1   # Demographic causes of adult sex ratio variation and their consequences for
2   parental cooperation

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Abstract:

The adult sex ratio (ASR) is a fundamental concept in population biology, sexual selection, and social evolution. However, it remains unclear which demographic processes generate ASR variation and how biases in ASR in turn affect social behaviour. Here, we evaluate the demographic mechanisms shaping ASR and their consequences for parental cooperation using detailed survival, fecundity, and behavioural data on 6,119 individuals from six wild shorebird populations exhibiting flexible parental strategies. We show that these closely related populations express strikingly different ASRs, despite having similar ecologies and life histories, and that ASR variation is largely driven by sex differences in the apparent survival of juveniles. Furthermore, families in populations with biased ASRs were predominantly tended by a single parent, suggesting that parental cooperation breaks down with unbalanced sex ratios. Taken together, our results indicate that sex biases emerging during early life have profound consequences for social behaviour.

Main text:

Sex ratio variation is a fundamental component of life-history evolution. At conception, birth, and adulthood, the ratios of males to females have long been hypothesized by evolutionary biologists and human demographers as catalysts for social behaviour and population dynamics[1,2]. In particular, the adult sex ratio (ASR) exhibits remarkable variation throughout nature, with birds and mammals tending to have male-biased and female-biased ASRs, respectively[3]. Recent studies also show extreme shifts in ASR due to climate change in fish[4], amphibians[5], and dioecious plants[6]. By influencing mate availability, ASR bias can alter social behaviour with divorce, infidelity, and parental antagonism being more frequent in sex-biased populations[7,8]. Moreover, in human societies, ASR variation is linked to economic decisions, community violence, and disease prevalence[9-11]. Yet despite the widespread occurrence of ASR bias and its significance in evolutionary ecology and social science, the demographic source(s) of ASR variation and their ramifications for social behaviour remain unclear[12].

Sex ratio theory is concerned with the adaptive consequences of sex-biased parental allocation to offspring[13,14], with the processes generating sex ratio bias after birth receiving less theoretical and empirical attention[15]. Here, we use a demographic pathway model to quantify ASR variation among avian populations and to determine whether this variation is predominantly caused by sex biases at birth, during juvenile development, or in adulthood. We parameterized our model with detailed individual-based life history data from *Charadrius* plovers – small ground-nesting shorebirds that occur worldwide. Plovers exhibit remarkable diversity and plasticity in breeding behaviour with sex roles during courtship, mating, and parental care varying appreciably among populations both between and within species[16,17]. This behavioural variation, coupled with their tractability in the field (Supplementary Video

77   1), allowed us to explore the sources and significance of demographic sex biases among

78   closely related wild populations in the light of social evolution.

79   **Results and Discussion**

80   Over a total of 43 observational years of fieldwork, we monitored the survival, fecundity, and

81   breeding behaviour of 6,119 individually marked plovers from six populations of five closely

82   related species worldwide (Fig. 1a). We then employed two-sex stage-structured population

83   matrix models to derive estimates of ASR at equilibrium from stage- and sex-specific

84   demographic rates of annual survival and reproduction (Fig. 1b)[18]. For each population, the

85   numbers of male and female progeny in our model depended on modal clutch size and

86   hatching sex ratio derived from our field data. Mark-recapture methods were used to estimate

87   the apparent survival of juveniles and adults while accounting for sex differences in detection

88   probability (the term "apparent survival" indicates that mortality cannot be disentangled from

89   permanent emigration)[19]. Fecundity was derived from a mating function that depended on the

90   extent of polygamy observed in each population and the frequency of available mates (see

91   *Methods* for details).

92   The hatching sex ratio, based on 1,139 hatchlings from 503 families, did not deviate

93   significantly from parity in any of the populations (Fig. 2a). Conversely, sex biases in

94   apparent survival varied considerably within and among species and, in most populations,

95   juvenile survival was more biased than adult survival – either towards males or females (Fig.

96   2a). Taken together, these sources of demographic sex bias rendered significant deviations in

97   ASR from parity for three populations (two male-biased and one female-biased; Fig. 2b).

98   Matrix models provide a flexible analytical environment to decompose the feedbacks

99   between state-dependent vital rates and population response – an important method used in

100 conservation biology for understanding life-history contributions to population growth and

101 viability[20]. In our case, we modified this approach to assess the relative contributions of sex

102 allocation and sex-specific survival on ASR bias[18]. We found that sex biases in apparent

103 survival during the juvenile stage contributed the most to sex ratio bias of the adult

104 population: in populations with significantly skewed ASR, sex biases in juvenile survival

105 contributed on average 7.2 times more than sex biases in adult apparent survival and 24.6

106 times more than sex biases at hatching (Supplementary Fig. 1). Moreover, variation in

107 hatching sex ratio had no effect on ASR – a result that provides empirical support for

108 Fisher's[13] prediction of unbiased sex allocation regardless of sex-biased survival of

109 independent young or adults.

110   In species where both parents have equal caring capabilities, the desertion of either

111 parent is often influenced by the availability of potential mates[21] – parental care by the

112 abundant sex is expected to be greater than that of the scarcer sex due to limited future

113 reproductive potential[22]. Detailed behavioural observations of 471 plover families revealed

114 high rates of parental desertion in populations with biased ASRs, whereas desertion was rare

115 in unbiased populations (Fig. 3). We evaluated our *a priori* prediction of a quadratic

116 relationship between parental cooperation and ASR variation using a regression analysis

117 incorporating a bootstrap procedure that acknowledged uncertainty in our estimates of ASR

118 and parental care (see *Methods* for details). We found that families in male- or female-biased

119 populations tended to express higher rates of parental desertion, while unbiased populations

120 were more likely to exhibit parental cooperation (Fig. 3a). This is supported by experimental

121 evidence of sex-biased mating opportunities in three of the populations studied here

122 (Supplementary Fig. 2; ref 23). Moreover, the relationship between parental cooperation and

123 local ASR bias was apparent in our within-species contrast of *C. alexandrinus*: the unbiased

124 Cape Verde population exhibited a higher rate of parental cooperation than the male-biased

125 population in Turkey (Fig. 3a). Counterintuitively, we also found a high rate of male-only

126 care in *C. pecuarius* despite ASR being female-biased (Fig. 3b), although in line with

127 expectations, *C. pecuarius* also showed the highest proportion of female-only care among our

128 studied populations (Fig. 3b, Supplementary Fig. 3b). This provides partial support for the

129 notion that breeding strategies may respond flexibly to local mating opportunities provided

130 by ASR bias, while also suggesting that other factors may play a role, such as the energetic

131 costs of egg production imposed on females or because of sex differences in parental

132 quality[24] or the age at maturation[25].

