). The intensity of colour represents higher nest densities.

Arcese, 2018, Specht et al., 2020). However, many long-term studies consider only the temporal variation in demography with less attention to how such changes may vary over space, particularly over fine-scale variation among different local breeding habitats (Murphy, 2001). As a consequence, there is an increasing focus on integrating temporal and spatial information on breeding patterns. Therefore, long-term studies that consider habitat variation in combination with temporal trends are needed to identify the biotic and abiotic factors that may drive demographic losses, variation in population persistence and facilitate effective conservation decisions.

Here, we use a small cosmopolitan ground-nesting shorebird, the Kentish plover (*Charadrius alexandrinus*) to understand processes that may influence population demography. We investigated patterns of nest survival based on 13 years of breeding data from a resident population of birds on the tropical island of Maio, Cabo Verde (15.17° N, 23.21° E). The Kentish plover is increasingly used as a model system in evolutionary ecology due to its highly variable breeding system (Kosztolányi et al., 2006; Székely et al., 2006; AlRashidi et al., 2010; Székely, 2019; Gómez-Serrano and López-López, 2014). The species is classified as 'Least Concern' in the IUCN list, but the overall global population is declining (IUCN, 2019) and information on long-term patterns in demography and nest survival are required. The breeding population of Kentish plovers at Maio is genetically distinct from mainland populations in Africa and Europe, increasing its importance as a unique target of conservation (Almalki et al., 2016). The Kentish plover population on Maio mainly breed in a large saline wetland composed of four different habitat types: grassland, semidesert, saltmarsh, and salt-extraction, that each vary in their substrate type, water surface and vegetation characteristics (McDonald et al., 2020, Pereira Neves, 2016). Such habitats face potential declines as a result of touristic development, urbanisation, and cattle grazing (WTTC, 2018). Kentish plover nests are placed in shallow scrapes on the ground, typically in open areas near water, making them vulnerable to both predation and disturbance. In Maio, eggs of Kentish plovers are depredated by nocturnal ghost crabs (*Ocypode cursor*), and also face increasing predation pressure from brown-necked ravens (*Corvus ruficollis*) as a generalist avian predator and introduced mammals such as feral dogs and cats (Engel et al., 2020). The island environment is xeric, and the plover population depends on seasonal rainfall for breeding, thus climate change may disrupt breeding conditions and breeding phenology (Kubelka et al., 2018).

The objectives of our study were: (1) to investigate long-term and seasonal patterns in timing of breeding, and (2) to determine annual variation in breeding densities across different nesting habitats. In addition, we also aimed (3) to estimate long-term trends in nest survival and (4) the spatial patterns of breeding success across different breeding habitats. Our overarching goal was to evaluate the patterns and potential causes of nest failures so that conservation organisations can develop targeted actions to protect ground-nesting shorebirds such as the Kentish plover that will be relevant to other similarly vulnerable populations of island birds.

2. Methods

2.1. Study site

Fieldwork was carried out during the 13-year period of 2007–2019 on the island of Maio, Cabo Verde (15° 13′N, 23° 10′W, see Fig. 1), a volcanic archipelago off the west coast of Africa in the eastern Atlantic Ocean. Kentish plovers in Maio can breed throughout the year, but the core breeding season is during a ~4-month period between September to December, with less frequent breeding occurring between January and August. Between 2007 and 2019, we found a total of 755 nests. The majority of nests were found between September to December (98%, 739 nests) and only 16 nests (2%) were found between January and August with egg laying dates between 26th March and 30th June. Therefore, throughout this study, we focus on the main breeding season during the wet season in September to December (Székely et al., 2008). The study area was the Salinas do Porto Inglês, a protected area classified as Protected Landscape since 2003, and a Ramsar Site since 2013 harbouring important biodiversity and the largest permanent wetland in Maio of ~535 ha (Oliveira, 2013; Pereira, 2016). About 100–200 breeding pairs can be found in that area, and pairs typically produce between 50 and 100 clutches each breeding season (Carmona-Isunza et al., 2015). The onset of breeding depends on rainfall during the months of July to September; generally, the months of October to June are dry with no rainfall. In dry years, breeding activity is low likely due to a lack of food availability. Here, we censored the year 2017 from most analyses because it was a particularly dry year with relatively few nesting attempts. The predation pressures on the local population of Kentish plovers are high and most egg losses are attributed to predation by brown-necked ravens and ghost crabs (González et al., 2017). The study area was composed of four distinct habitats that differ in their nest cover availability (McDonald et al., 2020, see Fig. 1): The *grassland* was comprised mainly of short grass with a small number of shrubs on a sandy substrate, providing good nesting cover. The *saltmarsh* represented an intertidal sand flat connected to the beach and colonized by an introduced halophyte plant, *Sesuvium portulacastrum,* a sprawling perennial herb that can reach up to 30 cm of height (Dehury et al., 2022), although in the saltmarsh the plant usually does not reach this full height and provides little nesting cover. The *semidesert* was constituted of mud, volcanic rocks, and acacia trees and the salt-extraction represented a saltern area where salt is being extracted as a local industry. During the breeding season, the *salt-extraction* site is often filled with water but features small protruding 'islets' where Kentish plovers can breed. The grassland and semidesert were located on the north side of the Salinas Porto Inglês, whereas the semidesert was located on the south side of the Salinas do Porto Inglês and the salt-extraction site was located between the semidesert, the saltmarsh and the grassland. The boundaries of these four different habitats were defined and their areas were calculated in program QGIS version 3.6.1 (QGIS Development Team 2019).

