




# Offspring sex-ratio and environmental conditions in a seabird with sex-specific rearing costs: a long-term experimental approach

Thomas Merklings<sup>1,2,3,6</sup>  · Scott A. Hatch<sup>4,5</sup> · Sarah Leclaire<sup>1,2</sup> · Etienne Danchin<sup>1,2</sup> · Pierrick Blanchard<sup>1,2</sup>

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## Abstract

Sex allocation studies among birds and mammals are notoriously inconsistent with theoretical predictions. One explanation is the difficulty of collecting data on costs and benefits of sex-ratio adjustments, which prevents the investigation of underlying assumptions. Some predictions may thus have been tested in species where they should not have been expected. Here, we focus on the “cost of reproduction hypothesis”, which states that parents with low investment capacity should avoid producing the most expensive sex to minimise the decrease in their residual reproductive value. In the black-legged kittiwake (*Rissa tridactyla*), sons are energetically more expensive than daughters. Using 10 years of data (1172 chicks from 790 broods) from a long-term feeding experiment, we predicted a stronger decrease in the probability of producing a son with deteriorating environmental conditions among Control than among supplementally Fed parents. To test this prediction, we used three proxies of environmental conditions and a recent sliding window approach. We found no support for our prediction. Hence, we investigated between-year sex-ratio variation in relation to feeding status to detect a response to an unmeasured environmental variable. There was no interaction between year and feeding status, nor any effect of feeding status itself. However, the probability of producing a male increased with time, which could be a response to an oceanic regime shift that occurred around our colony, but that our proxies failed to capture. Our study further highlights the difficulty of explaining sex-ratio variation in long-lived species with complex life-histories where multiple selective pressures can occur simultaneously.

**Keywords** Energy expenditure · Life-history trade-off · Oceanographic conditions · Parental effort · Reproductive cost

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✉ Thomas Merklings  
thomasmerklings00@gmail.com

Extended author information available on the last page of the article

## Introduction

Sex allocation theory considers the way parents invest in male and female functions according to their relative fitness costs and benefits (Trivers and Willard 1973; Charnov 1982; Frank 1990). Although it has been successfully applied in a wide range of taxa (reviewed in Hardy 2002; West 2009), general patterns in birds and mammals remain inconsistent (reviewed in Cockburn et al. 2002; Komdeur 2012). One explanation is that given the difficulty of collecting data concerning the potential costs and benefits of sex-ratio adjustment (Festa-Bianchet 1996; West 2009; Komdeur 2012), the underlying assumptions of sex allocation hypotheses have not always been tested (West 2009; Komdeur 2012; Douhard 2017; but see Bowers et al. 2015; Merklings et al. 2015 for attempts to go past that difficulty). Hence, the presence of sex-ratio adjustment may have been tested in species or populations where it would not be theoretically expected (Festa-Bianchet 1996; West 2009; Komdeur 2012).

The ‘cost of reproduction hypothesis’ (hereafter, ‘CRH’) is one of the proposed hypotheses explaining offspring sex-ratio biases (Myers 1978; Cockburn et al. 2002). It states that parents with low investment capacity (e.g., in poor body condition) should be less likely to produce the most expensive sex to minimise the risk of current reproductive failure and/or the decrease in their residual reproductive value. This hypothesis therefore assumes that one sex is costlier to rear than the other, but the test of this assumption is challenging because it requires data about the costs of rearing each sex (see Gomendio et al. 1990; Bérubé et al. 1996 for some exceptions). Sexual size dimorphism has often been used as a proxy for the differential cost of rearing sons and daughters (e.g., Anderson et al. 1993; Magrath et al. 2007). However, the magnitude of sexual dimorphism can be poorly correlated, or even uncorrelated, with the actual difference in rearing costs (e.g., Krijgsveld et al. 1998; Hewison and Gaillard 1999; McDonald et al. 2005). For instance, females blue-footed boobies (*Sula nebouxii*) are 27% heavier than males at fledging, but this is not due to a greater parental feeding expenditure towards daughters (Torres and Drummond 1999). In this species, one would then not predict any sex-ratio bias in relation to rearing costs patterns, despite a strong sexual dimorphism. Hence, the prediction of the CRH should be tested on species where sex-specific rearing costs have been demonstrated, using measurements of energy expenditure or parental food provisioning for example (Magrath et al. 2007), or, ideally, measures of parental reproductive value.

The rationale of the CRH has been tested using two main approaches. Researchers either compared parents with low and high investment capacity (e.g., Arnbom et al. 1994) or compared breeding seasons with low and high food availability (e.g., Wiebe and Borolotti 1992; Moreno-Rueda et al. 2014), and showed that sex-ratio was biased towards the cheaper sex among parents with low investment capacity or during breeding seasons with low food availability, respectively. However, very few studies have considered both factors concomitantly, although they could be expected to interact together, with, for example, poor environmental conditions having a stronger impact on individuals with low investment capacity. One exception is a longitudinal study on bighorn sheep (*Ovis canadensis*), which showed that senescent, but not prime-aged, females adjusted reproductive effort and offspring sex to environmental conditions, highlighting the benefits of long-term monitoring (Martin and Festa-Bianchet 2011). In a rather counterintuitive way, older females experiencing good environmental conditions reproduced every year but minimized the concomitant costs by overproducing the cheaper sex (i.e. female), while under poor conditions they were more likely to produce sons, but not every year. Finally, parental investment capacity

and environmental conditions could be confounded, with, for example, most individuals having low investment capacity during seasons with very low food availability, and conversely during seasons with very high food availability. As this could prevent a proper investigation of how both variables interact to influence sex allocation, a manipulation of parental investment capacity (e.g., Nager et al. 1999) could help circumvent such an issue.