133 There are several ways in which sex-biased juvenile survival could potentially lead to

134 a skewed ASR. Natal dispersal rates may differ between the sexes, as is typical of many

135 birds[26], which could contribute to our estimates of sex-biased apparent survival. Genetic

136 studies of several of the populations presented here are partially consistent with this

137 hypothesis, as island populations of *C. alexandrinus* and the endemic *C. thoracicus* have

138 reduced gene flow relative to comparable mainland populations[27,28]. However, sex-biased

139 juvenile survival in plovers has been reported elsewhere, even after accounting for

140 dispersal[29,30], implying that sex-differences in mortality are at least partly driven by intrinsic

141 factors, conceivably for example via genotype-sex interactions[31,32]. An alternative but not

142 necessarily mutually exclusive explanation is that males and females may differ in their

143 premature investment into reproductive traits, which could inflict survival costs for the larger

144 or more ornamented sex[33]. Although sexual dimorphism among adults is negligible in the

145 species we studied[34,35], sex-specific ontogeny does appear to vary in three of these

146 populations. In male-biased populations of *C. nivosus* and *C. alexandrinus*, female hatchlings

147 are smaller and grow more slowly than their brothers during the first weeks of life, whereas

148 juveniles of the unbiased *C. alexandrinus* population exhibit no such sex-specific differences

149 during early development[34].

150   The association between sex-specific demography and breeding system evolution

151   represents a causality dilemma because of the feedback that parental strategies impose on

152   ASR bias and *vice versa*[36]. On the one hand, mating competition and parental care may entail

153   costs via sexual selection that could drive differential survival of males over females and

154   have knock-on effects on ASR[37]. On the other hand, sex-specific survival creates unequal

155   mating opportunities via ASR that may influence mating patterns and parenting strategies[37].

156   Our study provides empirical support for the latter – sex biases emerge prior to sexual

157   maturity, suggesting that this evolutionary feedback loop is catalysed by intrinsic early-life

158   demographic variation. Moreover, our results add to the growing evidence of unbiased birth

159   sex ratios in nature[15] and provide a comprehensive empirical test of Fisher's[13] original

160   prediction that influential sex biases arise in life-history stages beyond parental control. By

161   unravelling the demographic foundations of adult sex ratio bias and their consequences for

162   parental cooperation, we hope to stimulate future studies to understand the complex

163   relationship between evolutionary demography and behavioural ecology.

164   **Methods**

165   *Field and laboratory methods*

166   We studied five *Charadrius* species comprising six populations from four sites worldwide

167   (Fig. 1a, Supplementary Table 1). In Mexico, we monitored the snowy plover (*C. nivosus*) at

168   Bahía de Ceuta, a subtropical lagoon on the Pacific coast. In Madagascar, we monitored the

169   Kittlitz's plover (*C. pecuarius*), white-fronted plover (*C. marginatus*), and the endemic

170   Madagascar plover (*C. thoracicus*), all of which breed sympatrically at a saltwater marsh near

171   the fishing village of Andavadoaka. Lastly, we monitored the Kentish plover (*C.*

172   *alexandrinus*) at two independent populations located at Lake Tuzla in southern Turkey and

173   at Maio in Cape Verde. The Mexico and Madagascar populations were monitored over a

174   seven-year period, whereas the Turkey and Cape Verde populations were monitored over six

175   and nine years respectively, thus totalling 43 years of data collection (Supplementary Table

176   1).

177   At each location, we collected mark-recapture and individual reproductive success

178   data during daily surveys over the entire breeding season that typically spanned three to four

179   months after a region's rainy season. Funnel traps were used to capture adults on broods or

180   nests[38]. We assigned individuals to a unique colour combination of darvic rings and an

181   alphanumeric metal ring, allowing the use of both captures and non-invasive resightings to

182   estimate survival. Broods were monitored every five days on average to assess daily survival

183   and identify tending parents. During captures, approximately 25–50 μL of blood was sampled

184   from the metatarsal vein of chicks and the brachial vein of adults for molecular sex typing

185   with two independent markers Z-002B[39] and Calex-31, a microsatellite marker on the W

186   chromosome[40]. Details of PCR conditions are given in ref. 34.

187   *Quantifying sex roles*

188   We evaluated sex role variation by summarizing for each population the proportion of all

189   families that were attended bi-parentally or uni-parentally by a male or female. We restricted

190   our field observations to include only broods that were at least 20 days old. Young chicks are

191   attended by both parents in all populations although, as broods get older, male or female

192   parents may desert the family[41]. As chicks typically fledge around 25 days of age, we

193   therefore choose broods of between 20 and 25 days of age to quantify parental care given that

194   at this age many parents already deserted the family but some still attend the young.

195   Furthermore, we restricted these data to include only broods that had at least two sightings

196   after 20 days. Given these criteria, our dataset consisted of 471 unique families distributed

197   throughout the six populations and pooled across all years of study (Supplementary Table 2).

198   To account for surveyor oversight while recording tending parents (e.g., observing only one

199   parent when two were present), we took a conservative approach by assigning a bi-parental

200   status to families that had both uni-parental and bi-parental observations after the 20th day. In

201   summary, desertion was most common in *C. nivosus* and *C. pecuarius*, whereas bi-parental

202   care was most common in *C. alexandrinus* (Cape Verde), *C. thoracicus*, and *C. marginatus*

203   (Fig. 3b, Supplementary Table 2). The *C. alexandrinus* population in Turkey had 50% bi-

204   parental and 50% desertion (Fig. 3b, Supplementary Table 2). *C. pecuarius* had the highest

205   incidence of male desertion (20%; Fig. 3b, Supplementary Table 2). To acknowledge

206   uncertainty in these parental care proportions given variation in sample size, we used a

207   method that estimated simultaneous 95% confidence intervals according to a multinomial

208   distribution[42] (Supplementary Table 2).

209   *Estimation of sex- and stage-specific survival*

210   Our structured population model considered sex-specific survival during two key stage

211   classes in life history: juveniles and adults (Fig. 1b). The juvenile stage was defined as the

212   one-year transition period between hatching and recruitment into the adult population. The

213   adult stage represented a stasis stage in which individuals were annually retained in the

214   population.

215   We used mark-recapture models to account for sex, stage, and temporal variation in

216   encounter (p) and apparent survival (ϕ) probabilities as they allow for imperfect detection of

217   marked individuals during surveys and the inclusion of individuals with unknown fates[40]. We

218   use the term "apparent survival" as true mortality cannot be disentangled from permanent

219   emigration in this framework[19]. We used Cormack-Jolly-Seber models to estimate juvenile

220   and adult survival, with one-year encounter intervals. Juvenile and adult survival models

221   were constructed from design matrices that included sex, year, and stage as factors.

222   Since we were primarily interested in stage- and sex-specific variation in survival, all

223   models included a $\phi \sim sex * stage$ component. Our model selection thus evaluated the best

224   structure explaining variation in detection probability by comparing all interactions between

225   sex, year, and stage (e.g., $p \sim sex * year * stage$). We constructed survival models with the R

226   package "RMark"[43] and estimated demographic parameters via maximum likelihood

227   implemented in program MARK[44]. We evaluated whether our data were appropriately

228   dispersed (i.e. *c-hat* ≤ 3; ref. 19) by employing the "median c-hat" goodness-of-fit bootstrap

229   simulation in program MARK[44].

