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TITLE PAGE

**Short title:**

Colony size effects on reproductive success

**Title:**

Costs and benefits of colony size vary during the breeding cycle in Black-headed Gulls

*Chroicocephalus ridibundus*

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**Abstract**

We studied the effects of colony size on individual reproductive success in a multi-site population of Black-headed Gulls where colony size ranged from 10 to 5000 pairs. By focusing on family size, the number of chicks attended by individually marked parents, and accounting for between-individual variation, we detected a negative colony-size effect during the very first days of life of the chicks that was compensated by a subsequent increase in the proportion of surviving chicks with colony size. We suggest that this result originates in the interplay between overcrowding costs acting on hatching success, and benefits of colonial breeding, most probably more efficient food-searching (foraging enhancement), acting on chicks' survival. However, the frequency of complete colony failure increased with decreasing colony size. Taking this hazard risk into account yielded a corrected estimate of the effect of colony size on breeding success, and indicated that the largest colonies were the most productive. This pattern is congruent with the previous finding that larger colonies are more attractive to dispersing breeders.

**Key-words:**

Breeding success; *Chroicocephalus ridibundus*; Coloniality; Density-dependence; Fecundity; *Larus*.

## 1 **Introduction**

2 Colonial breeding (breeding in high-density sites exempt of feeding resources with territories  
3 limited to the nest area) is quite widespread in birds and especially in seabirds. One of the  
4 striking patterns is the sheer variation that exists in colony size. A recurrent question among  
5 ornithologists is whether this variation simply reflects variation in ecological conditions  
6 (distribution of resources, availability of nest sites, etc.) or whether the choice to settle in a  
7 colony of a given size is a trait subject to selection. These questions are generally addressed  
8 by studying variation in reproductive success (*RS*), which appears to be a useful metric to  
9 study the fitness consequences and ecological correlates of colony size (but see Danchin and  
10 Wagner 1997).

11 In colonial birds, especially in Charadriiforms, provisioning rate is often considered  
12 among the main determinants of reproductive success (Uttley et al. 1994; Jodice et al. 2006;  
13 see also Graves et al. 1984; Hamer et al. 1993; Sadoul et al. 1996; van Dijk et al. 2009).  
14 Provisioning rate depends on foraging success, which is known to be enhanced *via*  
15 information exchange between conspecifics foraging in the same area (Ward and Zahavi  
16 1973; Clark and Mangel 1984; Richner and Heeb 1995; Brown and Bomberger Brown 1996;  
17 see further detail in the discussion section). Provisioning rate is therefore expected to increase  
18 with conspecific density on the foraging grounds (Pöysä 1992), and, as the density of foraging  
19 individuals increases around large colonies (Brandl and Gorke 1988), we expect an enhanced  
20 reproductive success in large colonies. However, some studies indicate the opposite effect,  
21 i.e., that competition forces individuals from large colonies to travel further and longer to find  
22 food than individuals from small colonies (Lewis et al. 2006), sometimes to the point where  
23 colony size negatively impacts on body condition of both adults and chicks (Santema et al.  
24 2009). Furthermore, competition is only one of the known or supposed costs of breeding in  
25 large colonies. These costs also include higher rate of transmission of disease and parasites,

26 higher levels of aggression and antagonistic behaviours, etc. (Brown and Bomberger Brown  
27 1996; Danchin and Wagner 1997).

28 It is thus not surprising that, among the large number of studies reviewed by Brown  
29 and Bomberger Brown (1996, p321-323), every pattern of variation in *RS* with colony size  
30 can be found, from no effect to a directional trend for a benefit to the largest or smallest  
31 colonies through a non linear effect with an optimal colony size. This variation among studies  
32 suggests that (*i*) the costs and benefits of colonial breeding are not the same in different  
33 systems and/or (*ii*) the observed patterns depend on the *RS* variable used and on the stage of  
34 the breeding season that is under study (proportion of failed nests, average clutch size,  
35 average number of fledglings per breeding pair, fledgling survival, etc.).

36 Our aim in this paper is to contribute to these debates by studying colony size effects  
37 on *RS* in a Black-headed Gull *Chroicocephalus ridibundus* (BHG) multisite population  
38 presenting a contrasted distribution of colony sizes. Indeed a single, large colony concentrated  
39 most pairs and increased in size during the study period (from around 2000 to around 5000  
40 pairs), whereas several small colonies (numbering on average 163 pairs  $\pm$ 171) decreased in  
41 both number and total size. More precisely, we examined (*i*) how the costs and benefits of  
42 colony size interacted throughout chicks' development and (*ii*) whether a potential cost of  
43 breeding in small colonies could have driven the aggregation of breeders in the largest colony.  
44 Although BHG are known to occasionally breed as solitary pairs there was no such record in  
45 the dataset. We therefore did not contrast solitary vs. colonial breeding in this study but we  
46 investigated the costs/benefits of colony size.

