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Age-effects on breeding phenology and success of Common Guillemots *Uria aalge* at a North Sea colony

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Short title: Age-effects in Common Guillemots

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Capsule Common Guillemots *Uria aalge* show delayed breeding and marked age-related changes in
reproductive success consistent with improved performance with experience.

Aims To determine age of first breeding and age-related effects on breeding phenology and success
of Common Guillemots.

Methods Resighting data from a long-term colour-ringing study of Common Guillemot chicks were
combined with observations of breeding phenology and success to follow the recruitment process,
breeding phenology and success of 62 birds at a major North Sea colony over a 30 year period.

Results The median age of first breeding of Common Guillemots was 6.6 years. There were no
detectable costs of first breeding on return rates or the likelihood of breeding the next season but
first time breeders bred later and less successfully. Age of first breeding and lifetime breeding
success both varied among individuals but there was no clear optimal age of first breeding and early
first breeding was not associated with higher lifetime breeding success.

Conclusions Common Guillemots in the Isle of May population delayed breeding for 3-4 years
beyond physiological maturity. The marked increase in breeding success with age was consistent
with improved performance with experience rather than selection for higher quality individuals.
Findings from this study will inform population models by providing improved estimates of age of
first breeding and age-related changes in reproductive performance.

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66   Age of first breeding and subsequent decisions on whether or not to breed in a given season are key

67   components of life-time reproductive success and can be influenced by both intrinsic and extrinsic

68   factors (Newton 1989, Stearns 1992, Viallefont *et al.* 1995). Age of first breeding is also an essential

69   prerequisite for the formulation of population models (Lebreton *et al.* 1992). However, the

70   parameter is often underestimated, particularly in studies where the duration of data collection is

71   short relative to the potential lifespan of the study species (Dillingham *et al.* 2012 and references

72   therein). The best method of obtaining an accurate estimate of the age of first breeding is to follow

73   cohorts of individually marked chicks until all surviving members have recruited into the breeding

74   population. Seabirds are characterised by high survival rates (typically >90% in adults) and deferred

75   maturity (typically 2 – 7 years, but >10 years in albatrosses and petrels) (Schreiber & Burger 2001).

76   Thus age of first breeding and age-related breeding effects can potentially play a key role in seabird

77 population dynamics (Pardo *et al.* 2013) but collecting the requisite data can be very time

78 consuming.

79   The Common Guillemot *Uria aalge* (hereafter Guillemot) is one of the most numerous and

80 well-studied seabirds in the North Atlantic and North Pacific (Cramp 1985, Gaston & Jones 1998,

81 Ainley *et al.* 2002). Survival rates are high (90-94% per annum in adults; Meade *et al.* 2013, Lahoz-

82 Monfort *et al.* 2014) and the age of first breeding is typically given as 5-7 years (Birkhead & Hudson

83 1977, Harris *et al.* 1994, Ainley *et al.* 2002). However, Guillemots have been recorded living up to

84 over 42 years in the wild so there is plenty of scope for very protracted prebreeding periods (EURING

85 2014). To our knowledge, no previous study has investigated changes in Guillemot breeding

86 performance in relation to age and breeding experience using known age birds. However, estimates

87 based on birds ringed as breeding adults and using years since ringing or years prior to death as

88 proxies for age, suggest that breeding success increases over the first 10 years and, along with

89 survival, declines in the oldest individuals (Crespin *et al.* 2006, Reed *at al.* 2008). In the present study

90 we used long-term data on individually marked Guillemot chicks at a North Sea colony to elucidate

91 (1) the age of first breeding in this population, (2) the process of recruitment and (3) age and

92 experience-related changes in the timing of breeding and breeding success. For a subsample of these

93 birds where we had complete breeding histories from recruitment to death, we were also able to

94 calculate the first estimates of lifetime breeding success for this species.

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96 **METHODS**

97 Fieldwork was carried out between 1983 and 2015 on the Isle of May, Firth of Forth, southeast

98 Scotland (56° 11'N, 2° 33'W). Over the study period the Guillemot breeding population varied

99 between 10,-20,000 pairs. Each year between 1983 and 2012, an average of 246 ± se 10 chicks were

100 marked with long-lasting hard metal rings on one leg and a colour-ring with a unique three digit

101 alpha-numeric inscription on the other leg. Searches for these birds were made throughout the

colony each subsequent summer up to and including 2015 to record when they were first seen back
on the Isle of May and to follow the process of recruitment into the breeding population (see later).
Concurrently, a detailed study was undertaken of c.700 pairs of Guillemots breeding in front of five
permanent hides (details in Harris & Wanless 1988). Breeding sites were numbered on photographs
and were checked at least three times a day during the laying period and at least once a day for the
rest of the breeding season. All colour-ringed birds recorded in these areas were followed in detail
so that for each individual that had been ringed as a chick and which subsequently recruited into
these areas we knew: (a) the year of hatching, (b) when the bird was first seen anywhere on the Isle
of May, (c) when it was first seen where it later bred, (d) its sex from observations of copulations
(unknown for six individuals), (e) its age when it (or its mate) first laid an egg, (f) the date of laying of
the single egg by the ringed bird (or its mate) relative to other pairs in the same study area (Wanless
& Harris 1988; unknown for the few birds breeding at sites that were difficult to see clearly) and (g)
whether or not it bred successfully (defined as the male parent accompanied by its chick aged >14
days leaving the site and not returning again that season (Varoujean *et al.* 1979)). Laying date and
breeding success of these birds continued to be recorded either until they disappeared, presumably
because they had died since Guillemots are extremely faithful to a very small area of the colony once
they have bred (Harris *et al*. 1996), or until the study ended. The intensity of observations
throughout the study meant that visits and/or breeding attempts by colour-ringed birds were very
unlikely to have been missed. The high intensity of observations also enabled return rate of these
known-age birds to be used to estimate survival rates from one season to the next.

Bird age was taken as the number of calendar years after ringing (e.g. a chick hatched in 1983
and found breeding in 1988 was five years old). Many of the most recent recruits and a few of the
older birds were still alive at the end of the study resulting in records of breeding age and years
breeding being right censored. To avoid the potential bias that long-lived birds have higher fitness,
thereby leading to spurious positive correlations with age and experience, we used within-subject
centring (van de Pol & Wright 2009) to separate within-subject effects (i.e. phenotypically plastic or

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128   facultative behavioural responses) from between-subject effects (i.e. evolutionarily fixed

129   behavioural responses based on the individual).

