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

2

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18 **Abstract**

19 The monotypic Crab Plover *Dromas ardeola* winters around the shores of the Indian Ocean
20 and breeds in colonies on islands around the Arabian Peninsula. The IUCN lists the world
21 population of Crab Plovers as stable, but long-term survey data or demographic estimates
22 regarding the species status are lacking. Here, we use survey and demographic data collected
23 from 2011-2015 to study the status of the population of Crab Plover at their most important
24 wintering area: the Barr Al Hikman Peninsula in the Sultanate of Oman. Our survey data
25 showed that the population of Crab Plovers initially increased and then stabilized. The overall
26 observed finite rate of population change ($\bar{\lambda}_{\text{obs}}$) was estimated at 1.004 (0.995–1.013 95%
27 Bayesian credible interval [BCI]), indicating a stable population (7,000–9,000 birds), that is
28 possibly at carrying capacity. Based on mark-recapture data, the mean annual apparent
29 survival probability of Crab Plovers was estimated to be 0.90 (0.85–0.94 95% BCI). We used
30 counts of adults and yearlings to estimate the mean annual fecundity rate at 0.06 young per
31 pair. Using these demographic values, the overall mean expected finite rate of population
32 change ($\bar{\lambda}_{\text{exp}}$) was estimated to be 0.949 (0.899 – 0.996 95% BCI), so there is a low chance
33 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
34 immigrate to Barr Al Hikman each year. Regional surveys show that yearling densities are
35 higher closer to the breeding areas, so immigrants could be birds that during their first winter
36 stayed close to their natal area. Our study support the IUCN listening of Crab Plover as stable,
37 but further population-wide monitoring is required. From a conservation point of view it is
38 important to continue monitoring because Crab Plovers breed and winter in a region that is
39 rapidly developing.

40

41 **Keywords:** apparent survival, Arabian Peninsula, Barr Al Hikman, *Dromas ardeola*,

42 fecundity, finite range of change, Integrated Population Model

43 Introduction

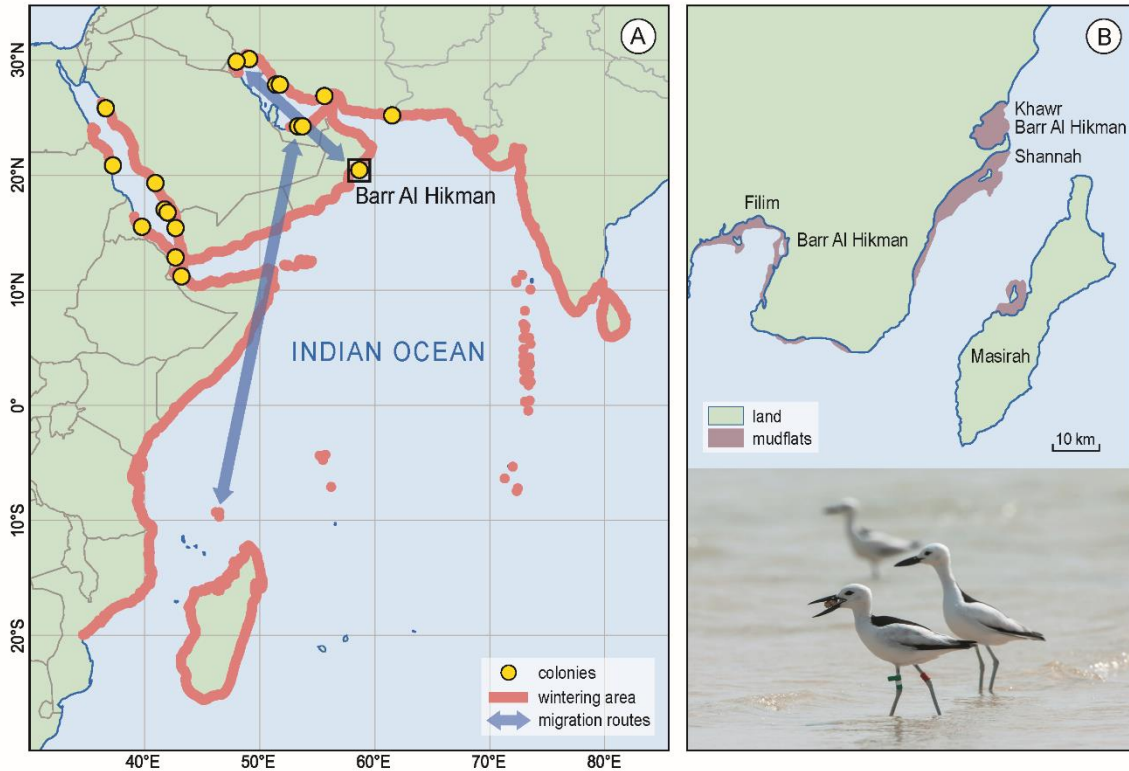
44 The coastal areas of the Arabian Peninsula and East-Africa provide essential breeding and
45 wintering habitat for a large number of shorebirds traveling within the Asian–East African
46 Flyway (Delany et al. 2009). In contrast to shorebird populations in other parts of the world
47 (Fernández and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