2.2. Field methods

All data collection followed a standard protocol for the breeding ecology of plovers (Székely et al., 2008). Nest searching was carried out using a mobile hide, a vehicle or on foot. Kentish plovers typically incubate their clutch for 25 days before eggs hatch and at first discovery of a clutch, eggs were floated in a jar filled with water and egg buoyancy was used to estimate stage of incubation, egg

laying dates from a standardised egg floatation chart (Table S1). The term egg laying date throughout this study refers to the estimated date of clutch completion. To estimate nest survival, nests were monitored at two- to four-day intervals. Nest fates were classified as follows: *hatched* if at least one egg produced a chick, *depredated* if there was confirmed evidence of a predation event determined by nest cameras or by visible predator marks/tracks left in the nest surroundings, disappeared if the eggs disappeared before the 18th day of incubation and were unlikely to have hatched, *abandoned* if the clutch had not been incubated for at least 24 h, and *unknown* if the eggs disappeared after the 18th day of incubation and there was no evidence as to whether the nest hatched or failed. All statistical analyses were performed in programme RStudio version 1.1.383 (RStudio Team, 2016), and data were visualised with package ggplot2 (Wickham, 2016). Estimates of demographic rates are presented as mean ± standard error unless stated otherwise.

2.3. Seasonal and annual breeding patterns

To test whether the timing of mean egg laying dates advanced or was delayed over the years and among habitats, we performed a Generalised Linear Model (GLM) using a Gaussian error distribution with an identity link function. The response variable was the Julian Day of egg laying and the explanatory variables included year as a continuous variable and habitat as a factor. We included an interaction between year and habitat to assess whether mean egg laying changed differentially according to different habitats.

To assess how the distribution of timing of breeding varied within seasons, we divided the breeding season into eighteen 5-day intervals (from the 1st September until the 30th November) for each year and calculated the number of nests initiated in each of the 5-day periods. We then included the counts, where higher values indicated that more breeding attempts were initiated during this interval, as a response variable into a GLM using Poisson error distribution with a log link function. Explanatory variables included year as a continuous variable, habitat as a factor and Julian day of the season (the 3rd day of the 5-day interval) both as a linear term and a quadratic term. We also included all two-way interactions between habitat, year, Julian day of the season and the quadratic term for Julian day in the model.

We investigated seasonal and long-term annual trends in overall reproductive investment of female Kentish plovers. We utilised variation in average egg volume per clutch as an indicator of reproductive investment (Watson et al., 2015). Egg volume (V) was calculated using the following formula: $V = L \times B^2 \times Kv$, where L is egg length in mm, B is egg width in mm and Kv is a constant for egg shape estimated to be 0.486 for the conical eggs of Kentish plover (Székely et al., 1994). To test for an effect of year, habitat, and laying date on average egg volume per clutch, we used a GLM with average egg volume per clutch as response variable and a Gamma error distribution with an inverse link function. Explanatory variables included year as a continuous variable, habitat as a factor and laying date in Julian Day. We included interaction terms between habitat and year, habitat and Julian Day and year and Julian Day.

Last, we investigated trends in clutch size across a season, across years and among habitats. We used a GLM with clutch size as a response variable and a Poisson error distribution with a log link function. Explanatory variables included year as a continuous variable, habitat as a factor and laying date in Julian Day. We also included interaction terms between habitat and year, habitat and day of the season and year and day of the season. For all the above GLMs we used the dredge function in R (Burnham and Anderson, 2002) to carry out model comparisons. Model selection was based on the differences in Akaike Information Criterion corrected for small sample sizes (AICc). We consider the models with the lowest AIC_c value as the top models and we discuss the results from these in the results. The full GLM results of the top models are included in Supplement B.

2.4. Breeding density

To investigate whether nest densities varied among years and habitats, we calculated the number of nests per hectare using maximum available area estimates for each separate habitat calculated in QGIS: grassland = 60.39 ha, semidesert = 199.88 ha, saltmarsh 76.68 ha, and salt-extraction = 161.90 ha. However, the salt-extraction area was a dynamic habitat and water levels can vary among and within years leading to differences of available nesting substrate in this particular habitat. In our analyses, we used the maximum available nesting surface which represents the area that would be available to nesting when there is no water present. In this way, we ensure to encompass all possible nesting surfaces. However, the total extent might not represent available nesting habitat at all times, so we also calculated minimum nesting surface available by using satellite images from Google Earth from one year available (February 2022). Specifically, we calculated the area of the potentially suitable nesting substrate of non-flooded land within the salt-extraction by drawing polygons around all land areas that consistently protrude above the water and calculated the total surface area of the polygons. Areas of land that protrude above water are clearly identifiable from lack of white salt residue of salt on Google images. The minimum available substrate area with high water levels was 35.90 ha, which is 22.17% of the entire salt-extraction area.