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131   Laying date was standardised (a) relative to the median date within each year for each study

132   area, to allow for annual variation in timing of breeding, and (b) within individuals to their specific

133   mean to allow for birds that bred consistently early or late. The relationship between relative laying

134   date and the number of times that a bird had bred was analysed using a linear mixed model with

135   individual fitted as a random effect.

136   Breeding success was analysed in relation to age and experience (defined as the number of

137   years since an individual had first bred where 1 = year of first breeding) using a Generalized Linear

138   Mixed Model (GLMM), where the dependent variable was binary (success or failure), individual and

139   calendar year were random terms, and the fixed effects were either bird age or the number of years

140   since first breeding. In 29 instances (5.8% of 502 records) involving 16 individuals, a bird was known

141   to be alive but not definitely proved to have bred and in these cases the bird was scored as being

142   unsuccessful in these years. To check that the right censored data did not bias the results, the

143   analysis of the effect of age or the number of breeding events on breeding success was repeated

144   after distinguishing three different 'phenotypes' of birds (a) last seen when 12 or less years old (the

145   median age of birds when last seen that disappeared before the end of the study), (b) last seen at 13

146   years or older (median 15.5 years), and (c) still alive at the end of the study (median 15.5 years)

147   regardless of when they had entered the data set. This last group inevitably includes many younger

148   individuals. As previously, both individual and year were fitted as random effects. Models were fitted

149   using GenStat version 17.

150

151   **RESULTS**

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153   **Age of first breeding and the recruitment process**

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154   Sixty-two colour-ringed birds recruited into in the study areas and all were paired with unringed and

155   therefore unaged mates. The youngest bird bred for the first time at 4 years and the oldest at 11

156   years (Table 1). Overall, the modal age of first breeding was 6 years (35% of all birds) and the median

157   was 6.6 years. The distribution of age of first breeding did not differ between the two sexes (χ^2 =

158   5.16, df = 6, P > 0.5 after pooling birds aged 10 and 11 years). At the end of the study eight colour-

159   ringed birds were prospecting in the study areas. The oldest was 6 years old so it seems unlikely that

160   there were any older birds still to recruit and thus that Guillemots in this population normally

161   recruited by the time they were 12 years old. Restricting the data to the 1983-2003 cohorts (i.e.

162   birds aged $\geq$12 years at the end of the study), gave a median age of first breeding of 6.7 years (Table

163   1).

164   All 62 birds were seen on the Isle of May for several years prior to recruiting into the study

165   areas (Fig. 1). The median ages when they were first seen anywhere in the colony and where they

166   later bred were 3.43 years (range 2-7) and 3.95 years (range 2-7), respectively. The earlier that an

167   individual returned to the Isle of May, and to where it subsequently bred, the younger it was when it

168   first bred (r = 0.31, P = 0.015 and r = 0.32, P = 0.010, respectively; both n = 62). Guillemots recruiting

169   to a site that was not occupied in the previous year (39% of cases) did so when they were

170   significantly younger than birds replacing birds at previously used sites (61% of cases; median age of

171   recruitment at unoccupied sites = 6.0 years, previously occupied sites = 6.95 years, χ^2 = 7.54, df = 2,

172   P = 0.023 after pooling birds aged 4 and 5 years, and 7 to 11 years). The type of site used was not

173   associated with sex (71%, n = 28 males recruited to previously occupied sites compared to 57%, n =

174   28 females; χ^2 = 1.24, df = 1, P = 0.27).

175   Excluding the four birds that were first recorded breeding in 2015, 91.4% of birds returned in

176   the season following their first breeding attempt, a value which did not differ significantly from

177   values after subsequent breeding attempts (mean = 85.2%: 95% CI 78.3, 92.0). The frequency of

178   nonbreeding by birds in the year following their first breeding attempt (37.8%, n = 53) was identical

179   to the value for years after subsequent breeding events (37.8%, n = 424).

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Changes in laying date and breeding success with age and experience

Laying date became progressively earlier over the first four breeding years (Exponential regression: $F_{2,435} = 14.78$, $P < 0.001$: Fig. 2) with the advance being most marked between the first and second years (3.4 days). There was no significant difference between the sexes in the advance in laying date with experience ($F_{1,420} = 0.2$, $P > 0.6$). After 12 years of breeding, individuals tended to breed later than in their prime (4-11 years of experience). There were no differences in the slopes of the 'within' individual effect and the 'between' individual effect (Table 2a: -0.995 ± se 1.2), so the effect of experience was not due to the early disappearance of some birds.

The median age of first successful breeding was 7.67 years (Fig. 1; range 6-15 years). Success of four- and five-year-olds was extremely low with only one of 12 attempts resulting in a fledged chick (Fig. 3a). There was no significant difference in the probability of success of the first breeding attempt of Guillemots that recruited to a previously occupied site (32%, $n = 38$) and those that recruited to a site that had been unoccupied the previous season (30%, $n = 24$; $\chi^2 = 0.04$, df = 1, $P = 0.84$).

After accounting for the random effects of individual and year, breeding success increased significantly with both age (Fig. 3a: Wald statistic, $\chi^2 = 11.08$, $P < 0.001$) and years since first breeding (Fig. 3b: Wald Statistic, $\chi^2 = 14.33$, $P < 0.001$). In neither case did the slope of the 'within' individual effect differ significantly from the 'between' individual effect (Table 2b & c: age = 0.0633 ± se 0.0525, years since first breeding = 0.0823 ± se 0.059). Thus there was no evidence that the increase in success with age/experience was due to 'poor quality' individuals dying when relatively young. This is illustrated graphically in Figure 3b which shows that there were no significant differences in the effect of experience between the three phenotype (those disappearing at 12 years or younger, those disappearing at 13 years or older and those still alive in 2015; slopes: Wald statistic 2.04, df = 2, $P > 0.3$; intercepts: Wald statistic 1.08, df = 2, $P > 0.5$).

