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Sex differences and breeding ecology of a burrow-breeding shorebird, the Crab Plover *Dromas ardeola*

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The Crab Plover *Dromas ardeola* is endemic to the Indian Ocean basin and breeds on islands around the Arabian Peninsula. Unique among shorebirds, it nests in an underground burrow where it lays a single white egg and feeds one chick. We investigated sex-related differences in body size and parental care of this species in Saudi Arabia. Molecular sexing of DNA samples of 66 adult Crab Plovers indicated that 26 were males and 40 were females. Males had significantly longer bill, wing and tarsus lengths than females, confirming previously published reports on sexual size dimorphism in Eritrea. Observations of molecular-sexed adults at four nests showed that both parents fed the chicks; however, females brought food to the nest-burrow more often than males (67.6% of all cases). We found that the temperature inside active nesting burrows was relatively stable at $35.0 \pm \text{SE}=0.18^\circ\text{C}$ ($n = 11$ nests) regardless of ambient temperature just outside the burrows. This suggests that burrows serve a purpose in incubation as well as in defence from predation. In the colony, adults were seen to prevent chicks from multiple burrows from leaving the nest when their own parents had left the colony, confirming a helper breeding system. We suggest areas for future investigation to further elucidate the breeding behaviour of this enigmatic and unique burrowing shorebird.

INTRODUCTION

The Crab Plover *Dromas ardeola* is a distinctive, medium-sized shorebird (weight: 230–325 g), with black and white plumage, a strong bill and long, black legs (Burton & Burton 2002). Sexual dimorphism occurs in size, though not in plumage, and males are generally larger than females (De Marchi *et al.* 2012). Juvenile Crab Plovers lack the characteristic adult patterns, instead emerging a uniform grey-brown with a smaller bill and shorter legs (Burton & Burton 2002).

The breeding ecology of Crab Plovers is unique among waders. They breed in colonies which are re-established each year on sandbanks (Chiozzi *et al.* 2011), in which they dig nest-burrows more than two metres long (Hockey & Aspinall 1996). The female lays a single large, white egg (in rare cases, two eggs) without any pigmentation (Hockey & Aspinall 1996, Delany *et al.* 2009, Tayefeh *et al.* 2013), a trait typical of species that nest in holes or hollow trees (Burton & Burton 2002, Jennings 2010). Reports suggest that the average incubation period is 33 days (De Marchi *et al.* 2008, Tayefeh *et al.* 2013). After hatching, a Crab Plover chick stays inside its burrow for several days (del Hoyo *et al.* 1996, Hockey & Aspinall 1997) and both parents deliver

food (Burton & Burton 2002, Hockey & Aspinall 1996). Chicks fledge at the age of seven weeks (Tayefeh *et al.* 2013), at which time they leave the colony with their parents and migrate together as a family (Delany *et al.* 2009, Hockey & Aspinall 1997). Crab Plovers are partial migrants (Delany *et al.* 2009, del Hoyo *et al.* 1996), and are the only reported waterbird species in which adults continue to provide food for their chicks during post-breeding migration; juveniles remain at least partly dependent on their parents to provide food for several months (Delany *et al.* 2009, De Sanctis *et al.* 2005, Fasola *et al.* 1996).

De Sanctis *et al.* (2005) suggested that the long duration of parental care may be attributed to the low reproductive yield of the parents, which is a consequence of the ecological limitations of the breeding areas; namely extremely hot environments. Their breeding range spans Kuwait, Iran, the United Arab Emirates, Oman, Yemen, Saudi Arabia, Somalia, Eritrea, Sudan and possibly western India, the Lakshadweep and Maldives (Almalki *et al.* 2014, Delany *et al.* 2009, De Marchi *et al.* 2006, Javed *et al.* 2012, Jennings 2010, Shobrak *et al.* 2002, Tayefeh *et al.* 2013) and the breeding season takes place during the hottest time of the year, between April and August (Hockey & Aspinall 1997, PERSGA/GEF 2003).

