

1 **Insights into the phenology of migration and survival of a long** 2 **migrant land bird**

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7 **Lay summary:**

8 For polygamous long-migrant birds, the choice of migration strategy depends on social
9 pressure and experience and influences the chance of survival. If you are a male, you'd better
10 leave early in the spring to secure the best site to show off. In fall, juveniles have a hard time
11 surviving to migration as they leave before the adults and lack experience on where to go and
12 where to stop to rest.

13

14 **Short title:**

15 Differential migration and survival in a polygynous bird

16

17 **Abstract**

18 The process of migration stems from an adaptation of climatic seasonality and animals have
19 developed various strategies to complete the journey between a wintering and breeding
20 ground. Understanding the migratory behavior and determining when and where mortality
21 occurs during the annual cycle is fundamental to understand population dynamics and
22 implement appropriate conservation measures. Based on a big data set and advanced statistical
23 methods, we inspected the phenology of migration of a polygynous land bird, the Macqueen's
24 bustard, *Chlamydotis macqueenii*. We explored its migration strategies between sex, age,

25 season and geographical origin. We show that departure for migration depended on age in the
26 fall with juveniles being the first to leave and on age and sex in the spring with juveniles
27 departing later and males induced to arrive early in spring to secure high-quality territories.
28 Birds breeding at higher latitudes were the first to leave in the fall and more likely to perform
29 longer stopovers. Bustards exhibited different strategies for spring and fall migrations: spring
30 migration was significantly longer than fall migration with more but shorter stopovers.
31 Survival was lower for juveniles experiencing their first migration and for all birds during fall
32 migration and on their wintering ground. Experience linked to social hierarchical pressures
33 and environmental conditions might be the key drivers of migration strategies and survival in
34 long-distance polygynous migrants. *Key-words:* E-SURGE, generalized linear mixed models,
35 Macqueen's bustard, movement ecology, PELT-TREE method, satellite tracking, stopover
36 ecology

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55 **Introduction**

56 The annual cycle of migratory birds stems from an adaptation to climatic seasonality and is
57 typically composed by three major events of variable timing, duration and sequencing:
58 breeding, molt and the return journey between wintering and breeding grounds, i.e., the
59 migration (Somveille et al. 2015). Different sets of rules determining the process of migration
60 (Alerstam et al. 2006, Duriez et al. 2009), called migration strategy, have been highlighted
61 and three main hypotheses were proposed (for a review see Ketterson and Nolan 1983) to
62 explain the differences in migration strategy between individual classes (e.g., age, sex,
63 reproductive status). The ‘Arrival Time’ hypothesis invokes that the reproductive fitness of
64 one sex is partly influenced by the acquisition of a territory in early spring, and, as high
65 quality territories are limited, the early arrival of individuals is an advantage to secure a
66 territory acquisition (Kokko 1999). The ‘dominance’ hypothesis (or ‘competitive release’
67 hypothesis) posits that food scarcity drives subordinate individuals to migrate further to limit
68 food competition (Rogers et al. 1989). The ‘body size’ hypothesis (or ‘thermal tolerance’
69 hypothesis) suggests that thermal efficiency dictates migratory tendency, with smaller
70 individuals being more likely to migrate further. These hypotheses stem from the study of bird
71 migration which has been largely dominated by studies on bird species benefitting from
72 intensive ringing programs (Bairlein 2001). However, for species with no other movement
73 monitoring options (limited field access: ocean and desert crossing species), the development
74 of remote monitoring tools such as satellite tracking brought a much needed salvation and has
75 opened new perspectives (Arizaga et al. 2014). This is the case of the Macqueen’s bustard,

76 *Chlamydotis macqueenii*, a partial migrant bird species (Goriup 1997), classified as
77 Vulnerable (BirdLife International 2014). From the early 90's, an intensive monitoring of
78 migrant individuals using satellite tracking was launched by the National Avian Research
79 Centre (Abu Dhabi, United Arab Emirates) and laid the foundations for the early study of the
80 species. Migrant populations were shown to breed from west Kazakhstan to China and winter
81 in the range of resident populations in South Central Asia and the Middle-East (Combreau et
82 al. 2001, Combreau et al. 2011b). On their breeding ground, migrant Macqueen's bustard
83 exhibit a polygynous mating system where males compete for display territories to which they
84 remain faithful during the breeding season (Riou and Combreau 2014). This monitoring effort
85 has been reinforced to this day, with more than 400 birds equipped with satellite transmitters
86 in central Asia. This unprecedented data set offers the opportunity to better highlight the
87 migration strategies among sex and age-classes in a rarely-studied system, i.e. a polygynous
88 land bird (but see Kessler et al. 2013, Garcia De La Morena 2015), in the light of the three
89 main hypotheses: arrival-time, dominance and body-size. Site fidelity and intra-sexual
90 competition are likely to be the main drivers for male migration timing and distance
91 (Schroeder and Robb 2003; Boyle 2008), suggesting the 'arrival time' hypothesis. Females
92 and juveniles, whose fitness depend less on securing a breeding site and whose survival might
93 be influenced by their smaller size (Martín et al. 2007), might have an obligate strategy due to
94 social hierarchical pressures of male dominance, suggesting the 'dominance' and 'body size'
95 hypotheses.