230   *Estimating hatching sex ratios*

231   To account for potential sex-biases arising prior to the juvenile stage (i.e. sex allocation or

232   sex-specific embryo mortality), we tested whether the hatching sex ratio deviated

233   significantly from parity. Each population was analysed separately using a general linear

234   mixed effect model with a binomial error distribution and a logit link function (R package

235   "lme4"[45]). In this model, the response variable was chick sex, the fixed effect was the

236   intercept, and brood identifier was included as a random factor to control for the non-

237   independence of siblings from the same nest. Because plover chicks are precocial, post-hatch

238   brood mixing can occur. Consequently, our dataset for analysing hatching sex ratio included

239   only complete broods (i.e. with no missing chicks) that were captured at the nest on the same

240   day of hatching (503 unique families with 1139 chicks, Supplementary Table 3). The fixed-

241   effect intercepts of all populations were not significantly different from zero, indicating that

242   hatching sex ratios did not deviate from parity (Fig. 2a).

243   *Matrix model structure*

11 | Eberhart-Phillips et al. *Origins and consequences of adult sex ratios*

244 We built two-sex post-breeding matrix models for each plover population that incorporated

245 two annual transitions denoting juveniles and adults (Fig. 1b). The projection of the matrix

246 for one annual time step (t) is given by:

$$\boldsymbol{n}_t = \mathbf{M}\boldsymbol{n}_{t-1} \tag{Eq. 1}$$

248 where $\boldsymbol{n}$ is a 4×1 vector of the population distributed across the two life stages and two

249 sexes:

$$\boldsymbol{n} = \begin{bmatrix} \text{♀ Juvenile} \\ \text{♀ Adult} \\ \text{♂ Juvenile} \\ \text{♂ Adult} \end{bmatrix} \tag{Eq. 2}$$

251 and $\mathbf{M}$ is expressed as a 4×4 matrix:

$$\mathbf{M} = \begin{bmatrix} 0 & R_{♀}(1-\rho) & 0 & R_{♂}(1-\rho) \\ \phi_{♀J} & \phi_{♀A} & 0 & 0 \\ 0 & R_{♀}\rho & 0 & R_{♂}\rho \\ 0 & 0 & \phi_{♂J} & \phi_{♂A} \end{bmatrix} \tag{Eq. 3}$$

253 where transition probabilities (ϕ) between life stages are the apparent survival rates of female

254 (♀) and male (♂) juveniles (J) and adults (A). The hatching sex ratio (ρ) describes the

255 probability of hatchlings being either male (i.e. ρ) or female (i.e. $1-\rho$), and was estimated for

256 each population from our field data (see above). *Per capita* reproduction of females ($R_{♀}$) and

257 males ($R_{♂}$) is expressed through sex-specific mating functions used to link the sexes and

258 produce progeny for the following time step of the model given the relative frequencies of

259 each sex[20]. We used the harmonic mean mating function which accounts for sex-specific

260 frequency dependence[46]:

$$R_{♀}(n_{♂}, n_{♀}) = \frac{kn_{♂}}{n_{♂}+n_{♀}h^{-1}} \quad , \quad R_{♂}(n_{♂}, n_{♀}) = \frac{kn_{♀}}{n_{♂}+n_{♀}h^{-1}} \tag{Eq. 4}$$

262 where k is the modal clutch size (3 in *C. nivosus*, *C. alexandrinus*, and *C. marginatus*, and 2

263 in *C. thoracicus* and *C. pecuarius*), h is an index of the annual number of mates acquired per

264   female (i.e. mating system, see below), and $n_♀$ and $n_♂$ are the densities of females and males,

265   respectively, in each time step of the model.

266   *Quantifying mating system*

267   Demographic mating functions are traditionally expressed from the perspective of males[46],

268   whereby h is the average harem size (number of female mates per male). Under this

269   definition, $h > 1$ signifies polygyny, $h = 1$ monogamy, and $h < 1$ polyandry; ref. 47).

270   Although both sexes can acquire multiple mates in a single breeding season, within-season

271   polygamy is typically female biased in plovers. Thus, in accordance with the predominantly

272   polyandrous or monogamous mating systems seen across these six populations, h was derived

273   from the average annual number of mates per female (μ):

$$\mu = \frac{1}{n}\sum_{i=1}^{n}\frac{m_i}{b_i} \qquad \textbf{(Eq. 5)}$$

275   where, n is the total number of females in a given population, b is the total number of years

276   female i was seen breeding, and m is the total number of mating partners female i had over b

277   years. Thus, if μ was less than or equal to one, females tended to have only one mating

278   partner annually, and h was set to 1. Alternatively, if μ was greater than 1, females were

279   polygamous and h was calculated as the inverse of μ:

$$h = \begin{cases} 1, & \mu \leq 1 \\ \mu^{-1}, & \mu > 1 \end{cases} \qquad \textbf{(Eq. 6)}$$

281   Our dataset to estimate h for each population only included females for which we were

282   confident of the identity of their mates, and had observed them in at least two reproductive

283   attempts. In summary, μ varied among populations (Supplementary Fig. 4), with *C. nivosus*

284   ($h = 0.82$), *C. alexandrinus* (Turkey; $h = 0.85$), and *C. pecuarius* ($h = 0.86$) having

285   polyandrous mating systems and *C. alexandrinus* (Cape Verde), *C. thoracicus*, and *C.*

286   *marginatus* all having monogamous mating systems (i.e. $h = 1$).

287 *Estimation of the adult sex ratio*

288 We estimated ASR from the stable stage distribution (**w**) of the two-sex matrix model:

289
$$\text{ASR} = \frac{w_{\male A}}{w_{\male A} + w_{\female A}}$$ **(Eq. 7)**

290 where $w_{\male A}$ and $w_{\female A}$ provide the proportion of the population composed of adult males and

291 females, respectively, at equilibrium. To evaluate uncertainty in our estimate of ASR due to

292 sampling and process variation in our apparent survival parameters, we implemented a

293 bootstrapping procedure in which each iteration: (i) randomly sampled our mark-recapture

294 data with replacement, (ii) ran the survival analyses described above, (iii) derived stage- and

295 sex-specific estimates of apparent survival based on the model with the lowest AIC_C (i.e.

296 $\Delta\text{AIC}_C = 0$; Supplementary Fig. 5), (iv) constructed the matrix model (Eq. 3) of these

297 estimates, (v) derived the stable stage distribution through simulation of 1,000 time steps,

298 then (vi) derived ASR from the stable stage distribution at equilibrium on the $1,000^{\text{th}}$ time

299 step. This approach ensured that parameter correlations within the matrix were retained for

300 each bootstrap and it also accounted for non-linearity in the mating function. We ran 1,000

301 iterations and evaluated the accuracy of our ASR estimate by determining the 95%

302 confidence interval of its bootstrapped distribution. Note that our method estimated ASR as

303 the asymptotic value predicted under the assumption that each population was at equilibrium

304 and thus we could not evaluate inter-annual variation in asymptotic ASR. Nonetheless, our

305 model-derived ASR estimate of the *C. nivosus* population falls within annual count-based

306 ASR estimates of this population[48], providing support that our method is robust. Count-based

307 estimates of ASR from the remaining populations in our study are unfortunately

308 uninformative due to our limited sample of marked individuals with known sex.