205   Breeding success was also higher among individuals breeding earlier in the season,

206   regardless of age and experience (Wald statistic = 15.89, $P < 0.001$). In general birds that were

207   successful laid two days earlier than unsuccessful breeders ($F_{1,433}$ = 12.18, $P < 0.001$).

208

209   **Lifetime breeding success**

210   The number of chicks fledged by the 34 birds that entered and left the population during the study

211   showed considerable variation ranging from nine individuals (26%) failing to fledge any young to one

212   male that fledged 19 chicks from 21 attempts (Fig. 4). The median number of chicks fledged was

213   3.09. There was no overall relationship between age of first breeding and lifetime breeding success

214   (r = -0.016, P = 0.52, Fig. 5). The number of chicks fledged by the 28 individuals still alive at the end

215   of the study period ranged 0 – 12 (median 5.5).

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218   **DISCUSSION**

219   Compared to breeding success and adult survival, age of first breeding has received much less

220   attention in studies of marine birds and as a consequence minimum rather than mean or median age

221   often has to be used in analyses (Weimerskirch 2002). The pattern of recruitment we recorded over

222   a 30 year period on the Isle of May accorded closely with previous shorter studies at this colony and

223   those elsewhere in the breeding range, with individuals first seen back when they were 2-3 years

224   old, becoming attached to a specific part of the colony when they were 3-5 years old and typically

225   making their first breeding attempt when they were 6-7 years old (Birkhead & Hudson 1977, Halley

226   *et al.* 1995, Lee *et al.* 2008). Only three Guillemots (one male, one female and one unknown sex)

227   were recorded breeding when they were 4 years old. However, in captivity Guillemots have bred

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228 (although not successfully) when they were 3 years old (Swennen 1977). Scattered records in the

229 literature suggest that birds in the wild have bred at 3 years but in all these cases there is

230 uncertainty about the validity of the record, e.g. the possibility of allo-parenting by neighbours, and

231 thus definite conformation of free-living Guillemots breeding at 3 years of age is lacking (Wanless &

232 Harris 1985, Harris *et al.* 1994, Lee *et al.* 2008). Our results, therefore, indicate that Guillemots have

233 a delayed onset of reproduction several years beyond the age of physiological maturity.

234   There appears to be little information on sex-related differences in age of first breeding in

235 seabirds. Among the auks, Gaston and Jones (1998) found that, on average, female Brünnich's

236 Guillemots *U. lomvia* bred when they were one year younger than males. In Common Guillemots the

237 process of recruitment was remarkably similar in the two sexes with no significant differences in the

238 age of first return to the island, the age at which birds moved into the area where they subsequently

239 bred or the age at which breeding first occurred and was first successful. However, the recruitment

240 process was influenced by the type of site a bird recruited to with Guillemots using a site that had

241 not been occupied in the previous season breeding a year earlier than those which first bred at a site

242 that had previously been occupied. To our knowledge this effect does not seem to have been

243 recorded previously in Guillemots. It suggests some sort of social constraint whereby birds need

244 additional time and/or experience to recruit to a site that has recently been bred at by other birds,

245 presumably associated with replacing a bird that had died or evicting the previous owner. Although

246 competition for the best breeding sites in Guillemot colonies is intense (Birkhead 1978), suitable

247 sites on the Isle of May do not appear to be limited since even when the population was declining in

248 the 2000s, new sites continued to be occupied and the colony boundary expanded (Harris *et al.*

249 1997, personal observations). Given the availability of sites, it is unclear why some Guillemots

250 apparently delay the age of first breeding by recruiting to a previously occupied site rather than

251 using a new one, particularly since there is no difference in breeding success of the first breeding

252 attempt in the two types of site.

253   Guillemots typically breed annually but individuals sometimes skip a year's breeding (Reed

254   *et al.* 2015). However, in contrast to the situation in the closely related Brünnich's Guillemot and

255   several other species of seabird, the frequency of skipping in Guillemots was not significantly higher

256   the year after first breeding compared to subsequent years (Wooller & Coulson 1977, Ollason &

257   Dunnet 1988, Viallefont *et al.* 1995, Gaston & Hipfner 2000). Similarly, we also found no significant

258   difference in return rates of first time and experienced breeders. Taken together these results

259   suggest that during the study period, costs of the first breeding attempt were not sufficient to

260   reduce subsequent overwinter survival or the likelihood of breeding the following season.

261   We did, however, find some marked differences in two key components of breeding

262   performance (laying date and breeding success). Thus, first time breeders bred significantly later in

263   the season than those with breeding experience and were less successful. However, in contrast to

264   Brünnich's Guillemots in which breeding became progressively earlier over the first 8 seasons

265   (Hipfner 1997), in Common Guillemots breeding advanced by 3-4 days between the first and second

266   attempt and by a further day in birds breeding 4-11 times. Most Guillemots breeding for the first

267   time failed to rear a chick but thereafter success increased steadily reaching 66% by the 10th attempt

268   and 75% by the 15th attempt. Thus whilst low success in the first year could potentially have been

269   due to poorer environmental conditions later in the season, subsequent improvements in success in

270   the absence of changes in laying date are indicative of intrinsic effects. Experimental studies in

271   European Shags *Phalacrocorax aristotelis* concluded that intrinsic effects were the main reason for

272   lower breeding success in first time breeders (Daunt *et al.* 1999) but this approach would be

273   challenging to carry out on Guillemots and would likely result in many eggs being lost.

274   In long-lived birds breeding success typically shows an inverse U-shaped relationship with

275   age, increasing during the first few years, then plateauing before declining in the oldest age classes

276   (Newton 1989, Forslund & Pärt 1995). An earlier study of Guillemots on the Isle of May based on

277   birds individually marked as adults and using years since ringing as a proxy for age, found that

278 success improved over the first 9-13 years and then remained stable for the next 6-10 years, before

279 declining after 19 years of breeding (about 25 years of age; Crespin *et al.* 2006). In our smaller

280 sample of known age birds there was no detectable decrease in success in the oldest birds, though

281 some of these were still alive and may not yet have reached senescence since only seven were older

282 than 21 years. Distinguishing whether the improvement with experience is directly due to age-

283 related improvements in breeding performance or is a consequence of lower quality (i.e. less

284 successful birds) having higher mortality and thus disappearing from the population, can be difficult

285 with observational studies. However, the method recently proposed by van de Pol & Wright (2009)

286 provides a powerful way of distinguishing between the two competing hypotheses by comparing

287 'within' and 'between' individual effects. In the case of Guillemots it indicates that the data are

288 consistent with genuine age-related improvements in performance rather than the selection

289 hypothesis, a conclusion supported by the simpler analysis classifying individuals into three

290 phenotypes.

