

Adult sex ratio bias in snowy plovers is driven by sex-specific early survival: implications for mating systems and population growth

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Data accessibility statement:

We provide all computer code and documentation as a PDF file written in Rmarkdown together with all raw datasets needed to reproduce our modeling and analyses. These can be downloaded from the GitHub repository found here: [https://github.com/leberhartphillips/Ceuta ASR matrix modeling](https://github.com/leberhartphillips/Ceuta_ASR_matrix_modeling)

1 **ABSTRACT**

2 Adult sex ratio (ASR) is a central concept in population biology and a key factor in sexual
3 selection, yet why do most demographic models ignore sex-biases? Vital rates often vary
4 between the sexes and across life history, but their relative contributions to ASR variation
5 remain poorly understood—an essential step to evaluate sex ratio theories in the wild and
6 inform conservation. Here we combine structured two-sex population models with
7 individual-based mark-recapture data from an intensively monitored polygamous population
8 of snowy plovers. We show that a strongly male-biased ASR is primarily driven by sex-
9 specific survival of juveniles, rather than adults or dependent offspring. This provides
10 empirical support for theories of unbiased sex allocation when sex-differences in survival
11 arise after the period of parental investment. Importantly, a conventional model ignoring sex-
12 biases significantly overestimated population viability. We suggest that sex-specific
13 population models are essential to understand the population dynamics of sexual organisms:
14 reproduction and population growth is most sensitive to perturbations in survival of the
15 limiting sex. Overall, our study suggests that sex-biased early survival may contribute
16 towards mating system evolution and population persistence, with implications for both
17 sexual selection theory and biodiversity conservation.

18 **SIGNIFICANCE STATEMENT**

19 Sex biases are widespread in nature and represent a fundamental component of sexual
20 selection and population biology—but at which point in life history do these biases emerge?
21 Here we report a detailed individual-based demographic analysis of an intensively studied
22 wild bird population to evaluate the origins of sex biases and their consequences on mating
23 strategies and population dynamics. We document a strongly male-biased adult sex ratio,
24 which is consistent with behavioral observations of female-biased polygamy. Notably, sex-
25 biased juvenile, rather than adult survival, contributed most to the adult sex ratio. Sex-biases
26 also strongly influenced population viability, which was significantly overestimated when sex
27 ratio and mating system were ignored. Our study therefore has implications for both sexual
28 selection theory and biodiversity conservation.

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29 Sex ratio variation in wild populations has important consequences for population dynamics
30 and hence biodiversity conservation (1). As reproduction in sexual organisms involves both
31 males and females, a shortage of either sex could compromise population viability (2). A
32 reduction in the number of breeding females directly reduces birth rates and hence population
33 productivity (3), whereas an overabundance of males may increase violence and aggression
34 such that both male and female survival is reduced (4). Although a small number of males
35 can potentially fertilize many mates, females in male-biased populations may need to
36 compete for breeding opportunities with high quality males which can induce additional
37 mortality (5). If males are in short supply, fathers also tend to reduce their parental
38 investment which could negatively impact offspring survival (6, 7). Additionally, a biased
39 sex ratio in either direction will decrease effective population size, which has adverse
40 consequences for genetic diversity (8). Therefore, depending on mating system, populations
41 with biased sex ratios may be more vulnerable to extinction than unbiased populations (9).

42 Recent studies also suggest that the adult sex ratio (ASR, the proportion of the adult
43 population that is male) impacts breeding strategies as the limiting sex has the advantage in
44 mating and parental decisions (10-12). For example, male-biased avian populations tend to
45 have polyandrous mating systems and male-biased parental provisioning (13). Although the
46 theory linking ASR to breeding system is relatively new, there are already supporting studies:
47 parental cooperation is associated with an unbiased ASR in birds (14) whereas ASR is a
48 strong predictor of sex-specific sexual activity and divorce rates in humans (15, 16).

49 Despite the importance of ASR in population biology, biodiversity conservation and
50 breeding system evolution, the origin(s) of ASR biases remain unclear. Biases in the ASR
51 can emerge via a number of mutually non-exclusive demographic pathways (11, 17, 18). For
52 instance, sex-biases may occur at conception or at birth (19), or the survival of male and
53 female juveniles may differ to the extent that fewer of one sex reaches adulthood (20).

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54 Furthermore, sex-differences in adult survival or maturation rates could create a shortage of
55 the sex that has higher mortality (4) or slower maturation (18), and if emigration is not
56 compensated by immigration, sex-differences in dispersal behavior could create local biases
57 in ASR (21).

