

**Demography of a stable population of Crab Plovers wintering in Oman**

Roeland A. Bom<sup>1,2</sup>, Jan A. van Gils<sup>1</sup>, Kees Oosterbeek<sup>3</sup>, Symen Deuzeman<sup>3</sup>, Jimmy de

Fouw<sup>1,4</sup>, Andy Y. Kwarteng<sup>2</sup>, Rosemarie Kentie<sup>1,5</sup>

*1. Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, and*

*Utrecht University, P.O. Box 59, 1790 AB Den Burg, Texel, the Netherlands*

*2. Remote Sensing and GIS Center, Sultan Qaboos University, P.O. Box 33, Al Khod PC 123,*

*Oman*

*3. SOVON Dutch Centre for Field Ornithology, Coastal Ecology Team, 1790 AB Den*

*Burg, Texel, the Netherlands.*

*4. Department of Aquatic Ecology and Environmental Biology, Institute for Water and*

*Wetland Research, Radboud University Nijmegen, Heyendaalseweg 135, 6525 AJ Nijmegen,*

*The Netherlands*

*5. Department of Zoology, University of Oxford, Oxford, OX1 3PS, UK*

*Corresponding author: [roeland.bom@nioz.nl](mailto:roeland.bom@nioz.nl)*

**Abstract**

The monotypic Crab Plover *Dromas ardeola* winters around the shores of the Indian Ocean and breeds in colonies on islands around the Arabian Peninsula. The IUCN lists the world population of Crab Plovers as stable, but long-term survey data or demographic estimates regarding the species status are lacking. Here, we use survey and demographic data collected from 2011-2015 to study the status of the population of Crab Plover at their most important wintering area: the Barr Al Hikman Peninsula in the Sultanate of Oman. Our survey data showed that the population of Crab Plovers initially increased and then stabilized. The overall observed finite rate of population change ( $\bar{\lambda}_{\text{obs}}$ ) was estimated at 1.004 (0.995–1.013 95% Bayesian credible interval [BCI]), indicating a stable population (7,000–9,000 birds), that is possibly at carrying capacity. Based on mark-recapture data, the mean annual apparent survival probability of Crab Plovers was estimated to be 0.90 (0.85–0.94 95% BCI). We used counts of adults and yearlings to estimate the mean annual fecundity rate at 0.06 young per pair. Using these demographic values, the overall mean expected finite rate of population change ( $\bar{\lambda}_{\text{exp}}$ ) was estimated to be 0.949 (0.899 – 0.996 95% BCI), so there is a low chance that  $\bar{\lambda}_{\text{obs}}$  and  $\bar{\lambda}_{\text{exp}}$  overlap.  $\bar{\lambda}_{\text{obs}}$  and  $\bar{\lambda}_{\text{exp}}$  would completely match if about 450 Crab Plovers immigrate to Barr Al Hikman each year. Regional surveys show that yearling densities are higher closer to the breeding areas, so immigrants could be birds that during their first winter stayed close to their natal area. Our study support the IUCN listening of Crab Plover as stable, but further population-wide monitoring is required. From a conservation point of view it is important to continue monitoring because Crab Plovers breed and winter in a region that is rapidly developing.

**Keywords:** apparent survival, Arabian Peninsula, Barr Al Hikman, *Dromas ardeola*, fecundity, finite range of change, Integrated Population Model

## Introduction

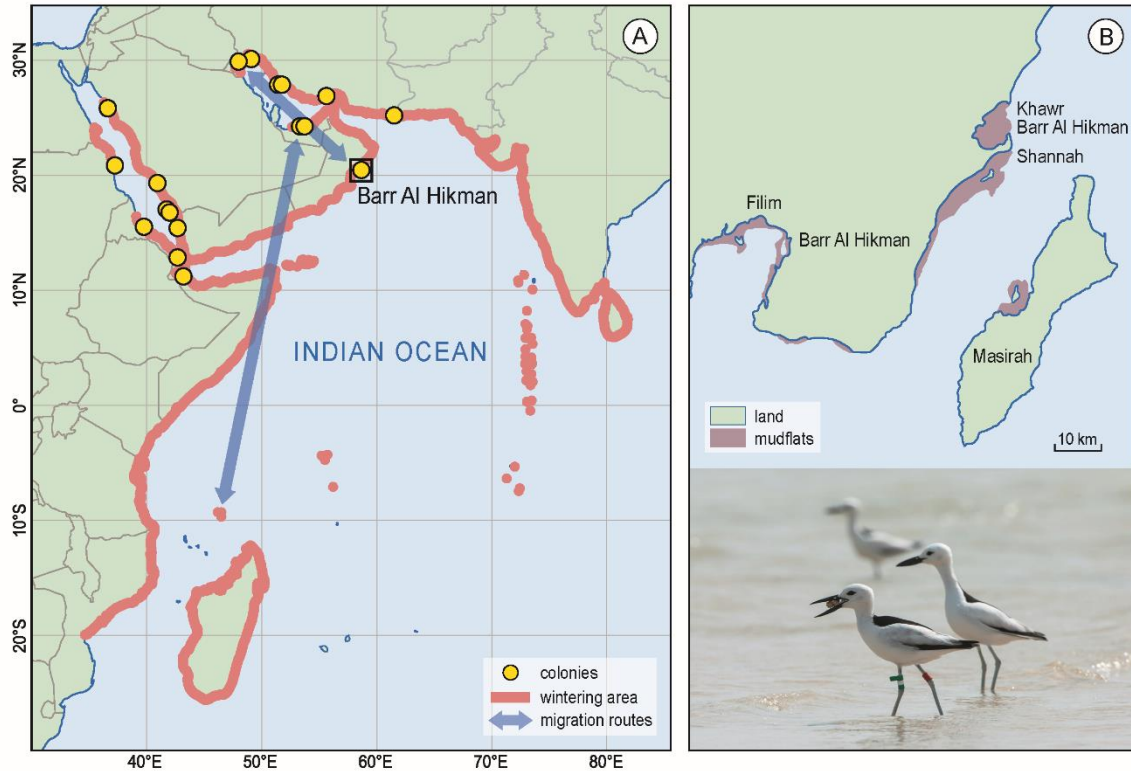
The coastal areas of the Arabian Peninsula and East-Africa provide essential breeding and wintering habitat for a large number of shorebirds traveling within the Asian–East African Flyway (Delany et al. 2009). In contrast to shorebird populations in other parts of the world (Fernández and Lank 2008; Piersma et al. 2016; van Roomen et al. 2015), the status of shorebirds breeding and wintering along the Arabian and East-African coasts remains largely unknown (Delany et al. 2009). Coasts along the Arabian Peninsula and East-Africa are rapidly changing under increasing human pressure (Halpern et al. 2008), including habitat loss, climate warming, and overfishing (Sale et al. 2011; Sheppard et al. 2010). To understand if shorebirds in this part of the world can keep up with their changing environment, long-term survey data and demographic estimates are urgently needed.