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

68 destruction of burrows, or harvesting of adults may seriously affect breeding success and
69 survival of Crab Plovers at the breeding areas (De Marchi et al 2006; Behrouzi-Rad 2013;
70 Tayefeh et al. 2013), whereas habitat destruction and overexploitation of preferred crab prey
71 may affect the species at the wintering areas (Safaie *et al.*, 2013). Based on counts at the
72 wintering areas, the world population of Crab Plovers has been estimated to be 60,000 to
73 80,000 birds (Wetlands International 2002). The population of Crab Plovers is currently
74 considered to be stable (IUCN 2017), but this has not been substantiated with data (Delany et
75 al. 2009).

76 In this study, we assessed the status of the population of Crab Plover wintering at the
77 Barr Al Hikman Peninsula in the Sultanate of Oman (Fig. 1a). The area supports 10-15% of
78 the world population of Crab Plovers and is therefore the most important wintering area for
79 the species (Delany et al. 2009). Based on survey data and demographic estimates collected
80 from 2011 to 2015, we developed an Integrated Population Model (IPM) (Schaub & Abadi
81 2011) in which we estimated observed and expected finite rates of population change (λ_{obs}
82 and λ_{exp}). IPMs combine population counts and demographic data in a single model, and are
83 particularly useful for studies with small datasets (Schaub et al. 2007), or studies where not all
84 demographic parameters could be accounted for by data collected in the field (Schaub &
85 Abadi 2011). Here we estimated λ_{obs} using existing survey data (de Fouw et al. 2017)
86 whereas λ_{exp} was calculated from newly estimated survival and fecundity rates. Apparent
87 annual survival rates were estimated based on sightings of 169 individually colour-marked
88 birds, and annual fecundity rates were based on the percentage of yearlings (first-winter birds)
89 in the population. In addition to survival and fecundity, population dynamics of local
90 populations also depend on immigration and emigration (Newton 1998). We did not measure
91 immigration and emigration directly, but calculated potential immigration rates by matching
92 observed (λ_{obs}) and expected (λ_{exp}) finite rates of population change (e.g., Doxa et al. 2012).

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



95
 96 *Fig. 1. The distribution of Crab Plovers is confined to coastal areas of the Indian Ocean (A).*
 97 *Breeding areas (yellow dots) are adapted from Bom and al-Nasrallah (2015), and wintering*
 98 *areas (red coast line) from Delany et al. (2009). Arrows show the known connections between*
 99 *breeding and wintering areas (Bom and al-Nasrallah 2015; Javed et al. 2011). The study*
 100 *area at Barr Al Hikman is shown in the black square and in (B), with the main localities that*
 101 *are mentioned in the text. The inset in (B) shows a colour-ringed Crab Plover.*

102

103 **Methods**

104 **Study area & data collection**

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

107 km² and can be found south of Shannah, in the Khawr Barr Al Hikman, near Filim and on
 108 Masirah Island (Fig. 1b). Local industries included fisheries and salt mining, but the area is
 109 relatively pristine. Crab Plovers can be found in the area almost exclusively in winter (Eriksen
 110 and Victor 2013). Six GPS tracks and four ring observations show that Crab Plovers
 111 wintering in Barr Al Hikman are connected to breeding areas in the Arabian/Persian Gulf in
 112 colonies in Kuwait and South-West Iran (Fig. 1a, Bom and al-Nasrallah 2015). Barr Al
 113 Hikman was surveyed for shorebirds including Crab Plovers in the four winters of 1989/90
 114 (Green et al. 1992), 2007/08, 2013/14 and 2015/16 (de Fouw et al. 2017) (Table 1).

