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3 **Renesting of Common Terns *Sterna hirundo* in the life history perspective**

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6

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8

9 **Abstract**

10 Replacement clutches may increase the annual reproductive output of individuals and the
11 population, but cause additional effort and may have fitness consequences. Whether longevity
12 and lifetime reproductive success are affected by renesting is unknown. In an individual-based
13 long-term study (1992-2009) we investigated common terns *Sterna hirundo* breeding at the
14 colony site “Banter See” on the German North Sea coast and marked with transponders. This
15 approach allowed us to study short-term as well as long-term consequences of relaying for
16 both the population and individuals. In five out of seven years characterized by higher
17 relaying activity, breeding success of replacement clutches was similar or even higher than
18 that of first clutches, but in the total study period only 4.5 % of all fledglings (4.4 % of natal
19 recruits) stemmed from replacement clutches. Demographic effects of relaying were minor. In
20 most years relaying birds were able to increase their annual reproductive output through the
21 replacement clutch. Relaying common terns were high quality individuals, arriving and laying
22 earlier, and characterized by higher age and body condition than non-relaying conspecifics.
23 Relaying probability decreased with delayed arrival and laying date of first clutch. Survival
24 to next year did not differ between breeders with or without a replacement clutch. In the
25 lifetime perspective, individuals with at least one renesting event had higher survival,
26 longevity, lifetime reproductive success and fitness compared to birds without a replacement
27 clutch. The higher lifetime reproductive success of the renesting individuals was achieved by
28 longer lifespan as well as by the reproductive output owing to relaying. The positive links
29 between survival, additional effort for replacement clutches and their success are obviously
30 due to the fact that only those individuals do relay that can cope with the additional effort for
31 production and care of the replacement clutch. In this way renesting is an indicator of high
32 individual quality and a benefit for fitness.

33

34 **Introduction**

35

36 Life history theory predicts that there is a trade-off between current and future reproductive
37 effort (Stearns 1992). This assumption implies that reproduction is costly (Williams 1966) in
38 terms of a reduced residual reproductive value, e.g. in form of reduced future reproductive
39 performance or survival. In birds experimental tests of the costs of reproduction have been
40 mostly concerned with trade-offs between chick rearing effort and subsequent survival and
41 fecundity (reviews in Lindén and Møller 1989, Stearns 1992). In recent years, however, avian
42 egg production also came into focus as a further demanding process which depletes a female's
43 body reserves (Houston et al. 1983, Bolton et al. 1992, Gayathri et al. 2004, Bauch et al. 2010)
44 and has consequences on future reproductive output, survival and fitness (Monaghan et al.
45 1998, Nager et al. 2001, Kalmbach et al. 2004).

46

47 A specific case of increased reproductive effort and cost is the production of a replacement
48 clutch within the same season, after loss of the first clutch or brood due to catastrophic and
49 stochastic environmental impacts such as predation, adverse weather events or flooding, or
50 induced by manipulative experiments. Replacement breeders are disadvantaged in two ways:
51 Firstly because they have to produce an additional clutch. Extra egg production and incubation
52 are demanding processes in terms of energy, time and nutrients. Monaghan and Nager (1997)
53 and Monaghan et al. (1998) found in several species that the production of only one extra egg
54 substantially reduced the capacity of female parents to rear the brood. Furthermore, in the season
55 following experimentally increased egg-production, female Lesser Black-backed Gulls *Larus*
56 *fuscus* were less likely to be resighted in the study plot and to produce a clutch compared to control
57 birds (Nager et al. 2001). In view of this, the advantage of laying replacement eggs after breeding
58 failure has to be traded off against additional costs of producing extra eggs. Secondly, the

59 production and care of the replacement clutch coincides with the progress of the breeding
60 season and concomitant deterioration of environmental conditions (reviewed by Moreno 1998,
61 Verhulst and Nilsson 2008). This is indicated by the negative seasonal trend in reproductive
62 success observed in many bird species and may be a direct effect of breeding time progress or
63 an effect of quality (individuals of high phenotypic quality breeding early in the season), or a
64 combination of the two (Verhulst and Nilsson 2008). On the other hand, renesting after breeding
65 failure offers the chance to still produce offspring in the same season and to increase lifetime
66 reproductive success (LRS) and fitness.

67

68 Owing to the costs involved in the production of additional eggs, replacement clutches should
69 be particularly expensive for the breeders and reserved to a smaller proportion of pairs
70 characterized by high individual quality. This is confirmed by the majority of studies dealing
71 with renesting: only a low proportion of females reneests declining with the date of egg loss in
72 the first clutch (Brünnich's Guillemot *Uria lomvia*, Hipfner et al. 1999, Connelly et al. 1993,
73 Wendeln et al. 2000, Roonem and Robertson 1997). Following the seasonal trend some species
74 reduce the size of the replacement clutch (Black Tern *Chlidonias niger*, Macikunas 1993, Tree
75 Swallows *Tachycineta bicolor*, Roonem and Robertson 1997, Black-legged Kittiwake *Rissa*
76 *tridactyla*, Gasparini et al. 2006, Red-backed Shrike *Lanius collurio*, Antczak et al. 2009) or
77 egg (Hipfner et al. 1999). High quality and effort of renesting breeders are reflected by studies
78 showing no difference between the size of first and replacement clutch (Common Tern *Sterna*
79 *hirundo*, Wendeln et al. 2000, Arnold et al. 2004; Starling *Sturnus vulgaris*, Christians et al.
80 2001, Red-backed Shrike, Antczak et al. 2009), or by laying even more or larger eggs than in
81 the first clutch (Willow Ptarmigan *Lagopus lagopus*, Sandercock and Pedersen 1994, Tree
82 Swallow, Roonem and Robertson 1997), or by fledging success of late replacement breeders
83 being similar or even superior to that of late nesting first breeders (Brünnich's Guillemot *Uria*
84 *lomvia*, Hipfner et al. 1999, Magpie *Pica pica*, De Neve et al. 2004, Common Tern, Arnold et

85 al. 2004). Replacement breeders start their first breeding attempt earlier in the season than non-
86 renesting pairs (Belted Kingfisher *Megaceryle alcyon*, Kelly and van Horne 1997, Kentish
87 Plover *Charadrius alexandrinus*, Amat et al. 1999, Common Tern, Wendeln et al. 2000, Red-
88 backed Shrike, Antczak et al. 2009, Mallard *Anas platyrhynchos*, Arnold et al. 2010) and are
89 characterized by higher quality or better condition (female Tree Swallows, Roonem and
90 Robertson 1997, Common Tern, Wendeln et al. 2000). Some studies present evidence of
91 replacement breeders being the older and/or more experienced individuals (Black-legged
92 Kittiwake, Wooller 1980, Tree Swallow, Wheelwright and Shultz 1994, Common Tern,
93 Wendeln et al. 2000, Mallard, Arnold et al. 2010).