Some nests could have been destroyed before discovery or overlooked by observers and our nest densities are therefore minimum estimates. To assess the effects of habitat and year on breeding densities, we performed a GLM using the natural logarithm of nest density as response variable with a Gaussian error distribution and an identity link function. Explanatory variables included year as a continuous variable and habitat was entered as a factor. We also tested for an interaction between year and habitat. A map of nest distributions with a heatmap for relative densities was produced using OpenStreetMaps (©OpenStreetMap contributors) in program QGIS. To calculate an index of habitat selection based on the area of available habitat, we used the widesI function of the R package adehabitatHS to carry out a Manly selection analysis (Manly et al., 2007; Calenge, 2011). A habitat is selected for if the Manly selectivity ratio W_i is > 1.

Table 1
Best performing models predicting the breeding activity of Kentish plovers in Maio, Cabo Verde between 2007 and 2019. Models were testing for effects of different predictors (a) on mean laying dates (breeding phenology) (b) on breeding frequencies (number of nests per 5-day intervals across the season as response variable), (c) on average egg volume per clutch, (d) on clutch size, and (e) on nest densities. Model selection was based on ΔAIC_c, which is the difference between Akaike Information Criterion values corrected for small sample sizes between each model and the top-ranked model. Only models of $\Delta AIC_c < 2$ are presented. Df is number of parameters in the model, *wi* is the Akaike model weight, Int. is intercept, Hab. is habitat and JD is Julian Day, Yr. is Year, for continuous terms retained in the model, their parameter estimates are shown and for categorical terms a + sign indicates if the variable was retained in the model.

Response	Rank	Parameter										Df	ΔAIC_C	*wi*
		Int.	Hab.	Year	Hab.*Year									
(a) Breeding phenology	1	127.70	+	0.07	+							9	0.00	0.861
		Int.	Hab.	JD	JD^2	Year	Hab.*JD	Hab.*JD^2	Hab.*Year	JD* Year	JD^2 * Year			
(b) Breeding frequency	1	290.90	+	1.16	-0.01	-0.22	+	+	+		< 0.01	17	0.000	0.271
	2	747.40	+	-2.16	< −0.01	-0.45	+	+	+	< 0.01		17	0.212	0.244
	3	-4492.00	+	35.22	-0.07	2.15	+	+	+	-0.02	< 0.01	18	1.053	0.160
		Int.	Hab.	Year	JD	Hab.*JD	Hab.*Year	JD* Year				Df	ΔAIC_C	*wi*
(c) Average egg volume per clutch	1	< 0.01		< −0.01	< −0.01			< 0.01				5	0.000	0.322
	2	< 0.01			< −0.01							3	0.810	0.215
	3	< 0.01		< 0.01	< −0.01							4	1.555	0.148
	4	< 0.01										2	1.803	0.131
		Int.	Hab.	Year	JD	Hab.*JD	Hab.*Year	JD* Year				Df	ΔAIC_C	*wi*
(d) Clutch size	1	0.94										1	0.000	0.479
	2	5.08		< −0.01								2	1.951	0.181
		Int.	Hab.	Year	Hab.*Year							Df	ΔAIC_C	*wi*
(e) Breeding density	1	116.20	+	-0.06								6	0.00	0.912

2.5. Daily nest survival

We estimated daily survival rates (DSR) using the R package RMark (Laake, 2013) as an interface to the nest survival procedure of program MARK (version 9.0). Of the 771 nests found between 2007 and 2019, a subset of 517 nests (67%) were included in the nest survival analysis because monitoring was adequate, and we had complete information on nest fate. We set up encounter histories for each nest with four input variables: (a) the day of the breeding season the nest was found, (b) the last day the nest was checked and still alive, (c) the last day the nest was visited and thus when nest fate was determined and (d) the fate of the nest (0 = hatched, 1 = failed) (Dinsmore and Dinsmore, 2007; Cooch and White, 2014). Nests that had at least one egg hatch were classified as successful, and nests that were depredated, disappeared, or abandoned were classified as failed. We censored nests if the fate was unknown. If a nest was successful, the dates (b) and (c) were set to be the same, whereas if a nest failed, then the dates (b) and (c) were different and bracketed the period of failure. For some of the failed nests, we did not know the exact day when the nest was last checked and active. Nests were checked every 2–4 days under our protocol, and we used an estimate of 3 days that a nest was last active prior to the end date. We excluded year 2017 from the analysis because it was a drought year without rainfall resulting in a small sample of only 12 nests with reduced clutch size and smaller eggs that had high rates of abandonment. Day 1 was defined as the earliest day we found the first nest across all the breeding seasons combined (day one = 11th September, and the last date the final nest was completed = 8th December for a total monitoring period of 89 days).

