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Unpredictable perturbation reduces breeding propensity regardless of pre-laying reproductive readiness in a partial capital breeder

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Theoretically, individuals of migratory species should optimize reproductive investment based on a combination of timing of and body condition at arrival on the breeding grounds. A minimum threshold body mass is required to initiate reproduction, and the timing of reaching this threshold is critical because of the trade-off between delaying breeding to gain in condition against the declining value of offspring with later reproductive timing. Long-lived species have the flexibility within their life history to skip reproduction in a given year if they are unable to achieve this theoretical mass threshold. Although the decision to breed or not is an important parameter influencing population dynamics, the mechanisms underlying this decision are poorly understood. Here, we mimicked an unpredictable environmental perturbation that induced a reduction in body mass of Arctic pre-breeding (before the laying period) female common eiders *Somateria mollissima*; a long-lived migratory seaduck, while controlling for individual variation in the pre-laying physiological reproductive readiness via vitellogenin (VTG) – a yolk-targeted lipoprotein. Our aim was to causally determine the interaction between body condition and pre-laying reproductive readiness (VTG) on breeding propensity by experimentally reducing body mass in treatment females. We first demonstrated that arrival body condition was a key driver of breeding propensity. Secondly, we found that treatment and VTG levels interacted to influence breeding propensity, indicating that our experimental manipulation, mimicking an unpredictable food shortage, reduced breeding propensity, regardless of the degree of pre-laying physiological reproductive readiness (i.e. timing of ovarian follicles recruitment). Our experiment demonstrates that momentary environmental perturbations during the pre-breeding period can strongly affect the decision to breed, a key parameter driving population dynamics.

A combination of environmental variables and intrinsic state interact to influence the life history trade-offs and decisions of individuals (McNamara and Houston 1996, Ricklefs and Wikelski 2002). Specifically, theoretical models predict that migratory individuals should optimize their reproductive investment based on a combination of body condition and timing of arrival on the breeding grounds (Rowe et al. 1994). The relationship among these variables have been formalized into the condition-dependent individual optimization model, in which individuals are predicted to require a minimum body condition to begin investing in reproduction (Rowe et al. 1994, Bêty et al. 2003). The timing of when individuals meet this theoretical condition threshold for reproduction will impact both the timing of reproduction and reproductive investment; individuals that are unable to reach this condition threshold early enough in the breeding season are predicted to skip reproduction in favour of self-maintenance (Drent and Daan 1980).

In long-lived species, empirical studies suggest that the decision to reproduce or not within a single breeding season (breeding propensity) is driven by a combination of individual body condition at arrival on the breeding grounds (Drent and Daan 1980, Reed et al. 2004, Warren et al. 2014), environmental conditions (Chastel 1995, Warren et al. 2014) and the timing of spring migration (Bêty et al. 2004). For example, breeding propensity was positively related to female body condition and negatively affected by drought episodes in lesser scaup *Aythia afinis* (Warren et al. 2014). As in the condition dependent individual optimization model, a threshold body condition mediating breeding propensity has been well established in organisms which rely extensively on internal reserves to successfully reproduce (capital breeder; Jönsson 1997). Such a threshold has been well documented in both mammal and reptile species (reviewed by Shine 2003, Bonenfant et al. 2009). Despite breeding propensity being considered a key demographic parameter (Sedinger et al. 2001), it is the least understood reproductive decision in avian species (Sedinger et al. 2001, Reed et al. 2004). This parameter has rarely been tested in birds because non-breeders are often entirely absent from the breeding grounds, making comparisons to breeding birds challenging (Chastel 1995), and individuals are difficult to both capture and manipulate prior to investment in reproduction (but see Weimerskirch 1992, Bêty et al. 2003). Furthermore, the proximate mechanisms underlying breeding propensity are currently poorly understood (Williams 2012, Crossin et al. 2013).

In avian species, experimental approaches testing the mechanisms linking pre-breeding body condition and breeding parameters (clutch size and laying date) are rare (but see Nooker et al. 2005, Descamps et al. 2011), with most studies manipulating female condition (i.e. body mass) via food supplementation (see Boutin 1990, Schoech and Hahn 2007 for reviews). Although these studies have been successful in directly manipulating female condition, food supplementation can indirectly affect aspects of individual state and territory quality, making results difficult to interpret (Williams 2012). Using physiological traits may be a more direct way of understanding reproductive investment or readiness because of their roles as underlying mechanisms influencing reproductive decisions (Ricklefs and Wikelski 2002).