47 The data we used for that purpose was the family size, i.e. the number of chicks  
48 attended by individually-marked parents. By using its variation with chicks' age, we had  
49 access to two variables for *RS*:

- 50 - the initial family size (IFS), which was considered as a proxy for the hatching success and  
51 chicks' survival during the first few days,
- 52 - the decrease in family size with age (DFS), which was considered as a proxy for chicks'  
53 survival rate during growth and until fledging. By using this variable instead of the family  
54 size just before fledging, we were able to use all the records of family size between  
55 hatching and fledging, hence to increase the sample size.

56 Predicting how IFS and DFS should vary with colony size in our BHG population  
57 required a few assumptions to be made on the main processes at stake. First, overcrowding  
58 costs in BHG are of three main kinds: increase in the level of competition for the access to  
59 high, secure nest locations, increase in alarm flight frequency and duration, and increase in  
60 antagonistic behaviours. Eggs and young chicks are supposedly more sensitive to these costs  
61 than older chicks: they can fall in the water or be predated from low, unsafe nests, they can  
62 die because of poor thermoregulation during alarm flights and they can suffer from aggression  
63 by neighbouring adults. In short, we assumed that overcrowding costs should impact more on  
64 IFS (eggs and young chicks) than on DFS (older chicks).

65 Second, the food resource available to chick-raising parents can vary with colony size,  
66 either positively through foraging enhancement, or negatively through density-dependence. If  
67 we make the assumption that food resource during the breeding season does not impact on  
68 clutch size and hatching success, we can predict that DFS but not IFS should be impacted by  
69 colony size effects on food resource (BHG as capital breeders, Drent & Daan 1980; Hamer et  
70 al. 1993 in another Larid species, but see Thyen and Becker 2006 and further details in the  
71 discussion section). Overall from the two preceding points we thus predict that IFS should  
72 decrease with colony size and that DFS should increase with colony size.

73 Third, predation risk is expected to decrease with colony size, due to among others the  
74 dilution effect (Hamilton 1971) and early-warning effect (Lazarus 1979). An increase with

75 colony size in the efficiency of anti-predator behaviours (mobbing) also likely occurs (Allainé  
76 1991). Predators' distribution can, however, alter these predictions. (i) If predators are strongly  
77 localised (territorial, dependent on rare habitat features...), the associated risk can eventually  
78 be independent of colony sizes. (ii) Alternatively, predators can concentrate their attacks on  
79 the densest sites where preys may appear more available (Larivière and Messier 1998).

80         These simple predictions can be further complicated by environmental stochasticity  
81 due to climatic accidents (Aebischer 1993), human perturbations (Calado 1996) or predator-  
82 driven failures (Ratcliffe et al. 2008). For example, climates partially drives the *RS* of  
83 *Fulmarus glacialis* (Lewis et al. 2009), which would probably have modified the effect of  
84 colony size in that system. In our BHG population, whole-colony failures, i.e. the desertion of  
85 a given colony before fledging, are relatively frequent (Table 1) and constitute a major  
86 external driver of *RS*. Their causes include man-driven droughts of the ponds and  
87 perturbations by terrestrial predators (Lebreton and Landry 1979). We further suggest that  
88 once a threshold proportion of breeders have failed, the remaining pairs desert the colony as  
89 well. The threshold proportion is supposedly more easily reached in small colonies (e.g., a  
90 single wildboar *Sus scrofa* will destroy most nests in a 100-pair colony, but its impact will be  
91 less visible in a 4000-pair colony). Thereby the risk of whole-colony failure should decrease  
92 with colony size, providing an advantage for breeding in large colonies. We combined the  
93 results from the family size data introduced above with an estimate of the probability of  
94 whole-colony failure. This made it possible to correct the estimate of *RS* for the occurrence of  
95 such failures and see how they affect the relationship between colony size and *RS* during the  
96 early and late parts of the breeding cycle.

## 97 **Methods**

### 98 Study site and species

99 The study site is located in the Forez basin, Loire department, central France. Each year  
100 between 1978 and 2008, from 9 to 34 colonies (mean 19.9) of BHG bred in man-made ponds  
101 situated in a farmland mosaic (see Lebreton 1987 for a more complete description of the study  
102 area). Gulls lay a clutch with a modal size of three eggs from mid-April to the beginning of  
103 June (Lebreton and Landry 1979). Chicks and adults have been ringed since 1978.  
104 One of the colonies (La Ronze) differed from other colonies due to its size (between 2000 and  
105 5000 pairs), while the other colonies numbered on average 163 pairs (SD: 171). Also,  
106 between 1978 and 2006 La Ronze was occupied continuously, contrary to smaller colonies  
107 which experienced either spontaneous desertion by the gulls and/or temporary man-induced  
108 perturbations that prevented breeding (droughts for management purpose). In 2007 La Ronze  
109 experienced such a drought; in 2008 the colony reappeared on that pond but numbered only  
110 500 pairs.

