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Published online: 05 Mar 2020.

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Romy Rice[1]*, José O Valdebenito[2], Meinolf Ottensmann[3], Noémie Engel[1], Andreia Adrião[4] and Tamás Székely[1,2,4]

[1] *Department of Evolutionary Zoology and Human Biology, University of Debrecen, Hungary*
[2] *Milner Centre for Evolution, University of Bath, United Kingdom*
[3] *Department of Animal Behaviour, Bielefeld University, Bielefeld, Germany*
[4] *Maio Biodiversity Foundation, Maio, Republic of Cape Verde*
*Correspondence: romyrice@yahoo.co.uk

The Cream-coloured Courser *Cursorius cursor exsul* is a data-deficient shorebird distributed across Eurasia and Africa. The subspecies *exsul* is endemic to the Cape Verde archipelago. In contrast with their mainland breeding sites, where coursers appear to be nomadic and rare throughout their range, the Cape Verde population is year-round resident and locally abundant. Here we investigate the breeding ecology of Cream-coloured Coursers in Maio, Cape Verde, where they breed in rocky semi-desert habitat. Over four consecutive breeding seasons (2015–2018), we found 52 nests, and ringed 56 adults and 100 chicks. Forty eight percent of 52 nests produced at least one chick; the main nest predators were Brown-necked Ravens *Corvus ruficollis* and domestic dogs *Canis familiaris*. Although coursers were thought to be sexually monomorphic, we found that adult males had longer tarsi than adult females. Coursers appeared to be socially monogamous and both sexes incubated the eggs and reared the young. Maio is currently a rural island with little development; however, the island is faced with the threat of touristic development. Therefore, research is required to understand how the courser population will respond to anthropogenic pressures in the future.

Écologie de reproduction de la Courvite isabelle au Cap Vert

La courvite isabelle *Cursorius cursor exsul* est oiseau de rivage distribué en Eurasie et en Afrique et pauvre en données. La sous-espèce *exsulis* est endémique de l'archipel du Cap-Vert. Contrairement aux sites de reproduction continentaux où les courvites semblent être nomades et rares dans l'ensemble de leur aire de répartition, la population cap-verdienne est résidente toute l'année et est localement abondante. Nous étudions ici l'écologie de la reproduction des courvites à Maio, au Cap-Vert, où ils se reproduisent dans un habitat rocheux semi-désertique. Au cours de quatre saisons de reproduction consécutives (2015–2018), nous avons trouvé 52 nids et bagué 56 adultes et 100 poussins. Quarante-huit pour cent des 52 nids ont produit au moins un poussin. Les principaux prédateurs de nidification étaient le corbeau brun *Corvus ruficollis* et les chiens domestiques *Canis familiaris*. Bien que les courvites aient été considérés comme sexuellement monomorphes, nous avons constaté que les mâles adultes avaient un tarse plus long que les femelles adultes. Les courvites semblaient être socialement monogames et les deux sexes couvaient les œufs et élevaient les jeunes. Maio est actuellement une île rurale avec peu de développement, cependant, l'île est menacée par le développement touristique. Par conséquent, des recherches sont nécessaires pour comprendre comment cette population de courvite isabelle répondra aux pressions anthropiques à l'avenir.

Introduction

Desert regions represent up to one third of the land surface on Earth. Despite its extent, little biodiversity can subsist, as a result of its extreme environmental conditions (Ward 2009). Accordingly, desert dwelling species usually present physiological adaptations that enable them to survive under intense solar radiation, low relative humidity and meagre primary productivity. Desert birds, for instance, show a reduced water loss, reduced metabolic rate, and small clutch size (Williams and Tieleman 2005). Climate change, expansion and intensification of arable agriculture, mining deserts for fuels, and habitat loss or fragmentation are some of the factors threatening desert dwelling species (Ayyad 2003; Kamp et al. 2016).

The Cream-coloured Courser *Cursorius cursor* is a ground-nesting desert wader from the Family Glareolidae. Based on morphological differences; three subspecies are currently recognised. The nominate race *C. c. cursor* is distributed across arid regions of Northern Africa, the Arabian Peninsula and the Canary Islands, *C. c. bogolubovi* is found in the Middle East, and *C. c. exsul* is restricted to the Cape Verde archipelago (Tavares 2013; Maclean and Kirwan 2019). Despite the wide distribution and breeding

range of the Cream-coloured Courser, little is known about its life history, breeding ecology and habitat preferences (Thomas et al. 2003; Palomino et al. 2008; Traba et al. 2013). The lack of knowledge is specifically apparent for the subspecies *exsul*. In the early 1990s, the population size was in the range of 750 to 1 000 breeding pairs (Maclean and Kirwan 2019), although more recent estimations are considerably lower with 150 to 350 breeding pairs, suggesting population decline, putting this species at risk of extinction (Dodman 2007). However, since the description of this subspecies almost 100 years ago by Hartert in 1920, little research has been carried out with the possible exception of brief reports (Bannerman and Bannerman 1968; Koch and Hazevoet 2000). The data deficiency, declining trend and lack of official conservation status of this subspecies categorises it as a species of conservation concern (Dodman 2007; BirdLife International 2016).

