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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 λ 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

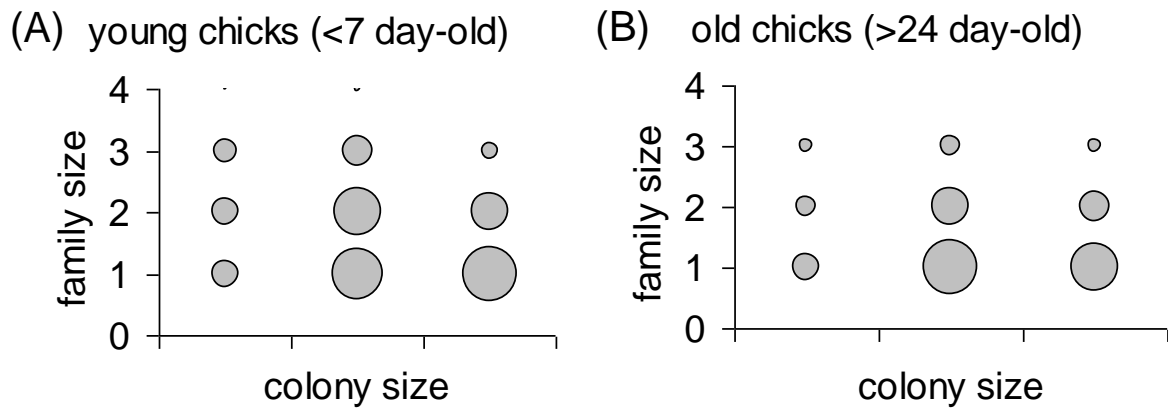


Fig.2

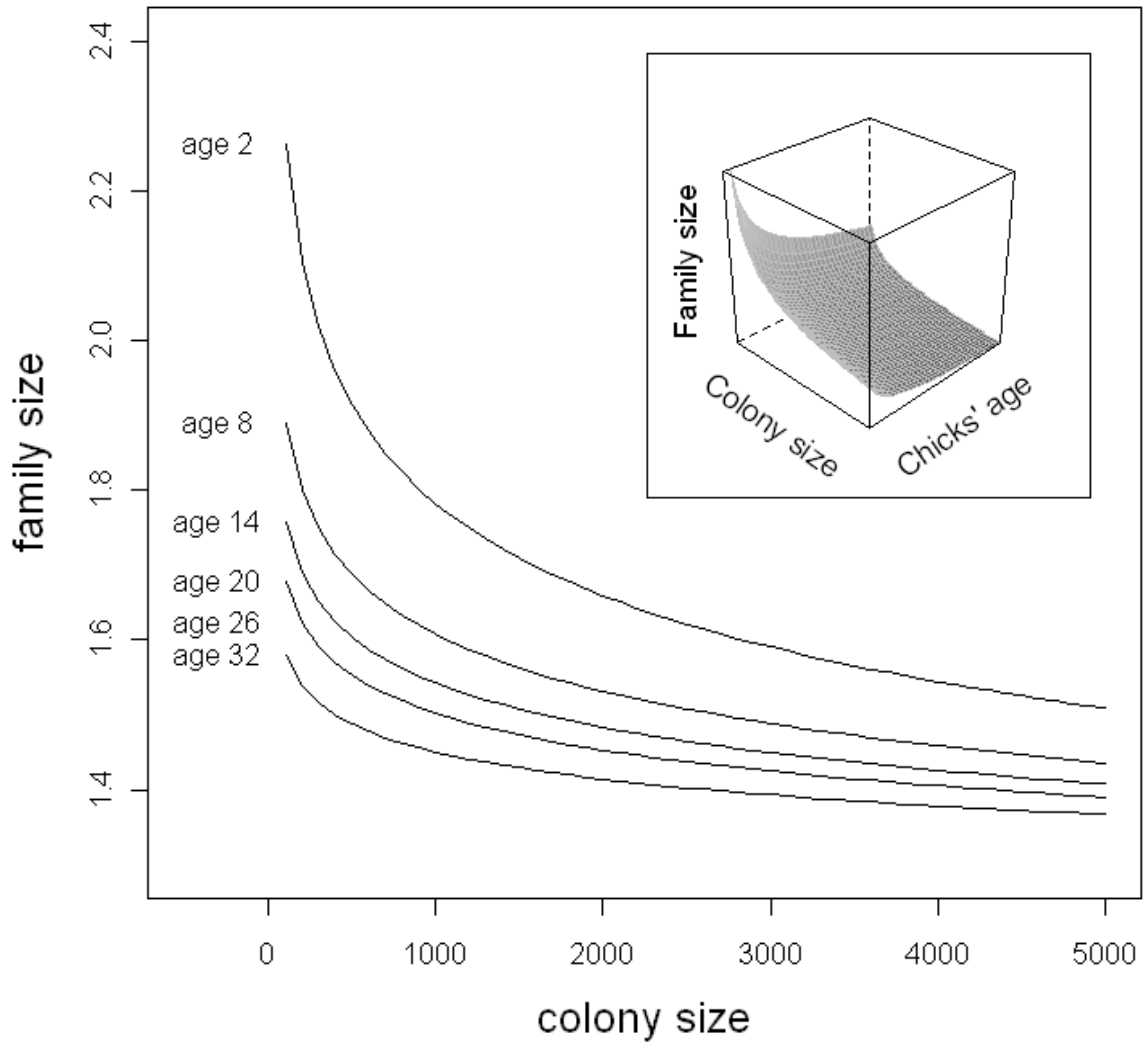
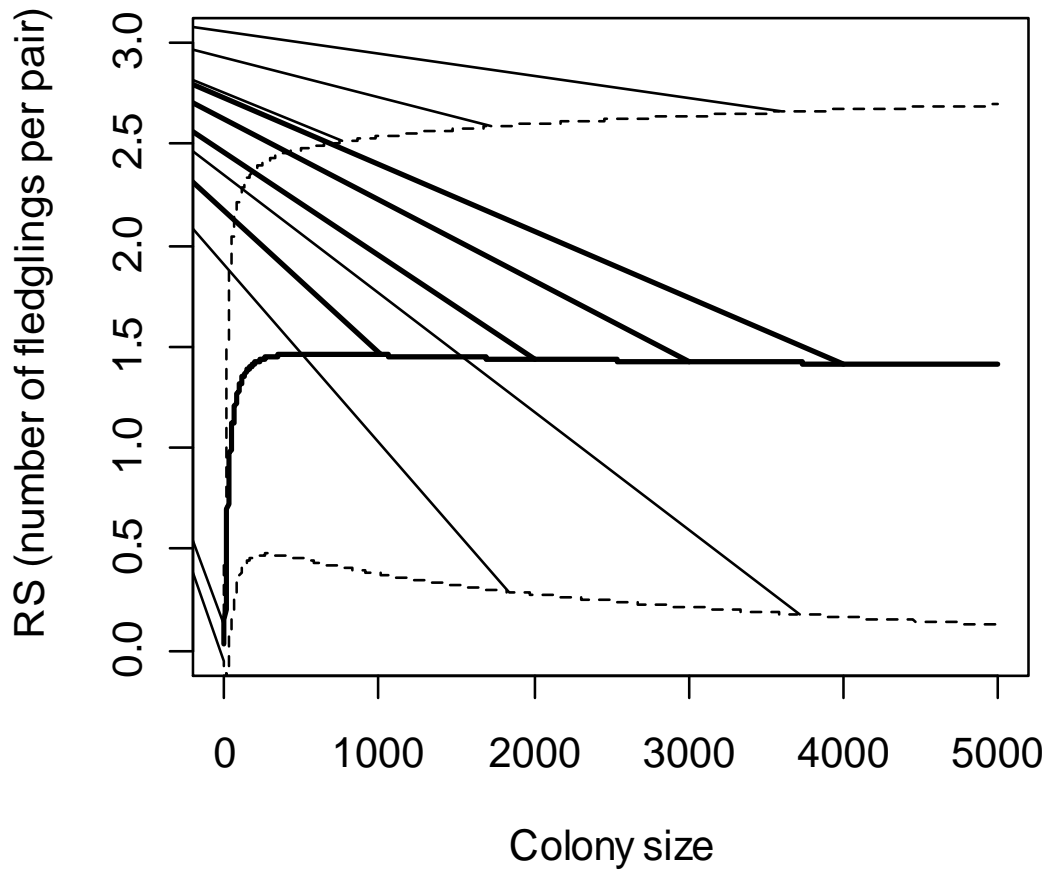


Fig. 3



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.