58 A number of studies of wild vertebrate populations have evaluated the independent
59 contributions of the above pathways to ASR bias (22-24). However, to fully understand ASR
60 bias requires these components to be modeled simultaneously to quantify their relative
61 contributions. In practice, large empirical datasets from natural populations incorporating
62 stage- and sex-specific vital rates are uncommon (25-27). Furthermore, males and females
63 often have different behaviors or ecological niches (28), which can make one or the other
64 easier to detect (9, 11). Fortunately, these sources of sampling bias can be accounted for
65 using mark-recapture methods (29).

66 Here, we investigate the demographic origins of ASR bias in a polygamous bird using
67 seven years of individual-based sex- and stage-specific life history data. Polygamous species
68 have a special significance in sex ratio studies as they are predicted to be at higher risk of
69 extinction (1, 30). We studied a small ground-nesting shorebird, the snowy plover
70 (*Charadrius nivosus*, ref. 31), which is endangered in parts of its Nearctic range and has a
71 sequentially polygamous mating system (32, 33). Using a two-sex matrix model, we show
72 that the ASR of this species is substantially more male biased than previously reported (34).
73 Sex-differences in chick and juvenile survival contribute most to ASR bias, suggesting that
74 ASR variation is particularly susceptible to factors that influence early life history stages.
75 Furthermore, we show that population growth is most sensitive to adult female survival under
76 a male-biased ASR, signifying that sex-specific early survival can affect population viability
77 via ASR variation. Importantly, our study suggests that sex-biased survival in early life has
78 ramifications for mating system variation and knock-on effects for population growth.

79

80 **RESULTS**

81 We conducted this study at Bahía de Ceuta, a subtropical lagoon on the coastal plain in north-
82 western Mexico (23°54'N, 106°57'W). Between 2006 and 2012, we uniquely marked and
83 monitored 1259 individuals (436 females and 390 males initially marked as chicks and 221
84 females and 212 males initially marked as adults). Although our marking methods were
85 limited to breeding adults and chicks, we detected no sex difference in the proportion of this
86 marked population that was non-breeding (paired t-test: $t = 0.429$, $df = 4$, $P = 0.69$, Fig. S1).
87 Therefore, this marked subset of the population represents a broadly representative sample
88 from which to draw inferences about the dynamics of the population at large and to elucidate
89 the contributions of sex- and stage-specific survival towards ASR bias.

90

91 *Mating system*

92 To understand the ASR in the context of mating system, we quantified sex-specific mating
93 strategies of snowy plovers at our study site. Although both sexes can be polygamous, female
94 snowy plovers typically desert broods to seek serial mates, leaving males to provide parental
95 care alone (33). Thus, we expected that females would acquire on average a greater number
96 of mates per year than males. Based on behavioral observations of 456 families with known
97 identities of both parents, this is precisely what we found (Fig. 1; Mann-Whitney-Wilcoxon
98 test: $W = 3264$, $P \leq 0.001$). As such, the mating system index in the mating function (Eq. 4 in
99 *Methods*) was polyandrous ($h = 0.82$).

100

101 *Sex-biased survival and ASR bias*

102 We estimated stage- and sex-specific survival rates using mark-recapture analysis to control
103 for imperfect detection in the field. Mark-recapture modeling revealed sex differences in

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104 encounter probability for juveniles and adults that would confound simple estimates of
105 survival and ASR based solely on return rates or uncorrected counts of males and females
106 (Table 1). Apparent survival was strongly male biased across all life-history stages, with male
107 survival being 11.5% higher than female survival at the chick stage, 51% higher for juveniles,
108 and 0.5% higher at the adult stage (Fig. 2a). Hatching sex ratio was slightly female biased but
109 did not significantly deviate from parity (average $\rho = 0.486$ [95% CI = 0.435–0.536], $P =$
110 0.588, $N = 340$ hatchlings from 116 full broods). Overall, our model indicated a strongly
111 male-biased ASR (mean = 0.632 [95% CI = 0.460–0.785]; Fig. 2b).

112

113 *Contributions to male-biased ASR*

114 To elucidate the stage-specific contributions of sex differences in survival to ASR bias, we
115 conducted a life table response experiment (LTRE), which revealed that all vital rates
116 contributed in the same direction (i.e. male-biased) but differed in magnitude. A sex
117 difference in juvenile survival made the largest overall contribution to ASR bias (Fig. 2c).
118 Specifically, the contribution of sex-biased juvenile survival towards ASR was 3.3 times
119 higher than sex-biased chick survival and 17.6 times higher than sex-biased adult survival.
120 Hatching sex ratio and mating system made negligible contributions (Fig. 2c).