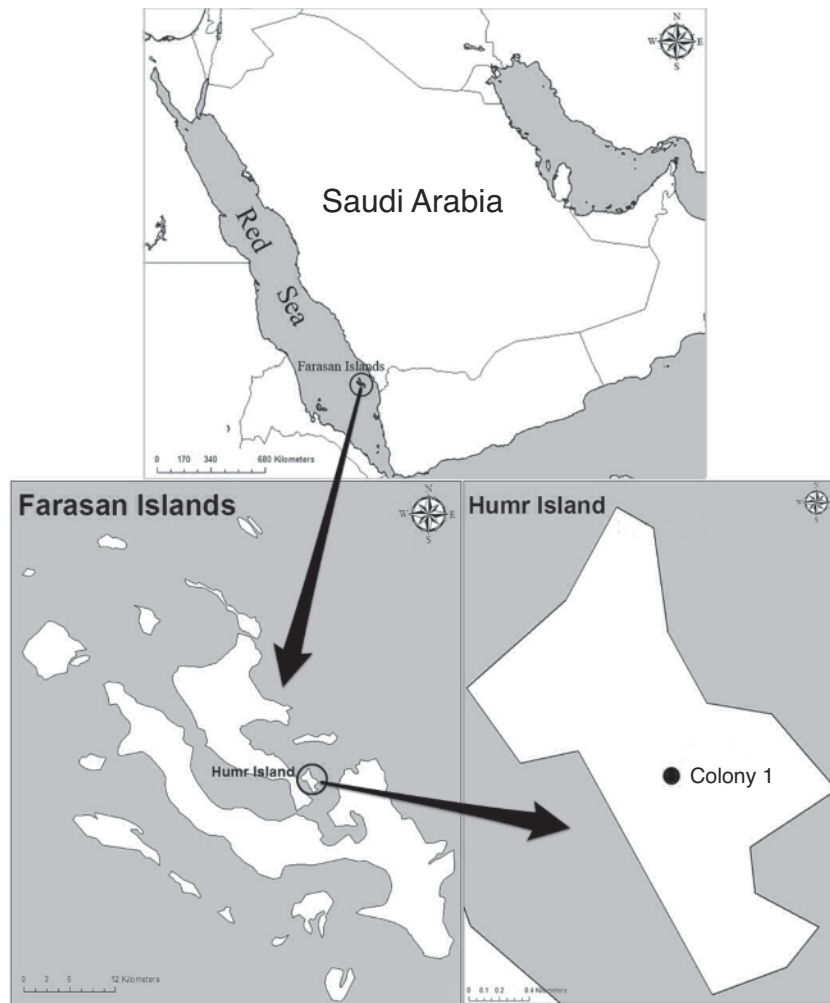


Fig. 1. Map showing location of Crab Plover breeding colony (black dot) on Humr Island, Red Sea.

Recent research suggests that the role of nest-burrows is to protect the eggs against high ambient temperatures (which can reach up to 45°C in the shade) providing near-optimal temperature and humidity for egg development (based on abandoned burrows, a temperature of 35.2°C and a humidity of 60.2% have been estimated; Aspinall & Hockey 1996, De Marchi *et al.* 2008). This minimizes the time required for incubating the eggs (28.3% of the time of the parents; De Marchi *et al.* 2008). When the chicks begin to leave their burrows, they avoid high temperatures and only come out in the early morning or late afternoon (Hockey & Aspinall 1996).

During the breeding season, Crab Plovers commonly forage singly or in loose groups on tidal mudflats or in shallow water (Burton & Burton 2002, Delany *et al.* 2009, del Hoyo *et al.* 1996). These foraging groups typically contain 20 to 30 individuals (Burton & Burton 2002) and foraging takes place during both day and night, in different locations in the intertidal zone (Burton & Burton 2002, Fasola *et al.* 1996). Their diet consists largely of crabs, but also includes other marine animals such as crustaceans, small molluscs and marine worms (del Hoyo *et al.* 1996, Fasola *et al.* 1996). The heavy and powerful bill gives this species the ability to crush larger crabs into pieces to eat, though smaller crabs are often swallowed whole (Soni & Bhuvra 2007). De Marchi *et al.* (2012) established that bill size differs between males and females, which might be related to the prey size caught by each sex (Rands 1996).

Our study aimed to further our understanding of sex differences and the breeding ecology of the Crab Plover with four main objectives. First, we measured the body size of males and females on the Farasan Islands in the Red Sea using molecular markers for sex determination. De Marchi *et al.* (2012) applied discriminant function analysis on Dahret Island in the Dahlak Archipelago, Eritrea, and we used the same approach to investigate whether morphological traits differ between the Dahlak Archipelago and the Farasan Archipelago. Second, we assessed the roles of males and females in parental care, by monitoring the delivery of food to chicks in nest-burrows according to the sex of the adults. Third, we determined the type of food items provided by the parents. Fourth, we measured temperatures both inside and outside active nest-burrows during the breeding season. We also investigated whether burrow temperatures differ in different regions.