309 Our mark-recapture analysis was based on the encounter histories of 6,119 uniquely

310 marked and molecularly sexed individuals (Supplementary Table 4). After implementing the

311   bootstrap procedure, we found that variation in the encounter probabilities of juveniles and

312   adults was best explained by sex, year, and age in *C. nivosus*, *C. alexandrinus* (Turkey) and

313   *C. pecuarius* (Supplementary Fig. 5). Encounter probability was best explained by age and

314   year in *C. alexandrinus* (Cape Verde) and *C. marginatus* (Supplementary Fig. 5). In *C.*

315   *thoracicus*, encounter probability was best explained by sex and year (Supplementary Fig. 5).

316   Our mark-recapture data were not over-dispersed (Supplementary Table 4).

317   *Life table response experiment of ASR contributions*

318   Perturbation analyses provide information about the relative effect that each component of a

319   matrix model has on the population-level response, in our case ASR. To assess how

320   influential sex biases in parameters associated with each of the three life stages were on ASR

321   dynamics, we employed a life-table response experiment (LTRE). A LTRE decomposes the

322   difference in response between two or more "treatments" by weighting the difference in

323   parameter values by the parameter's contribution to the response (i.e. its sensitivity), and

324   summing over all parameters[20]. We compared the observed scenario (**M**), to a hypothetical

325   scenario (**M₀**) whereby all female survival rates were set equal to the male rates (or *vice*

326   *versa*) and the hatching sex ratio was unbiased (i.e. $\rho = 0.5$). Thus, our LTRE identifies the

327   drivers of ASR bias by decomposing the difference between the ASR predicted by our model

328   and an unbiased ASR[18].

329   The contributions (C) of lower-level demographic parameters (θ) were calculated

330   following Veran and Beissinger[18]:

$$C(\theta) = \left(\theta_{\male} - \theta_{\female}\right) \times \frac{\partial \text{ASR}}{\partial \theta} \qquad \textbf{(Eq. 8)}$$

332   where $\frac{\partial \text{ASR}}{\partial \theta}$ is the sensitivity of ASR to perturbations in the demographic rate θ in matrix **M'**,

333   which is a reference matrix "midway" between the two scenarios[18]:

15 | Eberhart-Phillips et al. *Origins and consequences of adult sex ratios*

334 $$M' = \frac{M + M_0}{2}$$ **(Eq. 9)**

335   The two-sex mating function makes our model non-linear in the sense that the

336 projection matrix, and specifically the fertility elements (Eq. 4), depends on sex-specific

337 population structure. Perturbation analyses must therefore accommodate the indirect effects

338 of parameter perturbations on population response via their effects on population structure,

339 such as the relative abundance of males and females which can affect mating dynamics and

340 fecundity. To estimate the sensitivities of the ASR to vital rate parameters, we employed

341 numerical methods that independently perturbed each parameter of the matrix, simulated the

342 model through 1,000 time steps, and calculated ASR at equilibrium. This produced

343 parameter-specific splines from which $\frac{\partial \text{ASR}}{\partial \theta}$ could be derived. This approach appropriately

344 accounts for the non-linear feedbacks between vital rates and population structure, though it

345 does not isolate the contribution of this feedback[47,49].

346   Our LTRE revealed that across all populations, sex differences in juvenile apparent

347 survival made the largest overall contribution to ASR bias (Supplementary Fig. 1). Likewise,

348 for all populations, sex biases at hatching and in mating system had negligible effects on

349 ASR variation (Supplementary Fig. 1).

350 *Evaluating the association between ASR bias and parental cooperation*

351 To test the relationship between ASR bias and parental cooperation, we conducted a

352 regression analysis of the following quadratic model:

353 $$P_{\male\female} = \beta_0 + \beta_1 A + \beta_2 A^2 + \varepsilon$$ **(Eq. 11)**

354 where $P_{\male\female}$ is the proportion of families exhibiting parental cooperation, β_i are the

355 regression parameters (i.e. intercept and coefficient), A is the ASR, and ε is random error. We

356 chose a quadratic model *a priori* as we expected maximum parental cooperation at unbiased

357 ASR but minimum cooperation at both male- and female-biased ASRs (see inset in Fig. 3a).

358   This relationship was assessed with a bootstrap procedure that incorporated uncertainty in our

359   estimates of ASR and parental care. Each iteration of the bootstrap (i) randomly sampled an

360   ASR value from the 95% confidence interval of each population shown in Fig. 2b, (ii)

361   randomly sampled a parental care value from the truncated 95% confidence interval of each

362   population shown in Supplementary Table 2, then (iii) fitted the regression model. We ran

363   1,000 iterations of the bootstrap and evaluated overall relationships by visualizing the central

364   tendency of the regressions. We also evaluated the relationship between ASR variation and

365   male-only or female-only care using a similar bootstrap procedure of the following models:

366   $$P_{\male} = \beta_0 + \beta_1{}^A + \varepsilon \quad , \quad P_{\female} = \beta_0 - \beta_1{}^A + \varepsilon \qquad \textbf{(Eq. 12)}$$

367   where $P_{\male}$ and $P_{\female}$ are the proportions of families exhibiting male-only or female-only care,

368   respectively. In this case, we chose exponential models *a priori* as we expected a non-linear

369   increase in uni-parental care by the abundant sex under biased ASR (Supplementary Fig. 3a).

370   This analysis demonstrated that male-only care tended to be more common in populations

371   with male-biased ASR (mean $\beta_1 = 0.682$ [-0.366, 1.555 95% CI]) and female-only care

372   tended to be more common in female-biased populations (mean $\beta_1 = -0.205$ [-0.502, 0.037

373   95% CI]; Supplementary Fig. 3b). However, the overall magnitude of the effect of ASR

374   variation on female-only care was less than that of male-only care.

375   *Data and code availability*

376   All of our modelling and statistical analyses were conducted using R version *Kite-eating*

377   *Tree*[50] with significance testing evaluated at $\alpha = 0.05$. We provide all computer code and

378   documentation as a PDF file written in RMarkdown (Supplementary Material A) together

379   with all the raw datasets needed to reproduce our modelling and analyses (Supplementary

380   Material B). These can be downloaded from our GitHub repository:

381   https://github.com/leberhartphillips/Plover_ASR_Matrix_Modeling.

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520   **Author contributions:**

521   L.E.-P., T.S., J.I.H., and O.K. conceived the study. L.E.-P., C.K., M.C.C.-I., O.V., S.Z., A.K.,

522   M.C.L, I.C.C., and T.S. planned and collected the field data. L.E.-P., C.K., J.I.H., and T.B.

523   performed or supervised the molecular sexing. L.E.-P., T.M., and O.K. implemented the

524   demographic modelling. L.E.-P. wrote the manuscript and the RMarkdown file. All authors

525   contributed substantially to revisions of the paper.

526   **Figure legends**

527   **Figure 1. Modelling the demographic pathway of adult sex ratio bias among plovers**

528   **worldwide.** (**a**) Location of the six study populations. *C. pecuarius*, *C. marginatus*, and *C.*

529   *thoracicus* breed sympatrically in south-western Madagascar, whereas the two populations of

530   *C. alexandrinus* are geographically disparate, inhabiting southern Turkey and the Cape Verde

531   archipelago. The studied *C. nivosus* population is located on the Pacific coast of Mexico. All

532   populations inhabit saltmarsh or seashore habitats characterized by open and flat substrates.