The monotypic Crab Plover *Dromas ardeola* is endemic to the coastal areas of the Indian Ocean and the main breeding areas are located in the Arabian/Persian Gulf and the Red Sea (Bom and al-Nasrallah 2015). Crab Plovers breed in colonies on sandy islands where they nest in self-excavated burrows (De Marchi et al. 2008). Suitable breeding habitat seems scarce as only 56 breeding sites are known to exist worldwide (Bom and al-Nasrallah 2015). Crab Plovers are unusual among shorebirds as their modal clutch size is one, or rarely two eggs (Tayefeh et al. 2013). Crab Plovers exhibit extended parental care, which is biparental at the breeding areas (Almalki et al., 2015) and probably uniparental at the wintering areas (De Sanctis et al. 2005). Parental care extends up to 8 months, which is longer than any other shorebird (De Sanctis et al. 2005). A small clutch size and extended parental care are life-history characteristics typical of long-lived species with low fecundity rates (Newton 1998; Sæther and Bakke 2000; Sandercock 2003), but the demography of Crab Plovers has not been studied before. Potentially, as Crab Plovers require specific breeding- and wintering habitat, they may suffer from rapid environmental changes in coastal areas. Egg collecting,

destruction of burrows, or harvesting of adults may seriously affect breeding success and survival of Crab Plovers at the breeding areas (De Marchi et al 2006; Behrouzi-Rad 2013; Tayefeh et al. 2013), whereas habitat destruction and overexploitation of preferred crab prey may affect the species at the wintering areas (Safaie *et al.*, 2013). Based on counts at the wintering areas, the world population of Crab Plovers has been estimated to be 60,000 to 80,000 birds (Wetlands International 2002). The population of Crab Plovers is currently considered to be stable (IUCN 2017), but this has not been substantiated with data (Delany et al. 2009).

In this study, we assessed the status of the population of Crab Plover wintering at the Barr Al Hikman Peninsula in the Sultanate of Oman (Fig. 1a). The area supports 10-15% of the world population of Crab Plovers and is therefore the most important wintering area for the species (Delany et al. 2009). Based on survey data and demographic estimates collected from 2011 to 2015, we developed an Integrated Population Model (IPM) (Schaub & Abadi 2011) in which we estimated observed and expected finite rates of population change ( $\lambda_{\text{obs}}$  and  $\lambda_{\text{exp}}$ ). IPMs combine population counts and demographic data in a single model, and are particularly useful for studies with small datasets (Schaub et al. 2007), or studies where not all demographic parameters could be accounted for by data collected in the field (Schaub & Abadi 2011). Here we estimated  $\lambda_{\text{obs}}$  using existing survey data (de Fouw et al. 2017) whereas  $\lambda_{\text{exp}}$  was calculated from newly estimated survival and fecundity rates. Apparent annual survival rates were estimated based on sightings of 169 individually colour-marked birds, and annual fecundity rates were based on the percentage of yearlings (first-winter birds) in the population. In addition to survival and fecundity, population dynamics of local populations also depend on immigration and emigration (Newton 1998). We did not measure immigration and emigration directly, but calculated potential immigration rates by matching observed ( $\lambda_{\text{obs}}$ ) and expected ( $\lambda_{\text{exp}}$ ) finite rates of population change (e.g., Doxa et al. 2012).

We discussed the generality of our results by looking at population dynamics of Crab Plovers at other winter areas.



*Fig. 1. The distribution of Crab Plovers is confined to coastal areas of the Indian Ocean (A). Breeding areas (yellow dots) are adapted from Bom and al-Nasrallah (2015), and wintering areas (red coast line) from Delany et al. (2009). Arrows show the known connections between breeding and wintering areas (Bom and al-Nasrallah 2015; Javed et al. 2011). The study area at Barr Al Hikman is shown in the black square and in (B), with the main localities that are mentioned in the text. The inset in (B) shows a colour-ringed Crab Plover.*

## Methods

### Study area & data collection

Our study was conducted at the intertidal mudflats that surround the Barr Al Hikman Peninsula in the Sultanate of Oman (20.6° N, 58.4° E). The intertidal mudflats encompass 190

km<sup>2</sup> and can be found south of Shannah, in the Khawr Barr Al Hikman, near Filim and on Masirah Island (Fig. 1b). Local industries included fisheries and salt mining, but the area is relatively pristine. Crab Plovers can be found in the area almost exclusively in winter (Eriksen and Victor 2013). Six GPS tracks and four ring observations show that Crab Plovers wintering in Barr Al Hikman are connected to breeding areas in the Arabian/Persian Gulf in colonies in Kuwait and South-West Iran (Fig. 1a, Bom and al-Nasrallah 2015). Barr Al Hikman was surveyed for shorebirds including Crab Plovers in the four winters of 1989/90 (Green et al. 1992), 2007/08, 2013/14 and 2015/16 (de Fouw et al. 2017) (Table 1).

*Table 1. Survey results on wintering Crab Plovers at Barr Al Hikman, Oman, 1989-2016. In the present study, survey results collected over the period 2007/08 – 2015/16 were used to estimate the survey-based finite rate of population change.*

Year	No. of Crab Plovers	Source
1989-1990	2943	Green et al. 1992
2007-2008	6901	de Fouw et al. 2017
2013-2014	8759	de Fouw et al. 2017
2015-2016	8462	de Fouw et al. 2017

We collected mark-recapture data on Crab Plovers at Barr Al Hikman during ten winter expeditions between 2007/08 and 2015/16 (one winter included two expeditions). During seven expeditions, Crab Plovers were caught with mist nets and individually marked with colour rings. All catching took place on the mudflats close to the shore 3 to 22 km south of Shannah in the nights around a new moon. In 2008/2009 and April 2010, all newly captured Crab Plovers received a unique combination of a single colour ring (white or orange) with a single letter inscription on each tibia and a metal ring on the right tarsus. During later years, birds were marked with four coloured rings and a green flag on their tibia, and a metal ring on the tarsus. An initial mark-recapture analysis showed that there was no difference in

the resighting probability between the two types of colour rings as the Bayesian credible interval (BCI) for an effect of marker type overlapped zero (BCI 95% [-0.481; 1.459]).