METHODS

Study area

We investigated a colony of Crab Plovers on Humr Island in the Farasan Archipelago of Saudi Arabia (16°47'00"N, 42°00'42"E; Fig. 1) on 47 days between 19 May and 15 July 2012. Humr Island, 310 ha, is sandy, largely low and approximately flat with several reef platforms. Vegetation is sparse

and includes salt-tolerant plants such as *Halopeplis perfoliata*, *Zygophyllum album*, *Zygophyllum simplex* and *Suaeda monoica*. Mangroves, mainly *Avicennia marina*, exist along a wide area of the Humr Island coast. The weather from May to July is arid and hot with daily temperatures exceeding 50°C in direct sunlight.

The Crab Plover colony we studied comprised 265 active nest-burrows. We recorded three other bird species breeding on the island: Kentish Plover *Charadrius alexandrinus*, Saunders's Tern *Sterna saundersi* and Sooty Gull *Larus hemprichii*. We also found an abandoned Osprey *Pandion haliaetus* nest.

Trapping, morphometric measurements, behavioural observations and breeding ecology

Crab Plovers are easily disturbed by observers and are therefore difficult to capture, especially around their breeding sites. We captured Crab Plovers using mist-nets during the night. We used torchlight to dazzle the birds and drive them towards the mist-nets. Captured birds were removed immediately to reduce the possibility of injury.

Morphometric measurements were taken from 66 adult Crab Plovers captured between 6 June and 15 July. Three measurements (all in mm) were taken from each adult: (1) bill length (the exposed culmen) was measured with calipers from the edge of the feathers on the top of the bill to the bill tip; (2) the flattened and straightened length of the right wing was measured using a ruler from the carpal joint to the tip of the longest primary; and (3) the length of the right tarsus was measured with calipers from the notch on the knee to the distal end of the tarsometatarsus. Weight (in grams) was also measured, using a 600 g Pesola spring balance. However, we excluded weight measurements from morphometric analyses to determine differences between the sexes since weight may vary considerably between individuals and over time (even within days) and therefore they may not be good predictors of body size (van de Pol *et al.* 2009). All birds were ringed on the tibia with single metal rings provided by the Saudi Wildlife Authority and one–three coloured plastic rings for individual identification. Blood samples (25–50 µl) were taken from the brachial vein of adults and stored in Queen's lysis buffer (Székely *et al.* 2006) for molecular sex-typing.

To mark nest-burrows, we used numbered plastic spoons placed near the burrow entrances. We used the presence of fresh tracks at a nest-burrow entrance to distinguish inhabited burrows from uninhabited ones (De Marchi *et al.* 2006). To extract the eggs from the burrows for brief examination, we used a tool constructed by attaching a spoon to the end of a 1.5 m stick. The eggs were extracted from burrows at the beginning of the breeding season and were accessible at this stage since they were not positioned at the far end of the curved burrows. We collected and measured four eggs; two in June 2011 from the Albatrain Islands, which are located about 10 km northwest of Al Qunfudhah city, and two from Humr Island in 2012. As the breeding area was very fragile, we used sand-shoes – analogous to snow-shoes – for walking around the colony in order to avoid destroying burrows (Fig. 2).

A mobile hide was used for making behavioural observations to avoid disturbing the Crab Plovers. The hide was located about 30 m from the colony. Observations of bird behaviour were made during the day, and activities at the nest-burrows were also recorded using Bushnell Trophy



Fig. 2. Sand-shoes, analogous to snow-shoes, designed for walking around the colony in order to prevent damage to burrows.

Cam 270p HD (model119466) and Reconyx (SC950 HyperFire Security IR) cameras. It was difficult to determine by direct observation which nest-burrows belonged to the individually-marked birds as the burrows were close to one another and the birds were highly mobile within the colony. Therefore, the Bushnell camera was set up to record an image every minute to determine which nest-burrows the ringed birds were using. In this way, six burrows were identified as being inhabited by one ringed and one unringed parent (two contained eggs and four contained chicks). To determine the behaviour of parents at the nest-burrows, the Reconyx camera was positioned about 1 m from a nest-burrow entrance and set to record one image every five seconds for 24 hours and in several cases for 48 hours. The cameras were operated from the beginning of June until mid-July 2012.