### 111 Data collection

#### 112 -Family size data

113 Each year between 1979 and 2008 a subset of the active colonies (depending on access  
114 authorizations) was visited to look for ringed birds. We collected data simultaneously in La  
115 Ronze and in the smaller colonies but due to colony-specific laying dates more time was  
116 devoted to the large colony early in the season relative to small colonies. Field work lasted  
117 usually four or five weeks, between May 5 at the earliest and June 28 at the latest. However,  
118 data collection in the small colonies began only from 1995 onwards, with only a few sparse  
119 records before that year (see Table S1 in Appendix for details on when and where data were  
120 collected). We opportunistically recorded family size of individually-marked adult birds  
121 (metal rings on tibia) at various stages of the chicks' development while moving through the



122 colonies in a floating blind (Lebreton 1987). The number of chicks per pair (= the family size)  
123 was counted when the parents were feeding the chicks. Chicks' age in days was estimated  
124 with an accuracy of 2 to 4 days through detailed observation of size and plumage  
125 development (Lebreton and Landry 1979). As families were recorded while looking for  
126 ringed parents, it is unlikely that family size influenced on the detection probability of  
127 families. Of course, only families with at least one chick could be recorded (thereby excluding  
128 failed breeding attempts).

129 - Colonies' average *RS*

130 Each year, we visited most of the colonies at least twice (installation period and end of  
131 breeding cycle), including those that were not surveyed for family sizes. We recorded the  
132 number of pairs (colony size) and the colonies' average *RS*, quantified using a three-level  
133 index: 0 (no fledgling produced), 1 (low success), 2 (high success). Whole-colony failure is  
134 hereafter the occurrence of a '0'. This protocol provided us with an estimate of the proportion  
135 of birds that tried to breed even if they failed early and did not enter our dataset on family  
136 size.

137 Model for the family size data

138 The dataset included 1,255 family size records from 966 individually-marked birds  
139 over 31 years (Fig. 1). This dependent variable was worth 1, 2 or 3 (with a few marginal  
140 records of 4-chicks families possibly, but not compulsorily, due to chick adoption or intra-  
141 specific clutch parasitism). Generalized linear mixed models (GLMM) with Poisson-  
142 distributed error terms and log link function were fitted using the restricted maximum  
143 likelihood (REML) method implemented in the macro GLIMMIX in SAS 9.1.

144 We included the fixed effects of chicks' age, colony size and their interaction.  
145 Theoretically, the effect of colony size is not thought to be linear (see Clark and Mangel  
146 1984; Forbes and Kaiser 1994), which was taken into account via a log-transformation of

147 colony sizes. Similarly, chicks' death rate is expected to decrease with age, advocating the  
148 log-transformation of chicks' ages also. We corrected for the potential confounding effects of  
149 between-individual (966 individuals), -year (31 years) and -site (10 sites) variation with  
150 independent (i.e., non-nested) random effects. Temporal autocorrelation was accounted for  
151 using a first order autoregressive structure.

152 A large number of observers contributed to the data, but one of us (J.D.L.) contributed  
153 much more than other observers (collecting more than half of the data) and spent more time in  
154 the LR colony than other observers, but less time in the small colonies. Because old chicks are  
155 very mobile around their nest site, our method relied on a certain amount of subjectivity to  
156 decide when a family size had been accurately determined, suggesting non-negligible  
157 observer effect. We thus accounted for the observer effect with a fixed effect. Preliminary  
158 analyses indicated that contrasting J.D.L. to all other observers captured most of the between-  
159 observer variation.

160 We expected a low statistical power due to sparse data in several colony size  $\times$  chicks'  
161 age cells. Statistically significant fixed effects were considered to be those whose confidence  
162 interval (CI) did not encompass zero. For the random effect structure we used the Akaike  
163 Information Criterion (AIC) to discard non-significant effects.

#### 164 Model for the whole-colony failure data

165 We built a GLMM with binomial error term and logit link function, with occurrence of  
166 whole-colony failure as dependent variable and colony size as fixed effect, colony identity  
167 and year as random effects (with a temporal autocorrelation structure), using the restricted  
168 maximum likelihood (REML) method implemented in the macro GLIMMIX in SAS 9.1. This  
169 model produced an estimate of the probability of colony failure depending on colony size.  
170 Statistical significance of the effects was determined as in the previous section.