96 The chosen migration strategy will likely influence the annual survival of individuals, which
97 is the product of survival rates at the four periods of their annual cycle: breeding, fall
98 migration, wintering, and spring migration. Tracking data sets can be converted in capture-
99 recapture histories allowing advanced survival analyses (Duriez et al. 2009, Hardouin et al.
100 2014) taking into account such temporal breakdown. However, the extent of differential

101 migratory patterns and their relation to differential survival rates has rarely been explored
102 (Hutto 2000, Sillett and Holmes 2002, Lok 2011). Yet understanding the migratory behavior
103 and determining when and where mortality occurs during the annual cycle is fundamental to
104 understand population dynamics and implement appropriate conservation measures (Leyrer et
105 al. 2013, Klaassen et al. 2014).

106 Based on an eight-year satellite-tracking data set, we inspected the full picture of migration
107 and survival of the Macqueen's Bustard. Using recent advances in movement analyses, we
108 were first able to determine individual movement key timings. Then, using robust statistical
109 analyses and multistate capture-recapture modelling, we highlighted the influence of
110 individual traits (age and sex) and spatio-temporal factors (geographic origin and season) on
111 the migration strategy and survival of a polygynous long-migrant land bird species.

112

113 **Materials and methods**

114 DATA

115 A total of 414 wild migrant Macqueen's Bustards were captured during the breeding season
116 (end of March to end of June) between 2010 and 2013 in Uzbekistan (Navoi district, 39°N,
117 65°E) and between 2005 and 2013 in Kazakhstan (Central Kazakhstan: Shimkent area, 43°N,
118 67°E; East Kazakhstan: 46°N, 78°E; West Kazakhstan: Mangystau area, 42.75°N, 52°E;
119 Fig.1). Adult birds were trapped using loop cord snares. Males were trapped on their display
120 sites baited by a dummy female and females were trapped on their nest replacing live eggs
121 with wooden eggs (see method in Hardouin et al. 2014). Juveniles were trapped by hand
122 before fledging (see method in Combreau et al. 2002 and Hardouin et al. 2011). All birds
123 were weighted and ringed. Males weighted on average 2 kg \pm 1.7, females 1.3 kg \pm 1.3 and
124 juveniles 0.7 kg \pm 1.3. Birds were equipped GPS-PTT (platform terminal transmitter) solar-
125 powered satellite transmitters (Microwave Telemetry Inc, Columbia, MD, USA) of 22 to 45g

126 depending on bird weight (representing on average $3\% \pm 1$ of individuals weight (Kenward
127 2001). Transmitters were operated through the ARGOS system in Toulouse (CLS, France)
128 and programmed to record a GPS position every two hours and transmit once every two days.

129 Satellite tracking data from birds that did not migrate before the transmitter stopped
130 transmitting or with missing data (See Madon and Hingrat 2014) were not included in the
131 analysis. Hence a total of 158 wild adults and 41 wild juveniles were included in the analyses
132 (Table 1). Data were first filtered by precision: GPS and ARGOS locations of CLS classes 2
133 and 3 were selected. The last daily location was then retained for each individual to allow for
134 regular time spacing (i.e., an approximate 24h gap) between successive locations. Location
135 coordinates were then projected using the Asia north equidistant conic projection in ArcGIS
136 10.1 (ESRI 2012) to calculate distances between successive locations (in km), i.e., daily
137 distances, and build a daily distance time series for each bird.

138 The PELT-TREE method was used to break down the daily distance time series of each bird.
139 This recent framework combines a change point algorithm to find the changes in variance, the
140 so called change points, in the daily distance series for each bird and a classification tree to
141 classify the obtained segments. Here we considered three movement behavioral classes:
142 staging, migratory and non-migratory movements. Based on the training data used by the
143 classification tree, the mathematical rules to classify the segments into the three movement
144 classes were defined as follow: segments with mean < 17.642 km were classified as “staging”,
145 segments with mean > 17.642 km and < 100.284 km as “non-migratory” and segments with
146 mean > 100.284 km as “migratory” (See Madon and Hingrat 2014 for details).

