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1 **Spying on your neighbours? Social information affects timing of breeding and**
2 **stress hormone levels in a colonial seabird**

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- 27 • **Table S1.** Model set for the analyses on the effect of the proportion of neighbours from the
28 opposite food-treatment on laying date. The random effects is a random intercept for pair
29 ID.
- 30 • **Table S2.** Model set for the analyses on the effect of the proportion of neighbours from the
31 opposite food-treatment on egg mass. The random effect is a random intercept for pair ID.
- 32 • **Table S3.** Model set for the analyses on the effect of the proportion of neighbours from the
33 opposite food-treatment on baseline corticosterone levels (log-transformed) among
34 unsupplemented birds. The random effects is a random intercept for bird ID.
- 35 • **Table S4.** Model set for the analyses on the effect of the proportion of neighbours from the
36 opposite food-treatment on baseline corticosterone levels (log-transformed) among food-
37 supplemented birds. The random effects is a random intercept for bird ID.
- 38 • **Table S5.** AICc model selection table for the models explaining laying date. 'AICc' is the AIC
39 corrected for finite sample size; ' Δ AICc' is the difference between AICc of a given model to
40 that of the best model; ' ω AICc' is the probability of each model being the best model given
41 the data and the model set. The null model is given for comparison purposes. Laying date
42 was centred to improve model convergence. RE: random effect (1|PairID).

- 43 • **Table S6.** AICc model selection table for the models explaining laying date in the subset of
44 individuals that were captured. 'AICc' is the AIC corrected for finite sample size; ' Δ AICc' is the
45 difference between AICc of a given model to that of the best model; ' ω AICc' is the probability
46 of each model being the best model given the data and the model set. Laying date was
47 centred to improve model convergence. RE: random effect (1|PairID).
- 48 • **Table S7.** Model-averaged estimates of the variables explaining variation in laying date, in
49 the subset of individuals that were captured (i.e. with body mass data). Binary and
50 continuous explanatory variables were standardised to facilitate model comparisons. CI =
51 confidence interval. Estimates with a CI not overlapping zero are in bold.
- 52 • **Table S8.** AICc model selection table for the models explaining egg mass. 'AICc' is the AIC
53 corrected for finite sample size; ' Δ AICc' is the difference between AICc of a given model to
54 that of the best model; ' ω AICc' is the probability of each model being the best model given
55 the data and the model set. The null model is given for comparison purposes. RE: random
56 effect (1|PairID).
- 57 • **Table S9.** AICc model selection table for the models explaining baseline corticosterone (log-
58 transformed) among unsupplemented birds. 'AICc' is the AIC corrected for finite sample size;
59 ' Δ AICc' is the difference between AICc of a given model to that of the best model; ' ω AICc' is
60 the probability of each model being the best model given the data and the model set. RE:
61 random effect (1|BirdID).
- 62 • **Table S10.** AICc model selection table for the models explaining baseline corticosterone (log-
63 transformed) among food-supplemented birds. 'AICc' is the AIC corrected for finite sample
64 size; ' Δ AICc' is the difference between AICc of a given model to that of the best model;
65 ' ω AICc' is the probability of each model being the best model given the data and the model

66 set. RE: random effect (1|Bird ID). 'DifCortLaying' is the time difference between capture and
67 laying.

68 **Abstract**

69 A good overlap between offspring energetic requirements and [availability](#) of resources is required for
70 successful reproduction. Accordingly, individuals from numerous species fine-tune their timing of
71 breeding by integrating cues that predict environmental conditions during the offspring period.
72 Besides acquiring information from their direct interaction with the environment (personal
73 information), individuals can integrate information by observing the behaviours or performance of
74 others (social information). The use of social information is often beneficial because the accumulated
75 knowledge of conspecifics may represent a source of information more reliable than the intrinsically
76 more limited personal information. However, although social information constitutes the major
77 source of information in a wide range of contexts, studies investigating its use in the context of
78 timing of breeding are scarce. We investigated whether black-legged kittiwakes (*Rissa tridactyla*)
79 used social information to adjust the timing of egg-laying. [We manipulated social information using a](#)
80 [food-supplementation experiment, known to advance kittiwakes'](#) reproductive phenology. We
81 expected food-supplemented and unsupplemented pairs to delay and advance, respectively, their
82 timing of laying when surrounded by a majority of neighbours from the opposite food-treatment.
83 However, both unsupplemented and food-supplemented kittiwakes delayed egg-laying when
84 surrounded by a higher proportion of neighbours from the opposite food-treatment. This result
85 shows that kittiwakes use social information to time egg-laying, but that it is not used to match the
86 seasonal peak of food availability. We suggest that when social and personal cues give contradictory
87 environmental information, individuals may benefit from delaying laying to gather more information
88 to make better decisions about investment into eggs. Further, we explored a potential proximate
89 mechanism for the pattern we report. We show that baseline corticosterone, known to mediate
90 reproductive decisions, was lower in unsupplemented females facing [a](#) higher proportion of food-
91 supplemented neighbours. Altogether, our results suggest that to fine-tune their timing of laying,

92 kittiwakes use complex decision-making processes in which social and personal information
93 interplay.