We fitted 8 candidate models to investigate seasonal, yearly and spatial trends of DSR (effective sample size = 6390). Seasonal changes in nest survival are common in shorebirds (Sandercock et al., 2015), and we fitted a linear time trend model, a quadratic time trend model and one considering season as a group factor. Linear and quadratic models tested for variation in DSR that might be related to seasonal changes in vegetative cover, number of active nests, or predator activity. To explore annual variation and long-term trends in nest survival (Gaget et al., 2019), we built a model considering year as a categorical group and one that considered a linear effect of year over the 13-year study. To test for habitat-specific variation in DSR (Dinsmore et al., 2002), we included habitat as a categorical covariate with four levels for grassland, saltmarsh, salt-extraction and semidesert habitats. A factorial model with year and habitat was not possible to build because there were too many parameters due to the sparse number in nests some years, but we built an additive model including the main effects of habitat and years as a group on daily survival rates. Last, we also fit a null model that assumed that DSR is constant during the breeding season. To select the best model, we used hierarchical model selection based on the Akaike's Information Criterion (AIC_c) corrected for small sample sizes (Burnham and Anderson, 2002). Models with the lowest $\Delta QAIC_c$ and the highest Akaike weights (w_i) are the best supported models (Burnham and Anderson, 2002). Average yearly estimates were obtained using a model with year as a grouping factor.

For Kentish plovers, the typical exposure period for a 3-egg clutch is 25 days from the start of egg laying to the day the chicks leave the nest. To obtain a period estimate of nest survival (S_p), we raised the estimated DSR to the 25th power: $S_p = S_d^{25}$. We then used the delta method to calculate the SE of the period survival with the following formula: $SE(S_p) = \sqrt{SE(S_d)^2 \bullet (25S_d^{24})^2}$, where S_p is period survival and S_d is the real parameter estimate of the daily survival rate (Powell, 2007). Extrapolations from constant rates can be biased if daily survival rates vary with nest age or seasonally but that was not the case in our study (Weiser, 2021).

3. Results

3.1. Seasonal and annual breeding patterns

We found evidence of a significant interaction between the year of the breeding season and habitat on mean egg laying days (GLM,

Table 2
Summary of first egg laying date, last day of egg laying, the median egg laying date, and the duration of the breeding season (N = 677) of Kentish plovers in Maio, Cabo Verde from 2007 to 2019. Dates are shown in Julian Days of the year where 247 = 4th September, 274 = 1st October, and 312 = 8th November.

Year	First – Last egg laying date	Median date	Duration in Days	Number of Nests
2007	260 – 313	272	53	34
2008	255 – 312	264	57	19
2009	251 – 333	275	82	71
2010	244 – 314	269	70	136
2011	229 – 282	266	54	10
2012	252 – 306	288	54	69
2013	238 – 305	274	67	83
2014	243 – 325	278	82	70
2015	242 – 322	269	80	70
2016	246 – 332	284	86	65
2017	Drought year			12
2018	250 – 305	272.5	55	34
2019	257 – 295	276	38	16
Mean ± SE	247.3 ± 2.5 – 312.1 ± 4.3	274.0 ± 2.02	64.8 ± 4.4	677

Table 1, and S2), indicating that the long-term changes in timing of egg laying were habitat dependent. The interaction was largely driven by a delay in the onset of breeding in the saltmarsh across years (1.5 days per year) compared to nests laid in the grassland and semidesert habitats where timing of egg laying did not change across years (Table 1, S2, and Figs. S1, S2). Mean egg laying dates also varied among habitats, and Kentish plovers initiated breeding earlier in the grassland (mean Julian Day: 273.43 ± 0.92 SE) and semidesert (mean Julian Day: 275.37 ± 1.12), before starting to breed in the salt-extraction (mean Julian Day: 277.98 ± 1.30) and saltmarsh habitats (mean Julian Day: 285.91 ± 1.55). First and last egg laying dates were typically 4th September to 8th November with a median egg laying date of 1st October, and an average duration of 65 days for the breeding season per year (Table 2).

Across years, the number of nests laid in 5-day intervals throughout the season tended to decrease, however we identified a significant interaction between year and habitat indicating that the pattern was habitat dependent (GLM, Table 1, Table S3). The decrease in breeding frequencies was the highest in the saltmarsh and the lowest in the grassland (Table S3). The distribution of breeding frequencies typically followed a concave pattern within a season, initially increasing before decreasing (Fig. 1c). However, we also found significant interactions between habitat with day of the season on breeding frequencies (Table 1), indicating the frequency of nests being laid varied among habitats. The number of nests laid during a breeding season in the grassland, salt-extraction, and semidesert increased rapidly and then decreased (see Table S3 and Fig. 1c). In contrast, the number of nests laid in the saltmarsh tended to increase more slowly compared to grassland but breeding in this habitat continued for longer (Table S3 and Fig. 1c).