147 Based on the segmentation, we defined, for each bird, key timings of migration as follow:
148 departure date, i.e., start of migration, as the first day of migratory movement (or non-
149 migratory movement if immediately followed by a migratory movement) following a staging
150 period, in the opposite direction compared to the preceding migratory movement; arrival date,

151 i.e., end of migration, as the first day of staging after a migratory movement (or non-
152 migratory movement if immediately following a migratory movement), given that the next
153 migratory movement is in the opposite direction; and stopover as any segment of staging
154 behavior between the departure and arrival dates.

155 STATISTICAL MODELLING

156 Migration strategy

157 We explored the fall and spring migration strategy of the Macqueen's bustard in terms of six
158 response variables: 1- fall and spring migration departure dates, 2- migration distances, i.e.,
159 sum of the daily distances (in km) between the migration departure and arrival dates, 3-
160 migration duration, i.e., number of days between the departure and arrival dates, 4- number of
161 stopovers, i.e., number of staging segments between the migration departure and arrival dates.

162 The variable migration duration was further broken down into two variables in the analyses:
163 5- duration of migratory movement, i.e., total length in days of migratory and non-migratory
164 movement segments between the migration departure and arrival dates, 6- duration of
165 stopovers (Alerstam et al. 2006), i.e., total length in days of staging segments between the
166 migration departure and arrival dates.

167 We conducted two sets of linear (or generalized linear) mixed model (See (Bolker et al. 2008)
168 for a review) analyses on each response variable with individual and year as random factors
169 (Table 2) using four data sets: dataset 1- all individuals, dataset 2- sexed individuals, i.e.,
170 adults only, dataset 3- all individuals presenting at least 1 stopover, and dataset 4- sexed
171 individuals (adults only) presenting at least one stopover (Table 2).

172 With datasets 1 and 3, we used explanatory fixed factors "Age" (available for all individuals),
173 "Place" (corresponding to the breeding place for the adults and birth place for the juveniles),

174 “Season” (except for response variables fall and spring departure dates) to model the response
175 variables. Because Macqueen’s bustards may start breeding from one year old (Saint Jalme
176 and van Heezik 1996), only the first year of monitoring of juveniles was included in the
177 analyses to account for them as non-breeders. So factor “Age” refers to the reproductive status
178 of individuals. With datasets 2 and 4, we used factor “Sex”, along with factors “Place” and
179 “Season” (except for response variables fall and spring departure dates)(Table 2). Only the
180 interaction Sex*Season was considered, due to small sample sizes in levels of other
181 interactions and factors were considered significant when $p < 0.05$ or $|t| > 2$ (p being
182 unavailable in package ‘lmm’) (Baayen et al. 2008, Bolker et al. 2008). All analyses were
183 conducted in R (R Core Team 2014).

184 Survival

185 We used multistate capture-recapture models to estimate survival by describing the transition
186 between the states “alive” and “dead” (Lebreton et al. 1992). These models are defined in
187 terms of three processes (initial state, event and state processes) allowing the simultaneous
188 estimation of: the encounter probability (the probability that an individual is encountered in
189 site A and time t given that it is alive in site A and time t), the apparent survival (the
190 probability that an individual alive at site A and time t is still alive at time $t+1$) and transition
191 between sites, i.e., movements (the probability that an individual moves from site S at time t
192 to site Z at time $t+1$, given that it survived from time t to $t+1$; hence denoted “transition
193 matrix” or “movement probabilities” conditional on survival) (Lebreton and Pradel 2002).
194 Here we dealt with a mixture of live recaptures and dead recoveries (e.g., Duriez et al. 2009,
195 Le Gouar et al. 2011), reported when the transmitters were retrieved in the field. Hence
196 survival was modelled as a transition from the state “alive” to the state “newly dead”.
197 Encounter histories were split in four yearly occasions, each corresponding to one “movement
198 phase” with two fates, i.e., alive recaptures and dead recoveries. The four occasions

199 corresponded to the four seasonal phases of movement of a migratory animal determined by
200 the above key timings: on the breeding ground (period between the spring arrival date and fall
201 departure date), in fall migration (period between the fall departure date and the fall arrival
202 date), on the wintering ground (period between the fall arrival date and the spring departure
203 date) and in spring migration (period between the spring departure date and the spring arrival
204 date). We thus accounted for nine states: four alive states (1-4) and four newly dead states (5-
205 8) in the seasonal phases of movement and one unobserved dead state (9). Given that
206 individuals were equipped with GPS-PTT transmitter, the successive states occupied by an
207 individual can be observed directly and the encounter probability in the four alive states is
208 consequently equal to 1. In the transition matrix, movement and survival are considered as
209 two successive steps. Here, if a bird was found dead during a movement phase, it had
210 necessarily moved from the previous movement phase before dying. Therefore, movements
211 were estimated before survival in the transition matrix, i.e., the survival probability depends
212 on the site of arrival, e.g., in Duriez et al. (2009).