533   (**b**) Schematic of the stage- and sex-specific demographic transitions of individuals from

534   hatching until adulthood and their contributions to the adult sex ratio (depicted here is *C.*

535   *nivosus*). The hatching sex ratio (ρ, proportion of male hatchlings) serves as a proxy for the

536   primary sex ratio and allocates progeny to the male or female juvenile stage. During the

537   juvenile ('juv') stage, a subset of this progeny will survive (ϕ) to recruit and remain as adults

538   ('ad'). Dotted clusters illustrate how a cohort is shaped through these sex-specific

539   demographic transitions to derive the adult sex ratio (mortality indicated by grey dots). The

540   reproduction function, $R(n_\male, n_\female)$, is dependent on mating system and the frequency of

541   available mates (see *Methods* for details).

542   **Figure 2. Inter- and intra-specific variation in sex-biased demography.** (**a**) Hatching sex

543   ratios of successful clutches (proportion of chicks that are male) are shown as point estimates

544   ($\rho \pm 95\%$ CI; left y-axis), and sex bias (i.e. difference between males and females) in annual

545   apparent survival rates of juveniles (ϕ_{juv}) and adults (ϕ_{ad}) are shown as violin plots (right y-

546   axis). Horizontal lines within violin plots indicate the median and interquartile ranges of the

547   bootstrapped estimates (see *Methods* for details). (**b**) Bootstrap distributions of the derived

548   ASRs based on the sex- and stage-specific rates shown in panel a. Vertical bars on the right

549   side of histograms indicate the 95% CI of ASRs based on 1,000 iterations of the bootstrap

550   (mean ASR [95% CI]: *C. nivosus* = 0.644 [0.499, 0.778], *C. alexandrinus* [Turkey] = 0.586

551   [0.510, 0.652], *C. alexandrinus* [Cape Verde] = 0.469 [0.396, 0.543], *C. thoracicus* = 0.421

552   [0.171, 0.681], *C. marginatus* = 0.430 [0.340, 0.522], *C. pecuarius* = 0.386 [0.289, 0.498].

553   **Figure 3. Relationship between parental cooperation and the adult sex ratio.** (**a**) Faint

554   white lines illustrate each iteration of the bootstrap, which randomly sampled an adult sex

555   ratio and parental care estimate from each population's uncertainty distribution and fitted

556   them to the *a priori* quadratic model (shown in inset, Eq. 11). (**b**) Proportion of monitored

557   plover families that exhibit parental cooperation (white) or single-parent care by males

558   (green) or females (orange). Sample sizes reflect number of families monitored per
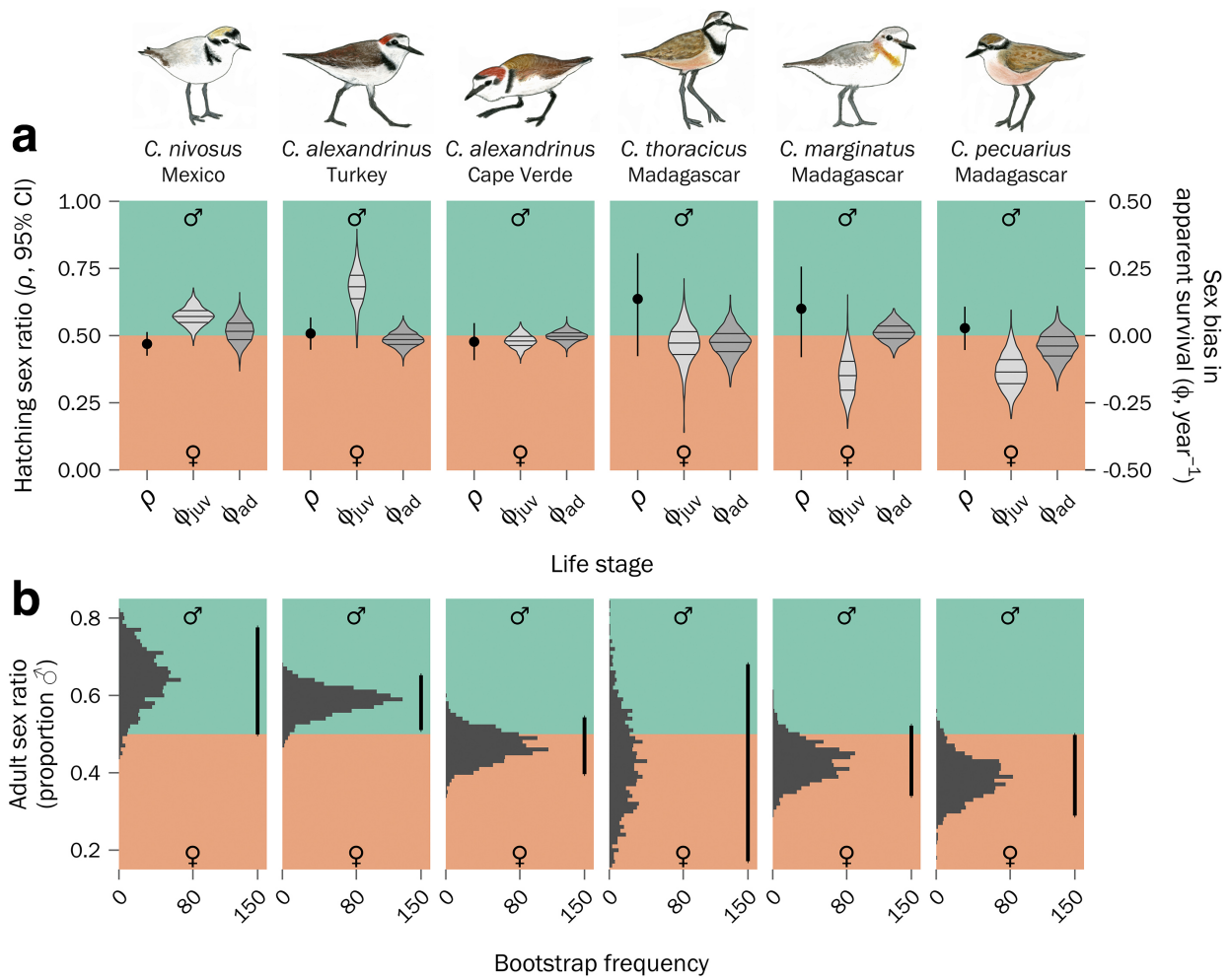
559   population.