121

122 *Consequences of ASR bias and polygamy on population viability*

123 Biased ASR and polygamy create conditions whereby reduced survival of the limiting sex
124 can compromise population viability, which has important implications for conservation. Our
125 perturbation analysis showed that population growth was most sensitive to adult survival
126 under all hypothetical scenarios of ASR and mating system (Fig. 3). Adult female survival
127 elasticities were highest under scenarios of male-biased ASR. As expected, there was no sex-

128 specific sensitivity of vital rates under an unbiased ASR and monogamous mating system.

129 However, elasticity was highest for adult males under an unbiased ASR and polyandry.

130 To elucidate the conservation consequences of disregarding sex-biases, we compared

131 the predictive accuracy of a detailed two-sex model incorporating polygamy to a

132 conventional one-sex model. Over the seven-year study period, average population growth

133 was below replacement ($\bar{\lambda}_{\text{obs.}} = 0.859 \pm 0.28 \text{ SD}$, Fig. 4). This observed rate of decline was

134 captured by the uncertainty distribution of the two-sex model ($\bar{\lambda}_{\text{two-sex}} = 0.849$ [95% CI:

135 0.802–0.897], Fig. 4). In contrast, the one-sex version of the model exhibited greater

136 uncertainty and significantly overestimated population growth ($\bar{\lambda}_{\text{one-sex}} = 0.947$ [95% CI:

137 0.883–1.01], Fig. 4).

138

139 **DISCUSSION**

140 We present a comprehensive demographic model based on detailed individual-based life-

141 history data from an intensively monitored bird population. By incorporating sex-specific

142 feedbacks between survival and frequency-dependent reproduction, our model predicted a

143 strongly male-biased ASR. This was complemented by our behavioral observations of a

144 polyandrous mating system. Therefore, our findings build upon recent empirical and

145 theoretical studies linking ASR to the evolutionary origins and consequences of mating

146 system variation (10-12), and also provide novel insights into the sex- and stage-specific

147 demographic components that contribute to ASR bias. Males had consistently higher

148 apparent survival than females across all life stages, but a sex difference in the apparent

149 survival of juveniles had the largest impact on ASR bias. Furthermore, population growth

150 was most sensitive to perturbations in adult female survival under the male-biased ASR.

151 Taken together, our results uncover the demographic pathways linking individual-level

152 variation in survival and sex roles to population-level dynamics.

153 Obtaining reliable survival estimates from natural populations is challenging due to
154 sex differences in behavior and life history. Our study addressed this uncertainty through
155 mark-recapture models and bootstrapping. A central assumption of our model is that our
156 marked subset of the population is representative of the entire population. This is appropriate
157 given that we marked the vast majority of chicks and breeding adults in the population.
158 Furthermore, we did not find a sex difference in the proportion of breeders versus non-
159 breeders (Fig. S1) indicating that our ASR estimate is not confounded by an excess number
160 of unmarked non-breeding females.

161 Females had higher rates of polygamy than males, which is in line with most
162 published records from other snowy plover populations (32, 35). This female-biased mating
163 system complemented a strongly male-biased ASR. ASR in this species has previously been
164 reported to be less extreme (34) than found here although the previous study was unable to
165 incorporate sex-specific chick and juvenile survival, which made the greatest contributions to
166 the ASR bias in this population (this study) and others (36). ASR bias is a widespread
167 phenomenon in wild vertebrate populations, with mammals typically being female biased
168 (mean ASR = 0.37 ± 0.15 SD) and birds typically being male biased (mean ASR = $0.55 \pm$
169 0.09 SD; Table S1; (37). Our ASR estimate for snowy plovers therefore lies within the
170 natural variation observed in other avian taxa (9).

171

172 *Importance of early sex-specific demographic processes*

173 Several hypotheses can be put forward to explain the observed pattern of male-biased early
174 survival. Focusing first on the chicks, male hatchlings are significantly larger than their
175 sisters in this population (38), potentially providing males with an advantage during early
176 development. Another mutually non-exclusive possibility is that male chicks could achieve
177 faster growth rates, as has been observed in Kentish plovers *Charadrius alexandrinus* (38),

178 for example, either by virtue of sex-specific parental care (39) or as a consequence of sex-
179 specific immunocompetence (40). Alternatively, predation could act sex-specifically,
180 although male and female chicks do not differ appreciably in appearance and behavior, and
181 we did not detect a sex difference in encounter rates (Fig. S2). Lastly, the sexes might differ
182 in premature investment in sexual traits (41) although this seems unlikely as sexual
183 ornamentation is moderate and body size differences are small (ref. 31; about 4%).