Crab Plovers were aged as yearlings (i.e. born in the previous summer) or adults (i.e. birds older than 1 year, Table 2) at first capture. Yearlings are easy to recognize by their spotted crown and hind neck and their greyish mantle (Cramp and Simmons 2004). We could not confidently age second-winter birds and we suspect that all yearling Crab Plovers had moulted into their adult plumage prior to our catching expeditions (Supplementary Material S1). During all expeditions, observation effort to resight the marked birds was concentrated along the coast south of Shannah, but during most expeditions all other sites in the area were visited and checked as well at least once.

*Table 2. Number of adult and yearlings Crab Plovers that were individually marked with colour rings at Barr Al Hikman per field visit.*

Period	no. of ringed adults	no. of ringed yearlings
Dec 2008- Jan 2009	58	11
Apr 2010	2	4
March 2011	5	6
Nov-Dec 2011	29	3
Nov-Dec 2012	9	0
Nov 2014	22	7
Nov 2015	12	1

From 2011-2015, during early winter (November-December), we collected data on the annual fecundity of Crab Plovers by regularly counting the number of yearlings and adults in foraging or roosting groups all along the coast south of Shannah. Roosting groups were only counted if all birds were visible, because it appeared that birds at flock edges were often foraging yearlings. We counted between 8 and 22 groups per year, and between 10 and 666 individuals per group (Table 3).

*Table 3. The number of groups in which the percentage yearlings of Crab Plovers were counted and the total number of birds counted. The final column give the model estimates of the percentage of yearlings in the population per year.*

	no. groups	total no. birds	% of yearlings <sup>154</sup>
	counted	counted	(mean $\pm$ 95% BCI)
2011/12	12	986	6.88 (5.41 – 8.53)
2012/13	12	766	6.77 (5.11 – 8.63)
2013/14	8	479	5.81 (3.89 – 8.14)
2014/15	22	1492	6.23 (5.10 – 7.49)
2015/16	11	2364	3.01 (2.42 – 3.80)



### Integrated population model

We combined survey data and demographic data in a Bayesian Integrated Population Model (IPM) (Schaub and Abadi 2011) to estimate the annual-dependent survey-based finite rate of population change ( $\lambda_{\text{obs}}$ ) and the annual-dependent demographic-based finite rate of population change ( $\lambda_{\text{exp}}$ ) for the five-year period 2011/12 – 2015/16.

#### *Survey-based finite rate of population change $\lambda_{\text{obs}}$*

$\lambda_{\text{obs}}$  was estimated from population counts as:

$$\lambda_{\text{obs}} = N_{t+1} / N_t$$

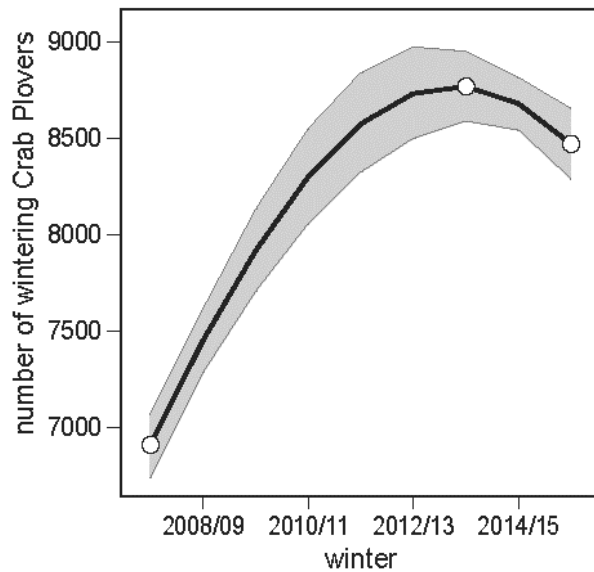
where  $N_t$  is the total population size at year  $t$  and  $N_{t+1}$  is population size in the year  $t + 1$ . To calculate  $N_t$  for winters in which no surveys were performed we simulated  $N_t$  by fitting a quadratic polynomial function with a Poisson distribution through the survey data over the period 2007/08 - 2015/16 in the Markov Chain Monte Carlo (MCMC) framework that we used in our Bayesian model (Fig. 2). We calculated year-specific  $\lambda_{\text{obs}}$  and also the geometric mean of  $\bar{\lambda}_{\text{obs}}$  over all five years. The geometric mean was calculated as:

$$\bar{\lambda}_{\text{obs}} = \left( \sum_{t=1}^T \lambda_t \right)^{1/T}$$

(Stevens 2009).

Our estimation of  $\lambda_{\text{obs}}$  assumes perfect detection or equal probability of detection. Imperfect detection is widespread in surveys of roosting birds (Sutherland 2006) and we cannot guarantee perfect detection during our Crab Plover surveys. Arguably, probability of detection between years is equal, as all surveys reported in Table 1 are comparable in the sense that they covered exactly the same area and that there has been overlap between

observers during all surveys (Fouw et al. 2017). In addition, Crab Plovers roost in well-defined congregations at the high-waterline and their conspicuous black-and-white plumage make them hard to miss. Furthermore, tracking data show that Crab Plovers have limited movements in their wintering area (unpublished data), making it unlikely that birds are counted twice when surveys are conducted over subsequent days.

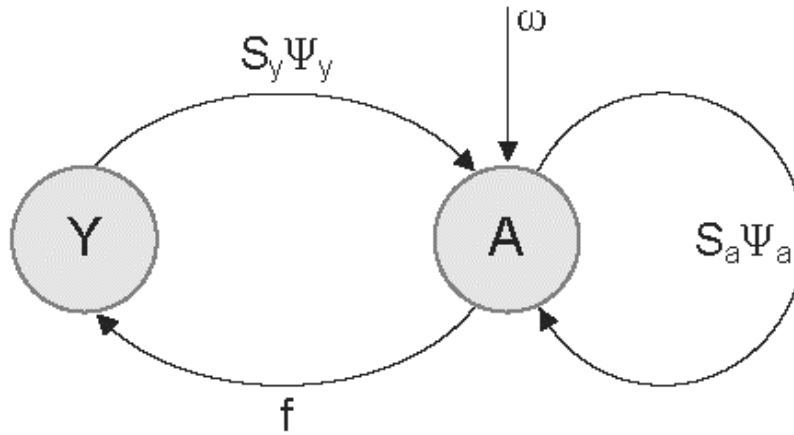


*Fig. 2. Number of wintering Crab Plovers in Barr Al Hikman in the study period based on surveys (open circles) and modelled population estimates. The thick line represents posterior means and shaded area represents 95% BCI.*

#### *Demographic-based finite rate of population change $\lambda_{exp}$*

We estimated  $\lambda_{exp}$  following assumptions shown in a post-reproductive census life cycle diagram (Fig. 3). Accordingly, as we could not age second-winter birds, the Crab Plover population at Barr Al Hikman in year  $t$  consists of yearlings (Y) and reproducing adults (A). The number of adults that will be in the area at year  $t+1$  depends on age-specific survival

194 probabilities ( $S_y$  and  $S_a$ ) and age-specific site fidelity ( $\psi_y$  and  $\psi_a$ ), and on immigration rate ( $\omega$ ).