94

95 Identifying benefits or costs of replacement clutches reflected in survival or fecundity of
96 renesting individuals requires a view beyond the year of the renesting event. Longitudinal
97 individual-based data collected in an integrated population study are needed, which are
98 preconditions rarely fulfilled in ornithology. Our study on the population ecology of the
99 Common Tern, a long-lived small seabird species, contains the potential to address hitherto
100 neglected long-term aspects of renesting on the individual and population level. The Common
101 Tern normally lays one clutch per season, occasionally in exceptional cases a second clutch, and
102 is able to replace the first clutch or brood if it is lost (see Wendeln et al. 2000, Becker and
103 Ludwigs 2004). Besides the characteristics of relaying Common Terns mentioned above, in
104 replacement clutches egg mass decreased and relaying intervals increased with the date when the
105 loss had occurred. Evidence of high levels of parental care of replacement clutches came from
106 body mass data in both genders: Female mass increase during courtship was higher in the second
107 attempt than in the first, whereas male mass was lower during the second courtship (Wendeln et
108 al. 2000). Therefore it seems that unlike in gulls (Nager et al. 2001) male terns may also
109 experience costs by renesting.

110

111 In our unique study colony at Banter See, on the German North Sea coast, during some years
112 between 1992 and 2008 numerous first clutches were lost due to predation or food shortage (see
113 Wendeln et al. 2000). In about two third of the pairs breeding at this site (90 – 530 pairs) at least
114 one partner is marked with a transponder allowing life-long automatic recording (Becker and
115 Wendeln 1997, Becker et al. 2001, 2008a, b). Consequently, detailed information on non-
116 manipulated replacement clutches, individual quality, reproductive performance and other
117 traits is available over lifetime (e.g. Wendeln and Becker 1999, Becker et al. 2008a, Bauch et
118 al. 2010). Furthermore, high return rates and recording probabilities (Ezard et al. 2006,
119 Becker et al. 2008b) allow us to study those aspects of reneesting which have to our
120 knowledge not been addressed in birds to date and which exceed a reneesting event of an
121 individual beyond the year of its occurrence: by following the entire lives of many reneesting
122 and non-reneesting marked individuals we are able to elucidate possible consequences of
123 reneesting on survival, LRS, fitness and demography.

124

125 After shortly describing occurrence and characteristics of reneesting in this colony, we address
126 the following questions in this paper, firstly at the population level: (1) Does reneesting change
127 the productivity of the colony? (2) What is the proportion of offspring originating from
128 replacement clutches and later recruiting to the colony? And secondly at the individual level:
129 (3) What traits characterize reneesting individuals? (4) Do individuals increase their annual
130 und lifetime reproductive success by reneesting? (5) Are there differences in survival, lifespan
131 and in fitness between reneesting and non-reneesting Common Terns?

132

133 **Methods**

134

135 The long-term study was performed at the Common Tern colony “Banter See” from 1992 –
136 2009 (90 – 530 breeding pairs). The colony site is located in the harbour area of

137 Wilhelmshaven, German Wadden Sea coast (53°30'N, 08°06'E; see Becker 1996 for details),
138 where the Common Terns breed on six artificial islands of concrete, each about 5x11 m in
139 size with a distance of about 1 m between the islands. The nesting area of each island is filled
140 with gravel and surrounded by a wall 50 cm in height on which 44 resting sites are attached
141 (30x30x30 cm in size).

142

143 *Recording breeders and non-breeders:* For individual lifetime identification we used
144 subcutaneously injected passive transponders (Becker and Wendeln 1997) and marked all
145 fledglings since 1992 and 101 adults trapped on their nests in the years 1992 to 1995. The
146 individual code of the transponder is recorded by special antennas and readers that are
147 connected via a network with a host computer in an adjacent field station. Each year, all
148 clutches are checked systematically for transponder bearing birds by placing an antenna for 1-
149 2 days at each nest. Breeders as well as non-breeders are registered on the resting sites that are
150 equipped with antennas (number of antennas increased from 12 in 1993 to 44 in 2002). In the
151 year 2003 e.g., 653 marked common terns were identified. In this way, we were able to
152 calculate local return rates which are used as an estimator of survival rates, as recapture
153 probabilities are close to one (see Becker et al. 2008b for reliability of the bird registration
154 system). The sex of the birds was determined by observation of copulations, and since 1998 in
155 fledglings by standard molecular methods. Survival rates of adults and subadults and
156 recruitment rates are high in this colony (Ezard et al. 2006; Becker et al. 2008b). Most
157 individuals recruit at an age of three or four years to the colony after at least one year
158 prospecting at the colony site (Ludwig and Becker 2002).

159

160 *Arrival date and body mass:* The date of annual arrival refers to the first record of an
161 individual on the resting boxes at the colony site. In order to record body mass and identity of
162 breeders and non-breeders simultaneously, 8 - 16 resting boxes were equipped with electronic

163 balances together with antennas. The combined data are stored automatically. In this paper,
164 we use the average body mass of a bird during the first 4 days after arrival and the average
165 body mass during the period of incubation as parameters of its condition (see Wendeln and
166 Becker, 1996, 1999; Limmer & Becker 2007).

167
168 *Reproductive biology:* During colony visits every 2-3 days, data on breeding biology were
169 collected at each nest site: Laying date, clutch size, egg volume index (callipers, breadth² *
170 length), and number of fledglings pair⁻¹ (mean fledging age is 26 d, Becker and Wink 2003).
171 The data are assigned to the marked breeders recorded at the respective nest.

172
173 *Timing:* Arrival date and laying date are given as day of the year. Furthermore, the time
174 between arrival and laying was analysed (Ludwig and Becker 2006).

175
176 *Recording replacement clutches:* For this paper only information from marked breeders is
177 used: At least one partner of a pair had to be marked in order to identify a renesting event;
178 mate change between first breeding and renesting is an exception (Ludwig and Becker 2008).
179 The main data base used in this paper originates from birds that had lost their first clutch or
180 brood due to environmental conditions, especially to predation or food shortage, and either
181 laid a replacement clutch or not (cf. Wendeln et al. 2000; predation by Brown Rat *Rattus*
182 *norvegicus* 1996, Long-eared Owl *Asio otus* 1997-8, 2005; food shortage 2004-5, 2007-8).
183 Based on the reproductive outcome of marked mothers between 1992 and 2003 the proportion
184 of offspring originating from first and replacement clutches was calculated (fledglings,
185 prospectors, recruits; only 2% of recruits are older than 5 years when they are breeding for the
186 first time, Becker and Ludwigs 2002).

187
188 *Survival analysis*

189 *Effect of breeding status on survival until next year:* We defined two breeding status groups,
190 (1) individuals laying one (first) clutch (with successful reproduction = rearing at least one
191 fledgling; or with breeding failure, lower level of effort), and (2) individuals laying a
192 replacement clutch with additional effort. The first clutch with success is assumed to be at a
193 similar level of parental effort as the replacement clutch. We focused on seven years with
194 high proportions of breeding failure. Within each year survival rate was calculated for each
195 status group as follows: Survival rate to next year = No. of breeders in year i which are still
196 alive in year $(i+1)$ / No. of breeders in year i . For reasons of comparability, only individuals
197 who initiated the first clutch before end of May were included (see Fig 3). The independence
198 between survival and breeding status was tested by Fisher's exact test.