184 The sex bias during the juvenile stage made the largest contribution to the ASR bias.
185 This corroborates the results of earlier avian studies showing that sex-specific first-year
186 survival may lead to an ASR bias (25, 36). Our study goes further than previous works by
187 decomposing the contributions from the first-year stage into chick and juvenile contributions.
188 Juvenile survival contributed most towards ASR bias, probably because these naïve
189 individuals face multiple challenges during the transition from parental independence to
190 sexual maturity, potentially including predation, harsh winter climates and food shortages, all
191 of which could disproportionately affect either sex. For example, in sexually size dimorphic
192 species including red deer *Cervus elaphus* and great bustards *Otis tarda*, male young are less
193 able to cope with severe winter weather (42) and food shortage (43), probably owing to the
194 metabolic demands of large body size. In snowy plovers, such a mechanism is unlikely given
195 the moderate size differences between males and females (31).

196 Another possibility is that sex-biased dispersal behavior could contribute towards sex-
197 differences in apparent juvenile survival, as natal dispersal is typically female biased in birds
198 (44), with snowy plovers being no exception (45, 46). However, dispersal and survival are
199 not necessarily independent phenomena, as dispersal often entails survival costs such as
200 increased predation risk and unfamiliarity of novel environments (47). Moreover, chicks are
201 unable to disperse beyond the breeding site, so their survival estimate approximated true
202 survival and thus implies a role of intrinsic sex differences in early survival. In addition, over

203 the seven years of this study, few adults were resighted in adjacent populations and these
204 individuals are unbiased with respect to sex. Finally, an independent study of snowy plovers
205 in Monterey Bay, California found that survival was male biased even after accounting for
206 sex-specific dispersal (34).

207

208 *Negligible effect of sex allocation*

209 The hatching sex ratio, based on 340 hatchlings, was unbiased and served as a proxy for the
210 primary sex ratio. Despite popular interest in sex-allocation theory (48, 49) relatively few
211 studies have convincingly demonstrated offspring sex ratio biases in wild populations (50).
212 Düsing (51), Fisher (52), and others (53-55) reasoned that if sex biases in survival emerged
213 after the period of parental investment, sex allocation should not deviate from parity. This is
214 precisely what we found, with ASR being strongly influenced by the sex-biased survival of
215 independent juveniles, rather than deviations in the hatching sex ratio (Fig. 2). Furthermore,
216 although the sex-biased survival of dependent chicks provided a noteworthy contribution to
217 ASR bias (Fig. 2), fathers provide uniparental care of chicks in this species, and therefore the
218 period of maternal investment typically ends at hatching. Given this parental care system, our
219 result further confirms theoretical expectations of an unbiased hatching sex ratio.

220

221 *Evolutionary feedbacks between ASR and mating system*

222 Mating systems are influenced by the availability of mates (11). A biased ASR creates
223 conditions whereby one sex is in limited supply, thus forcing the other sex to compete for
224 access to mates (7, 10). In shorebirds, ASR is a strong predictor of mating and parental
225 strategies (13), with the limiting sex tending to have greater mating opportunities and reduced
226 parental investment. These sex differences in the costs and benefits of parental care may
227 facilitate polygamy (6).

228 However, the relationship between sex ratio and mating system represents a causality
229 dilemma because of the positive feedback that polygamous mating systems impose on ASR
230 bias and *vice versa* (56). On the one hand, polygamy entails sex-specific costs due to sexual
231 selection which could drive the ASR bias, while on the other hand ASR bias creates uneven
232 mating opportunities and thus facilitates polygamy. We show that sex biases originate prior
233 to maturity (Fig. 5i), and are therefore likely influenced by natural selection. For example,
234 genotype-sex interactions could impact chick survival during development (57) rather than
235 during adulthood where sexual selection is expected to have a strong impact on survival.
236 Consequently, ASR bias appears to drive the mating system rather than *vice versa* (Fig. 5ii).
237 We cannot discount the possibility that sexual selection contributes towards sex biases in
238 early survival, for instance via differential early investment in secondary sexual traits (41),
239 but this seems unlikely as sexual dimorphism in plovers is negligible and, if anything, males
240 are more ornamented than females (31, 58).