The Cape Verde Archipelago is situated within the Sahelian arid belt and the climate is dry and hot with irregular rainfalls between August and October. The eastern islands, including Maio, are particularly arid, as a result of higher exposure from hot Saharan winds (SCVZ 2012). Cape Verde has a unique fauna and flora with high endemism both in terrestrial and marine ecosystems (Duda and Rolan 2005; Arnold et al. 2008; Duarte et al. 2008; Almalkl et al. 2016). Cape Verde is becoming a desirable tourist destination that has experimented increasing tourism with an average annual visitor growth of 11.2% (World travel and tourism council 2018, Instituto Nacional de Estatística de Cabo Verde 2018), which is likely to impact both terrestrial and marine ecosystems. Therefore, monitoring and understanding the breeding ecology of the endemic Cream-coloured Courser is of critical importance before increased anthropogenic disturbance and urban development arrive to this species' habitat.

Here we investigate the breeding ecology of *C. c. exsul* in Maio, one of the large rural islands in Cape Verde that has so far escaped intense touristic developments. Our overall objective is to collect data on breeding ecology and behaviour to assist conservation decisions. Particularly, we focus on (i) life history traits (e.g. body size, sex ratio, clutch size), (ii) breeding ecology (e.g. breeding season, nest distribution, breeding success), (iii) the breeding behaviour (i.e. incubation patterns and parental care), and (iv) identify threats that could have negative impacts on this population.

Materials and methods

Study site
Fieldwork was conducted on the island of Maio, Cape Verde (15°13′ N, 23°10′ W), during four consecutive years 2015–2018. Maio island has an area of 269 km² and a population of 6 980 inhabitants as of 2015 (Instituto Nacional de Estatística de Cabo Verde 2015). In 2015, we focused on the Ramsar site Salinas do Porto Inglês, an area comprising salt flats and rocky semi-desert areas, where intensive fieldwork was carried out between 14 September until 20 November in 2015, 6 September until 30 November in 2016, 11 September until 15 November in 2017 and 5 September until 31 November

in 2018. Because the breeding of coursers has been linked to rainfall elsewhere (Roberts 1966), we collected weather records from the nearest meteorological station located in Praia (approximately 35 km southwest of Maio) using the R package GSODR (Sparks et al. 2017).

Nest search and egg measurements
Nest searches were conducted using the protocol described in Székely et al. (2008) as a guideline. However, because coursers seem more wary than plovers, the methodology was adjusted, for example by extending the amount of time dedicated to waiting for an individual to return to the nest. Telescopes and binoculars from either a car or a mobile hide were used to observe fleeing adults, adults returning to the nest, and spotting broods.

Egg length and width were measured to the nearest 0.1 mm using 50 mm sliding callipers. The incubation stage was determined by floating each egg in fresh water (Székely et al. 2008). Eggs in one nest that were discovered during egg laying were floated every other day and the flotation stage was recorded with the known age of the egg each time, and based on these a calibrated egg flotation chart was produced (Appendix 1). We used Douglas' formula (1990) to calculate egg volume (V): $V = K_v \times L \times W^2$, where K_v = 0.5 (egg volume coefficient), L = egg length and W = egg width (Herzog et al. 2016). Clutch volume was calculated as the sum of all egg volumes per nest.

Nests were considered successful if at least one chick hatched, and unsuccessful if (a) all eggs were destroyed, (b) eggs were abandoned for more than 24 hours (without incubation), (c) a predation event was witnessed either via nest camera or visual observation, or (d) eggs disappeared before the 18th day of incubation without finding the ringed parents with chick(s). The 18th day of incubation is a few days before egg pipping usually begins, therefore is a conservative practical threshold to start expecting eggs to hatch. Nest fates were considered as unknown if all eggs disappeared close to the predicted hatching date and the parents were not observed with chicks, or if the nests were still active at the time when fieldwork was finished.