195  
 196 *Fig 3. The life cycle diagram used for a population model of Crab Plover wintering at Barr Al*  
 197 *Hikman. The two stages are the yearlings ( $Y \leq 1$  year, and adults ( $A$ ) birds  $> 1$  year. The*  
 198 *demographic parameters are age-specific survival ( $S_y$ ,  $S_a$ ), age-specific site fidelity ( $\psi_y$ ,  $\psi_a$ ),*  
 199 *annual fecundity ( $f$ ) and immigration of adults ( $\omega$ ).*

200  
 201 The number of yearlings in the area in year  $t+1$  depends on the annual fecundity rate ( $f_t$ ),  
 202 which is the proportion of yearlings per pair. We could not measure site fidelity ( $\psi$ ) and  
 203 immigration ( $\omega$ ) directly. Instead we estimated apparent survival ( $\phi$ ) as the product of true  
 204 survival ( $S$ ) and  $\psi$  (Lebreton et al. 1992) and immigration rate ( $\omega$ ) as the difference between  
 205  $\lambda_{\text{obs}}$  with  $\lambda_{\text{exp}}$  (see below).

206 We used a Cormack-Jolly Seber model to estimate apparent survival ( $\phi$ ), which  
 207 corrects for the probability that not each bird is seen each year (resighting rate,  $p$ ) (Lebreton et  
 208 al. 1992), which we constructed in a Bayesian framework (Kéry and Schaub 2012). We first  
 209 assessed the Goodness-of-Fit (GOF) in program Release in Mark to ascertain that the  
 210 underlying assumptions for mark-recapture models are met (Pradel et al. 2005). Test 2, which  
 211 tests the assumption that all individuals have an equal probability to be resighted and is

therefore referred to as a test of trap-dependence, was significant ( $\chi^2 = 40.7049$ ,  $df = 11$ ,  $p < 0.01$ ), and Test 3, which tests the assumption that all individuals have the same probability of survival to the next time step, was not ( $\chi^2 = 16.4881$ ,  $df = 9$ ,  $p = 0.0574$ ). To account for trap-dependence, we therefore used individual as random effect in the resighting probability (Kéry and Schaub 2012). The intensity of fieldwork varied each year, and resighting probability was modelled to vary among years. Test 3 of the GOF was almost significant, which could be caused by a differing apparent survival rate between adults and juveniles. We therefore tested preliminarily if apparent survival between yearlings and adults differed, which was not as the 95% BCI of their survival rates overlapped considerably ( $\phi$  yearlings = 0.867, 95% BCI [0.657-0.994],  $\phi$  adults = 0.893, 95% BCI [0.844-0.938]). Then, with a time-since-marking test, we tested whether catching influenced survival probability in the first year after catching, which could be caused by higher mortality or permanent emigration after the disturbance of handling, or by age-dependent survival probabilities (Sandercock 2006). We could find a weak effect of catching on apparent survival ( $\phi$  first year after catching = 0.821, 95% BCI [0.672-0.982],  $\phi$  years after first year after catching = 0.905, 95% BCI [0.855-0.950]). Given that there was overlap in BCI, all age classes and years after catching were treated as one group. Given our low sample size (Table 2), we did not calculate year-dependent annual apparent survival to avoid over parameterization.

We estimated year dependent fecundity ( $f_t$ ) as the proportion of yearlings within a group ( $Y/[Y+A]$ ), within the Bayesian framework. Because Crab Plovers lay (mostly) a single egg per year, fecundity could be estimated with a generalized model using a binomial error structure, and hence equals the fraction of success pairs (assuming that sex ratios of yearlings and adults in Barr Al Hikman are equal). As we estimated fecundity over the total number of birds older than one year (see below), we probably slightly underestimated the true fecundity in Crab Plovers, as Crab Plovers probably start breeding after their second winter (Bom and

al-Nasrallah 2015). However, given that fecundity rates in Crab Plovers are low (see below), this bias is probably small.

Because apparent survival between adults and yearlings did not differ, we could calculate  $\lambda_{\text{exp}}$  as:

$$\lambda_{\text{exp}} = \phi + \phi f_t$$

We estimated year specific  $\lambda_{\text{exp}}$  and the geometric mean of  $\bar{\lambda}_{\text{exp}}$  over all the years.

### *Immigration*

We regard immigrants as birds that have been in other areas during previous winters (hence, adult birds only). We calculated the per capita immigration rate  $\omega$  for each year except the first year as

$$\omega = (N_t - \lambda_{\text{exp}} * N_{t-1})/N_t$$

All parameters were estimated in one IPM. MCMC simulations for parameter estimation were obtained by running the JAGS program (Plummer 2003) implemented in the R environment (R Development Core Team 2013) using the *R2JAGS* package (Su and Yajima 2012). We used uninformative priors for all parameters. We ran three independent chains of 50,000 iterations of which the first 10,000 were discarded, and kept every 6th observation to avoid autocorrelation. We checked the R-hat for convergence of the parameters (in all cases < 1.01). Estimates are presented as the posterior means and with a 95% BCI.