Here, we used a long-term dataset to investigate the occurrence of a sex-ratio bias in relation to experimentally manipulated parental investment capacity and environmental conditions. We focused on the black-legged kittiwake (*Rissa tridactyla*), a species for which we have good evidence of sex-specific rearing costs, thereby offering a good system to test the predictions of the CRH (Merkling et al. 2015). Male kittiwakes are larger and heavier than females (Jodice et al. 2000; Helfenstein et al. 2004) and sexual dimorphism takes place during chick rearing (larger peak weight for sons than for daughters: 7.7% larger in Merkling et al. 2012; 13% larger in Vincenzi et al. 2013). In addition, parental daily energy expenditure and parental baseline corticosterone increased with the proportion of males in the brood (14% difference in energy expenditure between broods with at least one female and all-male broods, Merkling et al. 2015), as did oxidative stress and baseline corticosterone following a fostering experiment (Merkling et al. 2017), thereby supporting the underlying assumption of the CRH that one sex (here, male) is energetically costlier than the other. In line with the CRH, we previously focused on the prediction that kittiwakes with low investment capacity should avoid the production of costly sons. We used data from a long-term feeding experiment that started in 1996 to do so. In this experiment, a subset of the breeding pairs had been divided into two groups: parents receiving supplemental food throughout the breeding season (hereafter, ‘Fed’ birds) and control parents receiving no supplemental food (hereafter, ‘Control’ birds) (Gill and Hatch 2002). Control and Fed parents differ in parental investment capacity, with Control pairs having a lower fledging success (Vincenzi et al. 2015) and producing smaller chicks (Vincenzi et al. 2013) than Fed pairs, despite expending more energy in parental care (Welcker et al. 2015). Our prediction was confirmed over 3 breeding seasons (2006, 2007 and 2009) during which Control parents overproduced daughters, whereas Fed parents produced a balanced sex-ratio (Merkling et al. 2012). Unfortunately, the three breeding seasons considered were all assessed as “poor” (based on comparisons of fledging success), thereby preventing us from investigating the role of environmental conditions in sex allocation decisions. However, an interaction between parental investment capacity and environmental conditions is expected because poor environmental conditions (i.e. warmer oceanographic conditions) had a stronger negative effect on growth among Control than Fed chicks (Vincenzi et al. 2015), thereby suggesting that investment capacity decreased with food availability more strongly among Control than Fed parents. Hence, in the present study, we predicted that the decrease in the probability of producing a male with deteriorating environmental conditions should be stronger among Control than among Fed parents, i.e. we expected an interaction between feeding status and environmental conditions.

Since our previous study focusing on 3 breeding seasons, we have gathered a larger dataset comprising offspring sex-ratio data for Fed and Control pairs over 10 breeding years and offering a broader variance in environmental conditions [fledging success difference between Fed and Control pairs ranged from 0.01 to 0.77 chicks fledged ( $SD=0.26$ ), as compared to 0.38 to 0.67 ( $SD=0.15$ ) in our previous study (Merkling et al. 2012)], thereby allowing us to test our prediction. As proxies of prevailing environmental conditions, we used three indexes of oceanographic conditions available at different spatial and temporal scales (more details in methods). Because we had no previous knowledge of the biologically relevant temporal scale over which sex allocation decisions are made in this

species, we used a recently developed sliding window approach to test for a set of climatic window combinations (van de Pol et al. 2016).

## Materials and methods

### Study species and experimental protocol

This study was conducted from 2004 to 2016 (but 2008, 2014 and 2015 were not considered because of very low or non-existent sampling efforts) on an Alaskan population of individually marked kittiwakes as part of a long-term experiment begun in 1996 (Gill and Hatch 2002), in which a sample of birds are experimentally fed ad libitum three times a day (at 09:00, 14:00 and 18:00 local time) throughout the breeding season ('Fed') while comparable numbers are not and serve as controls ('Control'). Experimental feeding started between mid-April and early-May (~3 weeks before the first egg was laid in the colony) and lasted until fledging or loss of the nest contents. Supplemental food consisted of thawed Atlantic capelin (*Mallotus villosus*), a fish species similar to the kittiwakes' naturally preferred prey at this site (Hatch 2013). At each nest, food was offered through a plastic tube and was inaccessible to neighbouring birds (see details in Gill and Hatch 2002). The birds were fed until the parent(s) present at the nest stopped taking fish (see supplementary material for more details).

Nests were checked at least once daily to document events such as laying, hatching and chick mortality. Females lay 2 eggs on average (range: 1–3) between mid-May and late June (Coulson 2011). Nest site fidelity is high in kittiwakes (Coulson 2011) and only a few individuals occupied sites with a different feeding status between breeding seasons. The corresponding pairs ( $N=19$ ) were not considered in the analyses.