Body size of adults and chicks
After at least five days of incubation, adults were captured on the nest and ringed with one metal ring and a unique combination of two or three colour rings for identification. Wing length was measured to the nearest mm, whereas bill and tarsus length were measured to the nearest 0.1 mm and the bird was weighed with a digital balance to the nearest 0.1 g. Approximately 0.4 ml of blood was taken from the brachial vein for adults and from the metatarsal vein for chicks and stored in 98% ethanol. Blood samples were used for sex determination using molecular markers (Fridolfsson and Ellegren 1999).

Incubation and brood care
Bushnell® trophy trail cameras (model 119466) were used to record activities at nests; they were set up and disguised using nearby rocks and vegetation approximately 1 m away from the nest. Three nests were monitored using nest cameras for a minimum of 72 hours during the field season of 2016, capturing images every minute. A small patch

of black hair-dye (Ellis and Ellis 1975) was applied to the uppermost part of each wing of one parent at each nest, allowing us to distinguish between parents.

Nests were visited near the expected hatch date, and hatchlings were ringed in the nest if their mass exceeded 20 g. If chicks were too small to be ringed, we aimed to recapture and ring them approximately three days later. After hatching of the eggs, we attempted to follow broods by observing parental presence and behaviour. Every time a brood was observed (i.e. an adult with at least one chick, or two ringed adults known to have chicks), ring combinations of parents and chicks were noted, as well as location, date and time. Additionally, we found broods that hatched from unmonitored nests. These broods were also captured, measured, blood sampled and continuously monitored thereafter.

Brood sex ratio

The number of male chicks in broods of one and two chicks were calculated, and these distributions were tested against the binomial distribution (q. 0.5) to investigate brood sex-ratio bias.

Statistical analyses

Statistical analyses were conducted using R version 3.5.0 (R Development Core Team 2018). Prior to analyses, data were tested for normality using Shapiro-Wilk's test. We used Student's two-sample t-test to evaluate differences in sexual size dimorphism and paired t-test to investigate differences in male and female incubation timings. Significance was concluded at $p < 0.05$. All test results are presented as the mean ± standard error (SE).

To calculate the chick growth curve with tarsus length, analysis only included chicks that had known ages (i.e. their hatch date was known and the chick was measured and ringed in the nest). A generalised linear model (GLM) with binomial error structure was carried out to investigate the relationship between the age of the brood and parent presence, using only broods with known ages.

To calculate the age of broods found only after hatching, we took the tarsus length of the largest chick, and calculated the age using the calibrated chick growth curve (see Results). From the latter analysis we excluded an observation of a single chick of 17 days of age that was observed with no parents, because the latter record was likely erroneous. Plots were produced with the R package *ggplot2* (Wickham 2016).