171           Assuming independence between family size data and whole-colony failure data, and  
172 in order to obtain a model of *RS* accounting for colony size effects on both family size and the  
173 frequency of whole-colony failures, we multiplied the predictions from the two models  
174 constructed above. Confidence intervals on this expected *RS* were computed using a multiple  
175 (1000 times) resampling procedure, using the standard errors estimated at the previous stage  
176 to compute an expected distribution of models' parameters.

## 177 **Results**

### 178 Model for the family size data

179           Fixed effects of colony size, chick's age and their interaction all had confidence  
180 intervals only marginally encompassing zero, and were thus maintained in the final model  
181 (Table 2). Concerning random effects, year (with autoregressive structure) and individual  
182 effects proved significant with regards to AIC. The GLMM revealed an important variation  
183 between individuals: parent identity accounted for 20.4% of the total variance in the data.  
184 Year effect was much lower (2.3% of the total variance). Table 2 gives details of the  
185 estimated parameter values in the final model. The statistically significant effect of colony  
186 size indicates that IFS (family size shortly after hatching) decreased with colony size (Fig. 2).  
187 This is partly compensated by a decrease in DFS (chick mortality) with colony size  
188 (interaction term in Table 2; Fig. 2). Observer effects are presented in Table S2 in Appendix;  
189 they were discarded due to statistical non-significance.

### 190 Model for the whole-colony failure data.

191           As expected from an examination of the raw data (Table 1) the probability of complete  
192 colony failure markedly decreased with increasing colony size (Table 3: fixed effect), even  
193 after controlling for the colony identity and year using random effects. Concerning random  
194 effects, the GLMM revealed a significant variation between years: year accounted for 32.8%  
195 of the total variance in the data. Random effect of colony identity was discarded by AIC. The

196 temporal autocorrelation of colony failure probability appeared non-significant with regard to  
197 AIC and autoregression coefficient estimate.

198 Combining the two models.

199 The “composite” model of *RS* obtained by multiplying the predicted family size at  
200 fledging in successful families (from the model in Table 2) and the predicted probability of  
201 whole-colony failure (from the model in Table 3) suggested a strongly detrimental effect of  
202 breeding in colonies of 100-200 pairs or less but little effect of colony size on *RS* for colony  
203 size above 300 pairs (Fig. 3).

## 204 **Discussion**

205 Colony size effects on initial family size

206 Our first hypothesis (colonial breeding is costly at the egg and young-chick stages) is verified  
207 by the fact that IFS decreased with colony size. Given that the most abundant predators  
208 (Carrion Crow *Corvus corone*, medium-sized raptors such as Black Kite *Milvus migrans*,  
209 herons, snakes, Canids, Mustelids) prey mostly on eggs or young chicks, explaining this result  
210 by predation risk reduction would imply that small colonies are less subject to predation,  
211 which seems improbable (Hamilton 1971; Lazarus 1979; Allainé 1991), unless they attract  
212 less predators (Larivière and Messier 1998).

213 A second hypothesis is that females in large colonies have access to fewer resources  
214 and thus produce less and/or poorer-quality eggs than females in small colonies. Yet in the  
215 introduction we relied on the assumption that, at the egg-laying stage, females use mostly  
216 resources secured before settling in the colonies. This assumption that BHG are capital  
217 breeders (Drent and Daan 1980) is however contradicted by Thyen and Becker (2006) who  
218 found that in another BHG population clutch size changes with weather conditions during the  
219 breeding season.

220 A third explanation (that we consider the most likely) is that the larger the colony, the  
221 more intense the risk that eggs and young chicks are lost during alarm flights or during  
222 intense antagonistic behaviours. Here we thus assume that colony size and nest density are  
223 correlated (which seems relevant due to the much smaller variation in pond area compared to  
224 colony sizes). This is confirmed by our own observations (although no quantitative data are  
225 available yet) of more numerous fights among neighbours in large colonies and of occasional  
226 loss of eggs or small chicks during or after alarms because of such fights, or as small chicks  
227 that leave the nest during alarms are often attacked by neighbours when they cross their  
228 territories.

229 Even if we are unable to firmly choose among the potential explanations (resource  
230 limitation at the laying stage or increased loss of eggs and small chicks), our result that IFS  
231 decreases with colony size at least indicates that, at the egg-laying stage, overcrowding costs  
232 exceed any benefit of colony size.

233 Colony size effects on the decrease in family size with chicks' age

234 Our second prediction, that DFS decreases with colony size, is supported by the interaction  
235 between colony size- and chicks' age- effects. This interaction indicates that for each family  
236 the proportion of hatched chicks that survives to fledging increases with colony size. Any  
237 mechanism increasing chick survival but not hatching success can explain these results, and  
238 we consider here predation risk reduction and foraging enhancement.