213 Difficulties in attributing precisely the “movement phase” arose when a bird died after
214 starting migration, as it was not possible to determine whether it was still migrating or had
215 arrived on the wintering/breeding site before dying. Thus, we considered that an individual
216 was newly dead on the breeding ground: 1- when transmitters were retrieved on the breeding
217 ground or 2- when the individual was lost after the 1st of July (i.e., the signal was suddenly
218 lost or it was reported non-moving with the same position before loss of the signal but the
219 transmitter was not retrieved in the field). Similarly we considered that an individual was
220 newly dead on the wintering ground: 1- when PTT transmitters were retrieved on the
221 wintering ground or 2- when the individual was lost after the 1st of January.

222 Each step of a multistate model, i.e., initial state, event process and state process, can be
223 parametrized with environmental covariates or individual factors. Here we focused on

224 individual factors “Experience”, “Sex*Age” (males, females and juveniles), “Place” (Central
225 Kazakhstan, East Kazakhstan, West Kazakhstan and Uzbekistan) and time factors. Factor
226 “Experience” was related to age at capture and consisted in two groups: “first timers” and
227 “experienced birds”. The group “first timers” included the first year of monitoring of birds
228 equipped as juveniles on the breeding ground, hence first timers in terms of fall migration,
229 wintering and following spring migration. The group of “experienced birds” corresponds to
230 birds equipped as adults and to juveniles after a first year of monitoring (from their second
231 spring after their first fall migration). Time factor included “4 periods”: time divided in the
232 four movement phases. We also tested time divided into “2 periods” with time periods pulled
233 into 2 main periods “spring migration and breeding ground” and “fall migration and wintering
234 ground”, to account for the difficulties in attributing death to these successive periods.
235 Model selection was performed using program E-SURGE v1.8.9 (Choquet et al. 2009) with
236 an Akaike Information Criterion corrected for sample size calculated as follows: $QAICc =$
237 $(\text{deviance}/\hat{c}) + 2K + (2K(K+1))/(n-K-1)$, where K and n are the number of parameters and the
238 effective sample size respectively. The preferred model was the one with the smaller QAICc
239 value and two models were deemed to be equivalent when they differed by less than two. In
240 addition to the QAICc, we paid attention also to the biological plausibility and quality
241 (confidence intervals) of the estimates when selecting models. We used a generalized logit-
242 link function. Description of the model structure and matrix patterns used in the models
243 developed in E-SURGE is given in Appendix S1.

244

245 **Results**

246 Among Macqueen’s bustards equipped in Central Asia with GPS-PTT transmitter between
247 2005 and 2013, we obtained accurate data for our analysis from 201 birds (Table 1). Birds

248 were followed on average over two migrations ($se = 0.07$), i.e one year. Two females from
249 West Kazakhstan were followed during 10 and 14 migrations, i.e., five and seven years.

250

251 MIGRATION JOURNEY CHARACTERISTICS

252

253 Sex-based differential migration

254 Among adults, there was no difference in the timing of departure between males and females
255 in the fall but in the spring, males departed for migration 8 ($se = 2.98$, $lqmm\ p = 0.01$) days
256 earlier (Table 1). Migration distance was similar and both sexes were as likely to perform
257 stopovers. Migration duration, which included stopovers and movements, was significantly
258 shorter for males (glmm (logit scale) $\beta = -0.24$ ($se = 0.1$), $p = 0.02$) (Table 3). There was no
259 difference in terms of duration of movement but the time spent on stopovers by males was
260 significantly shorter (glmm (log scale) $\beta = -0.3$ ($se = 0.12$), $p = 0.01$).

261

262 Age-based differential migration

263 Juveniles departed for migration significantly earlier than adults in fall (6 days, $se = 2.79$,
264 $lqmm\ p = 0.03$) and later in spring (27 days, $se = 3.37$, $lqmm\ p < 0.05$) (Table 1). On average,
265 juveniles travelled as long as adults for both migrations in terms of distance and migration
266 duration and were as likely to perform stopovers. However, time spent on stopover was
267 significantly longer (glmm (log scale) $\beta = 0.36$ ($se = 0.17$), $p = 0.03$) (Table 3).