199

200 *Survival on lifetime scale:* The individual lifetime trajectories allow Kaplan-Meier and Cox
201 Regression analyses of survival and lifespan in reneesting and non-reneesting birds.

202 We grouped breeders by the number of replacement clutches during their life as follows: (a)
203 Non-reneesting birds: Individuals who only laid one first clutch during each breeding season;
204 this group includes birds who experienced no breeding failure during life and those who did
205 not relay after breeding failure; (b) reneesting birds: Individuals that laid at least one
206 replacement clutch during their lifetime. Kaplan-Meier analysis was used to examine the
207 effects of group (non-reneesting/reneesting) and gender on survival. A log rank test provided
208 overall tests on the equality of survival distributions.

209

210 We used three datasets (until year 2009): The basic dataset includes all breeders with known
211 gender, age and age at first breeding, born since 1989 whose entire reproductive trajectory is
212 known. Secondly, to exclude frail young breeders, a subset was selected including all breeders
213 ≥ 7 years of age and with a LRS of at least one fledgling. At an age of 7 years most breeders
214 are experienced (Limmer and Becker 2010). As a third dataset we used a subsample from the

215 renesting group, including only those individuals whose first renesting occurred before they
216 were 7 years old, to account for increasing probability of renesting with age.

217 In addition, we tested effects of covariates such as age and breeding status (first
218 clutch/replacement clutch) by Cox regression. Age at the replacement event is another
219 interesting covariate evaluated for the renesting events only.

220

221 *Recording lifespan, lifetime reproductive success and fitness:* We included individuals of
222 known age born since 1989 whose entire reproductive life trajectory was known, either life
223 was finished before the breeding season 2008 or the individual was alive in 2008. Both groups
224 were used to analyse lifespan. Individuals with completed lives before 2008 were the basis of
225 evaluating LRS and the contributions of renesting, those individuals with completed lives
226 until 2005 were the basis of evaluating LRS and fitness (no. of prospectors or recruits to the
227 colony; recruitment, however, is not completed and preliminary up to 2008, when the recruits
228 from 2005 are three years old; see Ludwigs and Becker 2002). Values of reproductive success
229 are presented on the individual level (offspring pair⁻¹/2). Individuals' lives were grouped to
230 those without renesting events, and with ≥ 1 replacement clutch.

231

232

233 *Statistical analyses:* These were performed with SPSS17 and R. According to the
234 assumptions, either parametric (GLM, t-test for related samples), or non-parametric tests were
235 used (Spearman rank correlation, Mann Whitney test, Wilcoxon test for related samples). To
236 test for effects of laying date and age on the probability to reneest, a logistic regression was
237 used (forward stepwise, likelihood ratio; including laying date, age and age*laying date as
238 covariates). Tests are two-tailed, and level of significance was set to $p \leq 0.05$. If not otherwise
239 stated, values are given as means ± 1 SE.

240

241 **Results**

242 **Relaying activity and success of replacement clutches**

243

244 The overall proportion of replacement clutches was 9.1 % for the total study period (n=2939
245 pair-years, Fig. 1). Proportions of relaying pairs were higher than average in seven of the 17
246 years under study reaching levels between 10.6 % and 22.4 % of the pairs (1996-1998, 2004,
247 2005, 2007, 2008). These years were characterized by low reproductive success.

248 Consequently, the proportion of reneesting pairs was negatively correlated with the annual
249 reproductive success of the colony ($r_s = -0.777$, $p < 0.001$, $n = 17$).

250

251 Replacement clutches were nearly as successful as first clutches (Fig. 2). Only in 2005
252 ($p = 0.001$) and 2008 ($p = 0.011$; Mann Whitney test) reneesting pairs produced significantly
253 fewer fledglings per clutch than conspecifics in their first breeding attempt. The average
254 annual reproductive success did not differ significantly between pairs with a first clutch
255 (excluding the clutches of reneesting conspecifics) and pairs which laid a replacement clutch
256 (0.60 ± 0.03 vs. 0.49 ± 0.06 fledglings pair⁻¹ year⁻¹; Mann-Whitney test $z = -0.702$, $p = 0.482$,
257 $n = 7$ years).

258

259 Did reneesting pairs increase their annual reproductive output by a replacement clutch? After
260 loss of their first clutch, the reneesting pairs increased their individual reproductive output
261 significantly in five out of the seven years by producing fledglings from replacement clutches
262 (cf. Fig. 2; 1996 $p = 0.007$, 1997 $p = 0.041$, 1998 $p = 0.005$, 2004 $p = 0.001$, 2007 $p = 0.001$, 2008
263 $p = 0.002$; Wilcoxon one-tailed tests for related samples). Only in the very poor season of 2005
264 there was no improvement at all, when all replacement clutches such as the 1st clutches of the
265 reneesting pairs failed. The average increase of reproductive success of the reneesting pairs was

266 0.40 ± 0.05 fledglings renesting pair⁻¹ year⁻¹ (Wilcoxon test, $z = -6.992$, $p = 0.001$, $n = 187$; cf.
267 Fig. 1).

268

269 **Does renesting change the average productivity of the colony?**

270

271 During the years of high renesting activities (see above and Fig. 1) the additional productivity
272 by renesting caused only a small increase in the colony mean, from 0.52 ± 0.09 to 0.59 ± 0.10
273 fledglings pair⁻¹ year⁻¹. Considering the entire study period from 1992 to 2008, the change in
274 productivity by renesting was even smaller: Assuming no renesting at all by birds whose 1st
275 clutch had failed, the productivity would have been reduced by just 0.04 fledglings pair⁻¹ year⁻¹
276 ¹ (productivity including renesting 0.97 ± 0.15 vs 0.93 ± 0.15 fledglings pair⁻¹ year⁻¹, $n = 17$
277 years).

278

279 **Proportion of offspring and colony members originating from replacement clutches**

280

281 Among the offspring produced by mothers from 1992 – 2003, only 4.5 % of fledglings
282 ($n = 984$) had their origin in replacement clutches (representing 7.3% of the clutches included,
283 $n = 995$). As return and recruitment rates did not differ between fledglings from first and
284 replacement clutches ($\text{Chi}^2 = 0.812$, n.s.; $\text{df} = 2$, $n = 984$), the proportion of natal birds in these
285 status groups was similar among first and replacement clutches, too (4.1 % of the prospectors,
286 $n = 406$, and 4.4 % of the recruits, $n = 275$, stemmed from replacement clutches).

287

288 **What traits characterize renesting individuals?**

289

290 94.6 % of the renesting females did lay their first clutch from end of April until end of May
291 (until pentad 30, $n = 111$, Fig. 3). The relationship between laying date of the first clutch and

292 renesting probability in females who started laying before end of May and had lost the 1st
293 clutch or the chicks was checked by a logistic regression. The model showed a decreasing
294 probability of relaying with advancing laying date ($\beta = -0.206$, Wald 52.95, $p < 0.001$, $n = 344$;
295 interaction age * laying date $\beta = 0.001$, Wald 11.57, $p < 0.001$; age n.s.).