291   Estimates of lifetime breeding success in seabirds are rare and we are aware of only one

292 other published value for an auk. Results from the study of Cassin's Auklet *Ptychoramphus aleuticus*

293 by Pyle *et al.* (2001) with a mean value of 3.7 chicks fledged and a range of 0-34 chicks are similar to

294 those for Guillemots. Both studies were carried out when the populations were declining for all or

295 part of the study period and the low values for lifetime breeding success probably reflect that

296 breeding conditions were poor (Harris *et al.* 2015). More recent estimates from the Isle of May when

297 the breeding population has been increasing, suggest that lifetime fledging success has also

298 increased with a median value of at least 5.5 chicks for individuals still alive at the end of the study.

299   Life history theory predicts that the timing of reproductive events during an individual's life

300 will affect its fitness (Caswell 1982). Starting to breed early can increase the number of reproductive

301 events over an individual's lifetime and thus potentially increase lifetime breeding success,

302 particularly in species with a clutch size of one such as the Guillemot. Although our study was based

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303 on a relatively small number of individuals, the intensity of observations gives us confidence that the

304 ages of first breeding and breeding performances recorded reflect the individual variation associated

305 with this population. Whilst the majority of Guillemots first bred when they were 6 or 7 years,

306 overall timing of first reproduction varied from 4 to 11 years. In species where age of first breeding

307 is variable certain ages can be associated with a high reproductive success (Newton 1989). However,

308 although lifetime breeding success in Guillemots showed considerable individual variation there was

309 no clear optimal age of first breeding, no evidence that success was higher in birds recruiting at the

310 median age and no relationship between age of first breeding and lifetime breeding success. A

311 recent study exploring the relationship between age of first breeding and lifetime reproductive

312 success across 34 species of birds, including a few seabirds, concluded that a delayed onset of

313 reproduction beyond maturity is an optimal strategy that is explained by a long lifespan and costs of

314 early reproduction (Mourocq *et al.* 2016). In our population the age when an individual started to

315 breed had no effect on lifetime breeding success hence delaying breeding was no more optimal than

316 earlier breeding.

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324

325 **REFERENCES**

326 **Ainley, D. G., Nettleship, D. N., Carter, H. R. & Storey, A. E.** 2002. Common Murre (*Uria aalge*). In

327   Poole, A. & Gill, F. (eds.), *The Birds of North America*. The Birds of North America, Inc.,

328   Philadelphia, PA.

329 **Birkhead, T. R.** 1978**.** Behavioural adaptations to high density nesting in the common guillemot *Uria*

330   *aalge*. *Anim. Behav.* **26:** 321-331.

331 **Birkhead, T. R. & Hudson, P. J.** 1977**.** Population parameters for the Common guillemot *Uria aalge*.

332   *Ornis Scand.* **8:** 145-154.

333 **Caswell, H.** 1982**.** Life history strategies. In Cherrett, M. (ed.) *Ecological Concepts* : 285-305.

334   Blackwell, Oxford.

335 **Cramp, S. E.** 1985**.** The Birds of the Western Palearctic, Vol. IV. Oxford University Press, Oxford.

336 **Crespin, L., Harris, M. P., Lebreton, J. D. & Wanless, S.** 2006. Increased adult mortality and reduced

337   breeding success with age in a population of Common Guillemot *Uria aalge* using marked

338   birds of unknown age. *J. Avian Biol.* 37**:** 273-282.

339 **Daunt, F., Wanless, S., Harris, M. P. & Monaghan, P.** 1999**.** Experimental evidence that age-specific

340   reproductive success is independent of environmental effects. *Proc. R. Soc. Lond. B* **266:**

341   1489-1493.

342 **EURING** (2014). http://www.euring.org/data-and-codes/longevity-list/guillemot (accessed 30 May

343   2016).

344 **Dillingham, P. W., Elliott, G. P., Walker, K. J. & Fletcher, D.** 2012**.** Adjusting age at first breeding of

345   albatrosses and petrels for emigration and study duration. *J. Ornithol.* **153:** 205-217.

346 **Forslund, P. & Pärt, T.** 1995**.** Age and reproduction in birds - hypothesies and tests. *Trends Ecol. Evol.*

347   **10:** 374-378.

348 **Gaston, A. & Jones, I. L.** 1998**.** *The Auks Alcidae.* Oxford University Press, Oxford.

349 **Gaston, A. J. & Hipfner, J. M.** 2000. Thick-billed Murre (*Uria lomvia*) No. 497. In. Poole, A. & Gill, F.

350   (eds.) *The Birds of North America*. Birds of North America, Inc, Philadelphia.

351 **Halley, D. J., Harris, M. P. & Wanless, S.** 1995**.** Colony attendance patterns and recruitment in

352   immature Common Murres (*Uria aalge*). *Auk* **112:** 947-957.

353 **Harris, M. P. & Wanless, S.** 1988**.** The breeding biology of Guillemots *Uria aalge* on the Isle of May

354   over a six-year period. *Ibis* **130:** 172-192.

355 **Harris, M. P., Halley, D. J. & Swann, R. L.** 1994**.** Age of first breeding in Common Murres. *Auk* **111:**

356   207-209.

357 **Harris, M. P., Wanless, S. & Barton, T. R.** 1996**.** Site use and fidelity in the Common Guillemot *Uria*

358   *aalge*. *Ibis* **138:** 399-404.

359 **Harris, M. P., Heubeck, M., Newell, M. A. & Wanless, S.** 2015. The need for year-specific correction

360   factors (k values) when converting counts of individual Common Guillemots *Uria aalge* to

361   breeding pairs. *Bird Study* **62**: 276-279.

362 **Harris, M. P., Wanless, S., Barton, T. R. & Elston, D. A.** 1997**.** Nest site characteristics, duration of

363   use and breeding success in the Guillemot *Uria aalge*. *Ibis* **139:** 468-476.