241

242 *Consequences of mating system and ASR on population growth*

243 In vertebrates, adult survival is often the most important parameter influencing population
244 growth because adults have the greatest reproductive potential (59). This was the case in our
245 population, but the effect of adult survival was sex-specific due to ASR bias and polygamy.
246 Under a male-biased ASR, adult female survival had the highest elasticity to population
247 growth, meaning that a small perturbation to adult female survival has a larger effect on
248 population growth than an equivalent perturbation in all other parameters. Attempting to
249 dissect the effects of ASR and mating system, we found that sex-specific elasticities of adults
250 were greatest under scenarios of male-biased ASR compared to scenarios of polyandry (Fig.
251 5iii). Conversely, in scenarios of unbiased ASR, both sexes had the same elasticities for all
252 parameters under monogamy, but under polyandry, adult male survival had the highest

253 elasticity. These contrasts highlight the reproductive constraints imposed on populations with
254 a biased ASR. When ASR is male-biased, polyandrous mating strategies optimize individual
255 fecundity, and thus maximize population growth (1). However, reproduction is dependent on
256 the availability of gametes, and thus a population with female-biased ASR and a polygynous
257 mating system may not be limited in the same way because a single male can produce many
258 more gametes than a single female and hence father more offspring. Therefore, similar
259 studies of polygynous populations are needed to critically test the predictions of mating
260 system, ASR, and population growth.

261

262 *Implications of two-sex vs one-sex modeling for biodiversity conservation*

263 Modeling population trajectories is an important tool for conservation and management (60).
264 Sex biases could potentially play an important role in population dynamics, particularly for
265 polygamous species, yet sex-structured models remain uncommon. Here, we compare a
266 conventional one-sex model to a two-sex model incorporating frequency-dependent
267 reproduction and sex-specific survival. We show that our two-sex model provides a better fit
268 to the observed data than a one-sex model. Moreover, while both models indicate negative
269 population trajectories, the one-sex model substantially underestimates the rate of population
270 decline and exhibits greater uncertainty. This has important conservation implications,
271 especially for sex-biased populations of threatened or endangered species, where failing to
272 incorporate sex-specific vital rates could lead to erroneous conclusions and overestimated
273 population viability.

274

275 *Conclusions*

276 With the rise of conservation-based monitoring of individually marked populations (61), a
277 wealth of demographic data present new scientific horizons for ecologists and evolutionary

278 biologists interested in sex-specific modeling. By combining extensive individual-based sex-
279 and stage-specific vital rates and structured population models, we show that a male-biased
280 ASR in a natural population is driven by male-biased survival of early life history stages (Fig.
281 5i). Our results indicate that ASR likely drives mating system (Fig. 5ii) although further
282 experimental and/or comparative studies are needed to establish the causal link. Both ASR
283 and mating system facilitate sex-specific sensitivities to population growth (Fig. 5iii), with
284 ASR having the strongest effect. Male-biased survival in snowy plovers is consistent with
285 recent comparative studies (62, 56) suggesting that many bird species may exhibit male-
286 biased ASR (9, 37). Thus, our study makes an important contribution to understanding a
287 widespread phenomenon in natural populations and highlights that ASR variation likely acts
288 as an important catalyst of mating system dynamics and population viability.

289

290 **METHODS**

291 *Field and laboratory methods*

292 Over the seven-year study period, we collected mark-recapture and individual reproductive
293 success data during daily surveys of the study site over the entire three-month breeding
294 season that typically spanned from mid-April to mid-July. Plover chicks and adults were
295 captured using funnel traps on broods or nests (63). We assigned adults a unique color
296 combination of three darvic rings and an alpha-numeric metal ring, allowing the use of both
297 captures and non-invasive resightings to estimate survival. Regular brood resightings
298 combined with regular recaptures aided analyses of daily survival for chicks. Given our
299 intensive nest search and capture efforts we are confident that we ringed the vast majority of
300 chicks (>95%) and breeding adults (>85%) in the local population. Nests and broods were
301 frequently monitored every two to seven days to assess daily survival and identify tending
302 parents. During captures, approximately 25–50 μ L of blood was sampled from the meta-tarsal

303 vein of chicks and the brachial vein of adults for molecular sexing with the Z-002B marker
304 (64) and verification with the Calex-31 marker located on the W chromosome (65). Details of
305 our PCR conditions are found elsewhere (38).

306

307 *Quantifying mating system*

308 We evaluated mating system of the population using a dataset that only included individuals
309 for which we (i) were confident of the identity of their mates, and (ii) had observed them in at
310 least two reproductive attempts that were either within the same season or in different
311 seasons. Sex differences in the per capita number of annual mates were evaluated using a
312 non-parametric Mann-Whitney-Wilcoxon test.

313

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

315 Our structured population model considered sex-specific survival across three key stage
316 classes in avian life history: chicks, juveniles, and adults (Fig. 6). The chick stage was
317 defined as the 25-day period between hatching and fledging during which offspring are
318 dependent upon parental care (66). The juvenile stage was defined as the one-year transition
319 period spanning from fledging to recruitment into the adult population. The adult stage
320 represented a stasis stage in which individuals were annually retained in the population.