### Chick sex and rank data

A total of 1172 chicks (from 790 different broods) in 10 breeding seasons were sexed (see details of the molecular methods in Merklings et al. (2012), additional details in the supplementary material and see 'Total dataset' in Table S1 for details on sampling). Some data had to be discarded (see supplementary material for justification). With the remaining data, we maintained two datasets for further statistical analyses. One dataset contained both complete (where both chicks had been sexed) and incomplete broods (where only one chick had been sexed, because the other one did not hatch or was lost before we could take a blood sample) ( $N=1012$ ; 'Unrestricted dataset' in Table S1) and the other contained only complete broods ( $N=678$ ; 'Restricted dataset' in Table S1). As suggested for offspring sex-ratio studies (Krackow and Neuhäuser 2008), we did the same analyses on the 'Unrestricted dataset' and the 'Restricted dataset' (Table S1) to see whether covariates explaining offspring sex-ratio variation changed. In the Restricted dataset, yearly overall sex-ratio varied between 0.20 and 0.71 among Control pairs (between 0.21 and 0.71 in the Unrestricted dataset) and between 0.33 and 0.61 among Fed pairs (between 0.38 and 0.63 in the Unrestricted dataset), whereas the yearly population sex-ratio varied between 0.35 and 0.59 (between 0.41 and 0.59 in the Unrestricted dataset). In addition, the random-effect variance explained by Year was higher among Control pairs (0.05 and 0.07 in the Unrestricted dataset) than among Fed pairs ( $<0.001$  in both datasets). Hence, as expected, there was

among-year variation in sex-ratio and it was larger among Control pairs, in line with the hypothesis that they would be more sensitive to environmental variation.

For each egg/chick, we also recorded its position in the laying sequence (first-laid/hatched = 'A-egg/chick'; second-laid/hatched = 'B-egg/chick'), which is later referred to as 'egg rank'.

## Environmental variables

As a proxy of prevailing environmental conditions and following Hatch (2013), we used a large-scale index of oceanographic conditions, the monthly Pacific Decadal Oscillation index (hereafter, 'PDO index': <http://jisao.washington.edu/pdo/PDO.latest>), measured during the period preceding laying [i.e. when the sex allocation decision is made, see Cameron (2004) and Sheldon and West (2004)]. It is a large-scale monthly index based on sea surface temperature sea level pressure and surface wind anomalies in the North Pacific Ocean and identifies 'Warm' and 'Cool' conditions, per its sign ([-] for cold phases; [+] for warm phases). 'Warmer' ocean conditions (i.e. high PDO values) have been associated with lower availability of kittiwakes' favoured prey in the region (Hatch 2013), as well as lower chick growth (Vincenzi et al. 2015) and survival (Hatch 2013) in that population. Previous sex-ratio studies have found relationships with large-scale proxies of environmental conditions, such as the North Atlantic Oscillation index (e.g., Post et al. 1999), which further justifies its use.

However, to increase our chances of having a reliable proxy and also because large-scale indexes have been criticised (e.g., van de Pol et al. 2013), we also considered two other variables, available on public repositories, at a smaller spatial and temporal scale: chlorophyll-A (hereafter, 'Chl-A') and sea surface temperature (hereafter, 'SST'). For each year, weekly Chl-A concentrations, a measure of ocean productivity and thereby seabird food availability (e.g. Grecian et al. 2016), was estimated from early March to the end of July using satellite-born moderate resolution imaging spectroradiometer data (MODIS Aqua) from the NASA Goddard Space Flight Center, accessed via the NOAA OceanWatch webpage (<http://pifsc-oceanwatch.irc.noaa.gov/thredds/dodsC/aqua/weekly.html>). Data were averaged over a region encompassing our study (Latitude: from 58 to 62°N; Longitude: from 149 to 146°W). Higher Chl-A concentrations indicate higher oceanic productivity, which in turn indicate higher food availability for seabirds (Grecian et al. 2016). Additionally, local daily maximum SST data, a commonly used index of local conditions in seabird studies (Sydeman et al. 2012) and related to annual productivity in European populations of kittiwakes (Frederiksen et al. 2007), were gathered from a buoy situated approximately 80 km away from Middleton Island (Station 46,061 at 60°13'39"N, 146°50'3"W; <http://www.ndbc.noaa.gov/>), in an area where kittiwakes are known to forage (Kotzerka et al. 2010). When data were not available for a given date, we used those from a nearby buoy (~40 km further away; Station 46,060 at 60°35'1"N, 146°47'1"W), and in the rare cases (<10) where neither had data for a specific date we calculated the average SST for the same date across the whole period. Lower SST values have been correlated with higher productivity in kittiwakes therefore indicating higher food availability (Frederiksen et al. 2007). For Chl-A and SST we also calculated their respective 'anomalies' using the difference between each observation and the average value over the whole study period for each week and day, respectively.

The presence of important inter-annual variation for each of environmental variable is confirmed in Figure S1 for the 2 months before laying (April and May).