Ground temperatures and temperatures inside active nest-burrows were recorded using iButtons (model no. DS1922L-F50), with an accuracy of $\pm 0.5^\circ\text{C}$ between -10°C and $+65^\circ\text{C}$, as tested by the manufacturer. Ground temperatures were measured using iButtons placed on the surface of the ground in the colony. We recorded nest-burrow temperatures using iButtons placed approximately 100 cm inside 11 active nest-burrows for 24 hours at 30-second intervals from late June to mid-July 2012. The devices were glued to a small wooden stick and inserted through the wall of the burrow to keep the iButton data logger inside the nest-burrow. The birds did not appear to be disturbed by them.

The types of food provided for chicks and the feeding frequency throughout the day were determined by deploying the Reconyx camera for 24 hours at each of four nest-burrows. We also collected some items discarded by the Crab Plovers from around the nest-burrow entrances. Prey size was estimated in two ways. First, based on the photographs, we evaluated prey size by comparison with the size of Crab Plover bills (approx. $5.5\text{ cm} \pm \text{SE}=0.05$; $n = 42$). Second, we directly measured discarded food items that we found in the colony around the nest-burrows.

DNA extraction and sex determination

DNA extraction from 66 blood samples was carried out using an ammonium acetate method (Nicholls *et al.* 2000; protocol online at http://www.shef.ac.uk/nbaf-s/protocols_list). DNA concentration was evaluated using a Nanodrop ND8000 spectrophotometer. Sex determination in birds is usually based on amplification (through polymerase chain

reaction – PCR) of fragments of a Z and W gene that differ in size, such that males (ZZ) and females (ZW) are easily distinguishable by the observation of the differently sized amplicons. For each sample, PCR amplification was conducted using two primer pairs, P2/P8 (Griffiths *et al.* 1998) and Z-002A F/Z-002A R (Dawson 2007) in a single duplex reaction with fluorescent dye labelled forward primers (HEX and 6FAM respectively). Using two different markers prevents errors resulting from the misinterpretation of sex-typing data due to allelic dropout or Z polymorphism (Dawson *et al.* 2001, dos Remedios *et al.* 2010, Toouli *et al.* 2000).

PCRs were performed in 2- μ l reactions including 10–15 ng dry DNA, 0.2 μ M of each primer (combined in 1 μ l of low TE buffer) and 1 μ l QIAGEN Multiplex PCR MasterMix, with a layer of mineral oil to prevent evaporation. PCR amplification was conducted on a DNA Engine Tetrad 2 Peltier Thermal Cycler using the following conditions: 15 min at 95°C, followed by 35 cycles of 30 s at 94°C, 90 s at 52°C, 60 s at 72°C, and a final cycle of 30 min at 60°C. Amplicons were visualized on an ABI 3730 48-well capillary Sequencer, with GeneScan 500 ROX size standard. Alleles were scored using GeneMapper software version 3.7 (Applied Biosystems).

Statistical analyses

The Nonparametric Test of Group Differences was used to *determine* whether there is a *significant difference* in the amount of food delivered by males and females.

Discriminant function analysis (DFA) was used to evaluate sexual size dimorphism. In this, outliers were checked using box plots. Missing values (22.1% of the total data set) were evaluated using the Expectation Maximization (EM) method (Strauss *et al.* 2003) since DFA cannot be applied to samples containing missing values. We applied EM for males and females whose sex was identified via molecular sexing. The Shapiro–Wilk test was applied to detect the normality of each variable, and all variables were normally distributed ($P > 0.05$). In order to test for differences in body size between males and females, MANOVA was applied using bill length, wing length and tarsus length as dependent variables and sex as an independent variable. In order to identify the significance of sex differences for each dependent variable, t-tests were applied. Correlation tests (Pearson correlation) were applied to examine correlations between

each two variable combinations since DFA supposes predictors should not be highly correlated with each other. We found that none of the three variables were highly correlated with each other (Pearson $r < 0.5$). A leave-one-out cross validation test was applied to check the accuracy of prediction. To identify the variable that differed most between males and females, DFA was performed on the three morphological characteristics using the package MASS, implemented in R (version 2.15.1) based on molecularly sexed individuals for which all three measurements were available (26 males and 40 females). The three morphological measurements from these birds were grouped together using DFA to generate a predictive function formula that can be applied to discriminate the sexes. Finally, a cut-off value was identified, with individuals with a higher value being classified as male, and individuals with a lesser value being classified as female.