## **Results**

The geometric mean  $\bar{\lambda}_{\text{obs}}$  for the five-year period 2011/12 – 2015/16 was 1.004 (0.995–1.013). The yearly  $\lambda_{\text{obs}}$  ranged between 0.98 and 1.02 and decreased over the years (Fig. 4). Annual apparent survival probability was 0.895 (0.847–0.940) for the period 2008/09 –

2015/16. The annual resighting probability increased from 0.080 (0.025 – 0.169 95% BCI) to 0.744 (0.097 – 0.915 95% BCI) over the years 2008/09 – 2015/16 (Supplementary Material S2). The estimated annual fecundity rate varied over the period 2011/12 – 2015/16 between 0.03 and 0.07 (proportion of yearlings), with 95% BCI ranging between 0.02 and 0.08. On average, the annual fecundity rate was 0.06 (Table 3). Based on the estimated apparent survival probability and fecundity rate, the geometric mean  $\bar{\lambda}_{exp}$  over the period 2012/13 – 2015/16 was 0.949 (0.899 – 0.996 95% BCI) and annually ranged between 0.92 and 0.96 (Fig. 4). As we did not estimate a yearly dependent apparent survival probability, variation in  $\lambda_{exp}$  was solely due to variation in the estimated fecundity rate, which was particularly low in the last year (Table 3). To explain differences between  $\lambda_{obs}$  and  $\lambda_{exp}$ , we estimated yearly per capita immigration rates of 0.056 (0.006 – 0.107 95% BCI) in 2012/13, 0.052 (0.027–0.104 95% BCI) in 2013/14, 0.034 (0.026–0.086 95% BCI) in 2014/15 and 0.051 (0.103–0.026 95% BCI) in 2015/16. Our estimated immigration rates correspond to 315-508 individuals per year.

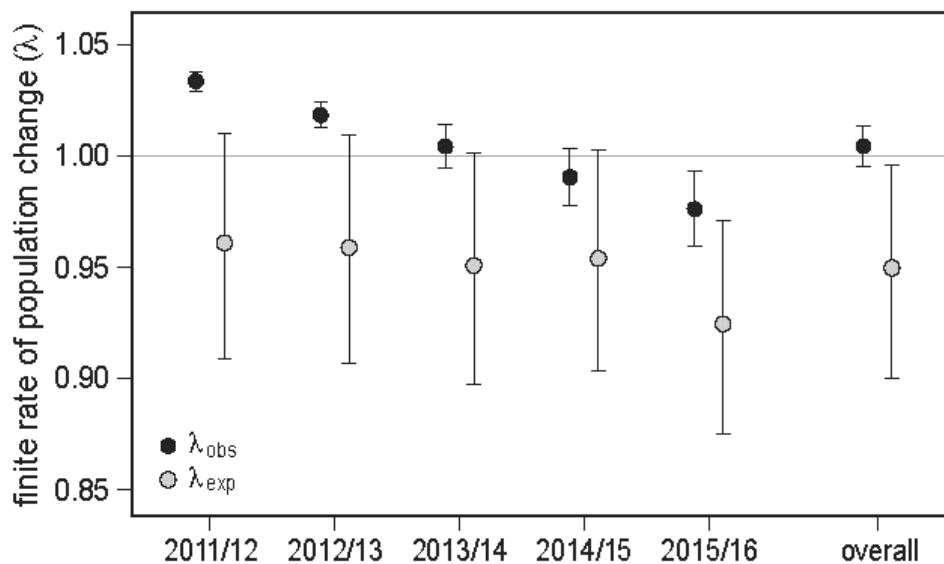


Fig. 4. Annual finite rates of population change based on population surveys ( $\lambda_{obs}$ , black dots) and based on demographic estimates ( $\lambda_{exp}$ , grey dots) and the overall  $\bar{\lambda}_{obs}$  and  $\bar{\lambda}_{exp}$ .

Error bars show 95% BCI. The grey line at  $\lambda = 1$  indicates the level at which the population would be stable. The difference between  $\lambda_{obs}$  and  $\lambda_{exp}$  was used to calculate immigration rates ( $\omega$ ).

## Discussion

### Annual survival

We estimated the annual apparent survival rate of Crab Plovers at 90%, which shows that, consistent with our expectations based on low fecundity rates, the Crab Plover is a long-lived shorebird (Sandercock 2003). Similar high survival rates are known from other large-bodied shorebirds including Eurasian Curlew *Numenius arquata*, Bar-tailed Godwit *Limosa lapponica*, Black-tailed Godwit *Limosa limosa* and Eurasian Oystercatchers *Haematopus ostralegus* (Conklin et al. 2016; Duriez et al. 2012; Kentie et al. 2016; Sandercock 2003; Taylor and Dodd 2013). Compared to other shorebirds, Crab Plovers exhibit more extreme life-history characteristics, including a clutch size of one egg and extended parental care, so it is perhaps remarkable that the annual apparent survival rate was similar high instead of higher than other large-bodied shorebirds. Since we could not separate true survival from permanent emigration, it could be that the true survival estimate is higher than our apparent survival rate (Lebreton et al. 1992). In general, shorebirds are extremely site faithful to their wintering area (Leyrer et al. 2013; Lourenço et al. 2016), but we do not know site fidelity for Crab Plovers as they move around in a part of the world where few observers are out on the shores looking for colour-ringed birds. An observation in winter 2012/13 in south India of a bird that was ringed by us in 2011/12 in Barr Al Hikman as an adult and never seen in the area afterwards, shows that permanent emigration can occur, suggesting that our apparent survival estimates are a conservative estimate of true survival in Crab Plovers. Note that the dispersal event to India

could also explain why the apparent survival in the first year was lower (but with overlapping BCI) than the estimated apparent survival over the years after the year of catching.

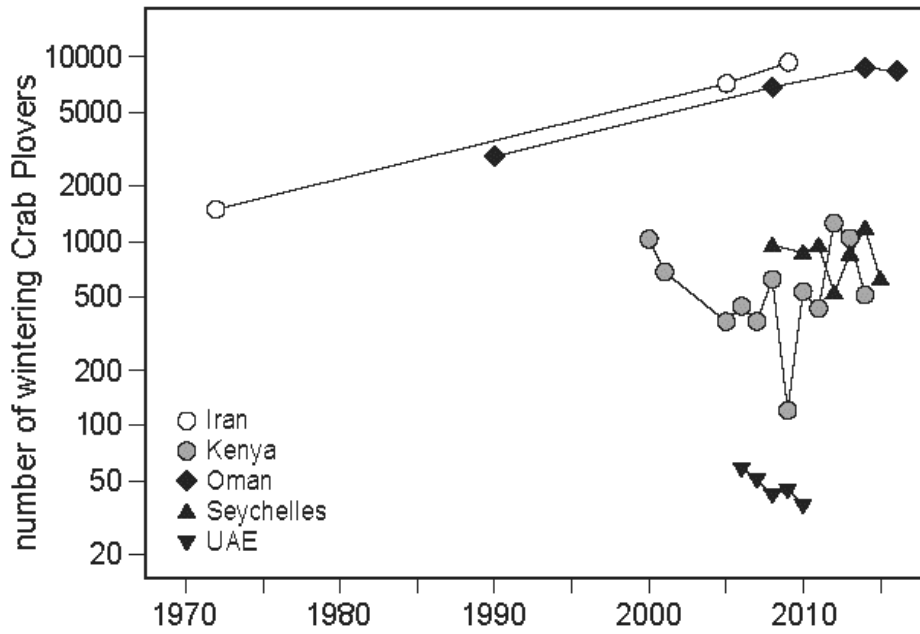
### **Finite rate of population change and immigration**