296

297 Comparing individuals whose first breeding attempt failed and was initiated before end of
298 May (Table 1), we found that renesting individuals were older, showed an earlier arrival by
299 5.3 d, started laying earlier by 7.8 d (females) and had a higher incubation mass by 5g than
300 failed individuals which did not reneest. These differences were significant also in most of the
301 seven single years under study. Gender, however, showed no significant effects in each
302 parameter if it replaced the individual as random effect. The other parameters, however, body
303 mass at arrival, clutch size, egg volume index of the first clutch and the time interval between
304 arrival and laying, showed no significant differences dependent on the renesting decision.

305

306

307 **Are there differences in survival and lifespan between renesting and non-renesting**

308 **Common Terns?**

309

310 *Survival to next year:* The individuals with replacement clutch had similar survival rates from
311 year x to year $x+1$ to individuals without replacement clutch, whether the latter had
312 reproductive success in the first clutch or not (Table 2).

313

314 *Cumulative survival and lifespan:* Focussing on the entire lifetime, lifespan of non-renesting
315 birds was shorter than that of individuals with at least one renesting event during life, which is
316 estimated by the Kaplan-Meier method ($n = 670$ breeders; 7.9 ± 0.3 years vs. 13.2 ± 0.5 years
317 of age; log-rank test, $\text{Chi}^2 = 125.92$, $p < 0.001$). This difference in lifespan holds true also for

318 those birds who reared at least one fledgling and reached an age of at least 7 years (n=366;
319 11.6 ± 0.4 years vs. 14.1 ± 0.5 years of age, $\text{Chi}^2 = 20.06$, $p < 0.001$). However, these
320 differences could be affected by an increasing probability of breeding failure and laying a
321 replacement clutch with age (the average age of laying a replacement clutch at the first time
322 during life is 7 years). To take that into account, we performed a second comparison including
323 only those individuals whose first reneating occurred before they were 7 years old. Again, the
324 reneating individuals had a significantly higher lifespan than the non-reneating conspecifics
325 (n=546 breeders, non-reneating birds 7.9 ± 0.3 years, see above; reneating birds 11.6 ± 0.5
326 years, $\text{Chi}^2 = 46.684$, $\text{df}=1$, $p < 0.001$; Fig. 4). 37.0% of the breeders (n=670) had produced at
327 least one replacement clutch during life. Gender showed no effect on lifespan ($p=0.251$).

328

329 To recognize possible effects of age and replacement event on survival of reneating birds we
330 used the bird-year data set and individuals with at least three years of breeding experience
331 (n=1695 bird-years). The Cox regression revealed that to get older one year did lead to 0.3
332 units of increase in hazard ($\text{exp}(\beta)=1.304$, $p=0.045$), and the hazard of a replacement event
333 was 2.1 times that of a first clutch ($\text{exp}(\beta)=2.106$, $p < 0.001$). In addition, if we only focus on
334 replacement events, the age of an individual at a reneating event had no significant influence
335 on survival (n=358, $\beta=0.276$, $p=0.215$).

336

337 **Do individuals increase lifetime reproductive success and fitness by reneating?**

338

339 The average annual reproductive success was slightly higher (n.s.) in individuals with at least
340 one reneating event during life compared to non-reneating individuals (Table 3). Within a
341 shorter lifespan the non-reneating individuals had produced 2.2 ± 0.2 fledglings, the reneating
342 individuals 2.7 ± 0.2 fledglings from their first clutches alone. Recognizing the supplementary
343 reproductive output from their replacement clutches, however, reneating individuals did

344 increase their lifetime reproductive success by 0.3 fledglings, or by 16.0 % on average (Table
345 3). In consequence, they arrived at a significantly higher lifetime reproductive success than
346 birds without replacement clutches.

347
348 In order to address the question whether the higher lifetime reproductive success of reneating
349 individuals also affects their fitness, we used a sample of individuals whose entire lives were
350 known and finished after 2005. We analysed no. of fledglings, prospectors and recruits they
351 had produced depending on reneating or not during their lives. In all breeders, reneating birds
352 reached longer lifespan (7.1 ± 0.2 vs 8.4 ± 0.4 years, $F_{1,142}=11.061$, $p<0.001$), more
353 fledglings, prospectors and finally recruits (Fig. 5) than the non-reneating conspecifics (no
354 significant gender effects).

355
356

357 **Discussion**

358
359 The results of this long-term study revealed that reneating in the Common Tern had only
360 minor effects on demography of the colony, but major importance at the individual level and
361 in the life-history perspective. Extra egg production by replacement breeders was found to
362 cause no disadvantage in terms of survival or future reproduction but is actually an indicator
363 of high individual quality and fitness.

364
365 Despite some years with high proportions of failed first breeding attempts by stochastic
366 events, the proportion of pairs relaying remained relatively low compared with other species
367 (Amat et al. 1999, Arnold et al. 2010): Only about one quarter of the pairs whose first clutch
368 or brood had failed, relayed, and almost all of these pairs had initiated the first clutch early in
369 the season. During this period the probability of relaying decreased with delayed laying date
370 of the first clutch (see below, Hipfner 1999, Arnold et al. 2010). Furthermore, relaying

371 propensity is influenced by the time a pair had spent to care for the clutch or brood prior to its
372 loss (de Forest and Gaston 1996, Hipfner et al. 1999, Wendeln et al. 2000); this, however, as
373 well as the timing of the replacement clutches itself were not subject of this study.

374

375 **Effects of renesting on productivity**

376 In most years, replacement clutches were as successful as first clutches (as found in the
377 Brännich's Guillemot, Hipfner 1999). One reason for that is that renesting Common Terns
378 had a higher fledging success than contemporaneous late - laying first time breeders (Wendeln
379 et al. 2000, Arnold et al. 2004). Furthermore, young from replacement clutches had no
380 reduced survival rates compared with young from first clutches, until they return to the colony
381 mostly at the age of two years (Ludwigs and Becker 2002). One reason for this is that
382 hatching or fledging date has no influence on subadult survival in the Common Tern (Nisbet
383 1996, Ludwigs and Becker 2006, Braasch et al. 2009). Together with the high reproductive
384 success of relaying pairs the comparably high survival rates of their young arising from
385 replacement clutches indicate that relaying individuals are parents of high quality (see below).

386

387 Because of the low proportion of relaying pairs among colony members, their often successful
388 replacement breeding attempts only had a minor impact on the annual productivity of the
389 colony. Over the study period, an increase in productivity through relaying by 0.04 fledglings
390 per year is a very low figure, which in most studies would be masked by the noise of
391 recording reproductive success and hardly affect population growth. The low figure of 4.5 %
392 of natal recruits arising from replacement clutches underlines that the influence of relaying on
393 demography is minor. This is in contrast to other species, e.g. the Mallard, with major
394 contributions of renesting to annual productivity (Arnold et al. 2010).