## Statistical analyses

We had no previous knowledge allowing us to decide over which period to consider our environmental variables. We thus used the *climwin* package (Bailey and van de Pol 2016; van de Pol et al. 2016) in R 3.3.1 (R Core Team 2015) to systematically compare a range of different temporal windows. This package uses an exploratory sliding window approach (e.g., Kruuk et al. 2015; Langmore et al. 2016) to investigate all possible ‘climatic’ windows and compare their relative importance to a model without any environmental variables using AICc. As we expected a different effect of our environmental variables on offspring sex-ratio depending on feeding status (i.e. a statistical interaction), we investigated models with a 2-way interaction between one environmental variable and feeding status, using the relative climate window approach (environmental windows for PDO, Chl-A and SST measured in months, weeks and days, respectively, before examining the biological response, Bailey and van de Pol 2016; van de Pol et al. 2016). For each environmental variable, we considered the mean and maximum values, but also the change in each environmental variable over a period of time (i.e. the “slope” aggregate statistics in *climwin*, see Schaper et al. 2012 for an example). We had no strong biological reasons to investigate quadratic or cubic effects, so we restricted our analyses to linear effects. Kittiwakes migrate back to their breeding grounds sometime between February and March (Hatch et al. 2009), so we decided to look for a signal of environmental conditions between February and clutch initiation (i.e. over a temporal window of approximately 5 months). All *climwin* analyses thus tested for a relationship between environmental variables and offspring sex over a similar period—for the PDO index, between 5 and 0 months before laying; for Chl-A and Chl-A anomaly, between 12 and 0 weeks before laying and for SST and SST anomaly, between 150 and 0 days before laying. Because Chl-A data were only available from early March we limited the analyses to 12 weeks before clutch initiation. To enable comparisons of effect sizes within and between models and following recent recommendations (e.g., Schielzeth 2010), we standardized environmental variables and feeding status by centring and dividing them by two standard deviations using the *arm* package (Gelman and Su 2014). All models were generalized linear mixed models (GLMM) with a binomial error distribution, a logit link function (i.e. chick sex was either 0 = female or 1 = male) and year, brood ID (nested in year), and pair ID as random effects. This was done to consider the non-independence of chicks born during the same breeding season or born from the same parents in the same or different years. All models were computed using the *lme4* package (Bates et al. 2011).

Each model (i.e. one for each possible temporal window) was compared to a reference model containing feeding status only and the corresponding  $\Delta$ AICc was calculated. Results were first assessed using the ‘plotdelta’ function, which represents the distribution of the  $\Delta$ AICcs across temporal windows (see results and supplementary material): a ‘true’ sensitivity of offspring sex-ratio to an environmental variable should be represented by many neighbouring, well supported (i.e. with AICc much smaller than the reference model), windows forming a broad peak on the output of the ‘plotdelta’ function (see van de Pol et al. 2016). Given the huge number of models compared, the probability of encountering false positives is high. So, for analyses where the  $\Delta$ AICc of the best window was  $< -6$  (i.e. suggesting an effect of the interaction between an environmental variable and feeding status), we compared the model output to the results of climate window analyses conducted on 15 randomised datasets using the ‘randwin’ function (Bailey and van de Pol 2016; van de Pol et al. 2016). This function calculates a metric called ‘P<sub>C</sub>’, which is the probability of



a climatic window being detected by chance (type I error) and considers the low number of randomisations. To explore the possibility of an effect of environmental conditions independent of feeding status, we repeated this procedure with models without the interaction (i.e. environmental variable + feeding status) and with models containing just an environmental variable.

Finally, we investigated between-year offspring sex-ratio variation in relation to feeding status and the effect of feeding status itself. The former allowed us to question whether kittiwakes responded to an unmeasured environmental variable and the latter can be used as a comparison to our previous study performed on a smaller dataset. We achieved the former in five different ways: (1) adding year as a factor, (2) as a linear term, (3) as a quadratic term and also (4) by using yearly fledging success among Control pairs as a proxy of environmental conditions prevailing over the entire breeding season and (5) classifying years as either ‘bad’ or ‘good’ (hereafter, ‘year quality’) based on the scatter plot between yearly Control fledging success and summer PDO index (June–August, following Hatch 2013; Vincenzi et al. 2015), which showed two clearly distinguishable cluster of points (some years with high fledging success and low PDO and others with an opposite pattern, see Figure S2). We used the same model structure (i.e. binomial GLMM with the same random effect structure) as in the other set of analyses. Thirty-five models were compared: we considered the 3-way interactions between year as a linear term or fledging success or year quality, and feeding status and egg rank, all 2-way interactions between the year terms or fledging success or year quality, and feeding status and egg rank, and all the additive models within them. We compared those models using an information theoretic approach based on AICc (Burnham and Anderson 2002), where the best model has the lowest AICc. As this approach can result in multiple models considered equally likely (i.e. with a  $\Delta\text{AICc} < 4$ ), we controlled for model selection uncertainty by computing model-averaged parameter estimates, standard errors, and confidence intervals without shrinking the parameters (Burnham and Anderson 2002). Briefly, we averaged the parameter estimates of each variable for all the models in which they appeared. These analyses were done using the *AICcmodavg* package (Mazerolle 2013).

## Results

In complete broods (i.e. the Restricted dataset from Table S1), Control birds produced 149 females and 155 males (222 and 212, respectively, when including incomplete broods, i.e. the Unrestricted dataset from Table S1) and Fed pairs produced 180 females and 194 males (287 and 291, respectively, when including incomplete broods).