We found evidence that mean egg volume per clutch decreased over the years and also decreased over a breeding season, however we also found a significant interaction between day of the season and year, indicating that the decrease in egg volume was less pronounced in later years (see Table 1, and S4). Mean egg length was $L = 28.98 \pm 0.11$ mm (N = 1790) and mean egg breadth was $B = 26.46 \pm 0.11$ mm (N = 1790). Annual variation in egg length ranged from 27.96 ± 1.05 mm to 29.36 ± 0.49 mm and egg width ranged from 25.91 ± 1.02 mm to 27.49 ± 0.97 mm (Table S5). The average egg volume per clutch over the breeding season was 8.38 ± 0.23 cm^3 (Fig. S3).

We found no evidence that clutch size differed among breeding habitats, changed during the breeding season or across the study period (see Table 1). Modal clutch size was 3 eggs, with little variation among years or across habitats (Fig. S4).

3.2. Breeding densities

Breeding densities decreased over the study period from 0.11 nests/ha in 2007–0.03 nests/ha in 2019 (GLM, year: −0.06, $p < 0.01$, see Table 1, and S6). The highest breeding densities were in the grassland, the first habitat where the plovers start breeding in a given season (see Table 1, and S3). Information on the exact location of nests was known for a total of 765 nests between 2007 and 2019 (see Fig. 1), of which 309 nests were found in the grassland, 187 in the semidesert, 159 in the saltmarsh, and 110 in the salt-extraction (see Table S7 for yearly details). Overall nest density was 0.17 ± 0.03 nests/ha, with habitat-specific estimates of 0.39 ± 0.09 nests/ha in the grassland, 0.07 ± 0.02 nests/ha in the semidesert, 0.05 ± 0.02 nests/ha in the salt-extraction when using the maximum area available and 0.41 ± 0.2 nests/ha when considering minimum substrate available, and 0.16 ± 0.03 nests/ha in the saltmarsh (see Fig. 1). There was strong habitat selection for grassland ($w_i = 3.33 \pm 0.15$ SE, 95% CI = 3.04–3.62) and saltmarsh ($w_i = 1.36 \pm 0.10$ SE, 95% CI = 1.16–1.56, Fig. S5). We found no evidence of a statistical interaction between year and habitat on breeding densities (see Table 1).

3.3. Daily survival rates of plover nests

Information on nest fate was available for 739 nests between 2007 and 2019. A total of 264 nests hatched and produced at least one chick (35.7%), 239 nests disappeared before the 18th day of incubation and it was assumed that they were unsuccessful (32.3%), 70 nests were depredated (9.5%) and 39 nests were abandoned (5.3%) (Fig. 2). Losses to nest abandonment were especially high in the drought year of 2017. The fate of an additional 127 nests could not be determined (17.2%) because nest monitoring was not systematic or because the eggs disappeared after the 18th day of incubation, and these nests were censored from our analysis. Annual hatching

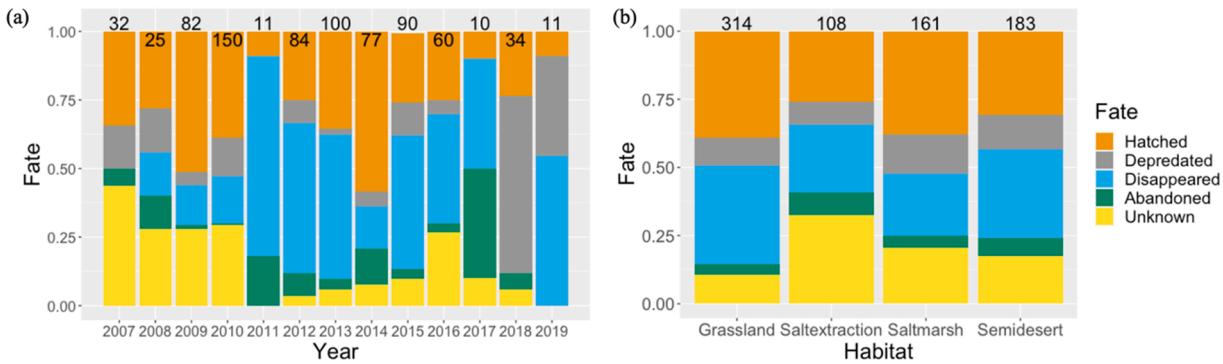

Fig. 2. The fates of Kentish plover nests in Maio, Cabo Verde (N = 766) among (a) the different study years 2007 – 2019 and (b) the four different habitats: grassland, salt-extraction, saltmarsh and semidesert. Number of nests included shown above the bars.

success ranged from 0.00 to 0.58 between 2007 and 2019 (N = 739).