395

396 **Characterization of renesting individuals**

397 At the individual level, however, re-nesting is of great importance to reproductive success.
398 Common Terns allocate high levels of parental care to replacement clutches (clutch size, high
399 effort measured by body mass change within individuals, Wendeln et al. 2000; high fledging
400 success, Arnold et al. 2004, this study). Several studies on long-lived bird species indicate that
401 long-term reproductive performance is linked to individual quality (e.g. Wendeln and Becker
402 1999, Barbraud and Weimerskirch 2006, McCleery et al. 2008, Sanz-Aguilar et al. 2008,
403 Aubry et al. 2009). We were able to compare several phenotypic traits characterizing
404 individual quality between relaying and non-relaying: The relaying birds were found to be the
405 older individuals (Wooller 1980, Wheelwright and Shultz 1994, but see Arnold et al. 2004 for
406 the Common Tern). With respect to timing, re-nesting birds were characterized by a five day
407 earlier arrival, an eight days earlier laying (cf. Kelly and van Horne 1997, Antzack et al. 2009,
408 Arnold et al. 2010) and by the tendency to reduce the time span between arrival and laying.
409 Arrival and laying date are strongly age dependent in the Common Tern (González-Solís et al.
410 2004, Ezard et al. 2007, Becker et al. 2008a) and other species (Brünnich's Guillemot,
411 Hipfner et al. 1997; Mute Swan, McCleery et al. 2008). However, as the logistic regression
412 reveals, the time when the first clutch was initiated was more important for the probability of
413 relaying than age per se.

414
415 Body mass is a measure of condition in the Common Tern and other small seabird species and
416 is linked to individual quality and reproductive success (Common Tern, Wendeln and Becker
417 1999, Blue Petrel *Halobaena caerulea*, Barbraud and Weimerskirch 2006, Puffin *Fratercula*
418 *arctica*, Erikstad et al. 2009). While mass recorded after arrival at the colony site did not
419 differ among relaying and non-relaying individuals, mass during incubation of the first clutch
420 was higher in relaying birds. No differences between relaying and non-relaying females were
421 apparent with respect to the reproductive parameters of clutch and egg size of the first clutch.
422 The phenotypic traits measured are linked with fitness components and indicate that relaying

423 birds were individuals of higher individual quality (cf. Hipfner 1999, Arnold et al. 2010),
424 characterized by older age, earlier arrival and laying as well as higher body mass than non-
425 relaying individuals.

426
427
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429

Do replacement clutches cause survival costs?

430 In none of the seven years with elevated replacement clutch production did individuals with a
431 replacement clutch in year x experience reduced survival to year $x+1$ compared to birds that
432 spent their effort on only one clutch or brood. Moreover, our longitudinal analyses of hazard
433 show: Individuals that had produced one or more replacement clutches during their breeding
434 career were characterized by lower hazard and higher lifespan than non-renesting individuals,
435 giving no indication of any survival costs in relation to reneating activity. The additional
436 studies of birds whose lives were completed corroborate this by showing that reneating
437 Common Terns had a significantly longer lifespan than non-reneating conspecifics, even if
438 frail and unsuccessful individuals dying soon after recruitment were excluded from the
439 analysis.

440

441 Mean lifespan of the groups investigated is close to that for a Common Tern population
442 (about 10 years, Nisbet and Cam 2002, Ezard et al. 2006); nevertheless we assume that the
443 difference in lifespan among reneating and non-reneating individuals might increase towards
444 the levels indicated by the Kaplan-Meier analysis (Fig. 4) covering also very old birds. The
445 age at a reneating event itself had no effect on the hazard, which was enlarged, however, by a
446 replacement clutch compared to the first clutch. But in comparison with non-reneating birds
447 this additional hazard by the reneating event had no visible consequence because survival of
448 reneating birds was constantly higher over life. The finding that survival was not negatively
449 affected by reneating indicates that delayed and long-term survival costs of laying extra eggs may

450 also be limited on a lifetime scale (cf. Kalmbach 2004). Further studies on long-lived seabirds
451 stress the importance of bird quality and suggest that even an increased input in reproduction may
452 have rather limited impact on survival, if individuals adjust their parental investment in a
453 flexible way according to their individual quality (Sanz-Aguilar et al. 2008, Erikstad et al.
454 2009).

455

456 **Is renesting in the Common Tern linked with costs of future reproduction?**

457 As in survival we found no evidence of this. Besides the increase of a breeder's annual
458 reproductive success by a replacement clutch, also in the lifetime perspective fitness
459 components show that renesting individuals were more productive than non-renesting
460 conspecifics. Neither the mean annual reproductive output of relaying individuals nor their
461 mean number of fledglings from first clutches (marginally significant) was higher than in non-
462 renesting conspecifics. Nevertheless these elevated values may indicate the tendency that
463 relaying birds are in general more productive irrespective of their renesting attempts.
464 However, the significantly higher LRS of renesting birds was due to both the additional
465 productivity from relaying and to their longer lifespan, a result independent of excluding frail
466 or unsuccessful breeders (Table 3, Fig. 5).

467

468 Since return and recruitment rates of young from first and replacement clutches were similar (see
469 above), it follows that the differences in LRS persisted at the level of subadults returned to the
470 colony as well as of recruits as direct measure of fitness. Thus renesting individuals were favoured
471 by selection and contributed more young to the next generation than non-renesting Common
472 Terns. The number of recruits from renesting birds (Fig. 5) is in the range of an individual's
473 contribution to the next generation sufficient to replace an individual in the population at the given
474 vital rates under the present environmental conditions (cf. Ezard et al. 2006).

475
476 Thus, in the situation of the “natural experiment of relaying”, Common Terns produced extra
477 eggs but did neither suffer from a reduced reproductive success in the same breeding season in
478 most years with high renesting activity, nor from an increased mortality up to the next breeding
479 season or beyond this. For understanding this apparent contradiction to the reproductive cost
480 hypothesis it is necessary to focus on the mechanisms that mediate between reproductive effort
481 and survival in terns. The absence of a survival cost owing to renesting suggests that the birds'
482 condition did not reach a critical level at the end of the breeding season. The physiological state of
483 a bird depends on the modus of energy acquisition for reproduction. Gulls e.g. rely on a
484 combination of stored reserves and dietary intake (Bolton et al., 1992, 1993). Increased effort will
485 deplete body reserves and a recovery in nutritional state during incubation is a slow process
486 (Houston et al. 1983) also in terns (Bauch et al. 2010), with a potential of increasing the subsequent
487 mortality risk (Nager et al. 2001). In contrast, in birds relying only on energy acquired recently,
488 the costs may not be reflected in the future survival probabilities of parents (Sibley and Calow
489 1986). Common Terns are rather income than capital breeders: they perform extensive courtship
490 feeding prior to laying (Nisbet 1973, Wendeln 1997) and do not store reserves; body mass
491 increase is restricted to the week before laying and dependent on courtship feedings (Wendeln
492 and Becker 1996). Hence, the body condition of Common Terns in the course of the breeding
493 season depends most probably on the balance between energy expenditure and current food
494 intake, but to a very limited extent to the energy stored.