Results

Breeding season and nest distribution

Most nests and broods were concentrated in two locations (Salinas do Porto Inglês and Lagoa Cimidor; Figure 1). In total, we found 52 nests in four breeding seasons (2015–2018; Figure 1). Breeding was first recorded in early September, peaked in mid-October and slowed towards the end of November (Figures 2 and 3). Amount of and distribution of rain between months were not uniform between years (Figure 4): for instance, in 2017 there was an extreme lack of rainfall, with none occurring during the
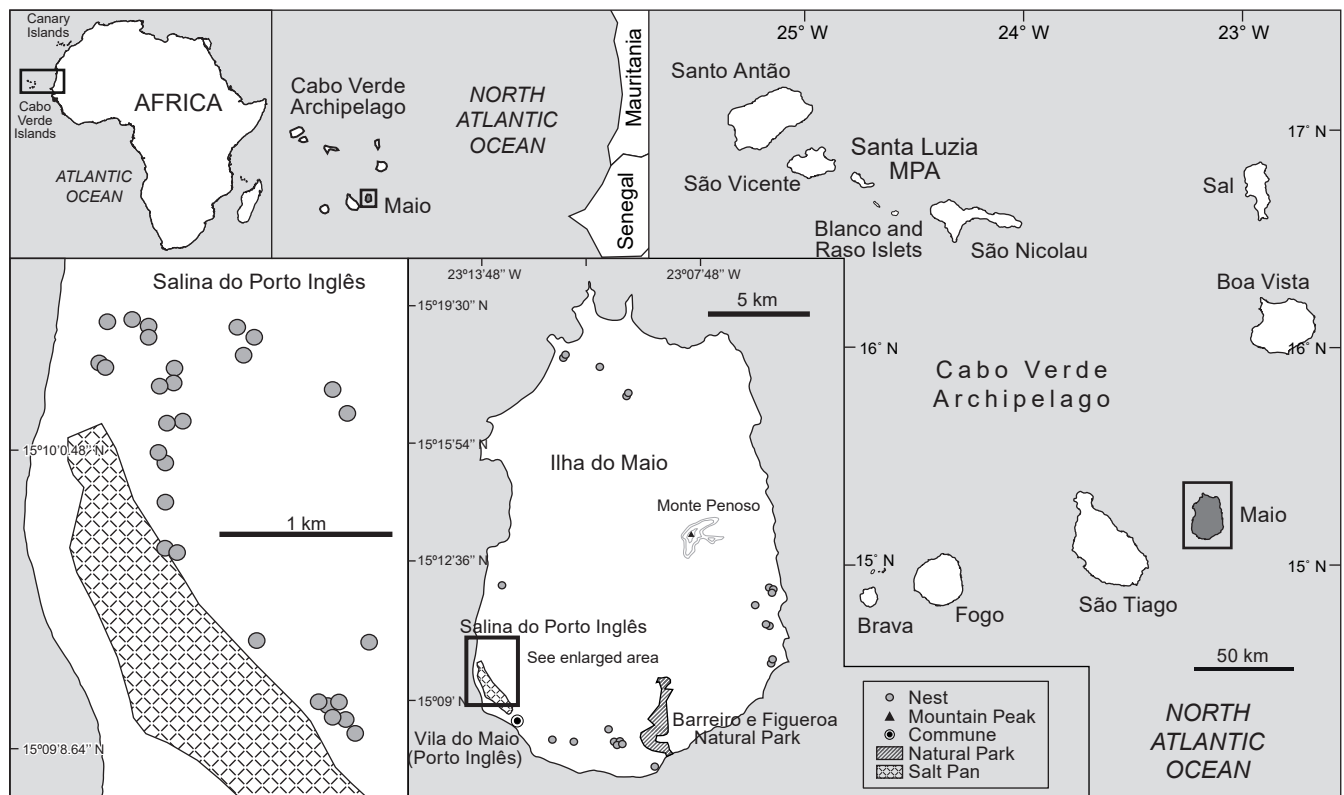

Figure 1: Distribution of Cream-coloured Coursers nests in Maio, Cape Verde (*n* = 52 nests)
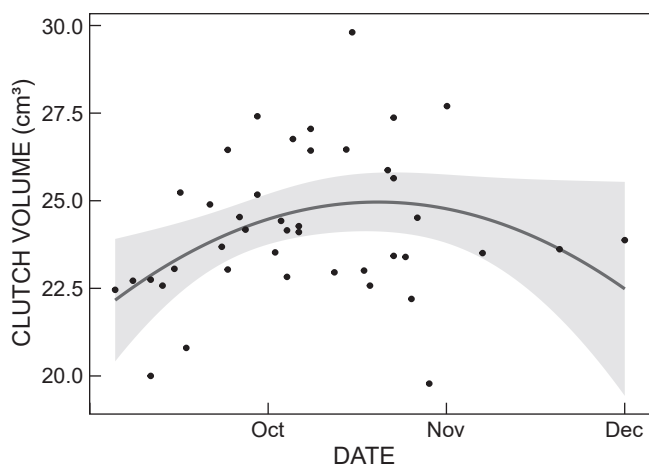
Figure 2: Clutch volume in relation to laying date. Regression line and standard deviation are shown. $y = 22.4 + 0.12\ x − 0.015\ x^2$; $y =$ clutch volume, x = days passed since first clutch laid
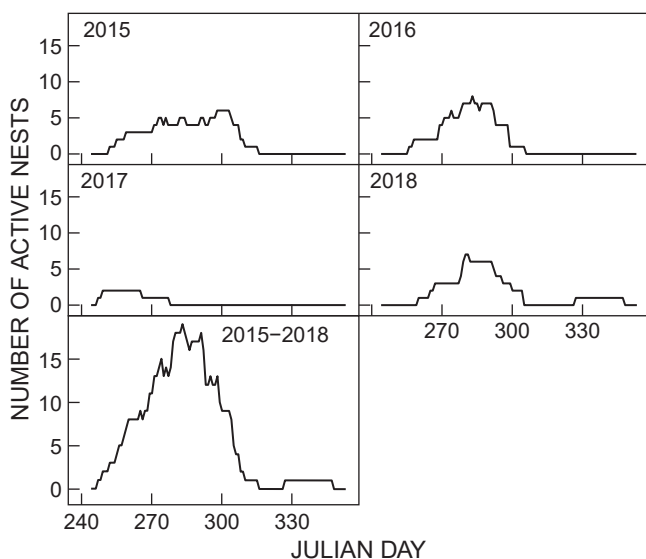

Figure 3: The number of active nests over the breeding season. Julian day refers to the number of days since the beginning of the year

breeding season. Correspondingly, only three nests were found that year, in comparison to 21, 16 and 12 nests in 2015, 2016 and 2018, respectively.