### Influence of feeding status and environmental conditions on offspring sex-ratio

Considering complete broods only (i.e. the Restricted dataset from Table S1), we found no support for our prediction that the probability of producing a male would decrease with decreasing environmental conditions more strongly among Control birds (i.e. no evidence for an interaction between feeding status and environmental conditions). Although the best models for an interaction between environmental conditions and feeding status (including the slope of SST and of SST anomaly) were much better than the reference model and seemed to corroborate our prediction (e.g., the ‘best’ model suggested that the probability of producing a male decreased among Control pairs, but not among

Fed pairs, when the increase in SST was larger, i.e. when conditions got worse), the randomisation test to control for false positives revealed that this was most likely not biologically true ( $P_c=0.49$ ; Table 1). A similar pattern was found for the model with the slope of SST anomaly (Table 1). The conclusion about the absence of a true biological signal was further confirmed by visual inspection of the  $\Delta AICc$ s, which revealed that potential environmental windows (i.e. models with very low  $AICc$ ) had neighbouring models with systematically lower statistical support (Figure S3). Models with the other environmental variables had  $AICc$ s very close to the reference model, providing no evidence for an interaction between feeding status and environmental variable in their effects on offspring sex (Table 1; Figures S4–S5).

Similar patterns were found in the analyses looking for a temporal window in each environmental variable, independently of feeding status (i.e. without the interaction between feeding status and each environmental variable): the best models were again those including the slope of SST or SST anomaly, but the windows detected were likely to be false positives and not ‘true’ biological signals (Table 2; Figures S6–S8).

Inclusion of incomplete broods (i.e. using the Unrestricted dataset from Table S1) led to similar conclusions to those on complete broods, i.e. there was no biological signal of an interaction between environmental conditions and feeding status. Contrary to the Restricted

**Table 1** Results of sliding window analyses of the interaction between environmental variables and feeding status on offspring sex in black-legged kittiwakes

Environmental variable	Aggregate statistic	$\Delta AICc$	Best window <sup>a</sup>	$P_c$	Estimate $\pm$ SE
SST	Slope	−13.69	17-10	0.49	Control: $-31.84 \pm 7.74$ Fed: $0.54 \pm 3.81$
SST anomaly	Slope	−12.72	17-10	0.65	Control: $4.15 \pm 1.04$ Fed: $0.06 \pm 0.51$
SST	Mean	−5.08	82-82		
SST	Max	−5.08	82-82		
SST anomaly	Mean	−4.14	82-82		
SST anomaly	Max	−4.14	82-82		
PDO index	Slope	−2.73	5-0		
Chl-A	Slope	−1.7	3-1		
Chl-A anomaly	Mean	−1.58	1-1		
Chl-A anomaly	Max	−1.58	1-1		
Chl-A anomaly	Slope	−1.5	9-7		
Chl-A	Mean	−0.58	1-1		
Chl-A	Max	−0.58	1-1		
PDO index	Mean	1.26	1-1		
PDO index	Max	1.26	1-1		

The mean, maximum, and increase in PDO index, Chl-A, Chl-A anomaly, SST and SST anomaly were considered. Table shows the environmental variable and associated aggregate statistic used in the models, the  $\Delta AICc$  value of the best window in each analysis ( $AICc$  compared to a model containing feeding status only), the best window, the probability that the best window is a false positive ( $P_c$ ) and the estimate  $\pm$  standard error (SE) of the effect of the environmental variable on offspring sex for Fed and Control birds. The latter two columns are filled only for variables with models of  $\Delta AICc < -6$ . All analyses were conducted with the package ‘*climwin*’ (see van de Pol et al. (2016) and Bailey and van de Pol (2016))

<sup>a</sup>Best windows are expressed in days (before laying) for SST and SST anomaly, in weeks for Chl-A and Chl-A anomaly and in months for PDO



**Table 2** Results of sliding window analyses considering the effect of environmental variables (with or without feeding status) on offspring sex in black-legged kittiwakes

Environmental variable	Aggregate statistic	$\Delta AICc^a$	$\Delta AICc^b$	Best window <sup>c</sup>	$P_c$	Estimate $\pm$ SE
SST anomaly	Slope	-6.92	-6.65	150-143	With feeding: 0.51 No feeding: 0.65	-4.72 $\pm$ 1.60 -4.62 $\pm$ 1.59
SST	Slope	-6.33	-6.18	150-143	With feeding: 0.56 No feeding: 0.55	34.31 $\pm$ 12.01 33.89 $\pm$ 11.94
SST anomaly	Max	-3.99	-4.05	41-34		
Chl-A anomaly	Mean	-2.84	-2.88	1-0		
Chl-A	Slope	-2.81	-2.76	4-1		
PDO index	Slope	-2.67	-2.73	5-3		
Chl-A anomaly	Max	-2.35	-2.36	1-1		
Chl-A	Mean	-2.3	-2.35	1-0		
SST anomaly	Mean	-2.29	-2.35	51-51		
SST	Max	-2.23	-2.28	148-33		
Chl-A anomaly	Slope	-2.23	-2.25	5-0		
Chl-A	Max	-2.22	-2.23	1-1		
SST	Mean	-1.31	-1.36	51-51		
PDO	Max	1.24	1.19	3-3		
PDO	Mean	1.24	1.19	3-3		