94 **Introduction**

95 Because a good overlap between offspring energetic requirements and peak of resources is required
96 for successful reproduction (Regehr and Montevocchi 1997; Visser et al. 2006; Hipfner 2008), the
97 timing of reproduction is a key life-history decision. Accordingly, individuals have evolved flexibility in
98 their timing of breeding, allowing them to track interannual variations in environmental conditions
99 (Reed et al. 2009; Dunn and Winkler 2010; Charmantier and Gienapp 2014). Such strategy requires,
100 however, the existence of reliable cues prior to breeding that predict the timing of food availability at
101 the time of offspring rearing. Accordingly, in passerines and seabirds, individuals have been shown to
102 fine-tune the timing of egg-laying by integrating information potentially predicting environmental
103 conditions during the offspring period, such as ambient temperature, food abundance or vegetation
104 phenology (Daan et al. 1988; Nager et al. 1997; Visser et al. 2009; Love et al. 2010; Ruffino et al.
105 2014).

106 The accuracy of the information acquired about the environment is thus crucial to optimize
107 the timing of reproduction. Besides acquiring information from direct interactions with the
108 environment (i.e. personal information, including body condition), individuals can acquire
109 information about environmental conditions by observing the behaviours and performance of others
110 (i.e. social information) (Danchin et al. 2004; Dall et al. 2005; Wagner and Danchin 2010). The
111 accumulated knowledge of conspecifics often represents a source of information more reliable than
112 the intrinsically more limited personal information (Boyd and Richerson 1988; Giraldeau et al. 2002;
113 Valone and Templeton 2002; Rendell et al. 2010). Compared to personal information, social
114 information can thus be beneficial by increasing the accuracy of an organism's appraisal of its
115 environment. Social information therefore constitutes a major source of environmental information

116 in a wide range of contexts, such as antipredatory behaviour (Sirot 2006; Beauchamp 2009), foraging
117 patch selection (Valone 1989; Brown and Laland 2003; Weimerskirch et al. 2010), and breeding site
118 selection (Danchin et al. 1998; Doligez et al. 2002; Valone and Templeton 2002; Kendal et al. 2005;
119 Boulinier et al. 2008). However, social information can be costly to acquire or use, or be outdated or
120 unreliable, and individuals are thus expected to be discriminative in their use of social information
121 (Laland 2004; Kendal et al. 2005; Rieucau and Giraldeau 2011). Accordingly, several studies show that
122 animals use social information only when prior personal information is unsatisfactory, such as when
123 it is uncertain or when its use is risky in terms of predation (Kendal et al. 2004; Van Bergen et al.
124 2004; Webster and Laland 2008; Heinen and Stephens 2016; Jones et al. 2019).

125 In the context of breeding decisions, the large amount of studies investigating the use of
126 social information in breeding site selection contrast with the handful of studies focusing on the
127 timing of breeding (Meijer and Langer 1995; Forsman et al. 2008; Forsman et al. 2011). In this paper,
128 we attempt to fill this gap by studying a colonial seabird, the black-legged kittiwake (*Rissa tridactyla*).
129 In this species, the fine-tuning of the timing of egg-laying to environmental conditions may be critical
130 because a mismatch between the inshore arrival of key forage fish species and chick hatching can
131 have devastating effects on breeding success (Regehr and Montevecchi 1997; Massaro et al. 2000).
132 Fish inshore arrival can often be predicted by environmental variables that affect spring bloom and
133 pre-spawning development, and that might be experienced by birds prior to laying (Carscadden et al.
134 1997; Carscadden et al. 2002; Regular et al. 2009; Davoren et al. 2012; Buren et al. 2014; Kovach et
135 al. 2015). To fine-tune their timing of egg-laying, kittiwakes are therefore likely to have evolved the
136 abilities to assess those environmental variables forecasting fish inshore arrival time. In line with
137 theoretical models predicting an important role of social information in intermediate-variable
138 environments or when individuals are uncertain about the environment (Boyd and Richerson 1988;
139 Nakahashi 2007; Galef 2009; Mclinn and Stephens 2010), the kittiwake has been shown to use social
140 information for breeding habitat selection (Danchin et al. 1998; Boulinier et al. 2008). We

141 hypothesized, therefore, that, to better estimate [their environment to adjust their timing of egg-](#)
142 [laying, this](#) species uses social information obtained from neighbours' phenotypic traits that vary
143 with environmental conditions.

144 We manipulated social and personal information by food-supplementing, or not, focal birds
145 and a variable proportion of their neighbours with capelin (*Mallotus villosus*) (capelin being a major
146 food source of kittiwakes in the studied population, Hatch 2013). Food-supplemented kittiwakes
147 have advanced reproductive phenology compared to unsupplemented birds (Gill and Hatch 2002; Gill
148 et al. 2002), suggesting that food supplementation enables the individuals to overcome a
149 physiological constraint limiting early laying or that food supplementation mimics the effects of
150 natural environmental conditions predicting an optimal earlier laying date. We therefore
151 hypothesized that some features of the phenotype of food-supplemented and unsupplemented birds
152 provide social cues associated with environmental conditions forecasting advanced or delayed
153 optimal laying date respectively. For instance, food-supplemented and unsupplemented birds differ
154 in their pre-laying behaviours, such as nest building and courtship feeding (Gill et al. 2002), and in
155 traits associated with body condition, such as integument coloration (Leclaire et al. 2019). Birds may
156 also use the direct decision of the neighbours (i.e. the egg-laying itself) or the vision of fish passing
157 through the feeding tube (Harvey et al. 1983) as social cues indicating environmental conditions.