115

116 *Table 1. Survey results on wintering Crab Plovers at Barr Al Hikman, Oman, 1989-2016. In*
 117 *the present study, survey results collected over the period 2007/08 – 2015/16 were used to*
 118 *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

119

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

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

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

139

140 *Table 2. Number of adult and yearlings Crab Plovers that were individually marked with*
 141 *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

142

143

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

150

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

	no. groups	total no. birds	% of yearlings ¹⁵⁴
	counted	counted	(mean ± 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)

155

156

157 **Integrated population model**

158 We combined survey data and demographic data in a Bayesian Integrated Population Model

159 (IPM) (Schaub and Abadi 2011) to estimate the annual-dependent survey-based finite rate of

160 population change (λ_{obs}) and the annual-dependent demographic-based finite rate of161 population change (λ_{exp}) for the five-year period 2011/12 – 2015/16.

162

163 *Survey-based finite rate of population change λ_{obs}* 164 λ_{obs} was estimated from population counts as:

165
$$\lambda_{\text{obs}} = N_{t+1} / N_t$$

166 where N_t is the total population size at year t and N_{t+1} is population size in the year $t + 1$. To167 calculate N_t for winters in which no surveys were performed we simulated N_t by fitting a

168 quadratic polynomial function with a Poisson distribution through the survey data over the

169 period 2007/08 - 2015/16 in the Markov Chain Monte Carlo (MCMC) framework that we

170 used in our Bayesian model (Fig. 2). We calculated year-specific λ_{obs} and also the geometric171 mean of $\bar{\lambda}_{\text{obs}}$ over all five years. The geometric mean was calculated as:

172
$$\bar{\lambda}_{\text{obs}} = \left(\sum_{t=1}^T \lambda_t \right)^{1/T}$$

173 (Stevens 2009).

174 Our estimation of λ_{obs} assumes perfect detection or equal probability of detection.

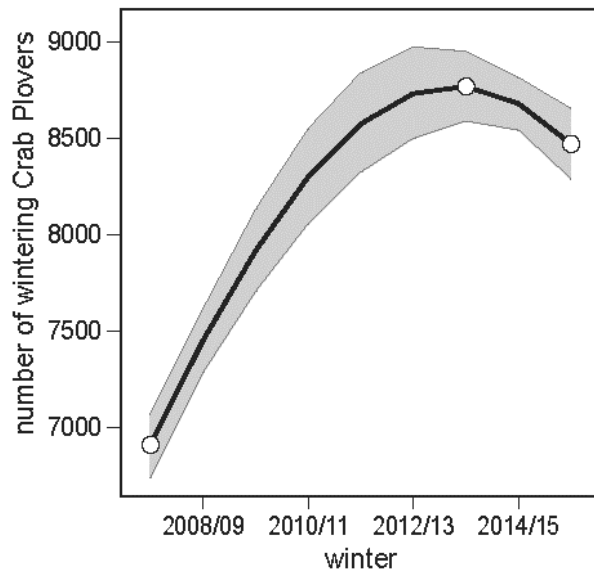
175 Imperfect detection is widespread in surveys of roosting birds (Sutherland 2006) and we

176 cannot guarantee perfect detection during our Crab Plover surveys. Arguably, probability of

177 detection between years is equal, as all surveys reported in Table 1 are comparable in the

178 sense that they covered exactly the same area and that there has been overlap between

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



184

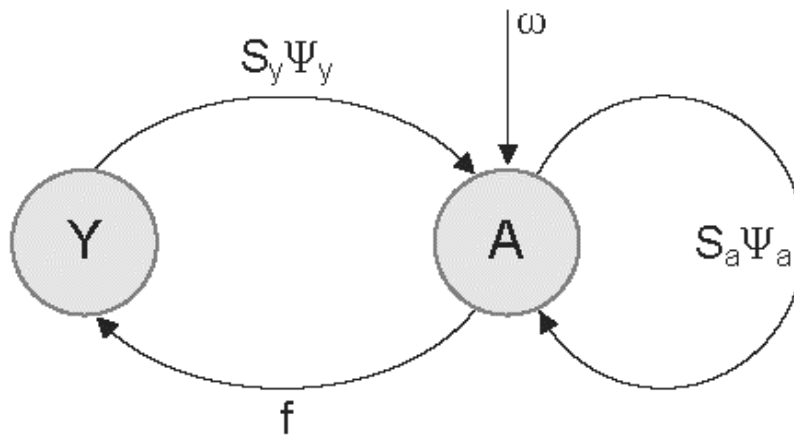
185 *Fig. 2. Number of wintering Crab Plovers in Barr Al Hikman in the study period based on*
 186 *surveys (open circles) and modelled population estimates. The thick line represents posterior*
 187 *means and shaded area represents 95% BCI.*

188

189 *Demographic-based finite rate of population change λ_{exp}*

190 We estimated λ_{exp} following assumptions shown in a post-reproductive census life cycle
 191 diagram (Fig. 3). Accordingly, as we could not age second-winter birds, the Crab Plover
 192 population at Barr Al Hikman in year t consists of yearlings (Y) and reproducing adults (A).
 193 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 (ψ_y and ψ_a), and on immigration rate (ω).