There are two key physiological markers (yolk precursors) that females produce at the onset of egg production specifically when they are recruiting and developing follicles: yolk-targeted very low-density lipoprotein (VLDLy) and vitellogenin (VTG). In non-breeding females, generic VLDL is produced by the liver and circulated in the plasma following foraging to meet the females general metabolic needs (Gibbons et al. 2004). When females begin recruiting follicles and initiate rapid follicle growth (RFG), they undergo a shift in lipoprotein metabolism from producing generic VLDL to VLDLy (Walzem et al. 1999). Simple assays that measure triglycerides do not easily identify differences between the two types of VLDL (Salvante et al. 2007) so VLDL is a somewhat less reliable measure of reproductive readiness (follicle development; Gorman et al. 2009). VTG is a yolk-targeted lipoprotein produced by all oviparous species only during the period of rapid follicle growth and provides a very accurate means of assessing the timing of the initiation of egg development (Vezina and Williams 2003). Finally, in common eiders *Somateria mollissima*, plasma (i.e. circulating) VTG has been shown to have a positive relationship with pre-laying body mass with heavier females (> 2 kg and closer to laying) exhibiting higher levels of VTG (Hennin et al. 2015). As such, VTG should be a good metric for estimating the likelihood that an individual will breed and help to identify fecund females whose reproductive status would otherwise remain unknown (Tranquilla et al. 2003).

We combined an experimental reduction of body mass in Arctic-nesting, pre-breeding female common eiders (Descamps et al. 2011) with plasma VTG to causally determine the interaction between individual condition and reproductive readiness on breeding propensity. Specifically, individuals were either released at capture, or held for 24 h in captivity, thereby likely modifying the condition (McNamara and Houston 1996) of manipulated individuals. By knowing the initial state of pre-laying individuals through plasma VTG (individuals engage in egg formation or not), our experiment can contribute to testing components of the condition dependent individual optimization model (McNamara and Houston 1996, Ricklefs and Wikelski 2002). Common eiders are a good model system to test these relationships because: 1) they are a long-lived, migratory species which exhibit a capital-income breeding strategy, 2) previous studies have shown that reproductive decisions were influenced by a body mass (Sénéchal et al. 2011, Hennin et al. 2015) threshold, and 3) if females cannot achieve a threshold body mass early enough in the breeding season to successfully complete reproduction, they have the flexibility within their life history to skip reproduction in favour of self-maintenance for that year (Yoccoz et al. 2002). We predicted that females that are heavier and have higher plasma VTG (likely closer to laying), would have a higher breeding propensity. Further, if body mass is a key driver of variation in breeding propensity, an experimental food shortage (i.e. reduction in body mass) should negatively affect breeding propensity regardless of pre-breeding physiological readiness as measured by plasma VTG.

Material and methods

In 2003 and 2004, before the laying period, female eiders were captured using flight nets at Mitivik Island, Nunavut, Canada (64°02′N, 81°47′W). The colony is located on a small (800 × 400 m) island that supports the largest known nesting colony of common eiders in the Canadian Arctic (up to 8000 pairs annually). This colony is the only one within a 100 km radius and we considered all eiders that were captured prior to laying as prospective breeders.

Females were caught in mid to late June to coincide with their timing of arrival on their breeding grounds (n = 76 and 146 in 2003 and 2004, respectively). There were no interannual recaptures in this dataset. Within 10 min of capture, ~ 300 μl of blood was collected from each female from the tarsal vein using either a 26 G needle and heparinized 75 μl capillary tubes (2003) or a heparinized vacutainer with a 26 G butterfly needle (2004). Samples were kept at 4°C until centrifugation after which plasma was stored at –20°C until further analysis. Following capture and blood sampling, females were measured (tarsus length and wing chord), weighed using a Pesola scale (± 25 g), given metal and coloured alphanumeric bands, and a unique combination of temporary nasal tags to ease individual identification in the colony post-release (Descamps et al. 2011). Nasal tags were attached using UV degradable monofilament and fall off at the end of the season (Hennin et al. 2015). After release, nasal-tagged hens were monitored twice daily from seven permanent blinds located around the periphery of the colony using spotting scopes and consistent behavioural observations from trained observes to determine reproductive status. We estimated the breeding propensity of female eiders as follows: individuals captured and resighted on a nest in the colony were classified as breeders, while individuals that have been caught, banded and nasal-tagged, but not subsequently resighted on a nest, were considered non-breeders.