158 Theoretical and empirical studies investigating who to copy show that individuals should
159 preferentially use the social information transmitted by the majority (Laland 2004; Pike and Laland
160 2010; Morgan and Laland 2012; Aplin et al. 2015). Therefore, if kittiwakes use social information and
161 follow the decision of the majority, we expect food-supplemented and unsupplemented birds to
162 respectively delay and advance laying date in relation to the proportion of neighbours from the
163 opposite food-treatment. Further, because egg production is energetically costly (Williams 2005),
164 there may be a trade-off between early laying and egg mass, if females are constrained by the time

165 needed to collect nutrients for the eggs (Perrins 1996). We therefore further expected the
166 advancement of egg-laying in unsupplemented birds to be associated with decreased egg mass.

167 At the proximate level, the timing of breeding is regulated by the activation of the
168 hypothalamic-pituitary-gonadal (HPG) axis, which can be inhibited by the stress hormone,
169 corticosterone (Wingfield and Sapolsky 2003; Lattin et al. 2016). Consequently, in several species,
170 including the black-legged kittiwake, experimental manipulation of female corticosterone levels
171 affects egg-laying date (Goutte et al. 2011). Corticosterone levels and the expression of
172 corticosterone receptors in the brain are also reduced by social information about increased food
173 availability (Cornelius et al. 2010; Cornelius et al. 2018). Corticosterone levels may therefore be a
174 mediator between socially-acquired information and the timing of breeding. To investigate whether
175 changes in laying date due to social information are associated with changes in corticosterone levels,
176 we tested how baseline corticosterone levels varied with food-treatments and the proportion of
177 neighbours of the opposite food-treatment.

178

179 **Materials and methods**

180 *Study site*

181 The study was carried out in 2011 and 2012 in a population of black-legged kittiwakes nesting on an
182 abandoned U.S. Air Force radar tower on Middleton Island (59°26'N, 146°20'W), Gulf of Alaska. The
183 tower is a 12-walled polygon where artificial nest sites have been created on the upper walls,
184 permitting observations from inside the tower through sliding one-way windows (Gill and Hatch
185 2002), and allowing us to easily capture and monitor the breeders. Large-scale oceanic index of
186 environmental conditions suggested that the 2012 pre-laying period (April-May) was relatively better
187 (i.e. more negative index) than 2011 in terms of food availability (Pacific Decadal Oscillation index

188 during the two pre-laying period: -0,395 in 2011 and -0,765 in 2012; see also Hatch 2013; Merklings et
189 al. 2019).

190

191 *Experimental design*

192 In total, 203 different pairs were involved in the study (145 pairs in 2011 and 149 pairs in 2012, most
193 pairs being studied in both years). To manipulate personal and social information about
194 environmental conditions, birds were assigned to two [food-treatments](#): unsupplemented birds (74
195 pairs in 2011 and 77 in 2012) and food-supplemented birds (71 pairs in 2011 and 72 pairs in 2012).
196 Food-supplemented birds were fed capelin, a common prey of kittiwakes (Hatch 2013), three times a
197 day (at 9:00, 14:00, and 18:00) until satiation. Fish were passed singly through a plastic tube passing
198 through the wall at each nest site (see fig. 2D in Gill and Hatch 2002). Each nest was visually
199 separated from the adjacent nests by wooden partitions in order to reduce the potential disturbance
200 caused by the experimental feeding and to reduce the probability [of other birds landing on the ledge](#)
201 [of the pair being fed](#). Despite these side partitions, birds can easily monitor the feeding status or
202 phenotype of other birds from the air, during or outside feeding trials. At each feeding session, we
203 fed whichever member of the pair was present on the nest. Feeding started several weeks after
204 settlement decision (which usually occurs mid to late March) and approximately 40 days before
205 laying (start of feeding: 15 April 2011 and 21 April 2012). Feeding stopped just after laying. For each
206 nesting site, food-treatment was assigned to maximise the variance in the proportion of neighbours
207 from the opposite food-treatment, leading to no spatial segregation of treatments. Assignment to
208 either food-treatment was similar in 2011 and 2012. Therefore, because kittiwakes are usually
209 faithful to their nesting site, most pairs received the same food-treatment in the two years (only 3
210 unsupplemented birds that switched mates were food-supplemented the following year).

211 The spatial distance between a bird and its neighbours can influence the detection of
212 neighbours' behaviour, and therefore the use of social information (Fernández-Juricic and Kacelnik
213 2004). Because we had no *a priori* knowledge of the relevant spatial scale for kittiwakes to gather
214 social information, we considered 3 spatial scales (Fig. 1): 1) 'local scale', where only the neighbours
215 directly surrounding the focal pair were considered (between 2 and 9 nests); 2) 'panel scale', where
216 all neighbours nesting on the same polygonal wall as the focal pair were considered (between 21 and
217 30 nests), and 3) 'global scale', where neighbours nesting on the same polygon wall as the focal pair
218 and on the two adjacent walls (between 50 and 88 nests) were considered. During both years, the
219 experiment comprised two sets of 3 polygonal walls situated at opposite sides of the tower (Fig. 1).
220 At the global scale, the proportion of neighbours of the opposite food-treatment for
221 unsupplemented pairs ranged from 25% - 60% (mean \pm SD: 43.6 ± 12.2 %), and for supplemented
222 pairs ranged from 40% - 76% (59.2 ± 10.5 %). At the panel scale, the proportion of neighbours of the
223 opposite food-treatment for unsupplemented pairs ranged from 24% - 69% (41.0 ± 16.2 %) for
224 unsupplemented pairs, and and for supplemented pairs ranged from 31% - 76% (47.6 ± 15.5 %). At
225 the local scale, the proportion of neighbours of the opposite food-treatment for unsupplemented
226 pairs ranged from 0% - 100% (35.7 ± 29.2 %), and for supplemented pairs ranged from 0% - 100%
227 (42.5 ± 27.8 %).

