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### **► To cite this version:**

Anika Immer, Thomas Merkling, Olivier Chastel, Scott Hatch, Etienne Danchin, et al.. Spying on your neighbours? Social information affects timing of breeding and stress hormone levels in a colonial seabird. *Evolutionary Ecology*, 2021, 35 (3), pp.463-481. <10.1007/s10682-021-10112-1>. <hal-03244466>

**HAL Id: hal-03244466**

**<https://hal.science/hal-03244466v1>**

Submitted on 7 Oct 2021

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

Anika Immer<sup>1§</sup>, Thomas Merkling<sup>1§</sup>, Olivier Chastel<sup>2</sup>, Scott A. Hatch<sup>3</sup>, Etienne Danchin<sup>1</sup>, Pierrick Blanchard<sup>1‡</sup>, Sarah Leclaire<sup>1‡\*</sup>

<sup>1</sup>Laboratoire Évolution & Diversité Biologique (EDB UMR 5174), Université Fédérale de Toulouse Midi-Pyrénées, CNRS, IRD, UPS. 118 route de Narbonne, Bat 4R1, 31062 Toulouse cedex 9 France

<sup>2</sup>Centre d'Etudes Biologiques de Chizé (CEBC), UMR 7372 – CNRS & La Rochelle Université, 79360 Villiers-en-Bois, France

<sup>3</sup>US Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK, 99508, USA

<sup>§</sup> Both authors contributed equally

<sup>‡</sup> Co-last authors

\* Corresponding author: [sarah.leclaire@free.fr](mailto:sarah.leclaire@free.fr); +33 05 61 55 67 53

Current addresses:

T Merkling: Centre d'Investigations Cliniques-Plurithématique 1433, Inserm U1116, CHRU Nancy, Université de Lorraine, Nancy, France.

SA Hatch: Institute for Seabird Research and Conservation, 12850 Mountain Place, Anchorage, Alaska 99516, USA.

20 **Running title:** Social information affects timing of breeding in kittiwakes

21 **Key words:** Public information; Timing of reproduction; Glucocorticoids; Egg mass; Experimental  
22 approach

23 **Word count:** 9871

24 **Number of figures and tables:** 3 figures and 4 tables

25 **Online appendix:**

26 A single pdf document containing:

- 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  
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- 38 • **Table S5.** AICc model selection table for the models explaining laying date. 'AICc' is the AIC  
39 corrected for finite sample size; ' $\Delta AICc$ ' is the difference between AICc of a given model to  
40 that of the best model; ' $\omega AICc$ ' 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).

- **Table S6.** AICc model selection table for the models explaining laying date in the subset of individuals that were captured. 'AICc' is the AIC corrected for finite sample size; ' $\Delta$ AICc' is the difference between AICc of a given model to that of the best model; ' $\omega$ AICc' is the probability of each model being the best model given the data and the model set. Laying date was centred to improve model convergence. RE: random effect (1|PairID).
- **Table S7.** Model-averaged estimates of the variables explaining variation in laying date, in the subset of individuals that were captured (i.e. with body mass data). Binary and continuous explanatory variables were standardised to facilitate model comparisons. CI = confidence interval. Estimates with a CI not overlapping zero are in bold.
- **Table S8.** AICc model selection table for the models explaining egg mass. 'AICc' is the AIC corrected for finite sample size; ' $\Delta$ AICc' is the difference between AICc of a given model to that of the best model; ' $\omega$ AICc' is the probability of each model being the best model given the data and the model set. The null model is given for comparison purposes. RE: random effect (1|PairID).
- **Table S9.** AICc model selection table for the models explaining baseline corticosterone (log-transformed) among unsupplemented birds. 'AICc' is the AIC corrected for finite sample size; ' $\Delta$ AICc' is the difference between AICc of a given model to that of the best model; ' $\omega$ AICc' is the probability of each model being the best model given the data and the model set. RE: random effect (1|BirdID).
- **Table S10.** AICc model selection table for the models explaining baseline corticosterone (log-transformed) among food-supplemented birds. 'AICc' is the AIC corrected for finite sample size; ' $\Delta$ AICc' is the difference between AICc of a given model to that of the best model; ' $\omega$ 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,