RESULTS

Timing of breeding and egg-laying

Crab Plovers started to dig their nest-burrows in mid-May 2012 and egg-laying was initiated at the end of May. The average egg length and width measurements were $64.3 \pm \text{SE} = 0.80$ mm and $45.1 \pm \text{SE} = 0.47$ mm respectively. Egg hatching was highly synchronized and the eggs started to hatch at the end of June. When the eggs hatched, the parents would throw the eggshell fragments outside the nest-burrow. From the eggshell fragments recorded at the end of June, we estimated that at least 64 eggs laid in the colony had hatched. At the beginning of July, new eggshell fragments were found outside the nest-burrows, but due to strong winds, we could not estimate the numbers accurately. The parents started to bring food to their chicks at the beginning of July.

Incubation temperature

The lowest and highest ground temperatures in the colony were recorded as 28.15°C and 55.56°C, respectively. The average temperature inside 11 active nest-burrows was $35.0 \pm \text{SE} = 0.18$ °C ($n = 11$ nest-burrows). The temperature inside the nest-burrows was almost constant from midnight to midnight but the outside temperature varied from around 30°C at night to 50°C in the middle of the day (Fig. 3).

Table 1. Data collected on Crab Plovers caught on Humr Island, Saudi Arabia, during May–July 2012 and sexed using molecular techniques.

	Number sexed	Bill measured	Wing measured	Tarsus measured	Weight measured
Male	26	15	25	19	22
Female	40	27	38	33	39
Total	66	42	63	52	61

Table 2. Body size parameters of adult Crab Plovers caught on Humr Island, Saudi Arabia, during May–July 2012, after estimating missing values using the expectation maximization (EM) method (SE = Standard Error). Note that as all these parameters are measures of size, it is appropriate to apply the Bonferroni correction. Therefore the null hypothesis should only be rejected if $p < 0.05/3 = 0.0166$.

	Male	Female	p-value, t test
	Mean \pm SE (N)	Mean \pm SE (N)	
Bill length (mm)	58.10 \pm 0.47 (26)	54.07 \pm 0.27 (40)	<0.0005
Wing length (mm)	213.51 \pm 0.75 (26)	209.72 \pm 0.82 (40)	0.001
Tarsus length (mm)	98.06 \pm 0.58 (26)	96.04 \pm 0.54 (40)	0.0139

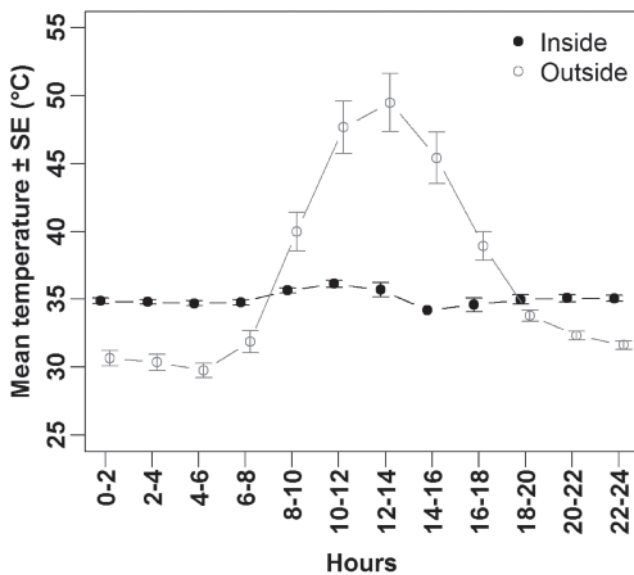


Fig. 3. Ambient temperature (\pm SE) outside seven Crab Plover nest-burrows on Humr Island, Saudi Arabia, and temperature at about one metre inside 11 active nest-burrows from midnight to midnight in two-hour periods during June 2012.

Molecular sexing and sexual size dimorphism

Sixty-six adult Crab Plovers captured on Humr Island were sexed using molecular techniques and found to comprise 26 males and 40 females (Table 1). Although no samples were available from individuals of previously known sex, all samples were amplified with both molecular markers and the results based on P2/P8 and Z-002A markers were consistent for all 66 samples.