268

269 Geographical origin-based differential migration

270 Birds departing from East Kazakhstan, migrated more than twice as far as birds from lower
271 latitudes (i.e., on average 2958 ($se = 35.84$) km for East Kazakhstan against 1228 ($se = 84.65$)
272 km for Uzbekistan) (Fig. 1, Table 3). As a consequence the median dates of departure

273 followed a latitudinal gradient for both the fall and spring migrations: birds from breeding
274 grounds at lower latitudes left later for migration. For the fall migration, the median date
275 departure of birds from higher latitudes departed significantly earlier. Compared to birds from
276 Central Kazakhstan, birds from East Kazakhstan departed 37 ($se = 3.44.21$, $lqmm\ p < 0.05$)
277 days earlier and birds from West Kazakhstan 9 ($se = 2.43.55$, $lqmm\ p < 0.05$) days earlier.
278 Birds from Central Kazakhstan departed slightly earlier (4 days) than birds from Uzbekistan
279 (Table 1). In the spring, the departure dates did not follow the latitudinal gradient. Adult birds
280 from Central Kazakhstan were the last ones to depart for migration on 8 March (67th day, $se =$
281 1.43): West Kazakhstan birds departed 6 days earlier ($se = 2$, $lqmm\ p < 0.05$), Uzbekistan
282 birds 7 days earlier ($se = 2.9$, $lqmm\ p = 0.02$), and East Kazakhstan birds 14 days earlier ($se =$
283 4.25, $lqmm\ p < 0.05$).

284 Birds with longer migratory journeys were more likely to perform stop-overs (Table 3). For
285 example, birds from East Kazakhstan which travelled on average 1328 km ($se = 92.05$, $lmm\ t$
286 = 14.43) more than birds from Central Kazakhstan, were 10 times more likely to perform
287 stopovers (glmm (logit scale) $\beta = 2.3$ ($se = 0.53$), $p < 0.05$), 90% of their migration legs
288 displayed at least one stopover and they spent significantly longer periods at stopover sites (on
289 average 28.68 ($se = 2.44$) days, glmm (log scale) $\beta = 0.63$ ($se = 0.15$), $p < 0.05$). On the other
290 hand, birds from Uzbekistan were less likely to stop for refueling (glmm (logit scale) $\beta = -$
291 1.66 ($se = 0.75$), $p = 0.03$) and only 28% of their migration legs included a stopover (Table 3).

292

293 Season-based differential migration

294 Macqueen's bustards appeared to exhibit different behaviors in spring and fall migrations.
295 Results indicated that spring migration was significantly longer than fall migration
296 (respectively 24.52 ($se = 1.03$) days against 20.66 ($se = 1.24$) days, glmm (log scale) $\beta = 0.24$
297 ($se = 0.023$), $p < 0.05$) (Table 3). However, spring migration was significantly shorter in terms

298 of movement duration for males (interaction sex*season, glmm (log scale) $\beta = -0.17$ ($se =$
299 0.07), $p = 0.015$). In terms of refueling strategy, birds were more likely to stop during the
300 spring migration (glmm (logit scale) $\beta = 1.8$ ($se = 0.26$), $p < 0.05$) and performed more
301 stopovers in the spring (glmm (log scale) $\beta = 0.66$ ($se = 0.099$), $p < 0.05$). However, time
302 spent on stopovers was longer during fall migration (glmm (log scale) $\beta = -0.07$ ($se = 0.04$), p
303 $= 0.058$).

304 SURVIVAL

306 The best fitting model for survival was the model including the interaction of “experience”
307 and the factor “4 periods” where time was divided in the four movement phases (Table 4).
308 First-timers, i.e. juveniles during their first year, had a lower probability to survive at each
309 time period. These differences in survival were especially apparent during their first fall
310 migration (0.62 $se = 0.07$ compared to experienced birds: 0.87 $se = 0.019$) and wintering
311 period (0.65 $se = 0.086$ compared to experienced birds: 0.89 $se = 0.019$). There were no sex-
312 biased mortality patterns (Table 5). Finally, the different migration strategies in fall and spring
313 appeared to impact survival with significantly higher probabilities of surviving the spring
314 migration for both first-timers and experienced birds (respectively 0.9 $se = 0.067$ and 0.97 se
315 $= 0.01$). Survival probabilities were also higher on the breeding ground for experienced birds
316 than on wintering grounds (respectively 0.96 $se = 0.009$ and 0.88 $se = 0.01$).

317

318 Discussion

319 Timing of migration and survival

320 The co-existence of different migratory strategies between age and sex groups has been
321 largely discussed and linked to constraints and selective forces in relation to reproductive

322 success, survival and competition. In polygynous species, male competition for display
323 territories during the breeding season is likely to be the main driver for male migration timing
324 (Schroeder and Robb 2003). Our results support the ‘arrival time’ hypothesis: in order to
325 optimize their fitness, Macqueen’s bustard males are induced to arrive early in spring to
326 acquire high-quality territories. Such fitness benefit probably out-weighs the cost of
327 migrating out the optimal temporal window, e.g., challenging conditions encountered during
328 late winter-early spring migration (Kokko 1999). Females, on the other hand, can arrive later
329 in spring without reducing their fitness (Kokko et al. 2006). This intersexual out of sync
330 migration timing, e.g., protandry in the spring (Schmaljohann et al. 2015), also warrants
331 females lesser intersexual competition for resources at stopover sites. Interestingly, these
332 differential migration timings do not lead to differences in survival between sexes although
333 for most bird species survival is thought to be higher for males (Sillert and Holmes 2002).