Breeding success
Complete clutches invariably consisted of two eggs ($n =$ 51 nests), although one nest was found with a single fresh egg (estimated to be incubated for one day), therefore likely representing an incomplete clutch, which had disappeared in the second visit. The mean clutch volume was 24.25 ± 0.32 cm³, and clutch volume and time of the breeding season displayed a quadratic relationship (Figure 2). Mean egg length and width were 33.5 ± 0.16 and 26.6 ± 0.10 mm, respectively (n = 52 nests, see Appendix 2).
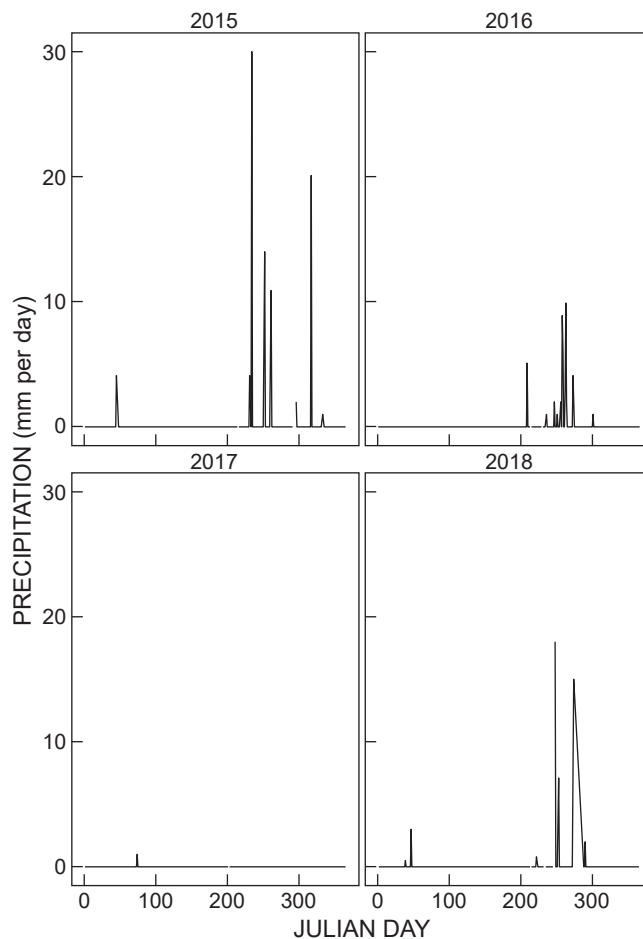

Figure 4: Daily precipitation levels over four years from the meteorological station Praia (14°54′00″ N , 23°30′00″ W), located approximately 35 km southwest of the study area

A total of 48.1% of nests produced at least one chick, 23.1% of nests, the eggs were predated, for 17.3% the fate was unknown, and for 11.5% of nests the eggs were abandoned (n = 52 nests in total). Of the 25 nests that hatched, 52% hatched two chicks and 48% hatched only one chick. Predators were identified using camera trapping or eye witness observations. Brown-necked Ravens *Corvus ruficollis* predated 11 nests and one clutch was eaten by a domestic dog (*Canis familiaris*, see nest camera images in Appendix 3).

Body size of adults and chicks
Male coursers had significantly longer tarsi than females (t = 2.583; p = 0.013; n = 44 adults) although body mass, wing and bill length did not differ between the sexes (Table 1). Body mass, tarsus and bill length of hatchlings are shown in Table 2. Growth rate of chick tarsus length was approximately linear within the age range in our samples (Figure 5): Tarsus length (in mm) = 1.44 × Age (in days) + 16.92 (R^2 = 0.897; p < 0.001; n = 33 chicks).