MANOVA of the birds' bill, wing and tarsus lengths indicated significant morphological differences between males and females ($F_{1,64} = 10.5$, $P < 0.0005$; Table 2). T-tests revealed that the bill, wing and tarsus lengths of males significantly exceeded those of females, bill lengths being

the most significantly different and tarsus lengths the least (Table 2). The results of direct DFA also showed that bill length is the most reliable single predictor of sex, whereas wing length and tarsus length are not so effective (Table 3). The coefficients of the three linear discriminant models were: (bill length \times 0.480237862) + (wing length \times 0.02213118) + (tarsus length \times 0.028304745). The overall discriminatory power of the model was high (83.3% of individuals were correctly classified). Using this discriminant model to classify the 66 individuals resulted in misclassification of 7 of 36 females (19%) and 4 of 19 males (21%).

Brood care

At the beginning of the breeding season, we observed several juvenile Crab Plovers at the colony on Humr Island, but we found no evidence that they took part in nesting activities as helpers or otherwise.

During chick-rearing, only one parent usually attended the nest-burrow entrance to provide food, although in a small number of cases both parents were present at the same time. In addition, there were many occasions when both parents were away from the nest-burrow and most adults left the colony at midday when ambient temperatures were highest.

Based on observations of individuals of known sex at four nests, the number of visits by the female and by the male were respectively 12 and 8 (60% by the female), 15 and 7 (68.2%), 15 and 6 (71.4%) and 17 and 7 (70.8%). This difference is not statistically significantly different from equal feeding rates (Wilcoxon's test, $p = 0.25$), probably due to the small sample size. After hatching, the parents usually remained outside the nest-burrows and fed their chicks from the nest-burrow entrances. On several occasions an adult was seen to prevent the chicks from other nest-burrows from leaving their burrows when their own parents were away from the colony.

Composition of food fed to chicks

Altogether 86 prey items were identified from Reconyx

Table 3. Classification accuracy using discriminant function analysis (number/total (and %) correctly assigned) based on measurements of single morphological characteristics in males, females and in all birds from a sample of 66 Crab Plovers (26 males and 40 females) caught on Humr island, Saudi Arabia, during May–July 2012 and sexed using molecular techniques.

Predictor of sex	Males	Females	All birds
Bill Length	23/26 (88.5%)	34/40 (85.0%)	58/66 (87.9%)
Wing Length	19/26 (73.1%)	21/40 (52.5%)	42/66 (63.6%)
Tarsus Length	17/26 (65.4%)	27/40 (67.5%)	45/66 (68.2%)

Table 4. Type and size of food items delivered to Crab Plover chicks on Humr Island, Saudi Arabia, during June–July 2012 identified using camera-trap photos at four nests. In addition, measurements are given of the remains of some prey items that were collected from around the nest burrow entrances.

Prey type	Prey identified from photos			Prey remains collected from burrow entrances	
	% of prey items	Prey sizes (cm \pm SE)	Number	Prey sizes (cm \pm SE)	Number
Crab	53.5	3.8 \pm 0.13	46	3.25 \pm 0.25	2
Fish	23.3	5.7 \pm 0.20	20	6.1 \pm 0.33	17
Prawn	3.5	5.5 \pm 1.3	3	5.1 \pm 1.6	4
Worm	2.3	Not measured	2		0
Unknown	17.4	4.1 \pm 0.28	15		0
Total	100		86		23



Fig. 4. Photo from the Reconyx Camera showing an adult Crab Plover feeding a crab to its chick just outside the nest burrow. On the right a numbered plastic spoon marks another burrow.

Camera photos while being fed to chicks by adults at four nests; these included crabs, fishes, prawns and worms (Table 4, Fig. 4). The remains of 23 other food items discarded around the nest-burrow entrances were also collected and measured the majority (17/23, 74%) of these were fish (Table 4). The photos showed that the parents brought only one prey item per feeding visit. On average each chick was fed $21.5 (\pm SE=0.96)$ times per day. Food was delivered during the day and night, but based on four nests, provisioning was higher by day than at night (Fig. 5).

Nest-burrow structure

At the end of the breeding season we dug up three used nest-burrows and found that the burrows extended 70 to 90 cm below ground level, were about 2 m long, and included a bend so that in some cases the direction of the end of the burrow was opposite to that of the entrance. The nest chamber was at the end of the burrow (Fig. 6).