334 Different factors, such as experience and body condition, are likely to influence migration
335 strategy and survival probability. The body size hypothesis assumes that smaller individuals
336 are less likely to withstand cold temperatures and to experience greater risks associated with
337 fasting in winter (Boyle 2008). This is corroborated by our results showing that, in fall,
338 juveniles leave breeding grounds earlier than adults. Juveniles might be constrained to leave
339 the breeding ground when food and environmental conditions deteriorate because of
340 competition, reduced foraging ability and site-familiarity (Bai and Schmidt 2012). They may
341 be physiologically less capable of undertaking full migration, e.g., different molt process
342 reducing juveniles flying abilities (Newton 2011) or of selecting optimal flight altitude
343 (Mateos-Rodríguez and Liechti 2012). In the Macqueen’s bustard, juveniles which depart
344 earlier do not benefit from social cues to initiate their first fall migration and they cannot use
345 social learning by following adults to locate suitable stopovers and wintering sites and
346 minimize predation risk (Nocera and Ratcliffe 2010, Cresswell 2014). As a consequence,

347 juveniles spent more time on stopovers and had lower survival probabilities during migration
348 as well as on wintering grounds. Greater first-year stochasticity in route-finding, suggesting a
349 bet-hedging strategy (Reilly and Reilly 2009), should nonetheless provide populations of
350 Macqueen's bustards with greater resilience abilities to large-scale changes (Cresswell 2014).
351 In the following spring, juveniles, which are probably less driven by a breeding pressure,
352 departed later than adults. Little is known about juvenile reproduction timing in Macqueen's
353 bustards. Studies on North African Houbara bustards, *Chlamydotis undulata undulata*,
354 showed that females initiated reproduction at 1.6 (standard deviation = 0.5) and males at 2.1
355 (standard deviation = 0.8) years-old (Hardouin et al. 2014). If the pattern of age at first
356 reproduction is similar in the Macqueen's bustard, it is likely that juvenile migration
357 phenology will be highly variable for the first 2 years (Combreau et al. 2011) and likely more
358 related to natal dispersal (Hardouin et al. 2012). By differing their departure from wintering
359 ground, they might also be able to optimize their survival, hence the high observed survival in
360 the spring migration, by reducing food competition with adults but also by benefiting from the
361 experience acquired in their first migration leg in fall and on wintering ground (Cresswell
362 2014).

363

364 **Refueling and survival**

365 With the development of bird tracking, it has been shown that many species use stopovers
366 along their annual migratory cycle (Guilford et al. 2009, Chevallier et al. 2011, Åkesson et al.
367 2012). Under the concept of optimal migration, rules for refueling decision at stopover sites
368 have been developed to determine the number of stopovers and time spent on stopovers in
369 order to optimize migration in a given set of constraints (Weber et al. 1999, Duriez et al. 2009,
370 Alerstam 2011). Surprisingly, very few studies have highlighted differential stopover
371 strategies between age, sex, season and geographical origin (Ellegren 1991, Dierschke et al.

2005, Alerstam et al. 2006) and our results demonstrated an effect of each of these factors. As expected, juveniles, that were inexperienced for their first migration, used longer stopovers, a result of different factors detailed above. Our results also highlighted a difference between males and females in terms of time spent on stopovers, with significantly shorter refueling periods for males. This suggests that males use a riskier strategy in spring with faster travel and shorter refueling times in order to optimize their arrival time (Åkesson et al. 2012) or that males have a higher refueling rate (Seewagen et al. 2013). However, these different strategies do not lead to differential survival between sexes. Seasonal differences in migration stopover patterns are also apparent, with individuals performing less but longer stopovers in the fall (Kokko 1999, Alerstam 2006). The longer stopover duration during the fall migration, also observed in some raptor species (Klaassen et al. 2014), might suggest that individuals molt during their fall stopovers and therefore that the role of fall stopovers is twofold: refueling and molting (Hutto 2000). In the case of the Macqueen's bustard, molting occurs in summer (between end of breeding and migration departure, Gubin 2008) and should not impact the species stopover strategy. Central Asian steppes are characterized by a high productivity during spring which rapidly decreases after summer (Eisfelder et al. 2014). On-route environmental conditions (food limitation and cold temperatures) might be the main drivers for longer stopovers in the fall (Alerstam 2006). In addition, bird condition might be affected by a potential "carry-over effect" of the breeding season (display investments for the males and the parental cares that drain energy reserves for the females). This could explain the observed greater mortality during the fall migration and wintering period, which could be exacerbated by uncontrolled hunting and poaching pressures (Combreau et al. 2001, Combreau 2007). On the other hand, the spring strategy involving short flights interspersed with fewer stopovers to load small fuel reserves assumes that birds will stop at all suitable sites along the migration route making migrants dependent on a chain of sites and

397 consequently more vulnerable to environmental changes in the spring. Under the principle of
398 “multiple jeopardy”, i.e., the probability that any one site is affected by environmental change
399 increases with the number of sites (Newton 2004), birds from higher latitudes (East and West
400 Kazakhstan) which cover greater migratory distances and rely on multiple stopovers (Navedo
401 et al. 2010), will be under greater threat from environmental changes and will be consequently
402 more likely to show declines.