From the intercept-only model where DSR was constant, we obtained an overall estimate for average survival across all years of DSR of 0.9569 ± 0.0025 SE (0.9520 – 0.9617 95% CI). Period survival for a nest surviving the period of 25 days until hatching was 0.332 ± 0.022 SE (0.292 – 0.377 95% CI). The best supported model fitting the nest survival data was an additive model with annual variation and habitat effects in DSR ($w_i > 0.86$, Table 3, Fig. S6). We had weak support for a trend model that daily nest survival decreased over the years (w_i =0.01, see Table S8 and Fig. 3), with nests in 2007 having DSR of 0.9784 ± 0.0107 whereas nests in 2019 had a DSR of 0.8967 ± 0.0401. The extrapolated nest success for 25-day exposure period declined from 0.579 ± 0.158 SE in 2007–0.066 ± 0.073 SE in 2019. The best model for seasonal changes was a quadratic trend over the breeding season with low survival rates at the beginning and the end of the season and higher survival rates mid-season (see Table S8 and Fig. 3). Daily nest survival rates varied among the four different habitats, but unexpectedly, were opposite to the patterns observed for habitat selection and nesting densities. The differences in DSR among habitats were relatively small but translated into large differences in nest success when extrapolated over a 25-day period: 0.415 ± 0.082 SE in salt-extraction, 0.375 ± 0.042 SE in semidesert, 0.322 ± 0.032 SE in grassland and 0.258 ± 0.046 SE in saltmarsh. Thus, despite evidence for avoidance and lower nest densities, daily nest survival and nest success tended to be higher in the salt-extraction and semidesert and lower in the preferred habitats of the saltmarsh and the grassland (see Table S8 and Fig. 3).

4. Discussion

We investigated long-term changes in the breeding ecology of a genetically distinct resident population of Kentish plovers on the tropical island of Maio, Cabo Verde. Our goal was to understand how a tropical coastal-breeding bird is responding to anthropogenic pressures on an oceanic island. Our long-term field study has identified that long-term changes in breeding phenology and breeding frequencies are dependent on fine-scale habitat variation, and that broad scale daily nest survival rates across these habitats have been decreasing over the past decade. Declining nesting success and reduced population densities might be worrying for this population as continued low productivity combined with other factors such as human disturbance, habitat destruction or unsuitable environmental conditions such as droughts can negatively affect population growth and without proper management may lead to local extirpation (Eberhart-Phillips and Colwell, 2014). Our data will facilitate conservation NGOs and conservation authorities to prioritise among the different breeding habitats and carry out management actions that will benefit the breeding population.

Precise timing is essential for successful reproduction and survival. Birds time their breeding accurately to environmental seasonality to maximise breeding success (Helm et al., 2006). Variation in food abundance (Both et al., 2006; McNamara et al., 2008), local weather conditions (Wesolowski and Cholewa, 2009), and the social environment (Helm et al., 2006) all interplay to offer cues to the birds about when to initiate breeding. We found that egg laying dates are increasing weakly over time, but the changes are habitat dependent: the largest delay in egg laying dates was identified in the saltmarsh. Hau et al. (2004) suggested that in unpredictable climates, breeding may be more flexible, depending on favourable environmental conditions such as the onset of rainfall. Kentish plovers in Maio depend on rainfall to breed and historically, Cabo Verde has undergone a pattern of alternation between dry and wet years (Monteiro, 2013). In recent years, Maio has suffered from droughts with no rainfall such as in 2017 (Costa, 2020), and climate change might lead to droughts becoming more frequent and more extreme (Monteiro, 2013). Dry conditions could be one of the reasons that the Kentish plovers are starting to breed later as they may delay breeding until the onset of seasonal rain that will enhance food availability. Our results suggest that while such effects may be possible, these effects may be habitat dependent such that magnitude of breeding delay is dependent on the local breeding habitat.

Habitat selection for nesting is not a straightforward process, but rather a multi-scale choice driven by trade-offs between costs and benefits for both the young and the parents (Ripari et al., 2022). A diversity of ecological drivers may determine habitat selection of Kentish plovers in Maio include food availability, microclimate, predation risk, social facilitation, and competition for suitable nesting

Table 3
Model selection results of daily nest survival for Kentish plovers in Maio, Cabo Verde, during breeding seasons 2007 – 2019 (N = 517). Models with the lowest $\Delta QAIC_c$ and the highest weight (w_i) are the best supported models.

	Model statistics[a]			
Model structure[b]	*K*	Deviance	$\Delta QAIC_c$	*wi* ≤
S(~Habitat+GroupYears)	**15**	**1670.41**	**0.00**	**0.86**
S(~GroupYears)	12	1679.99	3.57	0.14
S (~LinearYears)	2	1739.81	43.33	0.01
S (~Quadratic Season)	3	1758.96	64.49	0.01
S (~1)	1	1769.28	70.80	0.01
S (~Habitat)	4	1764.73	72.25	0.01
S(~LinearSeason)	2	1769.22	72.74	0.01
S(~GroupSeason)	88	1662.47	140.47	0.01

[a] Model statistics. Model fit was assessed by the number of parameters *K,* the deviance, the difference of $QAIC_c$ from the best fit model and Akaike weight w_i.