239 Predation risk reduction mechanisms can include dilution effect (Hamilton 1971) and  
240 early-warning effect (Lazarus 1979). An increase with colony size in the efficiency of anti-  
241 predator behaviours (mobbing) also likely occurs (Allainé 1991), thereby allowing individuals  
242 from large colonies to spend more time in other chick-care activities. However in the  
243 predation risk reduction scenario it seems hard to elucidate why the benefits act more on old  
244 chicks (DFS) than on eggs and very young chicks (IFS).

245 Foraging enhancement is therefore a more likely hypothesis explaining the observed  
 246 increase in chicks' survival with colony size. Congruent with this consideration is the fact that  
 247 the exchange of food information has been demonstrated in our study species (Andersson et  
 248 al. 1981) as well as in a closely related species that has similar feeding habits (Evans 1982).  
 249 These two studies are to our knowledge the only two testing the existence of information  
 250 transfers in *Chroicocephalus* gulls. Social foraging is also suggested by the finding in our  
 251 study population that neighbours in the largest colony tend to forage together (Prévot-Julliard  
 252 and Lebreton 1999), and by the consideration that white plumage makes it possible to detect  
 253 successful foragers at a great distance (Beauchamp and Heeb 2001). In the next paragraph we  
 254 thus provide a few additional elements on foraging enhancement in the Forez BHG.

#### 255 Locating food sources and foraging enhancement: a simplistic model

256 If there was one and only one feeding site available at any time, and if they were foraging  
 257 individually, gulls would have to patrol their home range of size  $S$ , at the speed  $V$  and with  
 258 the detection distance  $R$ . The instantaneous probability  $\lambda$  that a lone bird without prior  
 259 knowledge would find the feeding site is:  $\lambda \approx 2RV / S$ . With the plausible values  $S = 710\text{km}^2$   
 260 (a circle of approx. 15km radius: Brandl and Gorke 1988),  $V = 11.3 \text{ m}\cdot\text{s}^{-1}$  (Shamoun-Baranes  
 261 and van Loon 2006) and  $R = 500\text{m}$ , we obtain  $\lambda \approx 0.057 \text{ h}^{-1}$ , which would mean that a lone  
 262 bird needs on average 17.5 hours to find an appropriate feeding site. The selection pressure to  
 263 enhance foraging efficiency would thus be high. If  $N$  birds looked for the same site, and  
 264 neglecting the time needed for information transfers, the instantaneous probability that the  
 265 field is found would be  $N \times \lambda$  (Clark and Mangel 1984).

266 We must admit that the assumption of the uniqueness of the feeding site is quite  
 267 unlikely. Nevertheless, this simplistic model highlights the underlying idea that finding the  
 268 best food possible (i.e., securing the highest ratio energy or nutrients brought back to the  
 269 chicks vs. time or energy spent by the parents) takes too much time if foraging solitarily.

270 Furthermore, information transfer can allow a rapid specialisation on the best available  
271 resource at any time. We suggest information transfers as a possible explanation for our result  
272 that chick survival increased with colony size.

273 Correcting for whole-colony failures

274 The family size at age 32 days corresponds to the number of fledglings per pair. Our results  
275 indicated that, excluding complete breeding failures, BHG in our population produced  
276 between 1.4 and 1.6 fledglings per pair depending on colony size (curve labelled “age 32” in  
277 Fig. 2). This value lies in the high part of the range of reported values for BHG (0.3 to 2  
278 fledglings per pair: Patterson 1965; Lebreton and Landry 1979; Viksne 1980; Thyen and  
279 Becker 2006; van Dijk et al. 2009). This result is probably due to our not accounting for  
280 reproductive failures (pairs that do not produce any fledgling on a given year).

281         Reproductive failures are partially accounted for when correcting the previous  
282 estimates for the occurrence of whole-colony failures. The much more frequent occurrence of  
283 whole-colony failures in small colonies (Table 1) is an additional cost of breeding in small  
284 colonies, and it appears as the main determinant of the sharp decrease in expected *RS* at low  
285 colony sizes (Fig. 3). This low *RS* in small colonies is congruent with previous results that  
286 such colonies are less often chosen by dispersing experienced breeders (as opposed to  
287 inexperienced breeders; Péron et al. 2009), and that breeders from small colonies are less site-  
288 faithful than breeders from large colonies (Péron et al. submitted). Whether these results stem  
289 from colony size *per se* or a correlation between size and “quality” remains debatable. The  
290 result that whole-colony failure probability is neither temporally autocorrelated nor dependent  
291 on colony identity suggests that whole-colony failures can be viewed as an external hazard,  
292 i.e., independent of the true quality of the colony site. However in a low-quality habitat  
293 individuals are expected to be less site-faithful which could be sufficient to maintain colonies  
294 at a small size, and therefore colony size and colony quality could match exactly.