495
496 This independence of stored reserves could explain the lack of survival costs in the Common
497 Tern and other species (Kalmbach et al. 2004). Environmental variability is known to influence
498 reproductive effort and costs in long-lived birds (Erikstad et al. 1998, 2009) and it has been
499 suggested that costs may only be detectable in poor years (e.g. Bell and Koufopanou 1986,
500 Verhulst 1998, Wernham and Bryant 1998, Kalmbach et al. 2004). We cannot exclude that when

501 the access to food is limited, Common Terns would exhibit survival costs after reneating
502 activities. However, significant inter-year differences in fledging success in the respective years of
503 this study indicate that the study contained 'average' as well as 'poor' years (Fig. 2).

504 From his study on Brünnich's Guillemots Hipfner (1999) derived the conclusion that relaying,
505 adherent to laying late and departing late, inflicts relatively little additional costs. This is
506 confirmed by other studies proving the "quality" hypothesis (see Introduction, Verhulst and
507 Nilsson 2008, Kentish Plover *Charadrius hiaticula*, Amat et al. 1999; Kittiwake, Aubry et al.
508 2009) as well as by this study: Our data suggest that in non-manipulative situations birds adjust
509 their effort according to their own capacity without increasing the risk of mortality or decline
510 in future fecundity. This relationship is shown here on the annual and even corroborated on
511 the lifetime scale. Hence, the ability to withstand increased reproductive demands as induced by
512 reneating may be state-dependent (McNamara and Houston, 1996) and varying with individual
513 quality. Indeed, relaying birds were characterized by traits related to high intrinsic quality
514 enabling them to cope with the strains of producing and caring for additional eggs (Wendeln
515 et al. 2000). As with seasonal declines in clutch size in many species of birds or in the
516 proportion of pairs that attempt second broods (e.g. Great Tit *Parus major*, Verboven and
517 Verhulst 1996, Coot *Fulica atra*, Brinkhof et al. 2002), the relatively small and seasonally
518 declining proportion of relaying pairs might be an evolutionary safeguard to the reduced
519 fitness of late breeding poor quality adults and also of late fledged young (Hipfner 1999).

520

521 **Renesting in the life history perspective**

522 Our finding that reneating Common Terns are the more successful individuals - in units of
523 fitness – than those without reneating events in their life is in line with the positive link of
524 phenotypic traits and fitness components, as between body condition and reproductive
525 success (Wendeln and Becker 1999) or survival (Arnold et al. 2006), or between

526 reproductive success and survival (Arnold et al. 2006, Rebke et al. 2010). Positive
527 associations between an individual's annual reproductive performance or its LRS with
528 survival or lifespan were found in various studies accumulating in recent years (e.g. Black-
529 legged Kittiwake, Coulson and Porter 1985, Cam et al. 2002; Mute Swans *Cygnus olor*,
530 McCleery et al. 2008; Short-tailed Shearwater *Puffinus tenuirostris*, Bradley et al. 2000; Blue
531 Petrel, Barbraud and Weimerskirch 2005; Storm Petrels *Hydrobates pelagicus*, Sanz-Aguilar
532 et al. 2008). Costs, however, reflected by negative correlations between survival and
533 reproduction are rarely reported and restricted to young, inexperienced individuals during the
534 early breeding career (e.g. Chough *Pyrrhocorax pyrrhocorax*, Reid et al. 2003, Goshawk *Accipiter*
535 *gentilis*, Krüger 2005, Great Tit, Bouwhuis et al. 2009).

536

537 These findings support the “heterogeneity in individual quality” hypothesis (e.g. Aubry et al.
538 2009). In accordance with some of the studies cited above which cover the entire reproductive
539 career of individual birds, our present study shows that between-individual differences are
540 consistent over life: Individuals remained in the same part of the phenotype distribution
541 throughout life, and showed strong correlation of parameters over life, even if there is
542 considerable within-individual change during lifetime in traits relevant for fitness (Ezard et al.
543 2007, Limmer and Becker 2007, 2010, Rebke et al. 2010). High quality individuals characterized
544 by an advantageous set of inherent traits (fixed heterogeneity) are favoured by selection with the
545 consequence of positive links between various fitness components. This concept, however, is
546 under recent debate and some authors are favoring dynamic heterogeneity as mechanism
547 sufficient to explain inter-individual variability (Tuljapurkar et al. 2009, Steiner et al. 2010).

548

549 In conclusion, only those Common Terns do relay that can cope with the additional effort
550 needed to produce extra eggs and to care for a replacement clutch. Several traits measured in
551 this study document that relaying Common Terns are individuals of higher individual quality

552 than non-relaying breeders. Lifespan and fitness of the latter are reduced presumably because
 553 of selective disappearance of poor quality breeders. Evidently the benefits exceed the costs to
 554 be paid by relaying, and neither reduced care for the replacement clutch nor a decrease in
 555 survival nor in future reproductive output were found. In fact we infer that those individuals
 556 whose lifetime is characterized by renesting events exhibit higher fitness prospects.

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 559

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568

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- 741
- 742

743 Table 1: Characteristics of individuals which produced a replacement clutch or not. Only
 744 years with more than 10% replacement clutches (see Fig. 1) and individuals which started the
 745 first clutch before 30 May are included (cf. Fig. 3). Reproductive parameters are analysed
 746 only for females. For mass during incubation and clutch size, Mann-Whitney's U-test is used.
 747 Otherwise GLM with the fixed effects of replacement or not, year and interaction
 748 year*replacement, and with individual as random effect was used (age as log₁₀ values).
 749 Significant differences are given bold.
 750

Parameter	Replacement Clutch		F _{df} ; z	P
	Yes	No		
<i>All individuals</i>				
Age (years)	8.0±0.2 (n=195)	6.3±0.1 (n=469)	F _{1,219} =12.653 ^{1,3}	0.000
Arrival Date	115.6±0.5 (n=203)	120.3±0.3 (n=439)	F _{1,209} =19.012 ^{1,4}	0.000
Mass at Arrival (g)	132.4±0.9 (n=105)	131.7±0.6 (n=209)	F _{1,60} =0.078 ^{2,5}	0.781
Mass during Incubation (g)	136.9±1.6 (n=20)	131.9±1.5 (n=26)	z=-2.153	0.031
<i>Females</i>				
Time between arrival and laying (d)	21.6±0.5 (n=100)	23.7±0.4 (n=218)	F _{1,96} =1.843 ¹	0.429
Laying date	135.1±0.6 (n=111)	142.9±0.3 (n=233)	F _{1,108} =13.251 ¹	0.000
Clutch Size	2.61±0.06 (n=111)	2.61±0.04 (n=233)	z=-0.617	0.537
Egg Volume Index	38.8±0.2 (n=108)	38.6±0.2 (n=231)	F _{1,117} =0.138 ²	0.711

751 ¹ Significant effect of year and interaction year*replacement; ² year effect and interaction not significant; in all
 752 GLM-tests, individual as random effect was highly significant; ³⁻⁵ effect of gender as fixed effect used instead of
 753 individual (random effect) in an alternative model: ³ F_{1,655}=0.372, p=0.542; ⁴ F_{1,627}=23.699, p<0.001 (females
 754 arrived earlier than males); ⁵ F_{1,305}=0.388, p=0.534
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 759

760 Table 2: Survival rates from year x to year x+1 in Common Terns laying a first clutch (with
 761 and without reproductive success) and those laying both a first clutch and a replacement
 762 clutch (cf. Fig. 1). Only pairs who started their first breeding attempts until 30 May, are
 763 included.