Survey data suggest that the population of Crab Plovers at Barr Al Hikman over the period of study (2011/12 – 2015/16) was stable, as in this period the overall survey-based finite rate of population change  $\bar{\lambda}_{\text{obs}}$  did not differ from one (Fig. 4). A finite rate of change close to one indicates that the population at Barr Al Hikman is possibly at carrying capacity (Newton 1998). Note that prior to the study period, between 1989/90 - 2007/08, the population increased from 2,943 to 6,901 birds (de Fouw et al 2017; Table 1). As discussed by de Fouw et al (2017), the effort and area covered in 1989/90 did not differ from the more recent surveys; thereby the observed increase is thought to be genuine. Our demographic data did not cover the period 1989/90 - 2007/08, hence the origin of this increase remains unexplained.

Based on demographic data over the period of study (2011/12 – 2015/16), we estimated the overall demographic-based finite rate of population change ( $\bar{\lambda}_{\text{exp}}$ ) to be 0.95 (Fig. 4). The upper value of the 95% BCI of  $\bar{\lambda}_{\text{exp}}$  (0.996) slightly overlapped with the lower value of the 95% BCI of the overall  $\bar{\lambda}_{\text{obs}}$  (0.995), indicating that there is a small chance that  $\bar{\lambda}_{\text{exp}}$  did not differ from  $\bar{\lambda}_{\text{obs}}$ , (Fig. 4). Given the small overlap of the BCI, we reason that it is more likely that the observed population stability cannot be explained by our survival and fecundity estimates alone. Thus our study population likely received immigrants as part of a larger metapopulation, which matches our observation that Crab Plovers emigrate from Barr Al Hikman. The annual means of  $\lambda_{\text{obs}}$  and  $\lambda_{\text{exp}}$  predict net immigration ranging from 315 to 508 Crab Plovers per year. Immigrants could, for instance, originate from areas where the population of Crab Plovers is at carrying capacity, or Crab Plovers may immigrate to Barr Al Hikman when conditions at their original wintering site are deteriorating (de Fouw et al



2017). Limited data show that populations in other wintering areas are stable or increasing (Fig. 5), leaving the scenario open that immigrants could originate from other areas that are already at carrying capacity.



*Fig. 5. Survey-based population estimates of Crab Plovers in five countries on a log<sub>10</sub> scale. The large wintering population of Crab Plovers in Iran, which likely have shared breeding areas with the Barr Al Hikman population, was observed to increase (data from Amini and van Roomen 2009; Summers et al. 1987). A small population of wintering Crab Plovers in the United Arab Emirates decreased from 60 to 30 birds from 2006-2010 (Javed et al. 2012). Two winter populations along the shores in East-Africa (Miday Creek in Kenya, data C. Jackson) and Aldabra in the Seychelles (data: the Seychelles Islands Foundation) were apparently stable during the last decade.*

Immigrants could also be second-year Crab Plovers that during their first winter have stayed close to the breeding areas. Differential migration is widespread among migratory

shorebirds (Cristol et al. 1999; Nebel 2007). If this is the case, percentages of yearling Crab Plovers in wintering groups closer to the breeding areas should be higher than the 3-7 % of yearlings found at Bar al Hikman. Only few surveys of Crab Plovers exist, yet these surveys supported this possibility: A winter population near breeding areas in Eritrea consisted on average of 8% of yearlings (18 groups counted during winter over the period 2002-2009, total adults = 1160, yearlings = 99, G. De Marchi, unpublished data). A group of 104 wintering Crab Plovers in January 2016 close to the breeding areas in Kuwait consisted of 16% of yearlings (P. Fagel, pers. comm). Likewise, a group of 550 wintering Crab Plovers in the Gulf of Kutch in India consisted of 17% yearlings, but it is unknown if Crab Plovers breed in this area (Palmer and Briggs 1986). Thus, although the origin of immigrants remain unknown, available data suggest that immigrants are birds that stayed close to their natal area during their first winter.

## Conclusion

Our results support the current IUCN listing of the world population of Crab Plover as stable (IUCN 2017). Stability may be unexpected given that the species is under human pressure in their wintering grounds and especially in their breeding grounds where colonies remain subject to egg-collecting and harvest of chick and adults (De Marchi et al 2006; Behrouzi-Rad 2013; Tayefeh et al. 2013). We emphasize that survival and fecundity estimates indicate that the population of Crab Plovers wintering at Barr Al Hikman received immigrants, but their origin remains speculative. Finding the origin of these immigrants is a prerequisite to better understand the status of Crab Plovers wintering and breeding in the Arabian/Persian Gulf. Moreover, range-wide survey and ringing activities are needed to better understand the *global* status of Crab Plovers.

To our knowledge, our study is the first to report demographic parameters of a shorebird population wintering in the coastal areas of the Arabian Peninsula and East-Africa. The observed population stability contrasts with the rapid declining populations of many other shorebird species elsewhere in the world (Fernández and Lank 2008; Piersma et al. 2016; van Roomen et al. 2015); declines that are thought to be caused by environmental change, affecting particularly wintering- and stopover areas of shorebirds (Pearce-Higgins et al. 2017). Thus, shorebirds may still be able to find vital wintering grounds along the coasts of the Arabian Peninsula and East-Africa. From a conservation point of view, it is timely to protect those habitats and to continue monitoring the status of their inhabitants. Only then, unique birds such as the Crab Plover can be safeguarded for the future.