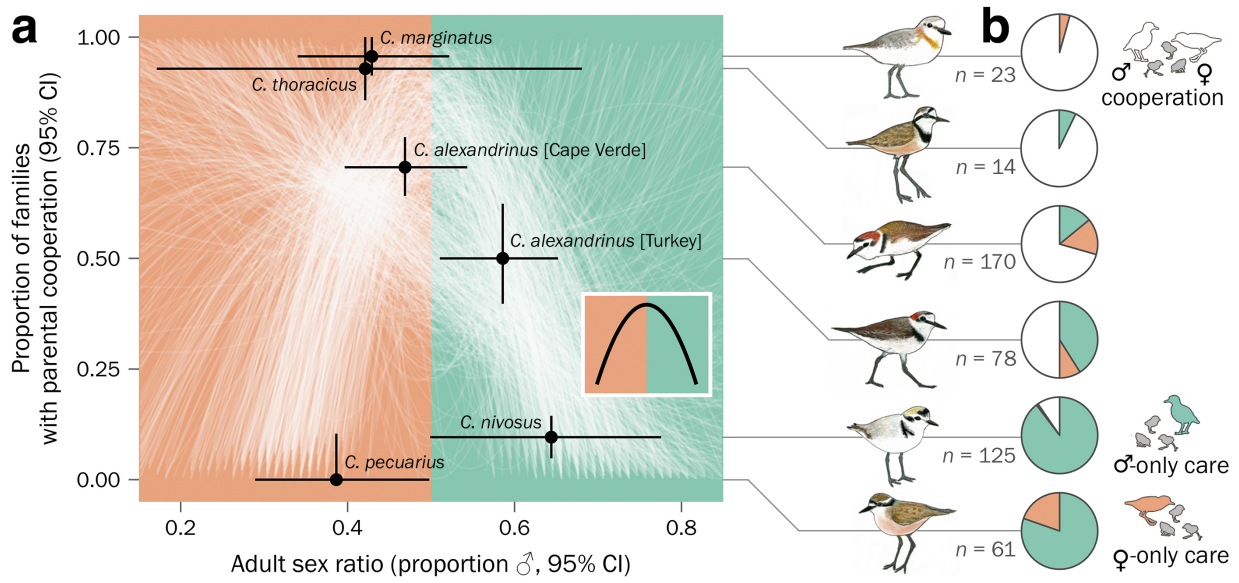560   **Figure 1**
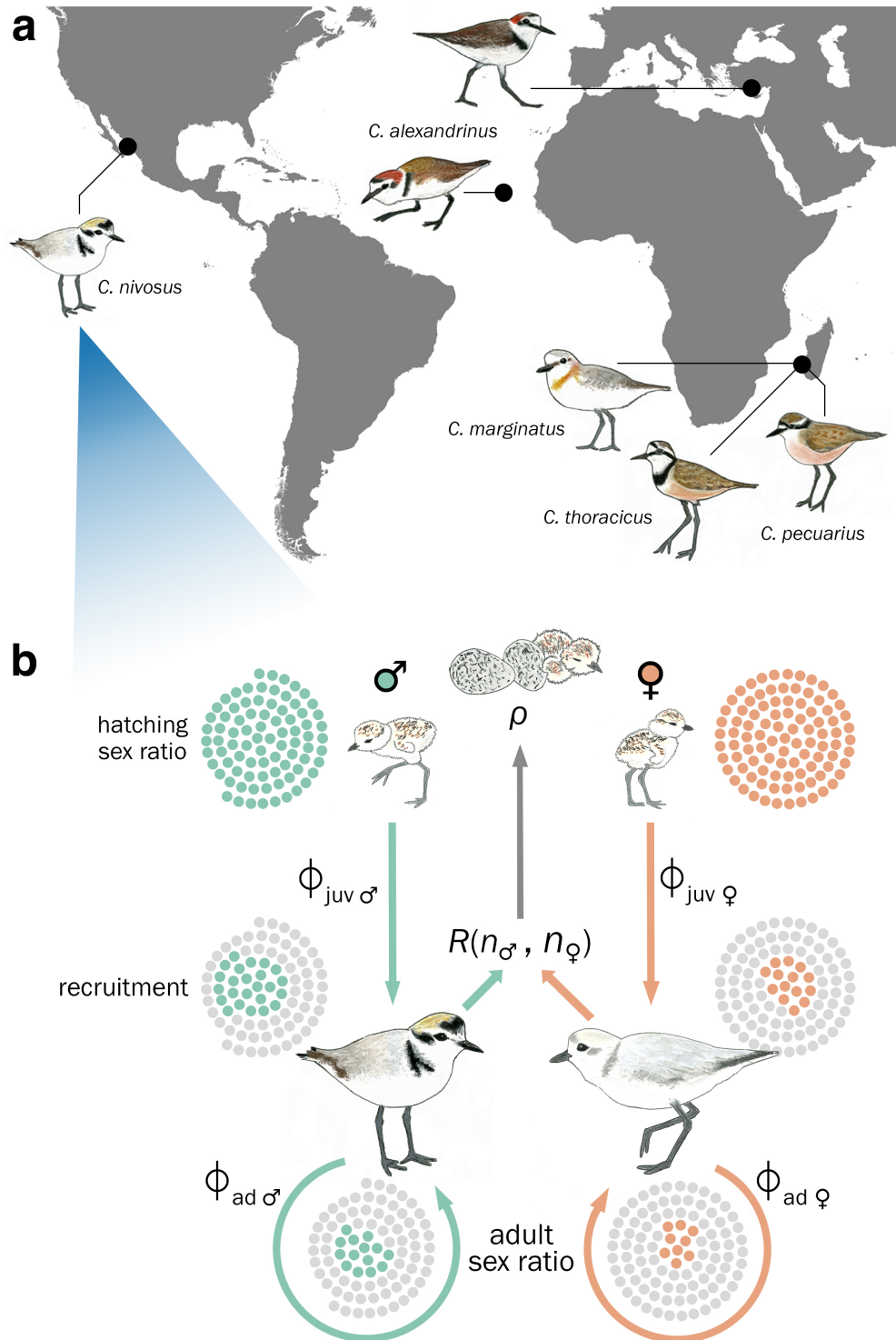
561   **Figure 2**

562 **Figure 3**

563   **Supplementary Information**

564   ***Supplementary Tables***

565   **Supplementary Table 1. Study site metadata: geographic location (see Fig. 1) and**

566   **duration of monitoring effort.**

Species	Population	Latitude	Longitude	Years monitored
C. nivosus	Mexico	23°54'N	106°57'W	2006-2012
C. alexandrinus	Turkey	36°43'N	35°03'E	1996-2001
	Cape Verde	15°8'N	23°13'W	2007-2015
C. thoracicus	Madagascar	22°6'S	43°15'E	2009-2015
C. marginatus	Madagascar			2009-2015
C. pecuarius	Madagascar			2009-2015
				43 years

567 **Supplementary Table 2. Summary of parental care sex roles.** Percentages reflect the

568 within-population proportion of families with a given parental care system.

Species	Population	Bi-parental [95% CI]	Female-only care [95% CI]	Male-only care [95% CI]	*n*
C. nivosus	Mexico	9% [5, 14]	1% [0, 6]	90% [85, 94]	125
C. alexandrinus	Turkey	50% [40, 62]	9% [0, 21]	41% [31, 53]	78
	Cape Verde	71% [64, 77]	15% [9, 22]	14% [8, 21]	170
C. thoracicus	Madagascar	93% [86, 100]	0% [0, 12]	7% [0, 36]	14
C. marginatus	Madagascar	96% [91, 100]	4% [0, 12]	0% [0, 7]	23
C. pecuarius	Madagascar	0% [0, 10]	20% [11, 30]	80% [72, 91]	61
					471

569 **Supplementary Table 3. Summary of hatching sex ratio data,** where ρ is the average

570 hatching sex ratio (expressed as the proportion of hatchlings in a brood that are male) and

571 95% CIs are calculated using a binomial distribution.