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 (ψ_y , ψ_a),*
 199 *annual fecundity (f) and immigration of adults (ω).*

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 (ψ) and
 203 immigration (ω) directly. Instead we estimated apparent survival (ϕ) as the product of true
 204 survival (S) and ψ (Lebreton et al. 1992) and immigration rate (ω) as the difference between
 205 λ_{obs} with λ_{exp} (see below).

206

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

212 therefore referred to as a test of trap-dependence, was significant ($\chi^2 = 40.7049$, $df = 11$, $p <$
213 0.01), and Test 3, which tests the assumption that all individuals have the same probability of
214 survival to the next time step, was not ($\chi^2 = 16.4881$, $df = 9$, $p = 0.0574$). To account for trap-
215 dependence, we therefore used individual as random effect in the resighting probability (Kéry
216 and Schaub 2012). The intensity of fieldwork varied each year, and resighting probability was
217 modelled to vary among years. Test 3 of the GOF was almost significant, which could be
218 caused by a differing apparent survival rate between adults and juveniles. We therefore tested
219 preliminarily if apparent survival between yearlings and adults differed, which was not as the
220 95% BCI of their survival rates overlapped considerably (ϕ yearlings = 0.867, 95% BCI
221 [0.657-0.994], ϕ adults = 0.893, 95% BCI [0.844-0.938]). Then, with a time-since-marking
222 test, we tested whether catching influenced survival probability in the first year after catching,
223 which could be caused by higher mortality or permanent emigration after the disturbance of
224 handling, or by age-dependent survival probabilities (Sandercock 2006). We could find a
225 weak effect of catching on apparent survival (ϕ first year after catching = 0.821, 95% BCI
226 [0.672-0.982], ϕ years after first year after catching = 0.905, 95% BCI [0.855-0.950]). Given
227 that there was overlap in BCI, all age classes and years after catching were treated as one
228 group. Given our low sample size (Table 2), we did not calculate year-dependent annual
229 apparent survival to avoid over parameterization.

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

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

239 Because apparent survival between adults and yearlings did not differ, we could
 240 calculate λ_{exp} as:

$$241 \lambda_{\text{exp}} = \varphi + \varphi f_t$$

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

243

244 *Immigration*

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

$$248 \omega = (N_t - \lambda_{\text{exp}} * N_{t-1})/N_t$$

249

250 All parameters were estimated in one IPM. MCMC simulations for parameter
 251 estimation were obtained by running the JAGS program (Plummer 2003) implemented in the
 252 R environment (R Development Core Team 2013) using the *R2JAGS* package (Su and Yajima
 253 2012). We used uninformative priors for all parameters. We ran three independent chains of
 254 50,000 iterations of which the first 10,000 were discarded, and kept every 6th observation to
 255 avoid autocorrelation. We checked the R-hat for convergence of the parameters (in all cases <
 256 1.01). Estimates are presented as the posterior means and with a 95% BCI.