Incubation and brood care
Camera images of three nests show that both parents incubate the eggs in marked shifts according to the time of

Table 1: Body size of adult Cream-coloured Coursers in Maio, Cape Verde. Statistics are two-sample Students t-tests with significant differences ($p < 0.05$) highlighted in bold

	Males (n = 22 individuals)		Females (n = 24 individuals)		p	t
	Mean ± SE	Minimum– Maximum	Mean ± SE	Minimum– Maximum		
Body mass (g)	113.8 ± 1.8	95.4–129.3	117.6 ± 1.9	97.5–136.2	0.160	−1.427
Wing length (mm)	156.3 ± 1.3	145.0–166.0	155.2 ± 1.0	147.0–163.0	0.470	0.723
Tarsus length (mm)	55.9 ± 0.5	51.6–59.8	54.1 ± 0.5	48.5–58.7	**0.013**	**2.582**
Bill length (mm)	21.6 ± 0.2	19.8–23.6	22.2 ± 0.2	19.9–24.0	0.066	−1.878

Table 2: Body size of freshly hatched courser chicks

	Hatchlings (n = 22 individuals)	
	Mean ± SE	Minimum–Maximum
Body mass (g)	9.5 ± 0.2	7.9–11.2
Tarsus length (mm)	17.2 ± 0.2	15.2–19.3
Bill length (mm)	7.1 ± 0.1	5.8–8.2

the day (Figure 6): males attend the nest throughout the night into the early morning, whereas females incubate during the hottest parts of the day between 10h00 and 14h00, often shading eggs. We also observed long periods when neither parent incubated the eggs for up to 8 h. Males incubated the nest for a mean of 13 ± 2.7 h per day, significantly more than the female mean 7.6 ± 1.6 h; t = 4.115; p = 0.003; n = three nests). The mean incubation period was 24 ± 3.2 days (n = 17 nests), with a minimum of 18 days and maximum of 31 days. The majority of nests were incubated between 21 and 26 days. One nest was incubated for 31 days, however, only one egg hatched from this nest.

We encountered 91 broods in total. We resighted 36 of these broods on 117 occasions: 88.9% of broods were resighted with both parents present and 11.1% with just one parent. There was no relationship between the age of the broods and the parent presence (GLM, z-test = −1.650; p = 0.099; n = 72 resightings). The oldest brood we observed was approximately 29 days old; at this age the chicks were able to fly (n = two chicks).

Brood sex ratio

The sexes of chicks from 28 out of 91 broods are shown in Table 3. The proportion of males in broods containing one chick was 0.636, and this was not different from 0.5 (binomial test p = 0.549; n = 11 chicks in 11 broods). The overall proportion of males in broods of two chicks was not different from 0.5 (binomial test p = 0.230; n = 34 chicks), nor the distribution of males in two chick broods (chi-square goodness of fit, χ^2 = 9; p = 0.111; n = 17 broods). The overall proportion of male chicks in all broods was 0.622, however, this was not different from the expected 0.5 ratio (Wilcoxon signed rank test V = 644; p = 0.102; n = 28 broods). The sex ratio of hatchlings at the nest was 0.6, and this did not differ from the overall chick sex ratio (Wilcoxon rank sum W = 460; p = 0.873; n = 20 chicks).

Discussion

Coursers in general are poorly studied, because of their nomadic behaviour, crepuscular life style and low breeding
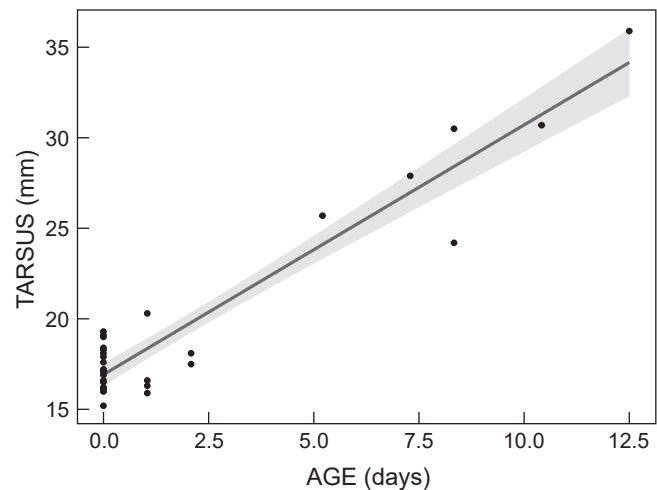
Figure 5: Chick tarsus length in relation to chick age in days. Grey shaded area represents the 95% confidence interval. Tarsus length (in mm) = 1.44 × Age (in days) + 16.92 (R^2 = 0.897; $p < 0.001$; n = 33 chicks)

densities (del Hoyo et al. 1996). Here we provide the first detailed report on the breeding ecology, parental behaviour and life history of the endemic population of Cream-coloured Coursers in Cape Verde, that might also be relevant for the species as a whole. Our study provided four key results.