364 **Hipfner, J. M.** 1997**.** The effects of parental quality and timing of breeding on the growth of nestling

365   Thick-billed Murres. *Condor* **99:** 353-360.

366 **Lahoz-Monfort, J. J., Harris, M. P., Morgan, B. J. T., Freeman, S. N. & Wanless, S.** 2014**.** Exploring

367   the consequences of reducing survey effort for detecting individual and temporal variability

368   in survival. *J. appl. Ecol.* **51:** 534-543.

369 **Lebreton, J.-D., Burnham, K. P., Clobert, J. & Anderson, D. R.** 1992**.** Modelling survival and testing

370   biological hypotheses using marked animals: a unified approach with case studies. *Ecol.*

371   *Monogr.* **62:** 67-118.

372 **Lee, D. E., Abraham, C. L., Warzybok, P. M., Bradley, R. W. & Sydeman, W. J.** 2008**.** Age-specific

373   survival, breeding success, and recruitment on Common Murres (*Uria aalge*) of the

374   California Current System. Auk **125:** 316-325.

375   **Meade, J., Hatchwell, B. J., Blanchard, J. L. & Birkhead, T. R.** 2013**.** The population increase of

376   Common Guillemots *Uria aalge* on Skomer Island is explained by intrinsic demographic

377   properties. *J. Avian Biol.* **44:** 55-61.

378   **Mourocq, E., Bize, P., Bouwhuis, S., Bradley, R., Charmantier, A., de la Cruz, C., Drobniak, S. M.,**

379   **Espie, R. H. M., Herenyi, M., Hotker, H., Kruger, O., Marzluff, J., Moller, A. P., Nakagawa,**

380   **S., Phillips, R. A., Radford, A. N., Roulin, A., Torok, J., Valencia, J., van de Pol, M.,**

381   **Warkentin, I. G., Winney, I. S., Wood, A. G. & Griesser, M.** 2016**.** Life span and reproductive

382   cost explain interspecific variation in the optimal onset of reproduction. *Evolution* **70:** 296-

383   313.

384   **Newton, I.** 1989**.** *Lifetime Reproduction in Birds*. Academic Press, London.

385   **Ollason, J. C. & Dunnet, G. M.** 1988**.** Variation in breeding success in Fulmars. In Clutton Brock, T. H.

386   (ed.) *Reproductive Success*: 263-278. Chicago University Press, Chicago.

387   **Pardo, D., Barbraud, C., Authier, M. & Weimerskirch, H.** 2013**.** Evidence for an age-dependent

388   influence of environmental variations on a long-lived seabird's life-history traits. *Ecol.* **94:**

389   208-220.

390   **Pyle, P., Sydeman, W. J. & Hester, M.** 2001**.** Effects of age, breeding experience, mate fidelity and

391   site fidelity on breeding performance in a declining population of Cassin's auklets. *J. Anim.*

392   *Ecol.* **70:** 1088-1097.

393   **Reed, T. E., Kruuk, L. E. B., Wanless, S., Frederiksen, M., Cunningham, E. J. A. & Harris, M. P.** 2008**.**

394   Reproductive senescence in a long-lived seabird: Rates of decline in late-life performance

395   are associated with varying costs of early reproduction. *Amer. Nat.* **171:** E89-E101

396   **Reed, T., Harris, M. & Wanless, S.** 2015**.** Skipped breeding in common guillemots in a changing

397   climate: restraint or constraint? *Front. Ecol. Evol.* **3:** 1-13.

398   **Schreiber, E. A. & Burger, J.** 2001**.** *Biology of Marine Birds*. CRC Press, Boca Raton.

399   **Stearns, S. C.** 1992**.** *The Evolution of Life Histories*. Oxford University Press, Oxford.

400   **Swennen, C.** 1977**.** *Laboratory Research on Sea Birds.* Netherlands Institute for Sea Research, Texel.

15

401   **van de Pol, M. & Wright, J.** 2009. A simple method for distinguishing within- versus between-subject

402   effects using mixed models. *Anim. Behav.* **77:** 753-758.

403   **Viallefont, A., Cooke, F. & Lebreton, J.-D.** 1995. Age-specific costs of first-time breeding. *Auk* **112:**

404   67-76.

405   **Wanless, S. & Harris, M. P.** 1985. Two cases of guillemots *Uria aalge* helping to rear neighbours'

406   chicks on the Isle of May. *Seabird* **8:** 5-8.

407   **Wanless, S. & Harris, M. P.** 1988. The importance of relative laying date on breeding success of the

408   guillemot *Uria aalge*. *Ornis Scan.* **19:** 205-211.

409   **Weimerskirch, H.** 2002. Seabird demography and its relationship with the marine environment. In

410   Schreiber, E. A. & Burger, J. (eds.) *Biology of Marine Birds*: 115-135. CRC Press, Boca Raton.

411   **Wooller, R. D. & Coulson, J. C.** 1977. Factors affecting age of first breeding of Kittiwake *Rissa*

412   *tridactyla*. *Ibis* **119:** 339-349.

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APPENDIX

Table 1. Sample sizes for plots shown in Figures 2 and 3

x-value	Figure 2	Figure 3a	Figure 3b		
			12 years or less	More than 12 years	Still alive
1	54		17	17	28
2	50		12	17	25
3	46		8	17	25
4	42	3	5	17	21
5	38	9	4	17	22
6	35	31	3	16	19
7	33	35		16	18
8	29	41		14	18
9	25	42		12	17
10	21	43		11	13
11	13	41		6	8
12	12	38		6	8
13	11	37		4	8
14	11	32		4	8
15	11	30		4	8
16	6	21		4	5
17	3	20		2	4
18		17		1	1
19		15			
20		12			
21		10			
22		7			
23		4			
24		3			
25		1			
26		1			
27		1			
28		1			
29		1			

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422   Figure 1. Age distribution at key stages in the recruitment process of 62 known-age Common

423   Guillemots. (a) Age (years) first seen on the Isle of May, (b) age first seen in study areas, (c) age of

424   first breeding attempt and (d) age of first successful breeding. (Twelve birds had not fledged a chick

425   by the end of the study.)