The mean, maximum and increase in PDO index, Chl-A, Chl-A anomaly, SST and SST anomaly were considered. Table shows the environmental variable and associated aggregate statistic used in the models, the  $\Delta AICc$  value of the best window in each analysis ( $AICc$  compared to a model containing feeding status only), the best window, the probability that the best window is a false positive (PC) and the estimate  $\pm$  standard error (SE) of the effect of the environmental variable on offspring sex for Fed and Control birds. The latter two columns are filled only for variables with models of  $\Delta AICc < -6$ . All analyses were conducted with the package 'climwin' (see van de Pol et al. (2016) and Bailey and van de Pol (2016))

<sup>a</sup>For additive models including an environmental variable and feeding status

<sup>b</sup>For models containing only an environmental variable

<sup>c</sup>Best windows are expressed in days for SST and SST anomaly, in weeks for Chl-A and Chl-A anomaly and in months for PDO

dataset, the best candidates for an environmental window were mean and maximum SST, which suggested that the probability of producing a male increased more among Control pairs than among Fed pairs when conditions got worse (Table S2). However, as for complete broods only, both the visual inspection of the  $\Delta AICc$ s and  $P_c$  strongly suggested that this was not a true biological signal (Table S2 and Figure S9). There was also no indication of an effect of any other environmental variable, whether in interaction with feeding status (Figures S10–S11) or by itself (Figures S12–S14), as confirmed by the patterns of the  $\Delta AICc$ s and the randomisation tests (Table S2–S3).

### Between-year variation in offspring sex-ratio

The interaction between year and feeding status did not explain offspring sex-ratio variation, nor did feeding status alone, or fledging success or year quality, alone or in interaction

**Table 3** Model-averaged estimates for all parameters in the subset of models explaining sex-ratio variation in complete and incomplete broods of kittiwakes (i.e. Unrestricted dataset from Table S1)

Parameter	Std. estimate	Uncond. SE	Lower CI	Upper CI
Intercept	−0.017	0.071	−0.157	0.122
'Fed' feeding status <sup>a</sup>	0.044	0.131	−0.213	0.300
Year <sup>b</sup>	0.403	0.131	0.146	0.659
B-chick <sup>c</sup>	0.170	0.128	−0.082	0.421
Year <sup>b</sup> ^2	0.073	0.243	−0.402	0.549
B-chick <sup>c</sup> : Year <sup>b</sup>	−0.364	0.258	−0.870	0.143
'Fed' feeding status <sup>a</sup> : Year <sup>b</sup>	−0.113	0.272	−0.647	0.421
B-chick <sup>c</sup> : Year <sup>b</sup> ^2	0.434	0.482	−0.511	1.378

'Std. estimate' denotes the estimate of the standardized variable (effect size); 'Uncond. SE' the unconditional standard error of the parameter

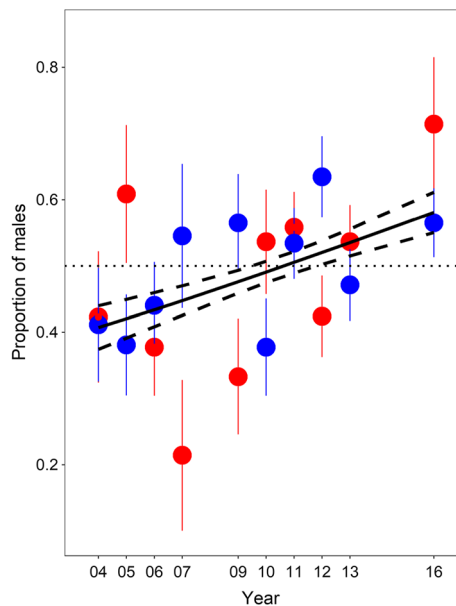
'Lower CI' and 'Upper CI' are the lower and upper bound of the 95% confidence interval. Estimates different from zero are in bold

<sup>a</sup>Relative to Control parents

<sup>b</sup>Year as a continuous variable (2004–2007, 2009–2013 and 2016)

<sup>c</sup>Relative to first-hatched A-chicks

**Fig. 1** Proportion of sons, in complete and incomplete broods (i.e. Unrestricted dataset from Table S1), in relation to year of study (2004 to 2007, 2009 to 2013 and 2016) in pairs of black-legged kittiwakes. Coloured dots and error bars (standard errors) represent the raw data, with dark grey (red for the online version) dots for the Control parents and light grey (blue for the online version) dots for the Fed parents. The black and dashed lines represent the model-averaged predictions and standard errors for the main effect of year, as there was no interaction with feeding status. The horizontal dotted line represents a 50% proportion of males



with feeding status. The best model contained Year as a linear term alone, while the interaction model had a  $\Delta AICc$  of 3.74, and even the null model was better (Table S4). Besides a weak positive effect of Year, all the other model-averaged estimates had confidence intervals overlapping zero (Table S5). This overall increase in the probability of producing a son with time was confirmed using the larger dataset including complete and incomplete broods (Table 3; Fig. 1), with Year as a linear term being in all the best models (Table S6).

However, the effect was weak as illustrated by the fact that the estimate was relatively small and Year explained only 1% of the variance (marginal  $R^2=0.014$ ; calculated following Nakagawa and Schielzeth 2013; and using the *MuMIn* package by Bartoń 2016).