321 We used mark-recapture models to account for sex, stage, and temporal variation in
322 encounter (p) and apparent survival (ϕ) probabilities as they allow for imperfect detection of
323 marked individuals during surveys and the inclusion of individuals with unknown fates (29).
324 We use the term “apparent survival” as true mortality cannot be disentangled from permanent
325 emigration in this framework (29). Furthermore, only a few nearby populations are regularly
326 monitored and we have limited evidence that marked individuals disperse. See *SI Methods*
327 for further details of our survival analysis.

328

329 *Matrix model structure*

330 We built a two-sex pre-breeding Lefkovich matrix model for the population that
 331 incorporated all three stages of plover life history into two annual transitions denoting first-
 332 years and adults (Fig. 6). Transitions of projection matrices are required to have equal
 333 temporal durations (67), and thus the chick stage (25 days) was combined with the juvenile
 334 stage (~11 months) as lower-level matrix elements to describe the transition of premature
 335 individuals into adulthood (Fig. 6). The projection of the matrix for one annual time step (t) is
 336 given by:

$$337 \quad \mathbf{n}_t = \mathbf{M}\mathbf{n}_{t-1} \quad (1)$$

338 where \mathbf{n} is a 4×1 vector of the population distributed across the two life stages and two
 339 sexes:

$$340 \quad \mathbf{n} = \begin{bmatrix} \text{♀ 1st year} \\ \text{♀ Adult} \\ \text{♂ 1st year} \\ \text{♂ Adult} \end{bmatrix} \quad (2)$$

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

$$342 \quad \mathbf{M} = \begin{bmatrix} 0 & R_{\text{♀}}(1 - \rho) & 0 & R_{\text{♂}}(1 - \rho) \\ \phi_{\text{♀C}} \phi_{\text{♀J}} & \phi_{\text{♀A}} & 0 & 0 \\ 0 & R_{\text{♀}}\rho & 0 & R_{\text{♂}}\rho \\ 0 & 0 & \phi_{\text{♂C}} \phi_{\text{♂J}} & \phi_{\text{♂A}} \end{bmatrix} \quad (3)$$

343 where transition probabilities (ϕ) between life stages are the survival of chicks (C), juveniles
 344 (J), and adults (A) for females (♀) and males (♂). The hatching sex ratio (ρ) describes the
 345 probability of hatchlings being either male (i.e. ρ) or female (i.e. $1 - \rho$). Per-capita
 346 reproduction of females ($R_{\text{♀}}$) and males ($R_{\text{♂}}$) is expressed through sex-specific mating
 347 functions used to link the sexes and produce progeny for the following time step of the model

348 given the relative frequencies of each sex (67). Here, we use the harmonic mean mating
349 function which accounts for sex-specific frequency dependence (68):

$$350 \quad R_{\text{♀}} = \frac{kn_{\text{♂}}}{n_{\text{♂}} + n_{\text{♀}}h^{-1}} \quad R_{\text{♂}} = \frac{kn_{\text{♀}}}{n_{\text{♂}} + n_{\text{♀}}h^{-1}} \quad (4)$$

351 where k is the modal clutch size (3 in the case of snowy plovers), h is an index of the mating
352 system ($h > 1$ signifies polygyny, $h = 1$ monogamy, and $h < 1$ polyandry), and $n_{\text{♀}}$ and $n_{\text{♂}}$ are
353 the densities of females and males, respectively, in each time step of the model. In
354 accordance with the predominantly polyandrous mating system, h was defined as the inverse
355 of the average annual number of mates per female:

$$356 \quad h = \frac{1}{\text{mates}/\text{♀}} \quad (5)$$

357 which we estimated from our behavioral observations of mating system (see above). To
358 account for potential sex-biases arising prior to the chick stage (i.e. sex-allocation), we
359 evaluated if the hatching sex ratio deviated significantly from parity (see *SI Methods* for
360 details).

361

362 *Estimation of the adult sex ratio*

363 We estimated ASR from the stable stage distribution (\mathbf{w}) of the two-sex matrix model:

$$364 \quad \text{ASR} = \frac{w_{\text{♂A}}}{w_{\text{♂A}} + w_{\text{♀A}}} \quad (6)$$

365 where $w_{\text{♂A}}$ and $w_{\text{♀A}}$ give the proportion of the population composed of adult males and
366 females, respectively, at equilibrium. To evaluate uncertainty in our estimate of ASR due to
367 sampling and process variation in our survival parameters, we implemented a bootstrapping
368 procedure that resampled our mark-recapture data (see *SI Methods* for details).