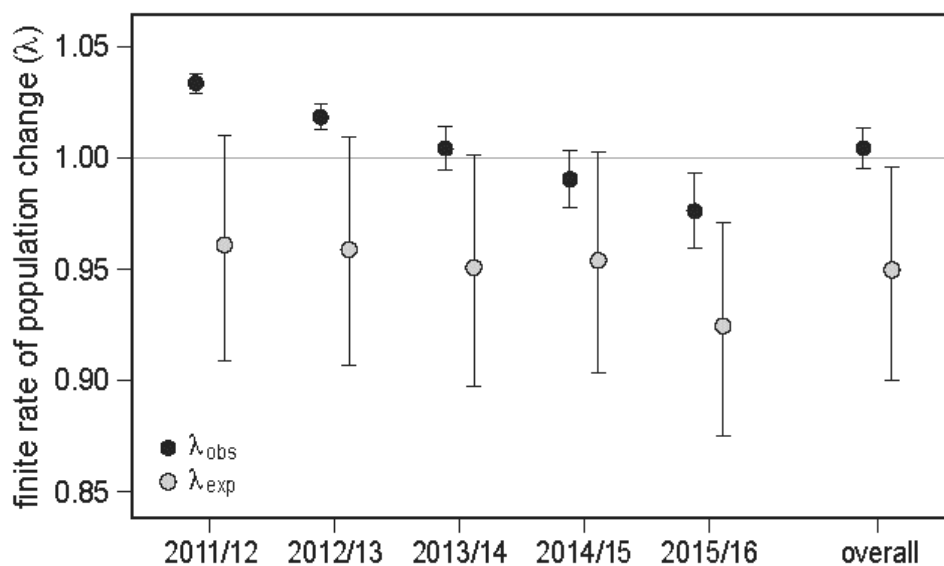
257

258 **Results**

259 The geometric mean $\bar{\lambda}_{\text{obs}}$ for the five-year period 2011/12 – 2015/16 was 1.004 (0.995–
 260 1.013). The yearly λ_{obs} ranged between 0.98 and 1.02 and decreased over the years (Fig. 4).

261 Annual apparent survival probability was 0.895 (0.847–0.940) for the period 2008/09 –

262 2015/16. The annual resighting probability increased from 0.080 (0.025 – 0.169 95% BCI) to
 263 0.744 (0.097 – 0.915 95% BCI) over the years 2008/09 – 2015/16 (Supplementary Material
 264 S2). The estimated annual fecundity rate varied over the period 2011/12 – 2015/16 between
 265 0.03 and 0.07 (proportion of yearlings), with 95% BCI ranging between 0.02 and 0.08. On
 266 average, the annual fecundity rate was 0.06 (Table 3). Based on the estimated apparent
 267 survival probability and fecundity rate, the geometric mean $\bar{\lambda}_{exp}$ over the period 2012/13 –
 268 2015/16 was 0.949 (0.899 – 0.996 95% BCI) and annually ranged between 0.92 and 0.96 (Fig.
 269 4). As we did not estimate a yearly dependent apparent survival probability, variation in λ_{exp}
 270 was solely due to variation in the estimated fecundity rate, which was particularly low in the
 271 last year (Table 3). To explain differences between λ_{obs} and λ_{exp} , we estimated yearly per
 272 capita immigration rates of 0.056 (0.006 – 0.107 95% BCI) in 2012/13, 0.052 (0.027–0.104
 273 95% BCI) in 2013/14, 0.034 (0.026–0.086 95% BCI) in 2014/15 and 0.051 (0.103–0.026 95%
 274 BCI) in 2015/16. Our estimated immigration rates correspond to 315-508 individuals per year.
 275



276
 277 Fig. 4. Annual finite rates of population change based on population surveys (λ_{obs} , black
 278 dots) and based on demographic estimates (λ_{exp} , grey dots) and the overall $\bar{\lambda}_{obs}$ and $\bar{\lambda}_{exp}$.

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

282

283

284 **Discussion**

285 **Annual survival**

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

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

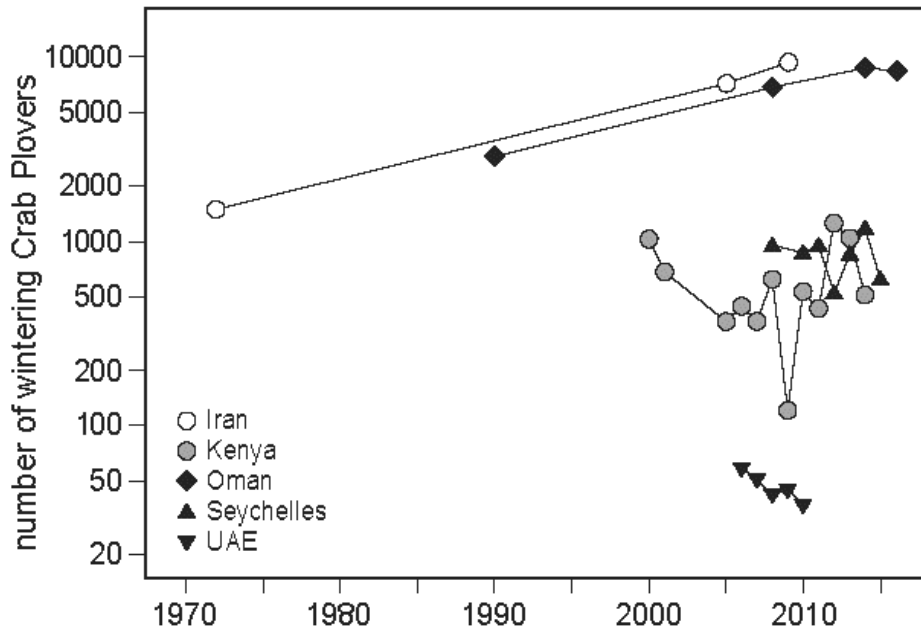
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307 **Finite rate of population change and immigration**