First, coursers have a consistent clutch size of two eggs, an unusual trait among shorebirds that usually produce four egg clutches (Shipley 1984; Sandercock 1997). It has been suggested that clutch sizes can be limited by the ability of parents to protect the clutches from both hot and cold temperatures. Experimental evidence is consistent with this hypothesis (Hills 1983; Delehanty and Oring 1993; Székely et al. 1994; Niizuma et al. 2005). Additionally, some studies have suggested that clutch size is limited by the trade-off between larger clutch size and lower chick quality (Sandercock 1997; Larsen et al. 2003). We suggest three non-exclusive explanations for the two-egg clutches in coursers. (i) This can be an adaptation to limited food supply that is characteristic in desert environments. Food availability has been correlated to clutch size in many avian species (Hussell and Quinney 1987; Clifford and Anderson 2001; Hoi et al. 2004). (ii) Courser eggs have thick shells, suggesting that producing an egg requires a substantial amount of calcium, potentially increasing courser's vulnerability to calcium deficiency. A restricted
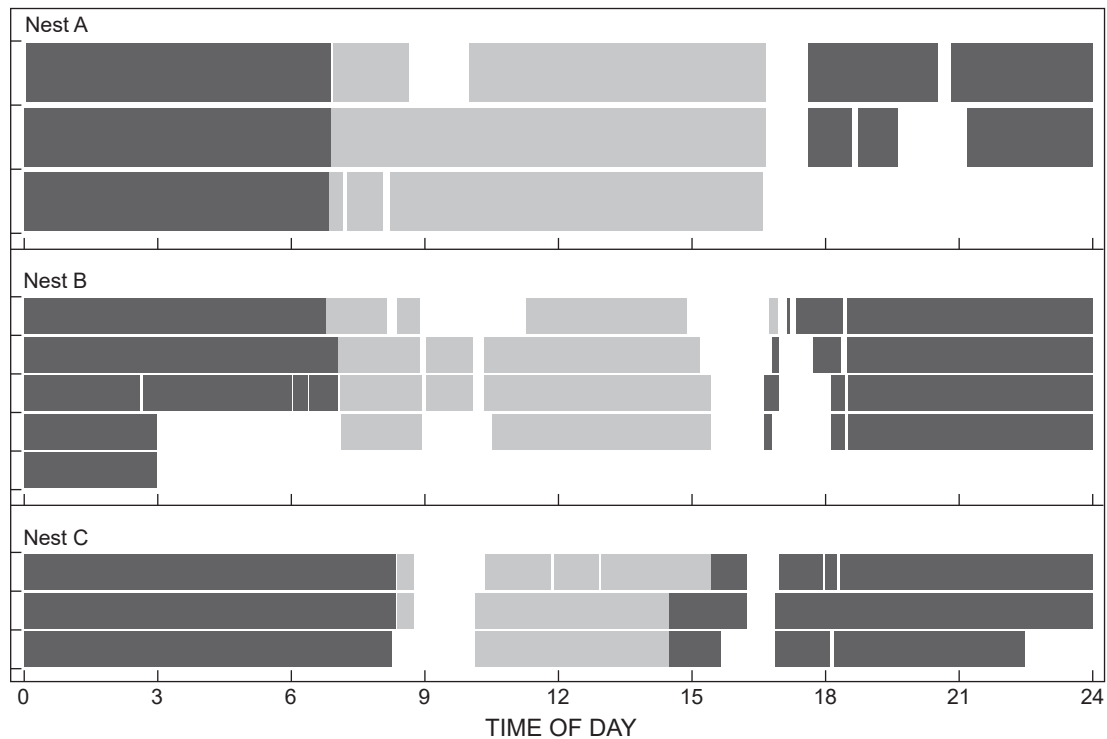
Figure 6: Attendance patterns at three nests (A, B and C) of Cream-coloured Coursers. Horizontal bars represent 24 h cycles, where male incubation is represented in dark grey and female incubation in light grey. Sections in white represent times during which no individual attended the nest. Nests A and C hatched, nest B was predated by a raven

Table 3: Brood sex ratio of Cream-coloured Coursers in Maio, Cape Verde. Brood type indicates the gender composition of broods

Two chick broods		One chick broods	
Brood type	% (*n* = 17 broods)	Brood type	% (*n* = 11 broods)
Male-Male	52.9	One Male only	63.6
Male-Female	17.7	One Female	36.4
Female-Female	29.4	only	

supply of calcium may limit the female's ability to produce large clutches (Patten 2007; Wilkin et al. 2009; Reynolds and Perrins 2010). (iii) Birds close to the equator often have reduced clutch sizes, the Moreau hypothesis (Lack 1968; Jetz et al. 2008). If coursers had a tropical origin, they could simply have retained this feature across all other climatic regions when the ancestors invaded various non-tropical habitats. The ultimate and proximate causes of small and invariable clutch sizes in coursers require additional investigations.