228 Laying date of the first egg (A-egg thereafter, as compared to B-egg for the second egg laid)
229 was recorded for all breeding pairs and all eggs were weighed within 12 h after laying (range of laying
230 date: May 21 - June 27 in 2011 and May 12 - June 25 in 2012, mean laying date: June 3 in 2011 and
231 June 1 in 2012). Four pairs laid three eggs, 245 pairs laid two eggs, 38 pairs laid one egg, while 7 pairs
232 laid no egg. Single eggs were laid later than A-eggs (mean \pm sd: June 6 ± 8 days vs. June 1 ± 6 days;
233 Wilcoxon test: $W_{245, 38} = 2954$, $P < 0.001$). All pairs (100%) that had a three-egg clutch were food-
234 supplemented, while only 26% of pairs that had a single-egg clutch were food-supplemented.

235 Therefore, because clutch size was not equally shared between food-treatments, we decided to
236 focus on pairs that laid two eggs only.

237

238 *Baseline corticosterone*

239 We captured a subset of individuals (16 males in 2011, 28 males in 2012, 19 females in 2011, and 32
240 females in 2012 including some individuals caught in both years) as close as possible to laying (using
241 nest shape as a predictor of imminent laying). At capture, bird mass was measured to the nearest
242 gram with a Pesola scale, and tarsus, head-bill and culmen were measured to the nearest 0.1 mm
243 with a caliper. A blood sample was collected from the alar vein using a 25G heparinised needle and a
244 1 ml syringe (maximum blood volume collected: 1 ml). Blood sampling occurred within 3 minutes of
245 capture, i.e. before the stress of capture would raise corticosterone levels (hereafter, 'cort') (Romero
246 and Reed 2005). These samples were thus representative of baseline cort. Blood samples were
247 centrifuged at 8 000 rpm for 10 minutes in the field, plasma were separated from red blood cells and
248 both fractions were frozen at -20°C until they were brought back to the lab and stored at -80°C.
249 Baseline cort was quantified via radioimmunoassay at the Centre d'Etudes Biologiques de Chizé.
250 Plasma concentrations of cort (ng/mL) were determined in one assay for each year following
251 methods described in Lormée et al. (2003), validated for black-legged kittiwakes by Goutte et al.
252 (2011). Cort was log-transformed to meet normality assumptions of models.

253 *Statistical analyses*

254 We investigated the effect of the interaction between social and personal information on pairs'
255 reproductive decisions around laying using linear mixed models in the *glmmTMB* package (Brooks et
256 al. 2017). We ran three sets of analyses, one for each of the three response variables (laying date -
257 centred to improve model convergence -, egg mass and log-transformed cort). We used a similar
258 approach to model selection for each set of analyses. However, some analyses included some extra
259 nuances that are specified below, after describing the common approach.

260

261 *a. Common modelling approach*

262 In the models used in our three sets of analyses, we never included more than one spatial scale in a
263 single model because there was slight collinearity between some spatial scales (Local- Panel: $r = 0.59$;
264 $P < 0.0001$; Panel-Global: $r = -0.27$; $P < 0.0001$, and Local-Global: $r = -0.05$; $P = 0.39$). All model sets
265 also included [food-treatment](#) (i.e. personal information), except the models explaining cort (see
266 below). In all model sets, 2-way interactions were the highest order considered (with an exception
267 for egg mass analyses, see below). Pair-bond duration (with all pair-bond durations > 5 years grouped
268 together) was also included as an explanatory variable in all analyses, as it is known to potentially
269 affect hormone levels and reproductive investment in kittiwakes (Coulson 1966; Lanctot et al. 2003).
270 In all model sets, we also added models with year (2011 or 2012) and its interaction with either the
271 proportion of surrounding pairs that experienced the opposite food-treatment (at each spatial scale)
272 or pair-bond duration (except in the models explaining cort; see below). All explanatory variables
273 were standardized (centred and divided by 2 standard deviations) using the *arm* package (Gelman et
274 al. 2016) and were therefore on the same scale (i.e. similar to effect sizes), which enables the direct
275 comparison of the parameter estimates within and across models. Non-independence of laying date
276 and egg mass data within pairs was accounted for by adding a random effect of Pair ID. Non-

277 independence of cort values from each individual sampled over both years was accounted for by
278 adding an individual ID random effect.

279

280 *b. Model selection*

281 Model selection was based on the information-theoretic approach where the trade-off between
282 goodness-of-fit to the data and model complexity was quantified using AICc for each model
283 (Burnham and Anderson 2003; Burnham et al. 2011). For the different sets of analyses, we explored
284 some carefully selected biological hypotheses that we tested at each spatial scale (see Table S1 for
285 laying date analyses which included 20 different models, Table S2 for egg mass analyses which
286 included 48 models, and Table S3 and S4 for cort analyses, which included 20 and 24 models for
287 supplemented and unsupplemented birds, respectively). As recommended, we considered all models
288 with $\Delta\text{AICc} < 4$ compared to the best model as equivalently explaining the data (Burnham et al.
289 2011). We also calculated a weight (ωAICc) for each model, which represents the probability that a
290 given model is the best approximating model among the subset of models (Symonds and Moussalli
291 2011). As multiple models were equally good, we accounted for model selection uncertainty by
292 computing model-averaged parameter estimates, standard errors, and confidence intervals without
293 reducing the number of parameters (Burnham and Anderson 2003). The strength of the effect of an
294 explanatory variable on the response variable was then assessed by checking whether the confidence
295 interval overlapped zero (Grueber et al. 2011). All the above calculations were based on maximum
296 likelihood estimation.