426

427   Figure 2. The mean relative laying date (± se) of Common Guillemots plotted against the number of

428   breeding years. The asymptotic regression (Relative lay date = -0.957+17.3*(0.263**Number of

429   breeding years) is fitted through all the 440 records. Sample sizes are given in the appendix.

430

431   Figure 3. Breeding success (chicks fledged/breeding attempt) of Common Guillemots in relation to

432   (a) age and (b) years since breeding started. The regression lines are fitted to the observed binomial

433   data rather than the mean breeding success shown by the points. In (b) three 'phenotypes' are

434   distinguished, birds that disappeared when they were 12 years or younger (circles), those that were

435   older than 12 years when they disappeared (diamonds), and those that were still alive in 2015

436   (crosses). Sample sizes are given in the appendix. In (a) squares indicate sample size <10 and in (b)

437   small symbols indicate sample size < 5. A common regression line is fitted since there were no

438   significant differences in slopes between phenotypes or differences in intercepts (see text).

439

440   Figure 4. Frequency distributions of (a) Lifetime breeding success (total number of chicks fledged

441   during a Common Guillemot's lifetime; *n* = 34) and (b) numbers of chicks fledged by birds still alive at

442   the *end* of the study (*n* = 28).

443   Figure 5. Lifetime breeding success in relation to their age of first breeding of 34 Common

444   Guillemots. Some points are slightly offset for clarity.

445   Table 1. Frequency distribution of ages of first recorded breeding of Common Guillemots on the Isle

446   of May.

		Age at first breeding (years)								
	n	4	5	6	7	8	9	10	11	Median
Male	28	1	5	10	3	3	5	0	1	6.46
Female	28	1	2	10	8	4	2	1	0	6.67
All including unknown sex	62	3	7	22	12	9	7	1	1	6.59
Chicks from 1983-2003 cohorts	55	2	6	19	10	9	7	1	1	6.69

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450   Table 2. Separating the within-individual effects from the between-individual effects on (a) relative

451   laying date in relation to years of breeding experience (because of the exponential relationship, see

452   Fig. 2, years of breeding experience was $\log_e+1$), (b) breeding success in relation to age, and (c)

453   breeding success in relation to years of breeding experience. In all cases there was no significant

454   difference in the slopes of the relationships comparing within individuals and between individuals.

455

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|	Coefficient	se	*P* - value
(a) Relative laying date			
Intercept	0.728	0.418	
Within individual effect	-2.55	0.552	< 0.001
Between individual effect	-1.563	1.064	0.140
Difference in effects	-0.995	1.200	n.s.
	Variance component		
Random individual effects	3.98	1.74	
(b) Age			
Intercept	0.2364	0.2003	
Within individual effect	0.0727	0.0318	0.023
Between individual effect	0.1360	0.0450	0.004
Difference in effects	0.0633	0.0525	n.s.
	Variance component		
Random individual effects	0.374	0.154	
Random year effects	0.485	0.216	
(b) Years breeding experience			
Intercept	0.2333	0.1987	
Within individual effect	0.0697	0.0318	0.029
Between individual effect	0.1520	0.0505	0.004
Difference in effects	0.0823	0.0590	n.s.
	Variance component		
Random individual effects	0.344	0.175	
Random year effects	0.487	0.218	

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461 Figure 1. Age distribution at key stages in the recruitment process of 62 known-age Common

462 Guillemots. (a) Age (years) first seen on the Isle of May, (b) Age first seen in study areas, (c) Age of

463 first breeding attempt and (d) Age of first successful breeding. (Twelve birds had not fledged a chick