Year X	Survial rate to year x+1 (n)			Fisher´s exact test
	No replacement without success	No replacement with success	Replacement	p-value
1996	0.85 (20)	0.88 (33)	0.96 (24)	0.463
1997	0.95 (20)	0.92 (53)	1.00 (13)	0.825
1998	0.95 (44)	0.98 (46)	0.91 (22)	0.342
2004	0.87 (168)	0.86 (80)	0.85 (48)	0.945
2005	0.89 (173)	0.96 (52)	0.92 (61)	0.306
2007	0.84 (123)	0.82 (148)	0.80 (44)	0.806
2008	0.90 (73)	0.88 (174)	0.97 (30)	0.388

764
 765

766 Table 3: Lifespan, annual and lifetime reproductive success (fledglings individual⁻¹) in
 767 Common Terns who had completed their life until 2007, reached at least 7 years of age and
 768 had produced at least one fledgling during life. GLM, with reneating decision and gender as
 769 fixed effects; the gender effect was not significant.

770

Reproductive Output	Non-reneating (n=91)	Renesting (n=66)	F _{1,153}	p
Lifespan (years)	8.8 ± 0.2	9.9 ± 0.3	12.305	0.001
Fledglings year ⁻¹	0.30 ± 0.02	0.33 ± 0.02	0.937	0.335
No. fledglings from 1 st clutch	2.2 ± 0.2	2.7 ± 0.2	2.540	0.113
Total No. Fledglings	2.2 ± 0.2	3.0 ± 0.2	7.146	0.008

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773 Figure Legends

774

775 Fig. 1: Proportion of renesting pairs in the Banter See colony from 1992 – 2008 (2939 pair-
776 years with at least one individual marked).

777

778 Fig. 2: Comparison of the breeding success from first clutches (without renesting pairs,
779 circles) and replacement clutches (dots) during seven years characterized by proportions of
780 more than 10% of pairs renesting. Pair-years first clutch n=1146, replacement clutch n=192; *
781 $p \leq 0.05$, *** $p \leq 0.001$, Mann Whitney test.

782

783 Fig. 3: Laying pattern of first clutches in females who renested (black columns) or not (grey
784 columns; n=493; data from 7 years with high proportions of renesting, cf. Fig. 1) after failure
785 of the first clutch. Laying date is grouped to pentads (5d periods of the year).

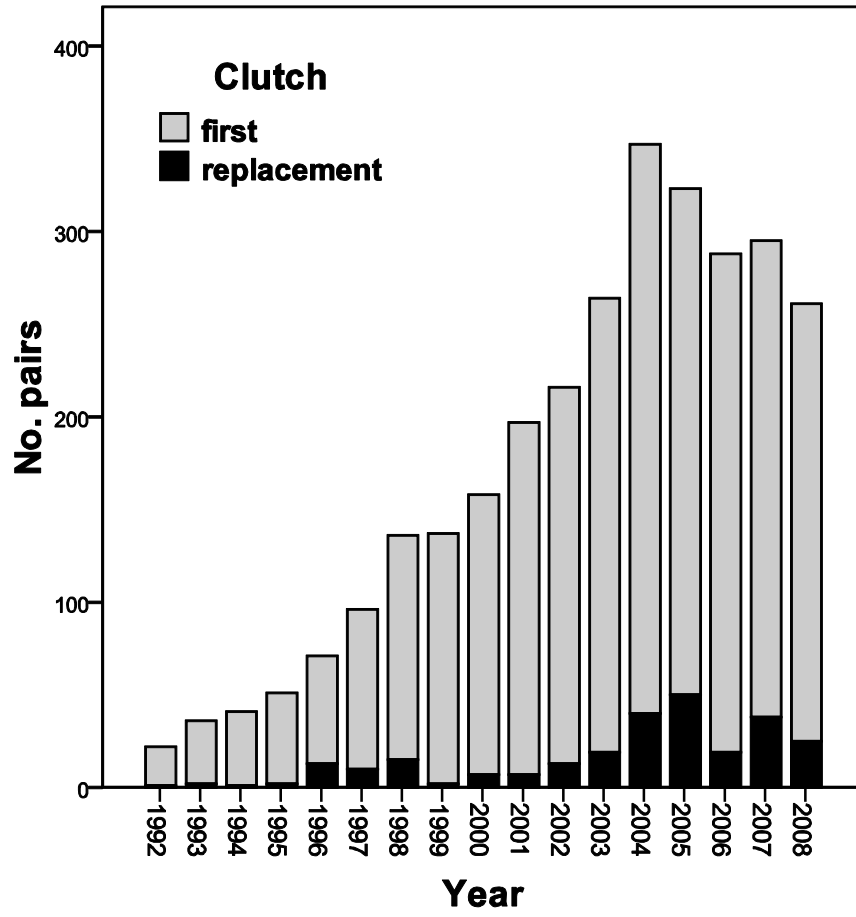
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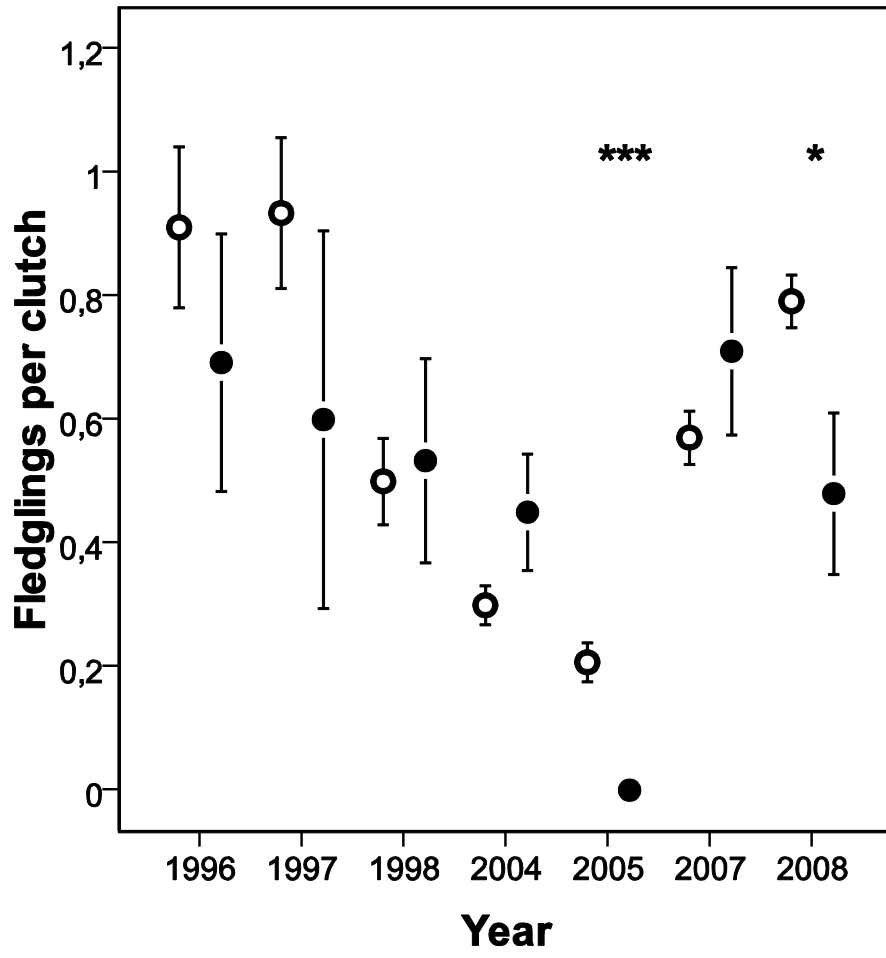
787 Fig. 4: Comparison of cumulative survival rates between non-renesting (n=422) and renesting
788 breeders (n=124) with first renesting < 7 years of age (Kaplan-Meier). Individuals with
789 replacement clutch are represented by the black lines, those without replacement clutch by the
790 grey lines. Dashed lines show 95% confidence intervals. These do not overlap, which
791 indicates that renesting birds do have significant higher survival rates than non-renesting
792 birds.