297

298 *c. Nuances for the analyses on laying date*

299 In the subset of individuals with body mass data (see 'Baseline corticosterone'), we also investigated
300 whether body mass influenced laying date. Using the same model set as for the main laying date
301 analyses, we also investigated the interactions between body mass and treatment or proportion of
302 surrounding pairs that experienced the opposite food-treatment (at each spatial scale). We ran those
303 models while controlling or not [controlling](#) for body size (to model body condition) [to determine its](#)
304 [effect on our result](#).

305

306 *d. Nuances for the analyses on egg mass*

307 In the models explaining egg mass (Table S2), egg rank (i.e. first-laid or second-laid egg) was included
308 as an explanatory variable and laying date as a covariate, because early-laid eggs are typically
309 heavier. In these models, we also included the three-way interactions between egg rank, feeding
310 treatment and pair-bond duration, and the three-way interactions between egg rank, feeding
311 treatment and the proportion of neighbours from the opposite food-treatment. Preliminary analyses
312 suggested a non-linear effect of pair-bond duration, so we included a quadratic effect. As some eggs
313 were from the same clutch, we initially added a brood ID random effect in addition to the pair ID
314 effect, but its estimated variance was practically zero and adding it led to convergence issues in some
315 models, so it was not included. Following our previous studies on sex allocation patterns in this
316 population (Merkling et al. 2012; Merkling et al. 2017), chick sex was also included in the models as
317 possibly explaining egg mass as well as egg rank. We also considered the 3-way interaction between
318 egg rank, chick sex, and feeding treatment. None of those models explained any variation in egg
319 mass, so we do not present those results.

320

321 *e. Nuances for the analyses on cort*

322 As expected, we observed that, during both years, food-supplemented birds started nest-building
323 and laying earlier than unsupplemented birds (Table S3 and S4; Gill and Hatch 2002; Gill et al. 2002).
324 Yet, for supplemented birds, the duration of nest building was longer than we anticipated. Because
325 we used nest shape as a predictor of laying, this led to earlier capture (and thus blood sampling for
326 cort) relative to egg-laying among food-supplemented birds than among unsupplemented birds
327 (mean \pm sd: 13.0 ± 7.4 days before laying vs. 9.6 ± 6.3 days before laying; Wilcoxon test: $W_{50,45} =$
328 1424 , $P = 0.026$). Because cort varies during the pre-laying period in seabirds (Hennin et al. 2015), we
329 ran separate cort analyses for each food-treatment to avoid the collinearity between food-treatment
330 and breeding stage. For each treatment, we started by testing whether some potential confounding
331 variables (laying date, the time difference between capture and laying, year and blood sampling
332 time) needed to be accounted for. The only significant variable was the time difference between
333 capture and laying among food-supplemented birds, so this is the only confounding variables that
334 was included in further analyses for food-supplemented birds. No confounding variables were
335 included for unsupplemented birds. In these individual-level analyses for cort, we also included the
336 explanatory variables body size and body mass and considered the two-way interactions between
337 each explanatory variable (proportion of neighbours from the opposite food-treatment, body mass,
338 body size, pair-bond duration) and parental sex. For each sex, an index of body size was calculated as
339 the first principal component of a principal component analysis including tarsus, head-bill, and
340 culmen length (explaining 65% of the variance for females and 63% for males). Body mass varied with
341 food-treatment and sex (food-supplemented females: 451 ± 26 g (mean \pm SD); unsupplemented
342 females: 439 ± 40 g; food-supplemented male: 447 ± 24 g; unsupplemented males: 435 ± 23 g), so
343 body mass was standardized (centred and divided by 2 standard deviations) within each sex and
344 food-treatment and then collated by food-treatment. One male was excluded from the analyses as it
345 was paired with a female that laid the first egg on June 27, while the others laid between May 20 and
346 June 18. As the sample size for the analyses explaining cort is relatively low ($n = 50$ food-

347 supplemented and n = 45 unsupplemented control birds), we kept the number of explanatory
348 variables to a minimum and did not consider anything more complex than 2-way interactions.

349

350 *f. Tests for spatial autocorrelation*

351 Given the spatial layout of our data with between-nest distances varying substantially and because
352 we were primarily interested in the effect of neighbouring nests on reproductive decisions, we made
353 sure that there was no need to account for spatial autocorrelation. For each set of analyses, we ran a
354 model including one spatial scale, treatment (except for cort analyses, which were separated by
355 treatment, see below), and the covariates and random effect proper to each analysis (see below).
356 We then plotted a variogram for the residuals and for the random intercepts using the *gstat* package
357 (Benedikt et al. 2016). A variogram calculates the semivariance between pairs of data points at
358 specific windows of distance and enables to see if points closer together are more likely to be similar
359 than those further apart (i.e. with a lower variance). In our case, the semivariance was quite stable
360 with distance (although it tended to decrease at the largest distances; see online repository Merklings
361 et al. 2020 for further details), so we decided not to include any random effects accounting for
362 spatial autocorrelation. Results did not change when accounting for spatial autocorrelation in models
363 (see online repository Merklings et al. 2020 for further details).