308 Survey data suggest that the population of Crab Plovers at Barr Al Hikman over the period of
309 study (2011/12 – 2015/16) was stable, as in this period the overall survey-based finite rate of
310 population change $\bar{\lambda}_{\text{obs}}$ did not differ from one (Fig. 4). A finite rate of change close to one
311 indicates that the population at Barr Al Hikman is possibly at carrying capacity (Newton
312 1998). Note that prior to the study period, between 1989/90 - 2007/08, the population
313 increased from 2,943 to 6,901 birds (de Fouw et al 2017; Table 1). As discussed by de Fouw
314 et al (2017), the effort and area covered in 1989/90 did not differ from the more recent
315 surveys; thereby the observed increase is thought to be genuine. Our demographic data did not
316 cover the period 1989/90 - 2007/08, hence the origin of this increase remains unexplained.

317 Based on demographic data over the period of study (2011/12 – 2015/16), we
318 estimated the overall demographic-based finite rate of population change ($\bar{\lambda}_{\text{exp}}$) to be 0.95
319 (Fig. 4). The upper value of the 95% BCI of $\bar{\lambda}_{\text{exp}}$ (0.996) slightly overlapped with the lower
320 value of the 95% BCI of the overall $\bar{\lambda}_{\text{obs}}$ (0.995), indicating that there is a small chance that
321 $\bar{\lambda}_{\text{exp}}$ did not differ from $\bar{\lambda}_{\text{obs}}$, (Fig. 4). Given the small overlap of the BCI, we reason that it is
322 more likely that the observed population stability cannot be explained by our survival and
323 fecundity estimates alone. Thus our study population likely received immigrants as part of a
324 larger metapopulation, which matches our observation that Crab Plovers emigrate from Barr
325 Al Hikman. The annual means of λ_{obs} and λ_{exp} predict net immigration ranging from 315 to
326 508 Crab Plovers per year. Immigrants could, for instance, originate from areas where the
327 population of Crab Plovers is at carrying capacity, or Crab Plovers may immigrate to Barr Al
328 Hikman when conditions at their original wintering site are deteriorating (de Fouw et al

329 2017). Limited data show that populations in other wintering areas are stable or increasing
 330 (Fig. 5), leaving the scenario open that immigrants could originate from other areas that are
 331 already at carrying capacity.



332
 333 *Fig. 5. Survey-based population estimates of Crab Plovers in five countries on a log₁₀ scale.*
 334 *The large wintering population of Crab Plovers in Iran, which likely have shared breeding*
 335 *areas with the Barr Al Hikman population, was observed to increase (data from Amini and*
 336 *van Roomen 2009; Summers et al. 1987). A small population of wintering Crab Plovers in the*
 337 *United Arab Emirates decreased from 60 to 30 birds from 2006-2010 (Javed et al. 2012).*
 338 *Two winter populations along the shores in East-Africa (Miday Creek in Kenya, data C.*
 339 *Jackson) and Aldabra in the Seychelles (data: the Seychelles Islands Foundation) were*
 340 *apparently stable during the last decade.*

341

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

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

356

357 **Conclusion**

358 Our results support the current IUCN listing of the world population of Crab Plover as stable
359 (IUCN 2017). Stability may be unexpected given that the species is under human pressure in
360 their wintering grounds and especially in their breeding grounds where colonies remain
361 subject to egg-collecting and harvest of chick and adults (De Marchi et al 2006; Behrouzi-Rad
362 2013; Tayefeh et al. 2013). We emphasize that survival and fecundity estimates indicate that
363 the population of Crab Plovers wintering at Barr Al Hikman received immigrants, but their
364 origin remains speculative. Finding the origin of these immigrants is a prerequisite to better
365 understand the status of Crab Plovers wintering and breeding in the Arabian/Persian Gulf.
366 Moreover, range-wide survey and ringing activities are needed to better understand the *global*
367 status of Crab Plovers.

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

378

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