DISCUSSION

Our study yielded several important results. To our knowledge, this is the first study to identify differences in food provisioning by male and female Crab Plovers identified by molecular sex-typing. Using the data gathered from four

nests we found females brought food to their chicks more frequently than males. In about 81% of bird species, both males and females contribute to the care of offspring; however, parental investment is often not shared equally between the parents (Cockburn 2006, Olson *et al.* 2008).

We also found, through analyses of sexual size dimorphism in molecularly sexed Crab Plovers, that males are larger than females in bill length, wing length and tarsus length and that bill length is the best predictor of sex. This finding is consistent with that of De Marchi *et al.* (2012) who found that males are larger than females for all morphological measurements they studied. However, they found that the best characters for distinguishing male and female Crab Plovers were head-bill length, bill length, bill depth, wing chord and weight, whereas tarsus length was a poor predictor.

Our results indicate that the main primary items fed of Crab Plover chick are (in descending order of importance) crabs, fishes, prawns and worms. This is consistent with the results of Aspinall (2010) who reported that about 95% of full-grown Crab Plovers depend on crabs, but chicks are occasionally fed fish and molluscs. Morris (1992) found that in Abu Dhabi, parent Crab Plovers mainly fed their young with crabs, and in some cases fish, but very rarely molluscs. Therefore, we can conclude that the Crab Plover's main prey is crabs. Indeed Aspinall & Hockey (1996) suggested that the distribution of Crab Plovers is restricted to tropical and subtropical areas due to the abundance of crabs.

Based on four nests, we found that the rate of delivery of prey to the chick was roughly twice as high by day than at night (Fig. 5). De Marchi *et al.* (2015) suggested that the foraging times of Crab Plovers are related to the tidal rhythm; similarly Geering *et al.* (2007) found that feeding activities by the majority of shorebird species are driven by tidal rhythm. However, the tidal range in the Red Sea is extremely small (Edwards 1987), so we were unable to evaluate the effect of tide on the provisioning of chicks in our study population.

On several occasions we observed Crab Plover adults preventing chicks from other nest-burrows from leaving their burrows while their parents were away from the colony. These findings suggest that there may be a cooperative care system operating among Crab Plovers. The present findings seem to be consistent with other research which suggested the existence of helpers at Crab Plover colonies. Helpers may increase vigilance and thus protect the Crab Plover chicks from potential risks (Hockey & Aspinall 1997,

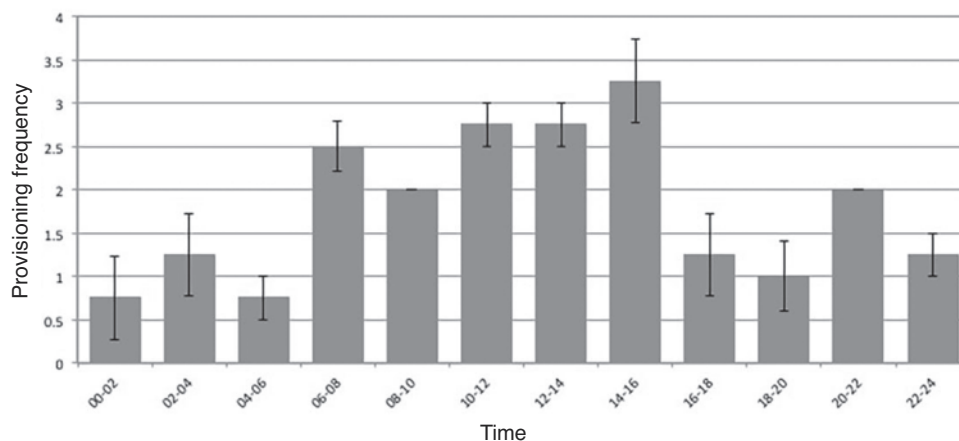


Fig. 5. Provisioning frequency (number of feeding visits by adults per nest per two-hour period $\pm SE$) from midnight to midnight at four Crab Plover nest-burrows on Humr Island, Saudi Arabia, during June-July 2012.