Species	Population	$N_{Families}$	$N_{Hatchlings}$	ρ	95% CI
C. nivosus	Mexico	198	484	0.469	[0.425, 0.514]
C. alexandrinus	Turkey	102	262	0.508	[0.447, 0.568]
	Cape Verde	107	197	0.477	[0.408, 0.547]
C. thoracicus	Madagascar	11	22	0.636	[0.423, 0.807]
C. marginatus	Madagascar	13	30	0.600	[0.419, 0.757]
C. pecuarius	Madagascar	72	144	0.528	[0.446, 0.757]

572 **Supplementary Table 4. Sample size and over-dispersion summary of mark-recapture**

573 **dataset used to estimate apparent survival.**

Species	Population	Juveniles[1]		Adults[2]		Total individuals	Median $\hat{c}$
		♀	♂	♀	♂		
C. nivosus	Mexico	438	388	221	212	1358	1.70
C. alexandrinus	Turkey	310	293	557	504	1664	1.49
	Cape Verde	377	383	254	213	1227	1.37
C. thoracicus	Madagascar	38	56	83	68	245	2.72
C. marginatus	Madagascar	76	96	99	95	366	1.31
C. pecuarius	Madagascar	274	286	382	416	1358	1.77
						6119	

574 [1]Individuals first marked as hatchlings (i.e. known age).

575 [2]Individuals first marked as breeding adults (i.e. 1+ years old).

576   *Supplementary Figure legends*

577   **Supplementary Figure 1. Contributions of sex-specific parameters to adult sex ratio**

578   **bias.** These results are based on a life-table response experiment (LTRE) that compared the

579   empirically-derived sex-specific model to hypothetical scenarios with no sex differences in

580   demographic rates (top panel: female-only rates, bottom panel: male-only rates). ASR is the

581   proportion of the adult population that is male, thus changes in female-biased parameters

582   have a negative effect on ASR and consequently their LTRE statistics are negative. Notation:

583   h = mating system index (Eq. 6), ρ = hatching sex ratio, Juvenile = sex-biased apparent

584   survival of juveniles, Adult = sex-biased apparent survival of adults.

585   **Supplementary Figure 2. Interspecific variation in sex-specific mating opportunities**

586   **among three plover species.** Experimental assessment of sex-differences in remating times

587   in three of the six populations analysed indicate that *C. alexandrinus* males in Tuzla, Turkey

588   ($n = 19$) take longer to find a mate than females ($n = 15$) after induced divorce. This trend is

589   reversed in *C. pecuarius* ($n_\male = 10$, $n_\female = 6$) whereas there are no differences in the *C.*

590   *marginatus* ($n_\male = 6$, $n_\female = 6$). Significant sex-differences are indicated by asterisks (***: $P <$

591   0.001, *: $P < 0.05$, n.s.: $P > 0.05$). Figure adapted from Parra et al. (ref. 23).

592   **Supplementary Figure 3. Relationship between uni-parental care and the adult sex**

593   **ratio.** (**a**) Predicted prevalence of male-only care (left panel) or female-only care (right

594   panel) in response to adult sex ratio variation. (**b**) Observed relationship between parental

595   care strategies and adult sex ratio estimates among the six studied populations. Faint white

596   lines illustrate each iteration of the bootstrap, which randomly sampled an adult sex ratio and

597   parental care estimate from each population's uncertainty distribution and fitted them to the *a*

598   *priori* exponential model (Eq. 12). (**c**) Proportion of monitored plover families that exhibit

599   parental cooperation (white) or uni-parental care by males (green) or females (orange).

600   Sample sizes reflect the number of families monitored per population, circled numbers

601   correspond to the data point labels shown in panel b.

602   **Supplementary Figure 4. Variation in annual female mating rates (μ) among the six**

603   **plover populations.** Sample sizes indicate the number of individual females in each

604   population that had at least two recorded breeding attempts with identified male(s) during the

605   study. Values below one represent females that bred over multiple years with the same mate

606   (i.e. between season monogamy), whereas values greater that one represent females that have

607   had more than one mate per year (i.e. within season polyandry). Values equal to one

608   represent individuals that have had one mate per year, but have switched mates between years

609   (i.e. between season polyandry but within season monogamy). White data points illustrate

610   individual females, and black points are population averages ($\mu \pm 1$ SD).

611   **Supplementary Figure 5. Summary statistics of bootstrapped mark-recapture modelling**

612   **of juvenile and adult encounter probability.** Left panels illustrate variation in AIC$_C$ w_i.

613   Right panels illustrate variation in ΔAIC$_C$. Model structure of encounter probability (p) is

614   shown as labels on the y-axes. See *Methods* for further details.
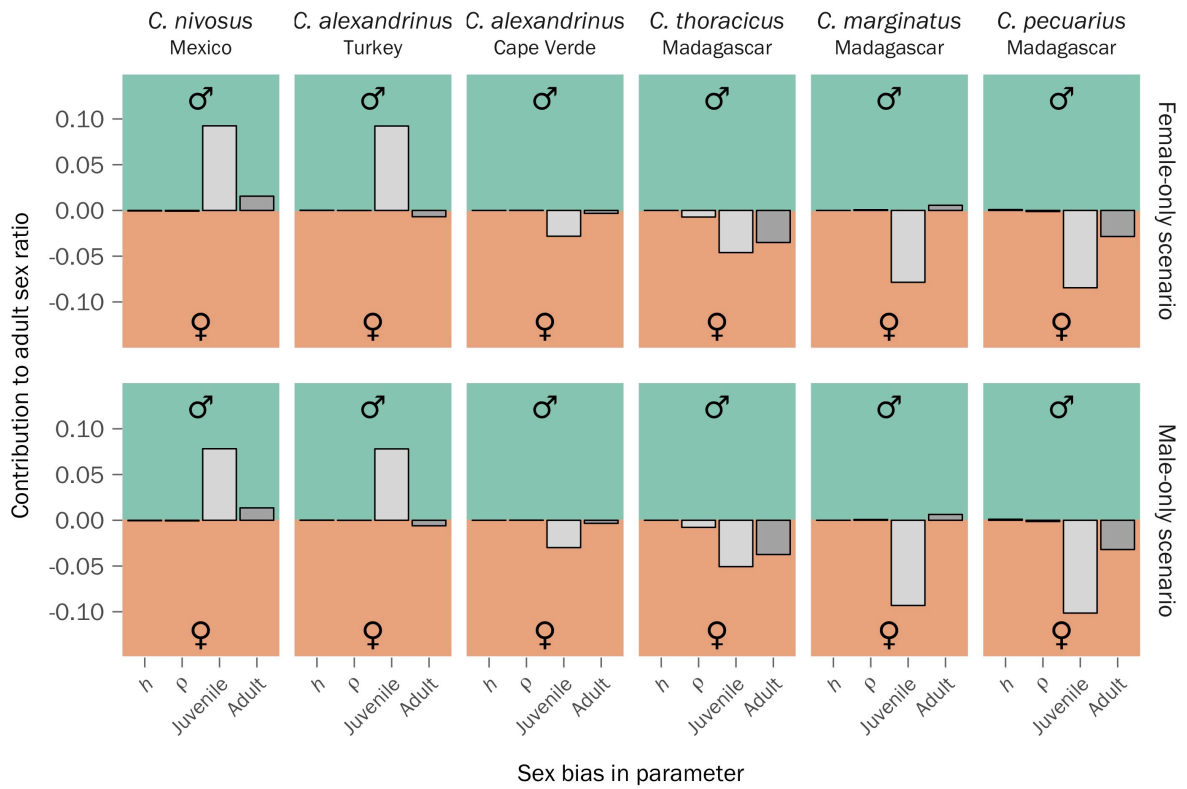
615   **Supplementary Movie 1**