364 All analyses were performed using R statistical software (R 3.6.3; R Core Team 2019).

365

366 **Results**

367 *Laying date*

368 Overall, unsupplemented birds laid later than food-supplemented birds (Table 1 and S5; Fig. 2). In
369 both food-supplemented and unsupplemented birds, laying date increased with the proportion of
370 neighbours from the opposite food-treatment at the global scale (Table 1 and S5; Fig. 2), but there
371 was no interaction between food-treatment and proportion of neighbours from the opposite **food-**
372 **treatment** at the global scale and no effect at the local or panel scale (Table S5). In addition, birds laid
373 earlier in 2012 than in 2011 (Table 1 and S5). In the sub-analyses investigating the effect of body
374 mass on laying date (in the subset of birds that were captured, see Methods), we found no effect of
375 body mass on laying date (-0,09 [-0,22; 0,04]; Table S7), as the null model was the best model (Table
376 S6).

377

378 *Egg mass*

379 Food-treatment and the proportion of neighbours from the opposite food-treatment did not
380 influence egg mass, regardless of the spatial scale (Table 2 and S8), but pair-bond duration was
381 associated with higher egg mass (Table 2 and S8). In addition, A-eggs were heavier than B-eggs and
382 females laid heavier eggs in 2011 than in 2012 (Table 2 and S8).

383

384 *Corticosterone levels*

385 In unsupplemented birds, cort decreased with the proportion of food-supplemented neighbours at
386 both the local and panel scales, but not at the global scale (Table S9 with no models including the
387 global scale). This relationship was non-linear and the decrease in cort was more pronounced for
388 higher proportions of food-supplemented neighbours (Table 3a and S9; Fig. 3). At least for the local
389 proportion of food-supplemented neighbours, this quadratic relationship seemed to be explained by
390 a sex-specific effect (Fig. 3a). In unsupplemented females, cort was lower when females were
391 surrounded by a higher proportion of food-supplemented neighbours, whereas cort in

392 unsupplemented males did not vary with the proportion of food-supplemented neighbours (Table
393 3a; Fig. 3a). At the panel scale, the interaction between sex and the proportion of food-
394 supplemented neighbours was weaker than for the local scale, but in the same direction (Table 3a
395 and S7; Fig. 3b).

396 Among food-supplemented birds, the proportion of unsupplemented neighbours did not
397 affect cort regardless of the spatial scale (Table 3b and S10). Cort levels were lower when birds were
398 sampled further away from laying (Table 3b). The model containing only the time difference between
399 capture and laying was the best model, thereby showing that none of the explanatory variables
400 strongly explained variation in cort (Table S10). Hence, although the estimates and confidence
401 intervals indicated that cort levels were lower in smaller and heavier males (Table 3b), we have low
402 confidence that those differences are biologically meaningful.

403 **Discussion**

404 Because kittiwakes are expected to fine-tune their timing of breeding to match the seasonal peak of
405 food availability, and because social information may constitute a reliable source of environmental
406 information, we expected individuals to advance or delay egg-laying according to some phenotypic
407 [traits associated with their neighbours' timing of egg-laying](#) (Meijer and Langer 1995; Forsman et al.
408 2008; Forsman et al. 2011). The phenotypic traits considered here may refer to any kind of
409 morphological trait (e.g. integument coloration) or behavioural trait (e.g. nest building, courtship
410 feeding) that may indicate change in breeding phenology (Leclaire et al. 2019, Gill et al. 2012). In
411 order to alter the traits of the neighbours, we used a food-supplementation experiment known to
412 advance reproductive phenology in the species (this study; Gill et al. 2002). As expected, food-
413 supplemented females surrounded by higher proportions of unsupplemented neighbours delayed
414 egg-laying. However, in contrast to expectations, unsupplemented females surrounded by high
415 proportions of food-supplemented neighbours also delayed egg-laying. This suggests that, although

416 kittiwakes use social information to time egg-laying, the proportion of neighbours from the opposite
417 **food-treatment** may represent additional information beyond the timing of **peak food abundance**.
418 For instance, the proportion of food-supplemented neighbours may represent information about
419 current food availability. In kittiwakes, body condition at egg-laying has been suggested to be a more
420 important selective force on laying date than matching peak food abundance with chick energetic
421 demands (Shultz et al. 2009). Therefore, unsupplemented females surrounded by food-
422 supplemented birds may benefit more from delaying laying to gain nutritional condition to lay better-
423 quality eggs compared to advancing laying to match seasonal **peak food abundance**. Recently, it has
424 been shown that, in this population of kittiwakes, none of the **pre-laying** environmental variables
425 considered (i.e. sea surface temperature, chlorophyll-B concentration and large-scale oceanic index)
426 are good predictors of environmental conditions during chick-rearing (Merkling et al. 2019). **This**
427 **suggests** that kittiwakes may not have been selected to adjust the timing of egg-laying to match peak
428 food abundance with chick energetic demands. According to this hypothesis, food-supplemented
429 kittiwakes surrounded by high proportions of unsupplemented neighbours would have delayed egg-
430 laying because of other selective forces. For instance, breeding synchrony is a characteristic of many
431 colonial birds and can provide several advantages, including increased success of chick adoption by
432 neighbours, formation of hatchling flocks and reduced predation risks for eggs and chicks through
433 predator swamping or mutual defence (Darling 1938; Emlen and Demong 1975; Wittenberger 1985).