[b] Model structure. S = nest survival, GroupYears = years as a categorical variable, LinearYears = linear effect of year, Quadratic season = quadratic time trend across the breeding season, 1 = Constant model, Habitat = the 4 distinct habitats, LinearSeason = linear time trend across the breeding season, GroupSeason = full time-dependence with day of season as a categorical variable.

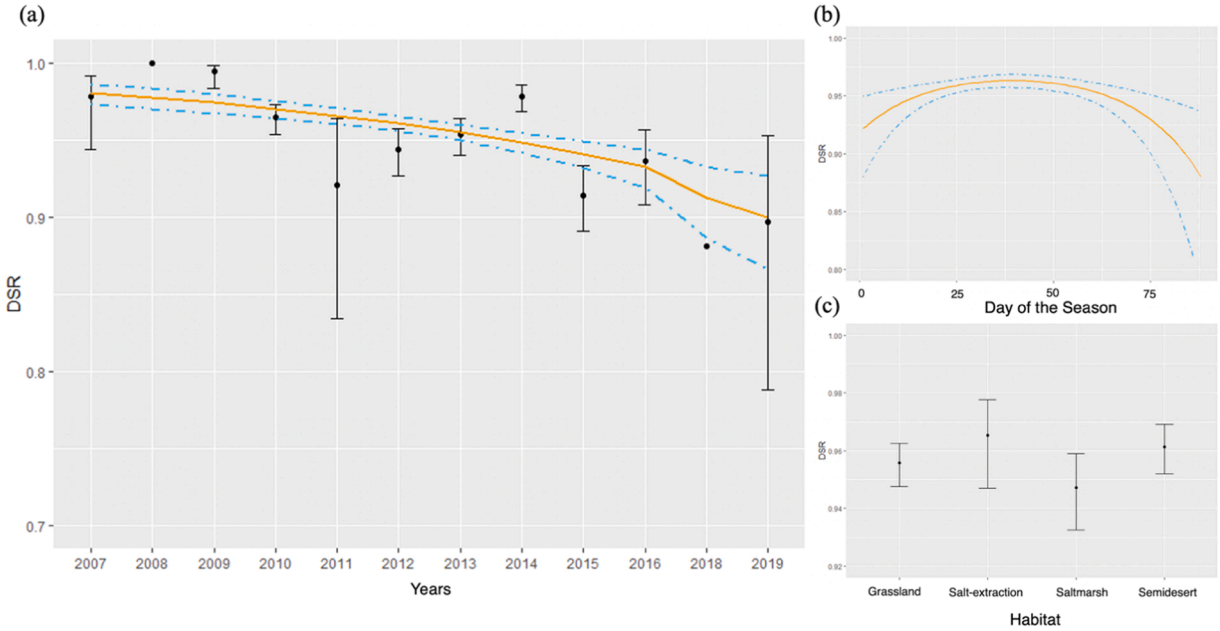

Fig. 3. Daily nest survival real parameter estimates ± 95% CI for Kentish plovers in Maio, Cabo Verde between 2007 and 2019 (a) plotted across the years from the alternate models with annual variation or a linear trend of year, (b) fitted with a seasonal time trend during the 89-day breeding season, and (c) plotted for the four different nesting habitats (N = 517 nests). One year with drought conditions (2017) was not included.

sites (Amat and Masero, 2004; Smith et al., 2007). If Kentish plovers in Maio choose a particular habitat based on food availabilities, temporal trends in food availability across habitats may explain between habitat differences in nesting frequencies (Dunn and Winkler, 2010). We found that breeding frequencies decreased over the years, but that decrease was also habitat dependent: the highest decrease was identified in the saltmarsh and the lowest in the grassland. Moreover, breeding frequencies varied among habitats within a season and the plovers start breeding earlier in the grassland, semidesert and the salt-extraction, which may therefore have the highest resources at the beginning of the breeding season before the resources eventually reduce. Alternatively, if habitats differ in predation risk, differences in breeding frequencies among habitats could reflect habitat preferences based on predator avoidance (Fontaine and Martin, 2006). For example, Kentish plover populations often show variation in patterns of nest cover (AlRashidi et al., 2011), where some nests are completely concealed by overhanging vegetation and other nests completely open. Previous work in Kentish plovers has indicated that nests with high vegetation cover have higher survival probability than nests with low vegetation cover (Gómez-Serrano and López- López 2014). In Maio, the grassland habitat provides many small shrubs and long grass that the plovers can place their nests under and may be favoured by nesting parents because this habitat offers concealment from visual predators (Engel et al., 2020). However, our results do not support a significantly higher DSR in grassland versus other habitats, suggesting the availability of nest cover does not explain higher breeding densities in the grassland. We suggest future work should explicitly explore predator densities and activity across different habitats to understand the role that predator presence may have on nest site selection. For example, the salt-extraction area is composed of a large water body with small protruding islets during years of rainfall, which may limit access to mammalian predators such as cats or dogs, but any effect is likely strongly dependent on water levels which are highly dynamic. Similarly, lower frequencies of nest survival in the saltmarsh could be related to higher concentrations of ghost crabs, which are egg predators (Engel et al., 2020).