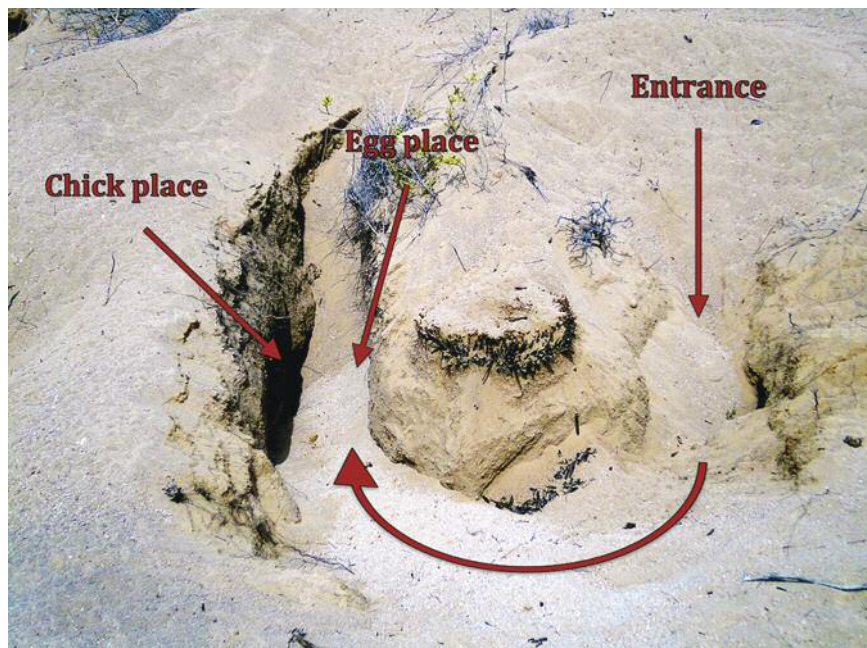


Fig. 6. Excavation revealed that from the entrance, the burrow sloped downwards and turned 180° before coming to the nest chamber.

Aspinall 2010). Covas *et al.* (2008) indicated that helpers can positively influence reproductive performance in many ways; for example, food provisioning or parental care can enhance the condition and survival of chicks. We identified several juvenile birds at the Crab Plover colony on Humr Island at the beginning of the breeding season. However, we have no evidence that these juveniles shared the care of chicks with the adults.

One possible benefit of colonial breeding in birds is enhancing their defence against predators, yet conversely, breeding in a colony also raises the visibility of the group to predators (Ashbrook *et al.* 2008, Urfi 2003). Nest defence can be considered a parental strategy to increase fitness by decreasing the probability that a predator will target their offspring (Redmond *et al.* 2009). However, the Crab Plovers we observed did not defend their colony against the attendance or attacks of Sooty Gulls. Furthermore, when we visited the colony, we noticed that all the Crab Plovers would leave the colony and move to neighbouring sites. Therefore, nesting in burrows may help the parents to protect their young without the need to interact with predators, thus avoiding any physical risk associated with an active defence. If offspring are well-protected underground, Sooty Gulls might not depredate the Crab Plover chicks but instead collect their discarded food.

The average temperature inside 11 active Crab Plover nest-burrows was relatively stable at around 35.0°C regardless of the ambient temperature outside. This finding is consistent with that of De Marchi *et al.* (2008), who found the average temperature inside nest-burrows at 100–200 cm from the entrance to be 35.2°C. Conway & Martin (2000) reported that the optimal temperature for egg development for the majority of bird species is between 36 and 40.5°C. De Marchi *et al.* (2008) suggested that the most obvious purpose of nesting in burrows is to protect the eggs from high temperatures. As a consequence, parents have to spend very little time incubating their eggs (De Marchi *et al.* 2008, De Marchi *et al.* 2014).

CONCLUSIONS

The demographic and behavioural data collected on Crab Plovers breeding on Humr Island, Saudi Arabia, in this study revealed several key findings: (1) the most reliable morphological trait indicating the sex of Crab Plovers in our study population was bill length; (2) both males and females provided food to the chicks but provisioning was carried out more often by females than males; (3) this study has gone some way towards enhancing our understanding of day-night cycles in chick feeding routines, with higher provisioning rates during the daytime than at night; and (4) the temperature inside active nest-burrows was rather stable and did not change significantly with above-ground temperature.

In future, cannon-netting could be used to catch a larger number of birds in the colony or at their feeding sites. While this study has provided valuable insights into the breeding ecology of a highly specialised, unique shorebird, several questions still remain. In particular, we suggest future studies should concentrate on: (1) investigating whether the Crab Plover can incubate and rear two eggs and chicks at the same time; (2) studying mate fidelity in Crab Plovers; (3) studying the nest architecture of the Crab Plover; and (4) investigating the identity and function of the helpers at Crab Plover colonies.

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