464 by the end of the study.)
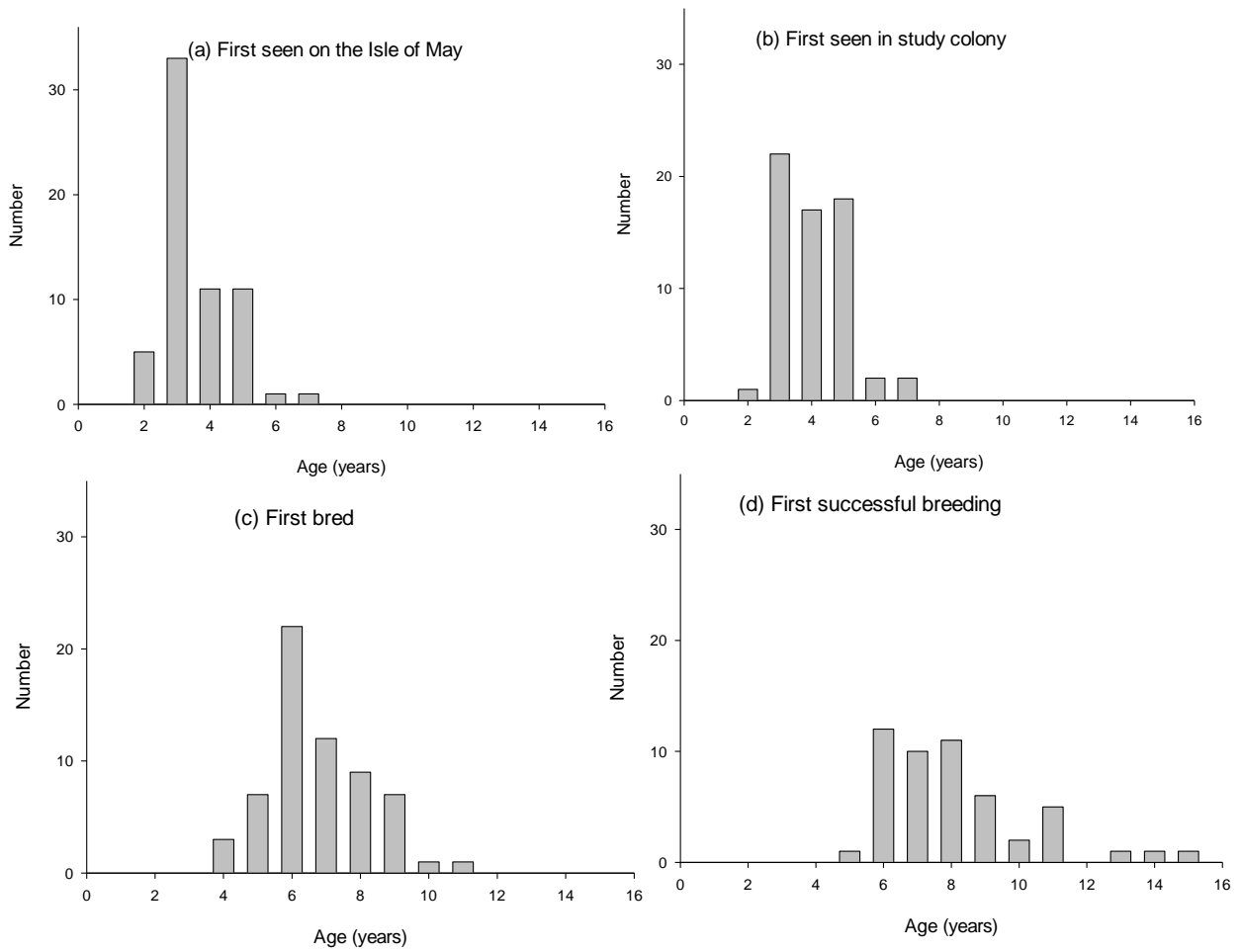
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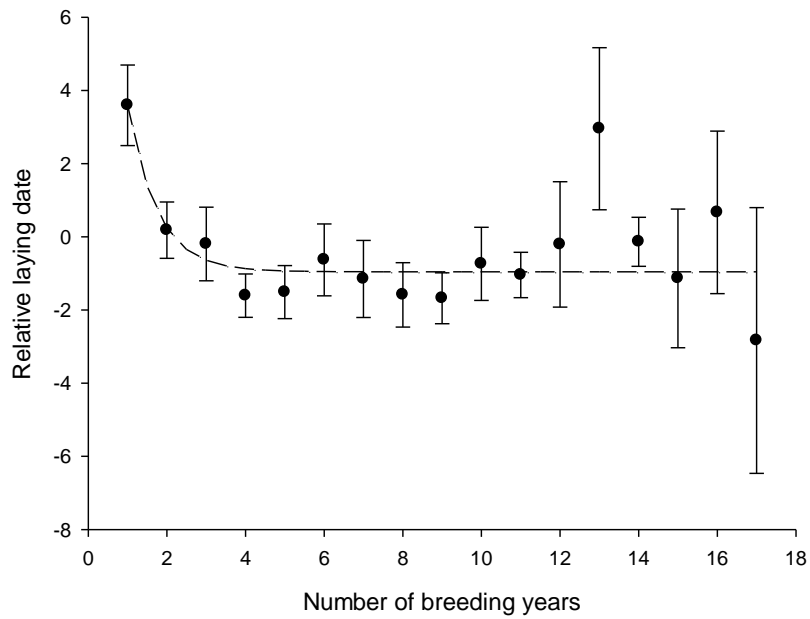469   Figure 2. The mean relative laying date (±SE) of Common Guillemots plotted against the

470   number of breeding years. The asymptotic regression (Relative lay date = -0.957+17.3*(0.263$^{Number\ of}$

471    $^{breeding\ years}$) is fitted through all the 440 records. Sample-sizes are given in the appendix.

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476

477 Figure 3. Breeding success (chicks fledged/breeding attempt) of Common Guillemots in relation to
478 (a) age and (b) years since breeding started. The regression lines are fitted to the observed binomial
479 data rather than the mean breeding success shown by the points. In (b) three 'phenotypes' are
480 distinguished, birds that disappeared when they were younger than 12 years (circles), those that
481 were older than 12 years when they disappeared (diamonds), and those that were still alive in 2015
482 (crosses). Sample sizes are given in the appendix. In (a) squares indicate sample size <10 and in (b)
483 small symbols indicate sample size < 5. A common regression line is fitted since there were no
484 significant differences in slopes between phenotypes or differences in intercepts (see text).
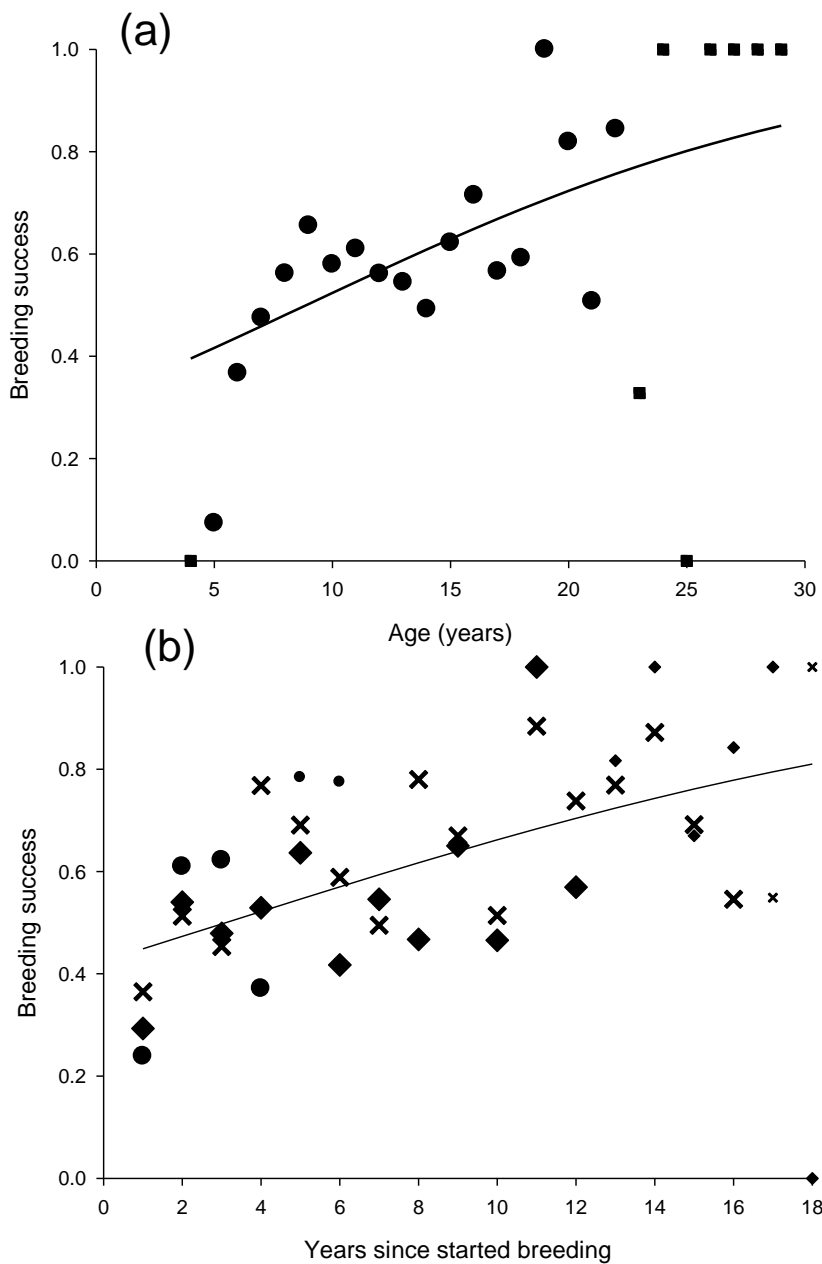
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487   Figure 4. Frequency distributions of (a) Lifetime breeding success (total number of chicks fledged