## 295 Conclusion

296           The 32-year long BHG dataset that we studied illustrated that the various costs and  
297 benefits of colony size varied during the breeding cycle, with costs exceeding benefits at the  
298 beginning of the cycle and benefits exceeding costs at the end of the cycle. Moreover the  
299 perturbation regime (environmental stochasticity) appeared as a main driver of breeding  
300 success and largely modified the final output of breeding in the various colony sizes, with the  
301 smallest colonies being the most exposed to perturbations. These findings put an interesting  
302 light on the inconsistencies between previous studies (reviewed in Brown and Bomberger  
303 Brown 1996; see also Lewis et al. 2009; Santema et al. 2009). They suggest that unaccounted  
304 differences in the regime of perturbation might have flawed previous results. Any interaction  
305 between colony size and the regime of perturbation can be predicted, with increases in the rate  
306 of perturbation with colony size possibly stemming from predators' attraction towards  
307 aggregated prey items, and decreases possibly originating from a threshold mechanism, as is  
308 suggested in our system, or from small colonies being settled in lower-quality habitats (Forbes  
309 and Kaiser 1994). Eventually the estimates of RS along the colony-size gradient in our system  
310 provided an explanation for the observed dynamics of our population. It seems indeed likely  
311 that individuals aggregated in the largest colony because this colony provided the best RS.  
312 Density-dependent mechanisms did not counter-balance this benefit. Results concerning  
313 breeding dispersal are in line with this consideration: colony size appears as a good predictor  
314 of colony choice (Péron et al.2009).

315

316 **Zusammenfassung**

317 **Kosten und Nutzen der Koloniegröße variiert während des Brutzyklus' von Lachmöwen**  
318 ***Chroicocephalus ridibundus***

319



320 An mehreren Koloniestandorten einer Lachmöwen-Population wurden die Effekte der  
321 Koloniegröße auf den individuellen Reproduktionserfolg untersucht. Die Koloniegröße lag  
322 bei 10 bis 5000 Paaren. Bezogen auf die Familiengröße (die Anzahl der betreuten Küken  
323 durch individuell markierte Eltern) und unter Berücksichtigung der interindividuellen  
324 Variation, wurde ein negativer Effekt der Koloniegröße während der ersten Lebensstage der  
325 Küken nachgewiesen. Dieser wurde kompensiert durch einen nachfolgenden Anstieg im  
326 Anteil der überlebenden Küken bezogen auf die Koloniegröße. Als Grund dafür vermuten wir  
327 die Wechselwirkung zwischen einem erhöhten Aufwand für den Schlupferfolg und die  
328 Vorteile einer Koloniebrut sowie einer möglicherweise effizienteren Nahrungssuche  
329 (Intensivierung der Nahrungssuche) für das Überleben der Küken. Allerdings erhöht sich die  
330 Häufigkeit vollständiger Koloniemisserfolge bei abnehmender Koloniegröße. Die  
331 Einbeziehung diese Risikos liefert eine verbesserte Abschätzung des Effektes der  
332 Koloniegröße auf den Bruterfolg und zeigt, dass die größten Brutkolonien die produktivsten  
333 sind. Dieses Muster entspricht vorherigen Ergebnissen, wonach größere Kolonien attraktiver  
334 sind für sich ansiedelnde Brutvögel.

335

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### Figures' legend

**Fig. 1:** Family size, chicks' age and colony size: raw data presentation (circle size represents the number of occurrences of a given family size). Colony size is the number of breeding pairs in the colony and chicks' age is in days since hatching. A: Chicks younger than 7 days. B: Chicks older than 24 days. Chicks fledge at 32 days on average. For clarity, colony size is presented in three classes (1-1000 pairs, 1001-2500 pairs and 2501-5000 pairs). Family size is the number of chicks per pair.

**Fig. 2:** Family size, chicks' age (in days) and colony size (in pairs): estimations of the GLMM. Family size is the number of chicks per pair. Chicks fledge at 32 days on average. The insert is a 3D representation of the same model.

**Fig. 3:** Post hoc model of reproductive success  $RS$  taking into account the variation with colony size in family size at fledging and in the probability of whole-colony failure. See method section for details. Dotted lines are confidence intervals computed by sampling 1000 times in the estimated variation of models parameters (Tables 2 & 3).