Second, hatching success was 48.1%, a high figure, compared with many shorebird populations, especially compared with the resident population of Kentish plovers *Charadrius alexandrinus* in Maio. This population was monitored using the same protocol, and had a lower hatching success of 23.0% (Que et al. 2015). Perhaps camouflage of the courser eggs or incubating adults offers an advantage in avoiding predation, compared

with neighbouring species. This would require additional analysis, however, to date no studies have addressed this topic.

Third, the lack of striking visual sexual differences between male and female Cream-coloured Coursers suggested that this species is sexually monomorphic. Here we found no sexual dimorphism in wing length, bill length, or body mass, however, tarsus lengths were different between adult males and females. As a desert species, coursers are probably under strong natural selection (Williams and Tieleman 2005), therefore the effects of sexual selection are limited to subtle sexual dimorphism. Differences in tarsus length could be a result of subtle sexual selection (Jehl 1970; Alatalo and Lundberg 1986), because longer tarsi could give the appearance of larger size when standing, a trait that may be advantageous for the courtship displays of this species, such as bowing and chasing. Fourth, incubation data from three nests identifies a daily incubation rhythm for this species. This 24-hour pattern showed that males incubated at night and females during the day, with not many incubation gaps, suggesting a near equal split of parental care. Bulla et al. (2016) observed that many biparental shorebird species express inter and intraspecific variation of incubation patterns, speculating that incubation bout patterns are influenced by social synchronisation and anti-predation strategies. Species that use parental camouflage as an approach to prevent nest predation should conform to the following strategies; decrease in activity around the nest,

less changeovers for incubation bouts and an increased bout duration for each parent. Bulla et al. (2016) also quantified the distance at which the parent remained on its nest in order to classify the level of parental crypsis. During our study we were able to observe a similar behaviour in some individuals that remained on the nest as close as we were able to capture the incubating bird by hand. This shows that the anti-predation and parental crypsis theory of incubation, as exhibited in other studies (e.g. Kreisinger and Albrecht 2008; Amat et al. 2012), seem to be displayed by coursers.

A possible limitation of our study was that fieldwork was carried out by several students and volunteers, and intensity may have varied between years and study areas. These constraints resulted from limited funding and the necessity to work out fieldwork methodology from scratch. In future, we plan to achieve more even coverage by using mobile hides to simultaneously work across multiple areas of Maio. Fieldwork in Cape Verde has only been conducted during September, October and November; therefore there is a gap in knowledge of courser breeding throughout the remainder of the year. Additional research is necessary, in order record year-round observations of possible breeding behaviour and reproduction in this population. Based on our four years of fieldwork, we believe the courser population in Maio is currently stable. Nevertheless, our findings are important when considering the assignment of protected areas and the necessity for reinforcing conservation policies. Currently the island of Maio is relatively undisturbed, compared with other islands in Cape Verde, welcoming annually only 0.2% of tourists arrivals in Cape Verde. However, a tourism surge is expected with the local port being expanded in 2019. Anthropogenic activities, such as off-road driving, road construction, and human settlements have been recognised as known threats to the coursers in the Canary Islands (Gonzalez 1999), and therefore are most likely threats for the courser population inhabiting Cape Verde. In order to understand the effects of the inevitable increase in anthropogenic activities on the courser population in Maio, increased research with a conservation focus is necessary.

In conclusion, our study provided detailed baseline knowledge of Cream-coloured Courser breeding ecology, life history traits and morphometric measurements. Research should be continued to further investigate in detail some of the general results found, for instance revisit the brood sex ratio. Additionally, the social structure of this population can be looked into in more detail, including mate fidelity, how many times mating occurs, and also site fidelity. Continuing research will enable an increased understanding of courser ecology, thus enabling more targeted conservation efforts.

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Appendix 1: Data used to produce an egg flotation chart for the Cream-coloured Courser

Float stage	Age
(days)	
0° (flat)	2
20°	4
40°	5
60°	10
80°	13
90° (tip touching surface)	16
+1 (5 mm of tip emerging from water)	19
Hatch	25