488   during a Common Guillemot's lifetime; *n* = 34) and (b) numbers of chicks fledged by birds still alive at

489   the end of the study (*n* = 28).
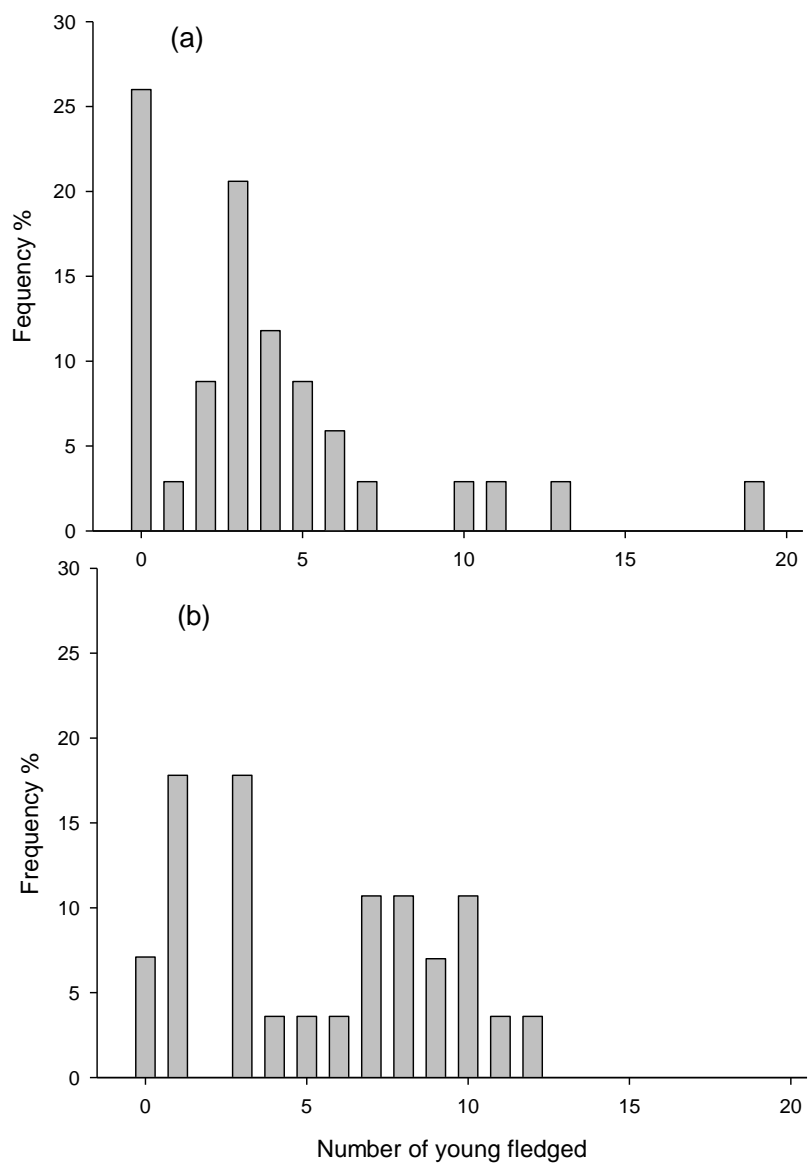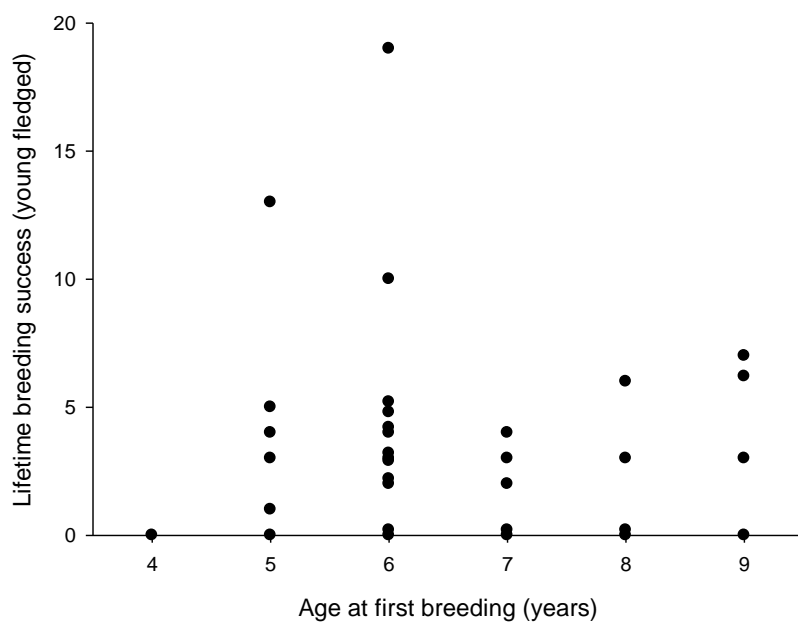

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498   Figure 5. Lifetime breeding success in relation to their age of first breeding of Common Guillemots.

499   Some points are slightly offset for clarity.

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