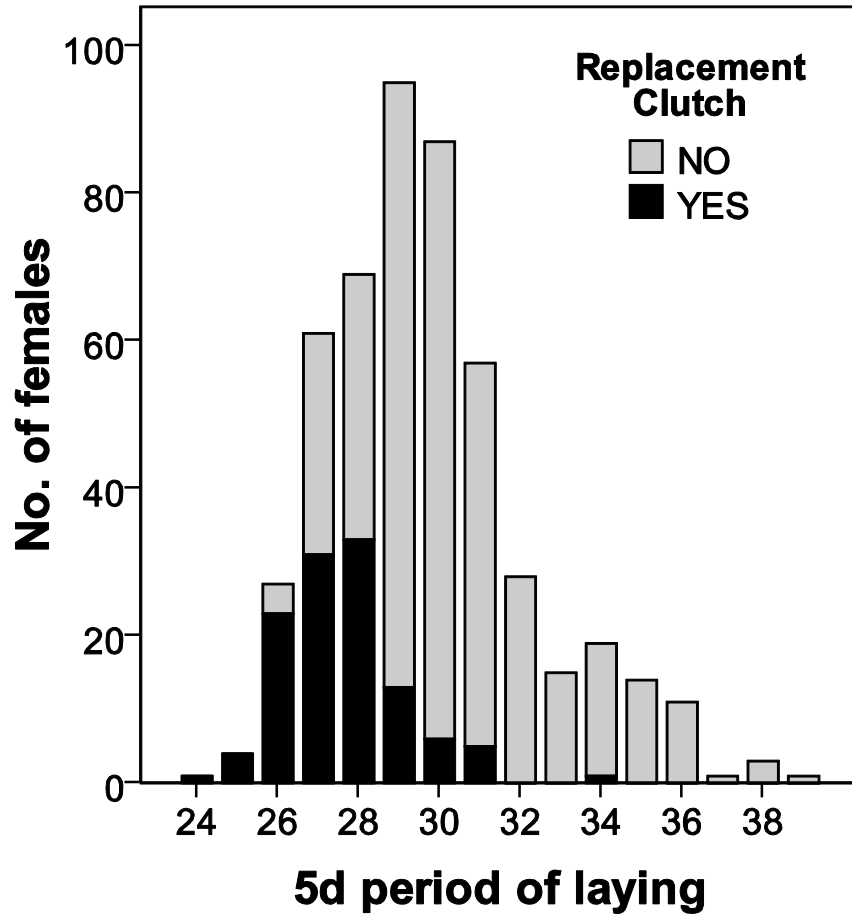
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794 Fig. 5: Lifetime reproductive success and fitness of Common Terns with completed lives
795 (1989-2005). No. of offspring per individual life, dependent on renesting or non-renesting. P-
796 values from GLM (gender had no significant effect, respectively).

797







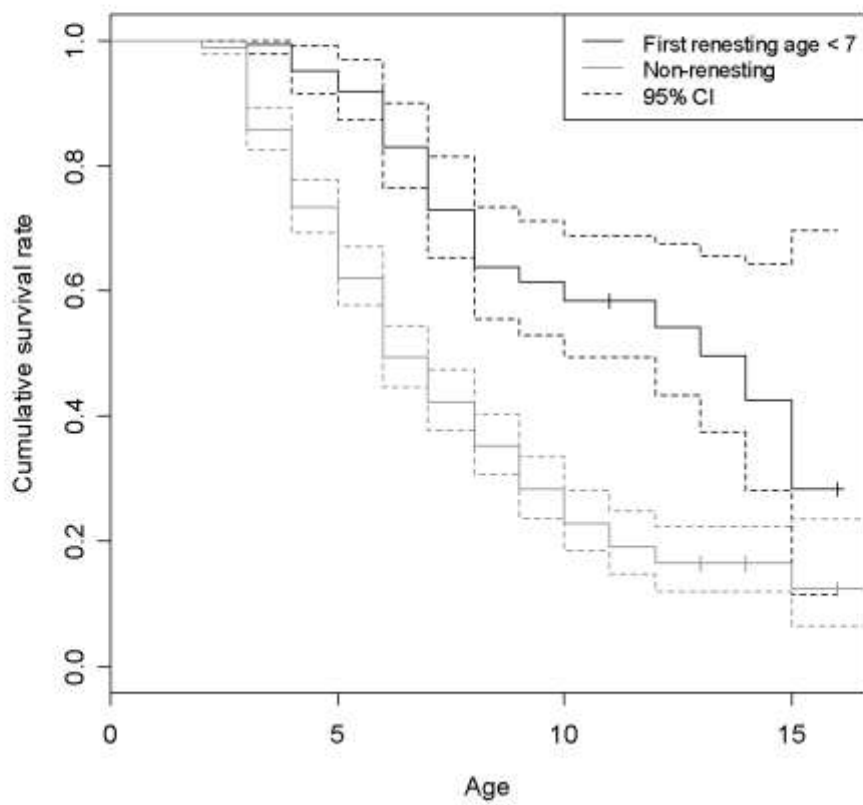


Fig. 4