434 In our study, **the proportion of neighbours from the opposite food-treatment varied**.
435 **Therefore**, not only the social information varied, but also the degree of inconsistency between social
436 and personal information. Our result may therefore be in line with females delaying laying when
437 social and personal cues give contradictory environmental information. Inconsistent information
438 have repeatedly been shown to increase uncertainty, and delay decision making in humans (Urbany
439 et al. 1989; Tversky and Shafir 1992; Farnan et al. 2008). Such a strategy may allow individuals to
440 gather more information to make better decisions. In numerous species, offspring fitness is

441 maximized when the prenatal and postnatal environments are accurately matched (Agrawal et al.
442 1999; Cleal et al. 2007; Monaghan 2008). For instance, in kittiwakes, some maternally-deposited egg
443 components are beneficial only for chicks growing under poor environmental conditions, and their
444 deposition needs thus to be finely adjusted to future food resources to avoid long-term costs
445 (Gasparini et al. 2007; Merklings et al. 2016). [Female kittiwakes facing high uncertainty about the](#)
446 [environment may therefore delay egg-laying to gather more information about the optimal](#)
447 [investment into eggs](#). Although we did not detect any effects of social information on egg mass,
448 females might have adjusted other crucial egg components. In birds, including kittiwakes, delaying
449 laying may, however, entail costs as it can reduce the time window for subsequent breeding activities
450 (Verhulst and Nilsson 2008) and reduce breeding success as chicks born late during the breeding
451 season are more likely to die (Merklings et al. 2014). Hence, the 3-day lag in laying date between [birds](#)
452 [facing consistent versus inconsistent information](#) may represent a trade-off between benefits of
453 decreasing uncertainty and costs of delayed egg-laying.

454 At the proximate level, variation in laying date can be due to variation in corticosterone
455 levels (Wingfield and Sapolsky 2003; Lattin et al. 2016). For instance, in kittiwakes, an experimental
456 decrease in corticosterone levels within the natural range advances laying date (Goutte et al. 2011).
457 We, therefore, expected birds delaying breeding to have higher corticosterone levels. However, we
458 found that unsupplemented birds facing conflicting information (and thus delaying laying) had
459 reduced corticosterone levels. [In contrast, the corticosterone levels of food-supplemented birds](#)
460 [were not affected by our manipulations, even if these birds also delayed egg-laying when facing](#)
461 [conflicting information](#). In addition, the effect of social information on corticosterone levels and
462 laying date did not operate at the same spatial scale. Overall, these results suggest that
463 corticosterone levels are not the main pathway linking social information to changes in laying date in
464 our study. In kittiwakes, although elevated corticosterone levels affect breeding decision of females
465 (Angelier et al. 2009; Goutte et al. 2010; Goutte et al. 2011), [their](#) effect on laying date are mixed

466 (Goutte et al. 2010; Goutte et al. 2011; Goutte et al. 2014). In contradiction to the generalization that
467 high corticosterone levels inhibit reproduction, a number of studies in several species have reported
468 a positive association between corticosterone levels and reproductive behaviours, suggesting that
469 elevated baseline corticosterone may enable birds to mobilize energy needed to fulfill the high
470 energy demands of reproduction (e.g. Moore and Jessop 2003; Ouyang et al. 2013; Bowers et al.
471 2016). By delaying laying, unsupplemented females facing conflicting information might require less
472 energy for reproductive activities at any time point before laying, and therefore have lower
473 corticosterone levels. We found that corticosterone levels were affected by social information in
474 unsupplemented females, but not in unsupplemented males. During the egg-laying period, males and
475 females greatly differ in their role and thus potentially in allostatic load (i.e. the sum of energy
476 demands), which is known to affect corticosterone levels (Juster et al. 2010). Female kittiwakes might
477 have higher allostatic load than males, and thus be more impacted by social information. Female
478 birds usually play a greater role in the fine-tuning of the onset of breeding than males, and sensitivity
479 to local environmental variations related to egg-laying has been suggested to be expressed
480 predominantly in females (Ball and Ketterson 2008).

481 In conclusion, our study provides experimental evidence for a complex decision-making
482 process in kittiwakes, where social and personal information interact to influence the timing of
483 breeding. We conclude that understanding how individuals weigh social versus personal information
484 to make decisions about reproduction is important for predicting the response of birds to
485 environmental variability.

486

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492

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500 figures and tables presented in the main text and supplementary information are available to
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502

503

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728 **Table 1.** Model-averaged estimates of the variables explaining variation in laying date. Binary and
 729 continuous explanatory variables were standardised to facilitate model comparisons. CI = Confidence
 730 Interval. Estimates with a CI not overlapping zero are in bold.

731

732

Parameter	Estimate \pm SE	Lower CI	Upper CI
Intercept	-0.03 \pm 0.47	-0.95	0.89
Unsupplemented birds^a	4.17 \pm 1.07	2.08	6.26
Proportion of opposite neighbours (global)	3.12 \pm 1.07	1.02	5.21
Year 2012^b	-2.04 \pm 0.58	-3.18	-0.90
Unsupplemented birds ^{b*} Proportion of opposite neighbours (global)	0.73 \pm 2.17	-3.52	4.99

733 ^a: as compared to supplemented birds

734 ^b: as compared to 2011

735 **Table 2.** Model-averaged estimates of the variables explaining variation in egg mass. Binary and
736 continuous explanatory variables were standardised to facilitate model comparisons. CI = Confidence
737 Interval. Estimates with a CI not overlapping zero are in bold. A-eggs are the first-laid eggs of a clutch,
738 while B-eggs are the second-laid eggs of a clutch.
739