### **Acknowledgements**

The presented work relies on the effort of many volunteers that were in the heat of the day out on the shabkha or mudflats to look for colour-ringed Crab Plovers. We thank all observers and in particular Irene Landman, Thijs Fijen, Jelle Abma, Jan van de Kam and Leon Kelder. Raymond Klaassen, Peter Olsson, Petter Ohlson and Gabriel Norevik provided indispensable help during catching. We thank Collin Jackson and the Seychelles Islands Foundation for sharing their data on Crab Plover surveys and Giuseppe De Marchi and Pekka Fagel for sharing their fecundity estimates. Dick Visser prepared the figures. Brett Sandercock, Giuseppe De Marchi and an anonymous reviewer gave excellent comments on previous versions of this manuscript. Our study was financially supported by Shell Development Oman, the Embassy of the Kingdom of The Netherlands in Muscat, the Research Council (TRC) of the Sultanate of Oman (ORG/EBR/12/002 grant awarded to AYK) and by NWO in the Netherlands (ALW Open Programme grant 821.01.001 awarded to JAvG). RK was funded by The Royal Society. Catching and banding of Crab Plovers was carried out under

393 permission of the Ministry of Environment and Climate Affairs, Sultanate of Oman. We are  
394 grateful to the assistant Director-General Ms. Thuraya Said Al-Sairiri, Director-General Mr  
395 Sulieman Al Akhzami and the former Director-General, Mr Ali Al-Kiyumi for their  
396 assistance.

## References

- Almalki M, Shobrak M, dos Remedios N, AlRashidi M, Székely T (2015) Sex differences and breeding ecology of a burrow-breeding shorebird, the Crab Plover *Dromas ardeola*. Wader Study Group Bull, 121:169–176.
- Amini H, van Roomen M (2009) Waterbirds in Iran 2009, Results of a mid-winter count in the provinces of Gilan, Mazanderan, Golestan, Fars, Khuzestan, Bushehr, Hormozgan & Sistan-Baluchistan. Department of Environment, Islamic Republic of Iran & Foundation Working Group International Waterbird and Wetland Research, The Netherlands.
- Behrouzi-Rad B (2013) Birds observation and nest count of Crab Plover *Dromas ardeola*, Western Reef Heron *Egretta gularis* and four tern species on Ghaber Nakhoda Island (Persian Gulf) in 2003 and 2012. Int J Mar Sci 42:344-351
- Bom RA, al-Nasrallah K (2015) Counts and breeding biology of Crab Plovers *Dromas ardeola* on Bubiyan Islands, Kuwait, in 2012–2014. Wader Study 3: 212-220
- Conklin JR, Lok T, Melville DS, Riegen AC, Schuckard R, Piersma T, Battley PF (2016) Declining adult survival of New Zealand Bar-tailed Godwits during 2005–2012 despite apparent population stability. Emu 116:147-157
- Cramp S, Simmons KEL (2004) BWPI: Birds of the Western Palearctic Interactive (DVD-ROM). Sheffield: BirdGuides Ltd.
- Cristol DA, Baker MB, Carbone C (1999) Differential migration revisited. Current Ornithology 15:33-88
- De Marchi G, Chiozzi G, Fasola M (2008) Solar incubation cuts down parental care in a burrow nesting tropical shorebird, the Crab Plover *Dromas ardeola*. J Avian Biol 39:484-486

- 421 De Marchi G, Chiozzi G, Semere D, Galeotti P, Boncompagni E, Fasola M (2006) Nesting,  
422 overwintering, and conservation of the Crab Plover *Dromas ardeola* in central Eritrea.  
423 *Ibis* 148:753-764
- 424 De Sanctis A, Biddau L, Fasola M (2005) Post-migratory care of young by Crab Plovers  
425 *Dromas ardeola*. *Ibis* 147:490-497
- 426 Delany S, Scott D, Dodman T, Stroud D (2009) An atlas of wader populations in Africa and  
427 Western Eurasia. Wetlands International, Wageningen
- 428 Doxa A, Besnard A, Bechet CP, Lebreton JD, Sadoul N (2013) Inferring dispersal dynamics  
429 from local population demographic modelling: the case of Slender-billed Gull in  
430 France. *Anim Conserv* 16: 684–693
- 431 Duriez O, Ens BJ, Choquet R, Pradel R, Klaassen M (2012) Comparing the seasonal survival  
432 of resident and migratory oystercatchers: carry-over effects of habitat quality and  
433 weather conditions. *Oikos* 121:862-873
- 434 Eriksen J, Victor R (2013) Oman bird list. The Official List of the Birds of the Sultanate of  
435 Oman. Seventh edition. Center for Environmental Studies and Research, Sultan  
436 Qaboos University, Muscat
- 437 Fernández G, Lank DB (2008) Effects of habitat loss on shorebirds during the non-breeding  
438 season: Current knowledge and suggestions for action. *Ornitol Neotrop* 19:633-640
- 439 de Fouw J, Thorpe A, Bom RA, de Bie S, Camphuysen CJ, Etheridge B, Hagemeijer W,  
440 Hofstee L, Jager T, Kelder L, Kleefstra R, Kersten M, Nagy S, Klaassen RHG (2017)  
441 Barr Al Hikman, a major shorebird hotspot within the Asian–East African flyway:  
442 results of three winter surveys. *Wader Study* 124:10-25
- 443 Green M, McGrady M, Newton S, Uttley J (1992) The shorebirds of Barr al Hikman and  
444 Ghubbat al Hashish, Oman, Unpublished Report

- 445 Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, Bruno JF, Casey  
446 KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EM, Perry MT,  
447 Selig ER, Spalding M, Steneck R, Watson R (2008) A global map of human impact on  
448 marine ecosystems. *Science* 319:948-952
- 449 IUCN (2017) IUCN Red List of threatened species. Version 2017-3. Downloaded on 31 May  
450 2017 at: <http://www.iucnredlist.org/details/22694081/0>.
- 451 Javed S, Khan S, Nazeer J, Ahmed S, Hammadi A (2011) UAE Crab Plover goes to Aldabra,  
452 Seychelles. *Phoenix* 27:4-5
- 453 Javed S, Khan SB, Tourenq C, Launay F, Merritt J (2012) Nesting, distribution and  
454 conservation of the Crab Plover, *Dromas ardeola*, in the United Arab Emirates. *Zool*  
455 *Middle East* 56:9-18
- 456 Kentie R, Senner NR, Hooijmeijer JCEW, Márquez-Ferrando R, Figuerola J, Masero JA,  
457 Verhoeven MA, Piersma T (2016) Estimating the size of the Dutch breeding  
458 population of Continental Black-tailed Godwits from 2007–2015 using resighting data  
459 from spring staging sites. *Ardea* 104: 213–225.
- 460 Kéry M, Schaub M (2012) Bayesian population analysis using WinBUGS: a hierarchical  
461 perspective. Academic Press, Amsterdam
- 462 Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing  
463 biological hypotheses using marked animals: a unified approach with case studies.  
464 *Ecol Monogr* 62:67-118
- 465 Leyrer J, Lok T, Brugge M, Spaans B, Sandercock BK, Piersma T (2013) Mortality within the  
466 annual cycle: seasonal survival patterns in Afro-Siberian Red Knots *Calidris canutus*.  
467 *J Ornithol* 154:933-943