## Discussion

There was no evidence corroborating our a priori prediction that the decrease in the probability of producing a male with deteriorating environmental conditions should be stronger among Control than among Fed parents. Regardless of the proxy of environmental conditions before laying, the interaction with feeding status could not explain variation in offspring sex-ratio, nor could the proxies of environmental conditions alone (i.e. independently of feeding status). Further, there was neither an interaction between fledging success or year (regardless of how we considered it) and feeding status nor an effect of feeding status alone, contrary to what we found previously (Merkling et al. 2012). The only effect we found was a linear increase of the proportion of sons with time.

Given the systematic sliding-window approach we used (i.e. testing for every possible time window over a 5-month period before clutch initiation) (van de Pol et al. 2016), we are confident that we did not miss any biologically relevant signal in our environmental variables during the period we considered, and thus should have been able to detect an interaction between environmental conditions and feeding status if there was one. Although we used proxies of environmental conditions known to correlate with food availability and offspring survival in seabirds (e.g., Frederiksen et al. 2007; Hatch 2013; Grecian et al. 2016), we cannot exclude that we are still missing a relevant proxy of environmental conditions and food availability linked to sex allocation decisions. Alternatively, correlations between environmental variables measured when sex allocation decision was determined (i.e. before laying: April or May, in 2 weeks period) and when sex-specific rearing costs occurred (i.e. during chick rearing: from mid-June to mid-August, in 4 weeks period) might have been too low (mean  $\pm$ SE:  $0.21 \pm 0.06$ ) to allow such tactic to be selected for in this population. Furthermore, a recent meta-analysis of 61 species of seabirds showed that reproductive phenology was insensitive to changes in SST (Keogan et al. 2018), but some populations experienced changes in the timing of reproduction, thereby suggesting that the birds responded to unmeasured environmental conditions. For instance, oceanographic conditions during the non-breeding season have been shown to impact reproductive performance in the black-browed albatross (*Thalassarche melanophris*; Desprez et al. 2018). Similarly, environmental conditions in the wintering grounds of the studied population could have a lagged influence on the condition of the birds at laying and thereby influence sex allocation decisions. However, detailed information about migration patterns is lacking, preventing us from properly exploring this possibility.

An alternative explanation for the lack of support for our prediction could be that the differences in energetic costs between sexes found in this population in 2011 and 2012 (Merkling et al. 2015, 2017) do not translate into fitness costs, which are extremely hard to estimate but ultimately what is important in terms of selective pressure. We assumed, along with most authors testing the CRH (e.g., Wiebe and Bortolotti 1992; Moreno-Rueda et al. 2014; Nichols et al. 2014), that the difference in energetic costs observed in our study species would correlate with a difference in fitness costs. However, the lack of support for our prediction may indicate that this assumption was incorrect. An ideal test would be to see whether parents rearing more males than they initially produced suffer a decrease in

their residual reproductive value or whether they can sustain the extra energetic costs without jeopardising their future reproduction and/or survival.

In addition, and not mutually exclusive from the first alternative explanation, there could be other selective pressures, as yet unidentified and unrelated to environmental conditions, having a superseding effect on rearing costs, which would have prevented us from explaining sex-ratio variation in response to environmental conditions. For example, we can expect the fitness benefits and costs of producing either sex to vary with factors such as age and breeding experience in a long-lived species such as the kittiwake. For instance, we found that energy expenditure during chick-rearing decreased with parental age for a given brood size (Merkling et al. 2015). Given this between-individual variation and because age and breeding experience are more predictable than environmental conditions, they could explain sex-ratio variation better than environmental conditions (e.g., Weimerskirch et al. 2005; Vedder et al. 2016). Moreover, given that, until now, the CRH has only been based on verbal arguments, it is difficult to have a high degree of confidence in the accuracy and the generality of its main prediction. Mathematical models for species with complex life-histories often reveal the difficulty to make accurate sex allocation predictions (Komdeur and Pen 2002; Pen and Weissing 2002). Here, models incorporating brood size and the fitness costs of producing either sex alongside its frequency-dependent fitness benefits would probably help to predict what parental strategy should be favoured by natural selection. Lastly, failure of our prediction could in part reflect low statistical power, as our sample size of 10 years of data is on the lower end of what has been suggested (van de Pol et al. 2016), especially given the likely moderate  $R^2$  expected in our case.

In our investigation of between-year sex-ratio variation, the increase in the probability of producing a son over time suggests that offspring sex-ratio responded to some unmeasured variable(s) similarly for both Fed and Control parents. This increase in the proportion of males produced in more recent years could be due to a 2008 oceanic regime shift (Hatch 2013), which led to an increase in food availability around the focal colony. This seems to confirm that, despite our best effort to find reliable proxies of food availability, we might still be missing something. Moreover, the absence of interaction between year and feeding status (and of an effect of feeding status alone) might indicate either that the differences in investment capacity between Fed and Control groups found by Welcker et al. (2015) are not as important as we thought or that the extra investment capacity of Fed birds played no role in their sex allocation decisions, though it may have lessened the impact of reproduction on their residual reproductive value. Contrary to what we reported previously in Merkling et al. (2012), there was no effect of feeding status alone in the larger dataset considered here, although it was present when restricting to the three breeding seasons previously considered (2006, 2007 and 2009), with Fed parents producing more sons than Control parents (Fig. 1). As our first dataset happened to comprise the two highest sex-ratio differences between Control and Fed pairs (2007 and 2009, Fig. 1), it is not surprising that including more breeding seasons and a greater range of environmental conditions caused the effect of feeding status alone to disappear. However, given our previously published results, in addition to the greater variance in environmental conditions between years and the pattern observed in Fig. 1, we expected to find an interaction between feeding status and Year as a factor, as there can be a statistical interaction without the main effect being present (e.g. if the two curves overlap). Yet, both the null model and the model with Year as a linear term alone explained the data better than interaction models, regardless of how we considered Year. In the information-theoretic approach we used here, the deviance explained by the interaction between feeding status and Year as factor was not enough to overcome the penalisation of the high number of parameters in this model. It should be noted that when