Density dependence may also play a role in habitat choice. Nest survival may have been linked to nesting densities through the numerical or functional responses of predators, or if breeding pairs were more likely to disperse after nest failure. Nest densities were highest in the grassland and the semidesert, the two habitats with earlier peaks in nesting frequencies. On the other hand, nest survival was highest in the salt-extraction, which has the lowest nesting densities. Here, breeding densities were based on the maximum available nesting substrate in the salt-extraction, and the restricted size of islands may not permit more than one or two breeding pairs occupying one islet, resulting in low densities. When selecting a breeding habitat, other social factors may also influence when and where nests are laid, if individuals use social cues for breeding from their conspecifics or prefer to nest in areas with conspecific aggregations (Farrell et al., 2012; Pärt et al., 2011). Alternatively, parents may base their choice on previous nest success and nest site selection of older birds might be based on previous experience with a site or mate (Flynn et al., 1999). In Maio, plovers that were successful in their previous breeding attempt were more likely to remain in the same habitat (McDonald et al., 2020). Last, anthropogenic factors may also influence nest site selection of parents. In recent years, the numbers of nests found in the semidesert have decreased from 52 in 2010 to only 2 in 2019. Changes may be due to habitat alterations and higher levels of human activity as the semidesert breeding grounds have been used as a waste dumping ground in recent years.

In Maio, long-term declines in nest survival may be due to multiple factors. First, an increase in transport infrastructure has made

human access to the island of Maio easier, and the entire Cabo Verde region and the Salinas do Porto Inglês attract tourists in higher numbers than decades ago when the islands were more inaccessible (Mitchell, 2008, ITA 2021). Moreover, human settlements may attract more mammalian or scavenging avian predators because they feed on refuse from human settlements. (Marzluff and Neatherlin, 2006; Coates and Delehanty, 2010; Rees et al., 2015). Last, the Salinas do Porto Inglês have experienced development during the past decade; an eco-museum and a fence (approx. 500 m) were built in the breeding grounds and the construction of a new expanded port has begun nearby. Together, disturbance from all these factors may contribute to the lower nest survival in our study area.

Our overall estimate of the probability of nesting success for a 25-day exposure period was 0.357. Predation is the main cause of nest failure in shorebirds and has been increasing worldwide over the past 70 years (Macdonald and Bolton, 2008, Roodbergen et al., 2012, Kubelka et al., 2018). Brown-necked ravens are the main predator responsible for egg losses at Maio island and are generalist omnivores that mainly forage by use of visual cues (Coates and Delehanty, 2010; Rees et al., 2015). Other nest predators at our study site included ghost crabs and small mammals. Conservation actions at Maio island to reduce predation with interventions such as improved waste management, protection of nests with nest exclosures, or predator management by fencing or removal of feral dogs or cats may be necessary in the future because high rates of predation can lead to population declines and local extirpation (Bennett and Owens, 2002, Blackburn et al., 2003, Colwell, 2010, Kubelka et al., 2018).

With human-induced environmental change increasing, our long-term study provided new insights into how island populations may be coping with increased pressures. Island populations have a 40-fold higher extinction risk compared to mainland populations (Fernández-Palacios et al., 2021), and resident species are especially vulnerable and might be more impacted by increasing pressures. Our demographic data revealing the productivity of different breeding habitats are essential to develop appropriate conservation strategies to ensure the viability of ground-nesting bird populations in tropical islands. We propose to use such data to design habitat- and species- appropriate management plans.

In conclusion, over the past decade, pressures have been increasing in Maio and Cabo Verde in general, similarly to many other tropical islands that have potential for beach-focused tourism. Our results in nest survival and breeding density indicate that Kentish plovers are experiencing demographic losses during nesting and that these losses have been steadily increasing. We suggest that conservation actions should be targeted at the nesting period and aim to protect the Salinas do Porto Inglês more intensely by reducing disturbance in that area. A focus on disturbance may be particularly useful in preparation for development of more intensive tourism at Maio. Also, it will be necessary to investigate juvenile and adult survival to determine whether recruitment or immigration can compensate for declines in nest survival. A population viability analysis will be essential to assess extinction risk and the future trends of decline or growth of this population. Integration of our demographic data for reproductive success with survival rates will help to identify the mechanisms for declines in this population and the viability analysis will give insights into the extinction risk over the next decade. If local management authorities and conservation organisations act in a timely manner, reductions in population viability linked to human pressure can be minimised.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Author contributions statement

NE and TS developed the concept of the paper, and then NE conducted the statistical analyses and wrote the first draft of the manuscript. GMC and BS provided advice on statistical analyses including model designs and R coding and contributed to writing the manuscript. RR, RMC, SR and TS contributed to structuring the paper and writing up. All authors contributed to edits and preparation of the final manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02522.

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