- 468 Lourenço PM, Alves JA, Reneerkens J, Loonstra AHJ, Potts PM, Granadeiro JP, Catry T  
 469 (2016) Influence of age and sex on winter site fidelity of Sanderlings *Calidris alba*.  
 470 PeerJ 4:e2517
- 471 Nebel S (2007) Differential migration of shorebirds in the East Asian–Australasian Flyway.  
 472 Emu 107:14-18
- 473 Newton I (1998) Population limitation in birds. Academic Press, London
- 474 Palmes P, Briggs C (1986) Crab-plovers *Dromas ardeola* in the Gulf of Kutch. Forktail 1:21-  
 475 28
- 476 Pearce-Higgins JW, Brown DJ, Douglas DJT, Alves JA, Bellio M, Bocher P, Buchanan GM,  
 477 Clay RP, Conklin J, Crockford N, Dann P, Elts J, Friis C, Fuller RA, Gill JA, Gosbell  
 478 K, Johnson JA, Marquez-Ferrando R, Masero JA, Melville DS, Millington S, Minton  
 479 C, Mundkur T, Nol E, Pehlak H, Piersma T, Robin F, Rogers DI, Ruthrauff DR,  
 480 Senner NR, Shah JN, Sheldon RD, Soloviev SA, Tomkovich PS, Verkuil YI (2017) A  
 481 global threats overview for Numeniini populations: synthesising expert knowledge for  
 482 a group of declining migratory birds. Bird Conserv Int 27: 6–34
- 483 Piersma T, Lok T, Chen Y, Hassell CJ, Yang H-Y, Boyle A, Slaymaker M, Chan Y-C,  
 484 Melville DS, Zhang Z-W, Ma Z, Fuller R (2016) Simultaneous declines in summer  
 485 survival of three shorebird species signals a flyway at risk. J Appl Ecol 53:479-490
- 486 Plummer M JAGS: A program for analysis of Bayesian graphical models using Gibbs  
 487 sampling. In: Proceedings of the 3rd international workshop on distributed statistical  
 488 computing, 2003. Vienna, p 125
- 489 Pradel R, Gimenez O, Lebreton J-D (2005) Principles and interest of GOF tests for multistate  
 490 capture–recapture models. Anim Biodivers Conserv 28:189-204
- 491 R Development Core Team (2013) R: A language and environment for statistical computing  
 492 R Foundation for Statistical Computing



- 493 Sæther B-E, Bakke Ø (2000) Avian life history variation and contribution of demographic  
494 traits to the population growth rate. *Ecology* 81:642-653
- 495 Safaie M, Kiabi B, Pazooki J, Shokri MR (2013) Growth parameters and mortality rates of the  
496 blue swimming crab, *Portunus segnis* (Forskål, 1775) in coastal waters of Persian Gulf  
497 and Gulf of Oman, Iran. *Indian J Fish* 60:9-13.
- 498 Sale PF, Feary DA, Burt JA, Bauman AG, Cavalcante GH, Drouillard KG, Kjerfve B,  
499 Marquis E, Trick CG, Usseglio P (2011) The growing need for sustainable ecological  
500 management of marine communities of the Persian Gulf. *Ambio* 40:4-17
- 501 Sandercock BK (2003) Estimation of survival rates for wader populations: a review of mark-  
502 recapture methods. *Wader Study Group Bull* 100:163-174
- 503 Sandercock BK (2006) Estimation of demographic parameters for live-encounter data: a  
504 summary review. *J Wildl Manag* 70: 1504–1509
- 505 Schaub M, Abadi F (2011) Integrated population models: a novel analysis framework for  
506 deeper insights into population dynamics *J Ornithol* 152:227-237
- 507 Schaub M, Gimenez O, Sierro A, Arlettaz R (2007) Use of integrated modelling to enhance  
508 estimates of population dynamics obtained from limited data. *Conserv Biol* 21:945–  
509 955
- 510 Sheppard C, Al-Husiani M, Al-Jamali F, Al-Yamani F, Baldwin R, Bishop J, Benzoni F,  
511 Dutrieux E, Dulvy NK, Durvasula SR, Jones DA, Loughland R, Medio D,  
512 Nithyanandan M, Pilling GM, Polikarpov I, Price AR, Purkis S, Riegl B, Saburova M,  
513 Namin KS, Taylor O, Wilson S, Zainal K (2010) The Gulf: a young sea in decline.  
514 *Mar Pollut Bull* 60:13-38
- 515 Stevens MH (2009) *A Primer of Ecology with R*. Springer Verlag, Berlin
- 516 Su Y-S, Yajima M (2012) R2jags: A Package for running jags from R. R package version  
517 003-08, URL <http://CRAN.R-project.org/package=R2jags>

- 518 Summers R, Underhill L, Pearson D, Scott D (1987) Wader migration systems in southern  
519 and eastern Africa and western Asia. Wader Study Group Bull 49:15-34
- 520 Sutherland WJ (2006) Ecological census techniques: a handbook. Cambridge University  
521 Press.
- 522 Tayefeh, F.H., M. Zakaria, G.D. Marchi, H. Amini, A. Moradi, P. Ahmadpour & S. Ghasemi  
523 (2013). Breeding biology of the Crab Plover (*Dromas ardeola*) on the Mond Islands,  
524 Northern Persian Gulf, Iran. Waterbirds 36:448–462.
- 525 Taylor RC, Dodd SG (2013) Negative impacts of hunting and suction-dredging on otherwise  
526 high and stable survival rates in Curlew *Numenius arquata*. Bird Study 60:221-228
- 527 van Roomen M, Nagy S, Foppen R, Dodman T, Citegetse G, Ndiaye A (2015) Status of  
528 coastal waterbird populations in the East Atlantic. Flyway Programme Rich Wadden  
529 Sea, SOVON, Wetlands International, Birdlife International, Common Wadden Sea  
530 Secretariat
- 531 Wetlands International (2002) Waterbirds Population Estimates, 3rd ed. Wetlands  
532 International, Wageningen