Parameter	Estimate \pm SE	Lower CI	Upper CI
Intercept	51.40 \pm 0.33	50.76	52.04
B-egg^a	-2.22 \pm 0.19	-2.59	-1.85
Pair-bond duration	1.39 \pm 0.62	0.18	2.60
Year 2012^b	-0.80 \pm 0.26	-1.32	-0.28
Laying date	-0.20 \pm 0.39	-0.95	0.56
Pair-bond duration ²	-0.96 \pm 0.72	-2.36	0.44
Unsupplemented birds ^c	-0.54 \pm 0.55	-1.62	0.54
B-egg ^c * pair-bond duration	-0.28 \pm 0.41	-1.08	0.52
B-egg ^c * pair-bond duration ²	0.62 \pm 0.67	-0.69	1.93

740 ^a: as compared to A-eggs

741 ^b: as compared to 2011

742 ^c: as compared to food-supplemented birds

743 **Table 3a.** Model-averaged estimates of the variables explaining variation in log-transformed cort in
 744 unsupplemented birds. Binary and continuous explanatory variables were standardised to facilitate
 745 model comparisons. CI = Confidence Interval. Estimates with a CI not overlapping zero are in bold.
 746

Parameter	Estimate \pm SE	Lower CI	Upper CI
Intercept	1.75 \pm 0.12	1.52	1.97
Male ^a	-0.20 \pm 0.12	-0.44	0.04
Proportion of opposite neighbours (panel)	-0.29 \pm 0.12	-0.53	-0.05
Proportion of opposite neighbours (panel) ^2	-0.74 \pm 0.31	-1.36	-0.13
Proportion of opposite neighbours (local)	-0.26 \pm 0.13	-0.52	0.00
Proportion of opposite neighbours (local) ^2	-0.45 \pm 0.23	-0.91	0.00
Male^a * Proportion of opposite neighbors (local)	0.50 \pm 0.25	0.00	0.99
Male ^a * Proportion of opposite neighbours (panel)	0.42 \pm 0.26	-0.09	0.92

747 ^a: as compared to females

748 **Table 3b.** Model-averaged estimates of the best subset models explaining variation in log-
749 transformed cort in food-supplemented birds. Binary and continuous explanatory variables were
750 standardised to facilitate model comparisons. CI = Confidence Interval. Estimates with a CI not
751 overlapping zero are in bold.
752

Parameter	Estimate \pm SE	Lower CI	Upper CI
Intercept	1.46 \pm 0.08	1.29	1.62
Time between capture and laying	-0.34 \pm 0.16	-0.65	-0.02
Male ^a	0.06 \pm 0.16	-0.25	0.37
Body size	-0.15 \pm 0.16	-0.46	0.16
Male^a * Body size	0.75 \pm 0.30	0.15	1.34
Pair-bond duration	0.11 \pm 0.17	-0.21	0.44
Body mass	0.12 \pm 0.16	-0.20	0.44
Male^a * Body mass	-0.77 \pm 0.31	-1.38	-0.17
Proportion of opposite neighbours (panel)	-0.07 \pm 0.17	-0.40	0.26
Proportion of opposite neighbours (global)	0.02 \pm 0.17	-0.30	0.35
Proportion of opposite neighbours (local)	-0.01 \pm 0.17	-0.35	0.33

753 ^a: as compared to females

754 **Figure captions**

755 **Figure 1.** Experimental design for the manipulation of the proportion of neighbours of each
756 treatment around a focal pair at different spatial scales. Unsupplemented pairs are represented by
757 blue squares, while food-supplemented pairs are represented by orange loops. Social information
758 was coded as the proportion of neighbours from the opposite food-treatment (e.g. the number of
759 food-supplemented pairs surrounding unsupplemented pairs or the number of unsupplemented
760 pairs surrounding food-supplemented pairs) and was calculated at three spatial scales. For example,
761 the focal pair surrounded by a red rectangle is food-supplemented and locally surrounded by two
762 food-supplemented nests and six unsupplemented nests resulting in a proportion of $6/8 = 0.75$ at the
763 local scale (pink rectangle). At the panel level (yellow rectangle), the proportion of pairs of the
764 opposite treatment is here $16/26 = 0.62$. Social information at the 'global' scale was calculated by
765 averaging over the focal panel and two neighbouring ones (green rectangle).

766

767 **Figure 2.** Laying date according to the proportion of neighbours from the opposite food-treatment at
768 the global scale in food-supplemented birds (dark blue) and unsupplemented birds (light blue). Solid
769 and shaded areas are bootstrap predictions and confidence intervals, respectively, from the best
770 model including treatment, proportion of neighbours from the opposite food-treatment at the global
771 scale and year.

772

773 **Figure 3.** Relationship between baseline corticosterone levels and the proportion of neighbours from
774 the opposite food-treatment (i.e. food-supplemented neighbours) in unsupplemented birds (males in
775 blue, females in red) at (a) the local spatial scale and (b) the panel spatial scale. On average,
776 unsupplemented birds surrounded by a high proportion of food-supplemented neighbours had lower
777 cort (quadratic relationship, black lines). This trend seems to be mostly due to the fact that female

778 cort (red line and points) strongly decreased with the proportion of food-supplemented neighbours
779 at the local scale (A panel), a trend that is not present in males (blue line and points). At the panel
780 scale (B panel), the interaction between sex and the proportion of food-supplemented neighbours
781 was not significant, although in the same direction as at the local scale and is thus represented with
782 dashed lines. Lines and shaded areas are bootstrap predictions and confidence intervals,
783 respectively, both back-transformed to the natural scale.

784