403

404 **Conclusion**

405 Little is known about the phenology of migration in polygynous land migrant bird species.
406 Our study provides the first direct evidence of complex migration behaviors and survival:
407 seasonal survival and migration strategies varying by sex, age, season and geographic origin
408 linked to social, hierarchical and physiological pressures. Since direct observations are not
409 possible yet on most parts of the migratory path and wintering ground, we have to rely solely
410 on remote tools and we demonstrate that technology coupled with robust statistical analyses
411 clearly shed light on migration strategies, a key element to implement appropriate
412 conservation measures. Mortality of both adults and juveniles occurs predominantly during
413 the fall migration and the wintering period, similarly to the migrating red knot *Calidris*
414 *canutus canutus* (Leyrer et al. 2013) and seems to be the driver of decline in many migratory
415 birds (Rappole and McDonald 1994, Carrete et al. 2013). Understanding the relative
416 importance of factors leading to the low survival rates observed during the fall migration and
417 winter (habitat quality versus anthropogenic threats) in relation to migration strategies and
418 stopover choices between populations or individuals will be essential to help improve the
419 current conservation and translocation efforts (see www.houbarafund.org).

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622 Table 1- Sample sizes by sex and geographical areas between 2005 and 2013 of PTT-equipped equipped
 623 individuals, subset of individuals included in the analyses with their monitoring lengths (and associated standard
 624 error) in terms of complete migration numbers, and timing of fall and spring migration as median departure dates
 625 (day of the year) with associated standard error.
 626

Country	Region	Sex	Number in					
			Individuals equipped	the analyses	Monitoring length	Mean fall date	Mean spring date	
Kazakhstan	West	female	43	37	3.1 (0.5)	14 oct (2.5)	6 mar (1.4)	
		male	19	19	2.5 (0.5)	19 oct (4)	26 feb (2.1)	
		Juvenile	23	19	1.5 (0.4)	30 sept (2.7)	24 mar (2.1)	
	Central	female	213	47	3.3 (0.4)	18 oct (1.6)	11 mar (1.5)	
			male	30	11	2.4 (0.4)	7 nov (3.6)	2 mar (2.7)
			Juvenile	34	26	0.6 (0.2)	18 oct (2.8)	1 ap (7.2)
		East	female	20	18	2.8 (0.5)	10 sept (2.6)	23 feb (3.5)
			male	9	9	2.8 (0.8)	22 sept (4.9)	18 feb (3.2)
			Juvenile	8	6	0.3 (0.3)	12 sept (4.6)	12 ap (na)
Uzbekistan	Navoi	female	13	6	2.5 (0.6)	17 oct (5.2)	4 mar (3.7)	
		Male	4	3	1.3 (1.3)	8 nov (3.4)	24 feb (16.5)	

Table 2- Modeling approaches (model type: lqmm = linear quantile mixed model on median; lmm = linear mixed model glmm = generalized linear mixed model; data distribution: “Family” (with the link for the glmm); R package and function) for the following migration response variables: fall and spring departure date, migration distance, duration of movement, number and duration of stopovers, using 4 datasets (“1” = all individuals, “2”= sexed individuals, i.e., adults only, “3” = all individuals presenting at least 1 stopover, “4” = sexed individuals presenting at least 1 stopover) and factor “Age”, “Place”(i.e., breeding place), “Sex” (adult birds) and “Season” as explanatory fixed factors and individual and year as random factors.

Response \ Explanatory	Age	Place	Sex	Season	Model type	Family (link)	R Package: function
	Fall departure date	1	1, 2	2		lqmm	Normal
Spring departure date							
Migration distance	1	1,2	2	1,2	lmm	Normal	lme4: lmer()
Migration duration	1	1,2	2	1,2	glmm	Poisson (log)	lme4: glmer()
Duration of movement	1	1,2	2	1,2	glmm	Poisson (log)	lme4: glmer()

Number of stopovers	1	1,2	2	1,2	glmm	Binomial (logit)/	lme4: glmer()
	3	3,4	4	3,4		Poisson (log), Poisson (log)	
Duration of stopovers	3	3,4	4	3,4	glmm	Poisson (log)	lme4: glmer()

Table 3- Mean (*and standard error*) of migratory distances (in km), migration duration (in days), duration of movement (in days) and proportion (%) of migratory legs with at least one stopover and among those, mean (*and standard error*) total duration (in days) and number of stopovers for the fall and spring migrations of wild Macqueen's bustards breeding in Asia (in Uzbekistan (Uzbek) and Kazakhstan: Betpakdalah (Betpak), Eastbalkash (Eatbal), Fetisovo (Fetis)), and equipped with PTT transmitter between 2005 and 2013.