**Figures**

Fig. 1

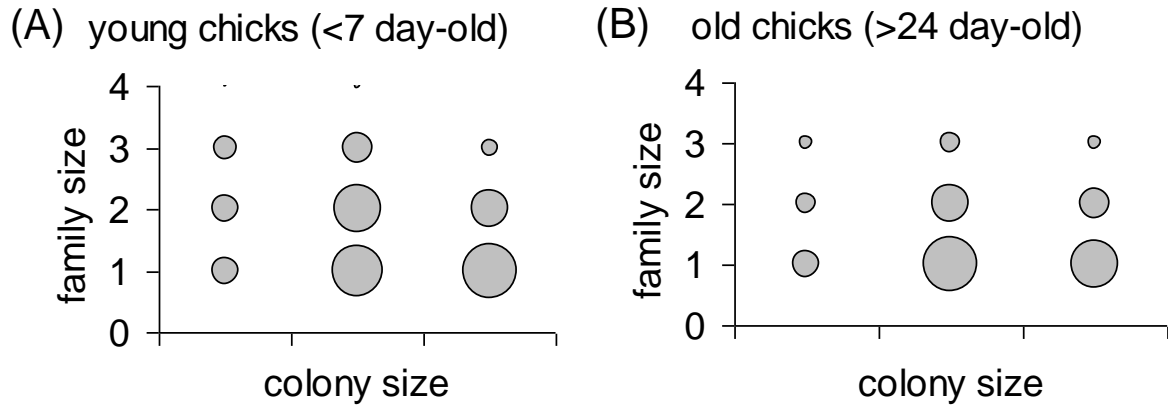




Fig.2

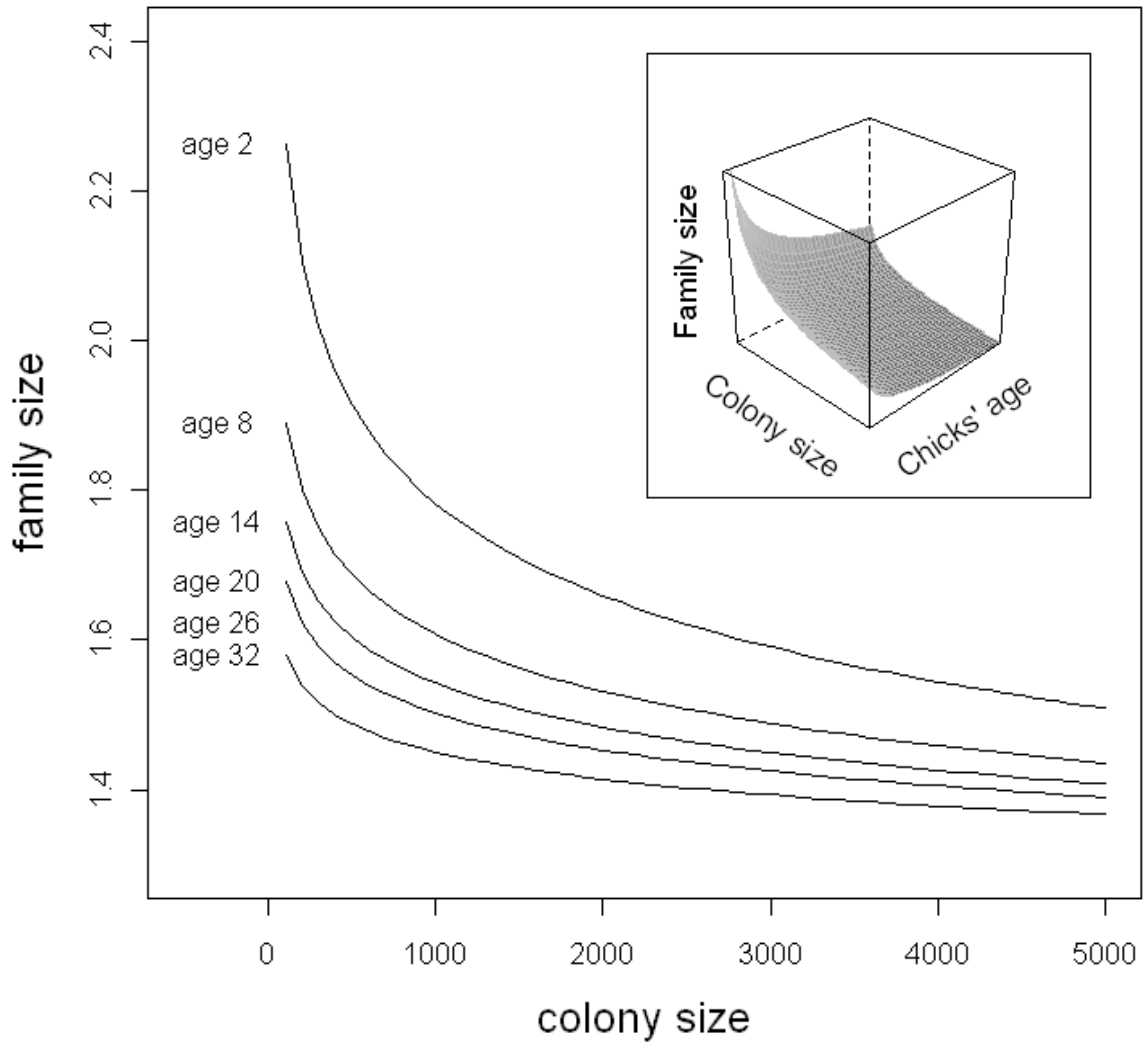
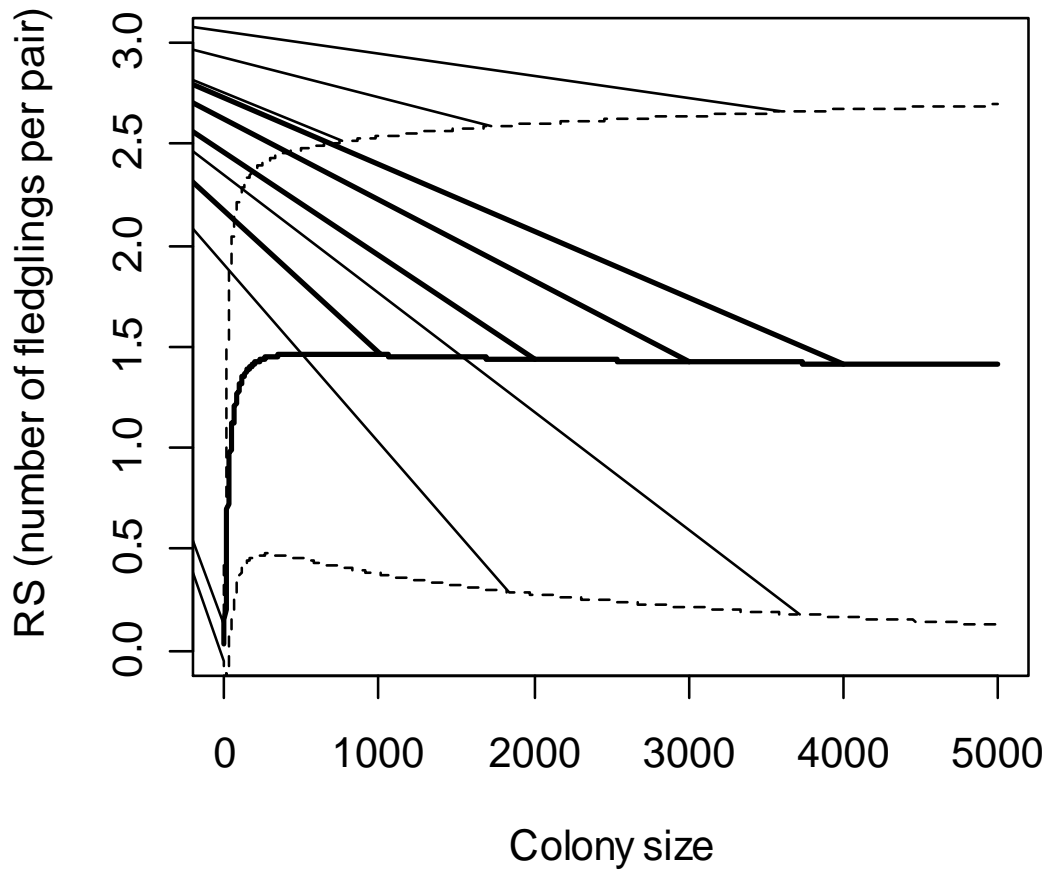