369

370 *Life table response experiment of ASR contributions*

371 Perturbation analyses provide important information about the relative effect that each
372 component of a matrix model has on the population-level response, in our case ASR. To
373 assess how influential a sex bias in parameters associated with each of the three life stages
374 was on ASR dynamics, we employed a life-table response experiment (LTRE). A LTRE
375 decomposes the difference in response between two or more "treatments" by weighting the
376 difference in parameter values by the parameter's contribution to the response (i.e. its
377 sensitivity), and summing over all parameters (67). Here, we compared the observed scenario
378 (\mathbf{M}), to a hypothetical scenario (\mathbf{M}_0) whereby all female survival rates were set equal to the
379 male rates and the hatching sex ratio was unbiased (i.e. $\rho = 0.5$). Thus, our LTRE identifies
380 the drivers of ASR bias by decomposing the difference between the ASR predicted by our
381 model and an unbiased ASR (25).

382 The contributions (C) of lower-level demographic parameters (θ) were calculated
383 following Veran and Beissinger (25):

$$384 \quad C(\theta) = (\theta_{\sigma} - \theta_{\text{f}}) \times \frac{\partial \text{ASR}}{\partial \theta} \quad (7)$$

385 where $\frac{\partial \text{ASR}}{\partial \theta}$ is the sensitivity of ASR to perturbations in the demographic rate θ in matrix \mathbf{M}' ,
386 which is a reference matrix "midway" between the two scenarios (67):

$$387 \quad \mathbf{M}' = \frac{\mathbf{M} + \mathbf{M}_0}{2} \quad (8)$$

388 The two-sex mating function makes our model non-linear in the sense that the
389 projection matrix, and specifically the fertility elements (Eq. 4), depend on sex-specific
390 population structure. Perturbation analyses must therefore accommodate the indirect effects
391 of parameter perturbations on population growth via their effects on population structure. To
392 estimate the sensitivities of the vital rate parameters to ASR we employed numerical methods
393 that independently perturbed each parameter of the matrix, simulated the model through 1000
394 time steps, and calculated ASR at equilibrium. This produced parameter-specific splines from

395 which $\frac{\partial \text{ASR}}{\partial \theta}$ could be derived. Our approach appropriately accounts for the non-linear
396 feedbacks between vital rates and population structure, though it does not isolate the
397 contribution of this feedback (26, 69).

398

399 *Population growth consequences to ASR bias and a polygamous mating system*

400 Biased ASR and polygamous mating systems can restrict the reproductive potential of a
401 population due to a scarcity of the limiting sex (70). Thus, population viability can be
402 indirectly affected by ASR and mating system via the sex-specific effects that vital rates have
403 on population growth under a biased ASR or a polygamous mating system, or both (71). To
404 investigate the relative influence that a biased ASR or a polygamous mating system has on
405 population growth, we conducted a sensitivity analysis of all sex-specific parameters using
406 four scenarios of the two-sex model: (i) polyandrous and male-biased ASR (i.e. the observed
407 scenario), (ii) polyandrous and unbiased ASR, (iii) monogamous and male-biased ASR, and
408 (iv) monogamous and unbiased ASR. In polyandrous scenarios, h was set to the value from
409 field observations, whereas in monogamous scenarios, $h = 1$. In scenarios of unbiased ASR,
410 male survival rates were assigned to both sexes (i.e. \mathbf{M}_0 above), whereas the original sex-
411 specific structure was retained in male-biased scenarios.

412 Under each scenario, sensitivities of λ to perturbations in each parameter (θ) were
413 estimated numerically as described above. Sensitivities were rescaled into elasticities (e),
414 which describe the proportional response of λ to a proportional perturbation of a demographic
415 parameter (67). This way, the sensitivity of parameters become directly comparable.

416 Elasticities were calculated as:

417
$$e(\theta) = \frac{\theta}{\lambda} \times \frac{\partial \lambda}{\partial \theta} \quad (9)$$

418 where $\frac{\partial \lambda}{\partial \theta}$ is the sensitivity of λ to perturbations in parameter θ .

419

420 *Comparison of two-sex versus one-sex models*

421 Two-sex population models are rarely used in conservation biology because of the detailed
422 data required to correctly parameterize them (70). As such, vital rates are typically estimated
423 for only one sex or generalized across both sexes. However, in polygamous species,
424 reproductive success varies according to the relative frequencies of mates (71), which is
425 dictated by ASR and sex-specific survival. Therefore, ignoring sex-specific vital rates in
426 polygamous species could misinform conservationists and wildlife management of
427 population viability.