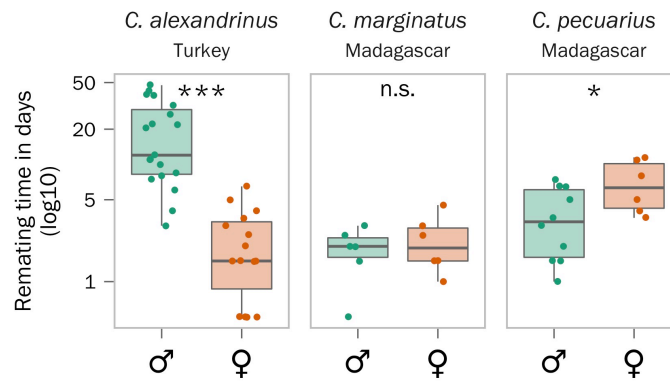616   **Field methods for capturing and monitoring plovers** (11min 46sec)**:**

617   https://drive.google.com/file/d/0B4RO-u-356yiRjNSQ0RUMWpxYlU/view?usp=sharing

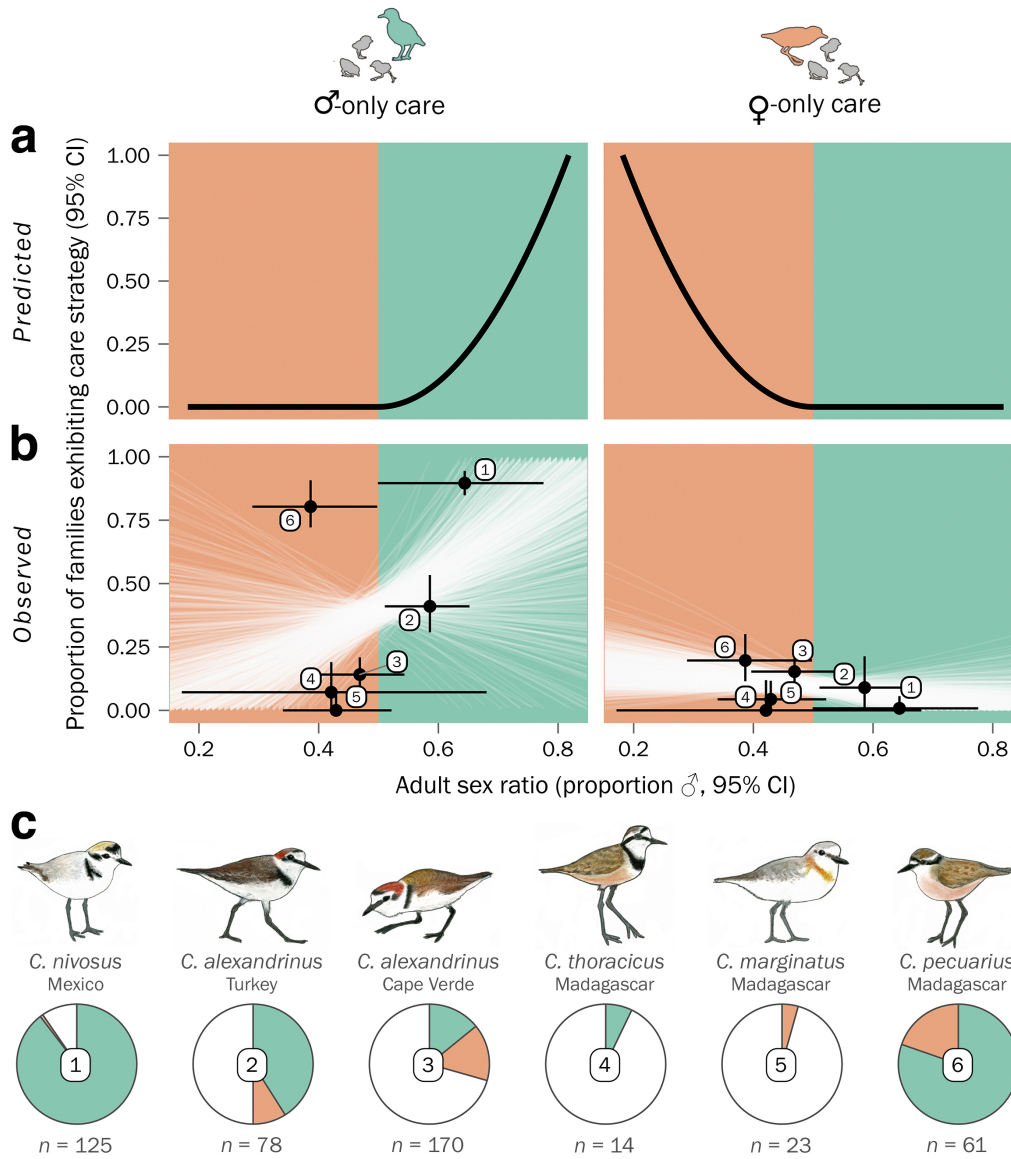618 **Supplementary Figure 1**

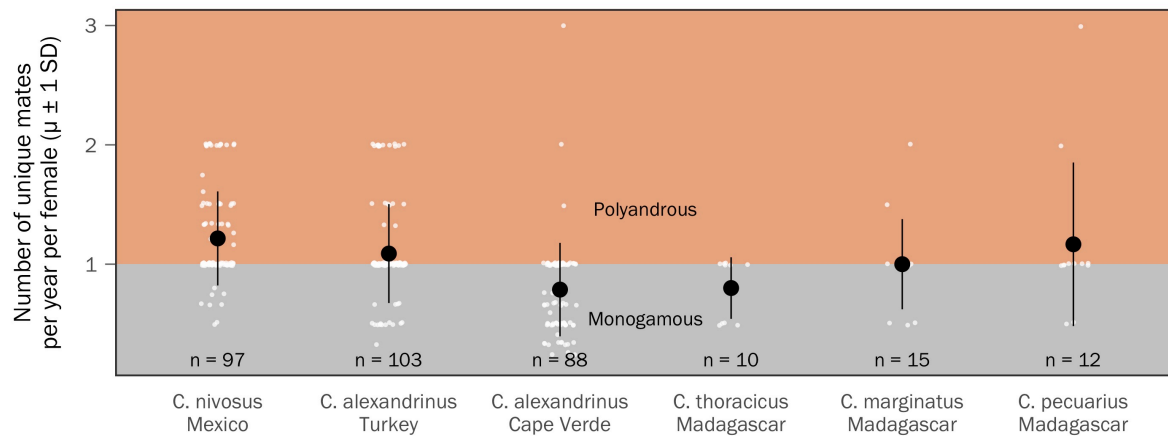619 **Supplementary Figure 2**

620   **Supplementary Figure 3**

621 **Supplementary Figure 4**

Supplementary Figure 5