Fig. 3



**Tables****Table 1:** Proportion of failed (0), low-success (1), and high-success (2) colonies across four ranges of colony size.

Size \ success	0	1	2
0-15	0.80	0.12	0.08
16-200	0.22	0.44	0.34
201-1000	0.03	0.24	0.73
>1000	0.00	0.06	0.94

Colony size is the number of pairs.

**Table 2:** Final GLMM for family size.

Random effects		
	SD	
Parent's identity	0.053	
Year	0.006	
Residual	0.20	
Between-year autoregression coefficient	0.57	
Fixed effects		
	Estimates	95% CI
Chicks' age	-0.24	-0.49 ; 0.007
Colony size	-0.12	-0.19 ; -0.055
Colony size × Chicks' age	0.024	-0.008 ; 0.056

The dataset is constituted of 1255 records of family size from 966 parents, for 31 years and 10 colonies ranging from 56 to 5000 pairs. Chick's age and colony sizes are log-transformed. SD refers to random effects' estimated standard deviation value. CI refers to fixed effects' confidence interval.

**Table 3:** Final GLMM for colony failure probability.

Random effects		
	SD	
Year	0.40	
Residual	0.82	
Fixed effects		
	Estimate	95% CI
Colony size	1.07	0.86 ; 1.27

The dataset is constituted of 527 records of colony success for 31 years and 10 colonies ranging from 56 to 5000 pairs. Colony sizes are log-transformed.