428 To explore how population growth varies under a two-sex model and a conventional
429 one-sex model, we compared deterministic population growth of the two-sex model (**M**) to
430 that of a one-sex model in which rates were averaged over both sexes (**A**):

431
$$\mathbf{A} = \begin{bmatrix} 0 & F \\ \phi_C \phi_J & \phi_A \end{bmatrix} \quad (10)$$

432 where F is the average annual per capita fecundity of females (expressed as hatchlings), and
433 ϕ is the sex-averaged survival of chicks (C), juveniles (J), and adults (A). Deterministic
434 growth (λ) was calculated as the dominant eigenvalue of **A** and as the asymptotic value of
435 $\sum w_{t-1} / \sum w_t$ for **M**. To acknowledge uncertainty, we utilized the bootstrapped survival
436 analysis described above by estimating the λ of each iteration under the structure of **A** or **M**.
437 We contrasted the central tendency and spread of these distributions to one another and to the
438 arithmetic average λ of the actual population trend over the seven-year study period.

439 All of our modelling and statistical analyses were conducted using R version “Bug in
440 Your Hair” (72) with significance testing evaluated at $\alpha = 0.05$. We provide all computer
441 code and documentation as a PDF file written in Rmarkdown together with all the raw
442 datasets needed to reproduce our modeling and analyses (*SI Dataset*).

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634 **Figure legends**

635 *Figure 1.* Sex bias in mating system illustrated as the per capita annual number of mates
636 acquired by male and female snowy plovers (Mann-Whitney-Wilcoxon test: $W = 3264$, $P <$
637 0.001 , $N = 456$ families).

638 *Figure 2.* (a) Bootstrap distributions of stage-specific sex biases in apparent survival
639 estimates, with internal lines indicating median and interquartile ranges, and shades of grey
640 corresponding to first-year (light grey) or adult (dark grey) parameters shown in Fig. 6; (b)
641 Bootstrap distribution of the derived ASR, with the horizontal bar above the distribution
642 indicating the 95% confidence interval of the ASR estimate based on 1000 iterations (mean
643 ASR = 0.632 [95% CI: 0.460 – 0.785]); (c) relative contributions of model components to
644 ASR in our life table response experiment (LTRE) which compared the empirically-derived
645 sex-specific model to a theoretical model in which survivorships did not differ between the
646 sexes. Our measure of ASR was expressed as the proportion of the adult population that is
647 male, thus changes in female-biased parameters have a negative effect on ASR and thus their
648 LTRE statistics are negative.

649 *Figure 3.* Sex-specific sensitivity analysis of population growth (λ) under four scenarios of
650 ASR and mating system. Notation: h = mating system index, ρ = hatching sex ratio, ϕ =
651 apparent survival.

652 *Figure 4.* Distributions of deterministic population growth (λ) under a two-sex frequency-
653 dependent matrix model (black) and a conventional one-sex matrix model (red) compared to
654 the observed average annual population growth ($\bar{\lambda}$) over the seven-year study period (blue
655 vertical line). Horizontal bars above each distribution represent the 95% confidence intervals
656 of the bootstrap simulation for each model.

657 *Figure 5.* Schematic representation of the sex- and stage-specific demographic feedbacks
658 between ASR, mating system, and population viability. In our study system, ASR bias is
659 driven by sex-specific survival of early life-history stages (i), and likely facilitates a
660 polygamous mating system (ii). Both, ASR bias and polygamy, contribute to sex-specific
661 elasticities of population growth (iii), with ASR having the strongest effect as illustrated by
662 arrow width.

663 *Figure 6.* Snowy plover life cycle flow diagram illustrating sex-specific survival (ϕ) among
664 three life stages (chick = C , juvenile = J , and adult = A) and the link between the sexes via the
665 frequency-dependent mating function (R , see methods). The hatching sex ratio (ρ , proportion
666 of male hatchlings) serves as a proxy for the primary sex ratio and allocates progeny to the
667 male or female chick stage. Lower-level parameters (i.e. chick and juvenile survival)
668 constitute the transition of first-year individuals illustrated in light grey.

669 **Tables**

670 *Table 1.* Summary statistics of sex- and stage-specific estimates of the snowy plover

671 population. Notation includes: N = number of individual encounter histories used for mark-

672 recapture modelling, ϕ = apparent survival, and p = encounter probability. Estimates are

673 shown as the median and 95% confidence interval of each bootstrapped distribution.

Sex	Stage	N	ϕ	p
Female	Chick	416	0.48 (0.41–0.55)	0.56 (0.53–0.58)
	Juvenile	234	0.15 (0.11–0.19)	0.48 (0.34–0.62)
	Adult	221	0.68 (0.62–0.74)	0.52 (0.40–0.65)
Male	Chick	372	0.53 (0.47–0.60)	0.55 (0.53–0.58)
	Juvenile	243	0.22 (0.18–0.27)	0.66 (0.48–0.74)
	Adult	212	0.69 (0.63–0.74)	0.66 (0.54–0.77)