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

## **Introduction**

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

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

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

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



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

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

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

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

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

## **Materials and methods**

### *Study site*

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

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

### *Experimental design*

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

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

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

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

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

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

#### *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:  $13.0 \pm 7.4$  days before laying vs.  $9.6 \pm 6.3$  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:  $451 \pm 26$  g (mean  $\pm$  SD); unsupplemented  
 342 females:  $439 \pm 40$  g; food-supplemented male:  $447 \pm 24$  g; unsupplemented males:  $435 \pm 23$  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-

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

#### *f. Tests for spatial autocorrelation*

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

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

## **Results**

### *Laying date*

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

#### *Egg mass*

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

#### *Corticosterone levels*

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

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

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

## Discussion

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

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

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

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

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

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

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

## **Acknowledgements**

We thank Lena Agdere, Elise Albert, Romain Durieux, Laurent Gaillard, Emilie Lefol and Emmanuelle Voisin for their help in the field. At the CEBC we thank Colette Trouvé and Charline Parenteau for

corticosterone assay. We thank Jean-Baptiste Ferdy, François Rousset and Thierry Onkelinx for their help in statistical analyses.

## **Declarations**

The study was financed by a 4-year grant from the French Polar Institute Paul-Emile Victor (IPEV 'Programme 1162 SexCoMonArc'), and is part of the 'Laboratoire d'Excellence' (LABEX) entitled TULIP (ANR-10-LABX-41). We declare no conflict of interest. This experiment was conducted under the approval of the USGS Alaska Science Center Animal Care and Use Committee, in accordance with US law and under permits from the US Fish and Wildlife Service (No. MB210495) and the State of Alaska (No. 11-108 and No. 12-115-A1). All data, code and models that were used to generate results, figures and tables presented in the main text and supplementary information are available to download from dedicated repositories on the Open Science Framework (Merkling et al. 2020).

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

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

<sup>a</sup>: as compared to supplemented birds

<sup>b</sup>: as compared to 2011



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

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

<sup>a</sup>: as compared to A-eggs

<sup>b</sup>: as compared to 2011

<sup>c</sup>: 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 <sup>a</sup>	-0.20 $\pm$ 0.12	-0.44	0.04
<b>Proportion of opposite neighbours (panel)</b>	<b>-0.29 <math>\pm</math> 0.12</b>	<b>-0.53</b>	<b>-0.05</b>
<b>Proportion of opposite neighbours (panel) ^2</b>	<b>-0.74 <math>\pm</math> 0.31</b>	<b>-1.36</b>	<b>-0.13</b>
<b>Proportion of opposite neighbours (local)</b>	<b>-0.26 <math>\pm</math> 0.13</b>	<b>-0.52</b>	<b>0.00</b>
<b>Proportion of opposite neighbours (local) ^2</b>	<b>-0.45 <math>\pm</math> 0.23</b>	<b>-0.91</b>	<b>0.00</b>
<b>Male<sup>a</sup> * Proportion of opposite neighbors (local)</b>	<b>0.50 <math>\pm</math> 0.25</b>	<b>0.00</b>	<b>0.99</b>
Male <sup>a</sup> * Proportion of opposite neighbours (panel)	0.42 $\pm$ 0.26	-0.09	0.92

747 <sup>a</sup>: 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
<b>Time between capture and laying</b>	<b>-0.34 <math>\pm</math> 0.16</b>	<b>-0.65</b>	<b>-0.02</b>
Male <sup>a</sup>	0.06 $\pm$ 0.16	-0.25	0.37
Body size	-0.15 $\pm$ 0.16	-0.46	0.16
<b>Male<sup>a</sup> * Body size</b>	<b>0.75 <math>\pm</math> 0.30</b>	<b>0.15</b>	<b>1.34</b>
Pair-bond duration	0.11 $\pm$ 0.17	-0.21	0.44
Body mass	0.12 $\pm$ 0.16	-0.20	0.44
<b>Male<sup>a</sup> * Body mass</b>	<b>-0.77 <math>\pm</math> 0.31</b>	<b>-1.38</b>	<b>-0.17</b>
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 <sup>a</sup>: as compared to females

## Figure captions

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

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

**Figure 3.** Relationship between baseline corticosterone levels and the proportion of neighbours from the opposite food-treatment (i.e. food-supplemented neighbours) in unsupplemented birds (males in blue, females in red) at (a) the local spatial scale and (b) the panel spatial scale. On average, unsupplemented birds surrounded by a high proportion of food-supplemented neighbours had lower 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.

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