Individual				Breeding place				Season	
Age		Sex		Betpak	Eastbal	Fetis	Uzbek	Fall	Spring
adult	juvenile	A.female	A.male						
<i>Migration distance</i>									
1894	1465	1901	1873	1684	2958	1678	1228	1866	1875
(29.21)	(129.81)	(32.43)	(66.23)	(34.28)	(35.84)	(26.82)	(89.49)	(39.69)	(42)
<i>Migration duration</i>									
22.77	18.26	23.65	19.82	19.84	39.75	19.51	9.11	20.61	24.58
(0.83)	(2.95)	(0.98)	(1.48)	(1.15)	(0.94)	(0.94)	(1.46)	(1.22)	(1.02)
<i>Duration of movement</i>									
10.72	10.18	10.89	10.17	9.9	13.97	10.56	6.72	10.8	10.58
(0.26)	(1.02)	(0.31)	(1.42)	(0.36)	(0.74)	(0.38)	(0.77)	(0.36)	(0.35)

Proportion of migratory legs including at least one stopover

63	40.74	64.15	59.43	58.2	89.87	57.29	27.78	46.85	77.97
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Number of stopovers performed among migration legs with at least one stopover

1.5	1.55	1.51	1.46	1.45	1.8	1.36	1.2	1.38	1.58
(0.03)	(0.1)	(0.03)	(0.06)	(0.04)	(0.09)	(0.04)	(0.11)	(0.03)	(0.04)

Total duration of stopovers performed among migration legs with at least one stopover

19.1	19.82	19.87	16.24	17.08	28.68	15.62	8.6	20.95	17.95
(0.73)	(2.52)	(0.85)	(1.42)	(1)	(2.3)	(0.77)	(0.89)	(1.25)	(0.78)

Table 4- Best models for Macqueen's bustard survival selected with E-SURGE with associated number of identifiable parameters (# Id Par.), deviance, QAIC and QAICc.

Model	Parametrization of survival	# Id Par.	Deviance	QAIC	QAICc
1	experience*2 periods	6	920.6	932.6	932.6
2	experience*4 periods	10	916.2	936.2	936.3
3	sex*age*2 periods	8	928.6	944.6	944.8
4	sex*4 periods	14	922.9	950.9	951.2
5	experience*place*4 periods	29	896.7	954.7	956

Table 5- Estimates of survival with associated standard errors (se) and CIs (lower bound: “CI-“, upper bound: “CI+”) for Macqueen’s bustard with the 3 best models selected (Table 4) by E-SURGE. Note that the survival for first-timers is 1 (model 2) for the breeding ground as they have necessarily survived to be included and do not have a following breeding period as they are followed only the first year.

Model	Covariate 1	Covariate 2	Estimate	CI-	CI+	se
1	experienced	Spring mig/breeding	0.96	0.94	0.97	0.009
	experienced	Fall mig/wintering	0.88	0.85	0.9	0.01
	First-timer	Spring mig/breeding	0.95	0.81	0.99	0.04
	First timer	Fall mig/wintering	0.63	0.52	0.7	0.05
2	experienced	breeding	0.95	0.92	0.97	0.014
	experienced	Fall mig	0.87	0.83	0.91	0.019
	experienced	wintering	0.89	0.84	0.92	0.019
	experienced	Spring mig	0.97	0.94	0.99	0.01
	First-timer	breeding	1	1	1	0
	First-timer	Fall mig	0.62	0.48	0.74	0.069
	First-timer	wintering	0.65	0.47	0.79	0.086
	First-timer	Spring mig	0.9	0.68	0.97	0.067
3	Male	Spring mig/breeding	0.97	0.92	0.99	0.015
	Male	Fall mig/wintering	0.87	0.8	0.91	0.029

Female	Spring mig/breeding	0.95	0.93	0.97	0.015
female	Fall mig/wintering	0.88	0.85	0.91	0.015
Undet	Spring mig/breeding	0.97	0.89	0.99	0.021
Undet	Fall mig/wintering	0.71	0.61	0.78	0.051

Fig. 1- Places of origin (trapping locations) of Macqueen's bustards equipped in Uzbekistan and in Kazakhstan (East, Central and West Kazakhstan) between 2005 and 2013. Black dots are daily locations of 150 wild adults and 51 wild juveniles retained for analyses.