using a less conservative approach (i.e. likelihood-ratio tests), as we did in our first study, the interaction between feeding status and Year as factor is significant ( $p=0.01$ ; but effect sizes overlap zero) in the Unrestricted dataset (i.e. considering complete and incomplete broods, as in Merklings et al. 2012) but not in the Restricted dataset ( $p=0.09$ ).

Hence, overall, we found no support for our a priori prediction that kittiwakes should adjust offspring sex-ratio in response to the interplay between their own investment capacity and environmental conditions. Moreover, contrary to what we previously found in a subset of the data used here, there was no effect of supplementary feeding on offspring sex-ratio either. Interestingly, an absence of effect of supplementary feeding on sex-ratio has also been found in other avian species (Hörnfeldt et al. 2000; Desfor et al. 2007), including species closely related to kittiwakes in which a bias occurred only after inducing females to lay more eggs than the average clutch size (Nager et al. 1999; Kalmbach et al. 2001).

Sex allocation studies in birds and mammals differ notably from other taxa in yielding inconsistent patterns (Cockburn et al. 2002; West 2009; Komdeur 2012). Focusing on species with known potential fitness benefits of sex-ratio adjustment has confirmed the ability of those species to overcome the constraints of chromosomal sex determination and bias sex-ratio according to theoretical predictions (e.g., Komdeur et al. 1997; West and Sheldon 2002; Bowers et al. 2015), with a likely role of steroid hormones in the female, especially testosterone (Merklings et al. 2018), as part of the underlying mechanism (Navara 2013, 2018). However, some species do not adjust sex-ratio according to predictions despite the evident potential for fitness benefits (e.g., Blanchard et al. 2005; Cockburn and Double 2008; Khwaja et al. 2018). As mentioned, this could be due to weaker than expected selective pressure (e.g. difference in rearing costs not large enough) and/or weaker selective pressure than derived from opposing and unidentified factors such as age and breeding experience.

Such interplay between selective pressures has been highlighted in other studies which suggest that sex allocation patterns are more complex than previously thought, especially in long-lived species (Schindler et al. 2015; Douhard et al. 2016b; Edwards et al. 2016). For instance, most theoretical and verbal models applied to birds and mammals overlook the complexity of their life-histories, how modes of parental care and sibling competition might influence benefits and costs of sex-ratio adjustment, and consider only one parent, thereby potentially leading to overly simplistic predictions not accounting for the possibility of secondary sex-ratio adjustment (Komdeur 2012; Vedder et al. 2016) or of sexual conflict over sex-ratio adjustment for example (Douhard et al. 2016a; Douhard 2017; Malo et al. 2017). In conclusion, there is a need for future theoretical models to better incorporate the complexity of avian and mammalian life-histories and interactions among competing selective pressures influencing sex allocation. As in other fields of evolutionary ecology, long-term monitoring of individuals will be crucial for proper testing of these new predictions (Clutton-Brock and Sheldon 2010).

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## Compliance with ethical standards

**Conflict of interest** The authors declare no conflicts of interest.

**Ethical approval** All the work was conducted under the approval of the USGS Alaska Science Center Animal Care and Use Committee and the IPEV Ethical Committee, in accordance with United States laws and under permits from the U.S. Fish and Wildlife Service and the State of Alaska. Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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## Affiliations

**Thomas Merkling**<sup>1,2,3,6</sup>  · **Scott A. Hatch**<sup>4,5</sup> · **Sarah Leclaire**<sup>1,2</sup> · **Etienne Danchin**<sup>1,2</sup> · **Pierrick Blanchard**<sup>1,2</sup>

<sup>1</sup> Laboratoire Évolution and Diversité Biologique (EDB UMR 5174), Université de Toulouse; CNRS, IRD, 118 Route de Narbonne, Bat 4R1, 31062 Toulouse Cedex 9, France

<sup>2</sup> Université Toulouse 3 Paul Sabatier, CNRS, IRD; UMR5174 EDB, 118 Route de Narbonne, 31062 Toulouse, France

<sup>3</sup> Division of Ecology, Evolution and Genetics, Research School of Biology, The Australian National University, 44 Daley Road, Canberra, ACT 2601, Australia

<sup>4</sup> U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK 99508, USA

<sup>5</sup> Institute for Seabird Research and Conservation, 12850 Mountain Place, Anchorage, AK 99516, USA

<sup>6</sup> Present Address: Department of Natural Resource Sciences, McGill University, 2111 Lakeshore Rd, Ste Anne-De-Bellevue, QC H9X 3V9, Canada