Among the 222 captured females, 79 served in the treatment group (23 in 2003 and 56 in 2004). Those females were randomly chosen and kept in outdoor pens (wooden structure surrounded by wire mesh, 1.2 × 2.5 × 1.2 m) for 24 h with access to fresh water, but no food, to experimentally reduce body condition, thereby mimicking an environmental perturbation restricting food access. Since female eiders will fast while in captivity, it is not possible to have a 'true' control group in which females were held captive, but body mass maintained. Instead, control females were captured and released immediately after the measurements and sampling procedures (Descamps et al. 2011). Body mass at capture did not differ between treatment and control females (mean ± SEM; treatment: 2045 ± 21 g; control: 2061 ± 19 g). Previous research in this colony has shown that correcting body mass for body size accounts for only 1% of the variation in body mass (Descamps et al. 2010). As such, uncorrected body mass was used as a proxy of endogenous reserves (i.e. body condition) in pre-breeding birds.

Samples were analysed for zinc (Zn) using a commercially-available kit (Zinc Kit; Wako Chemicals, VA, USA) as a measure of the plasma concentration of the yolk precursor vitellogenin (VTG) developed for chickens (Mitchell and Carlisle 1991), and validated in common eiders (Hennin et al. 2015). Each plate was run with a kit-provided Zn standard (2 μg ml^{-1}) and a control sample of laying-hen plasma (Sigma-Aldrich, USA). The inter- and intra-assay coefficients of variation for total Zn were 3.11 and 3.57%, respectively and 12.49 and 9.17% for depleted Zn, respectively.

We used generalized linear models (binomial family) to test the effect of 1) body mass (either at capture: BM1 or at release: BM2), 2) treatment (TRT: control vs fasting), and 3) vitellogenin concentration (VTG) on breeding propensity (0 = not resighted on a nest and 1 = resighted on a nest). We did not correct for over dispersion since the c-hat was close to one (c-hat = 1.0045). In all models, capture date (or release date for treated birds) was included to account for differential timing of arrival at the colony and year was included as a fixed factor. Capture date is a good predictor of the timing of arrival, especially for early-caught birds, and predict laying date of females in our colony (Descamps et al. 2011). Any detected effect of our treatment could either be due to a reduction in body condition or the stress experienced during captivity. To determine whether captivity stress played a confounding role, we ran all of our models with BM1 and again with BM2 to compare the effects of mass at capture (BM1) vs mass at release (BM2) (Descamps et al. 2011). If the treatment was a confounding effect, we predicted to see a large treatment effect on BM2 (post-treatment) compared to BM1. Change in mass was not a reliable index of our treatment because it not only accounted for endogenous reserve loss, but also for other losses such as droppings and water. Therefore, using either BM1 or BM2 reduced the magnitude of this potential bias. We based our interpretation by comparing models selection using both BM1 and BM2 but also provided similar results with mass loss in the appendix. We included quadratic terms on both BM and VTG to test for non-linear relationships. If a quadratic term was detected, we followed the methods of (Muggeo 2003) to calculate the threshold value and its confidence interval. We ranked our models using Akaike's information criterion corrected for small sample size (AICc) and used model averaging to obtain parameter estimates (Burnham and Anderson 2002, Burnham et al. 2010). We used AICcmodavg package in R 3.0.3 (R Development Core Team).

Data available from the Dryad Digital Repository: < http://dx.doi.org/10.5061/dryad.7k3p2 > (Legagneux et al. 2016).

Results

For all captured hens, body mass at capture was 2054 ± 14 g, and VTG was 2.75 ± 0.1 μg Zn ml^{-1}. Body mass and VTG were positively related (Pearson correlations between VTG and body mass at arrival or at release were 0.45 and 0.44, respectively). Body mass was affected by the treatment, decreasing markedly by –119.7 ± 6.0 g d^{-1}. Pre- and post-treatment body mass had different effects on breeding propensity (Table 1). When the model selection was performed using pre-treatment body mass, the effect of treatment was ranked highest (interacting with VTG; Table 1). However, when using post-treatment body mass, the treatment effect was relegated in the model selection ranking. The % of AICc weights supporting an effect of treatment was 76% when models used pre-treatment body mass and 47% when post-treatment body mass was used (Table 1). Using mass loss instead of body mass, the model with an interaction between body mass loss and VTG levels was ranked highest (Supplementary material Appendix 1, Table A1; Fig. A1).

Five competing models explaining variation in breeding propensity, which were equivalent on the basis of ΔAICc $<$ 2 (Table 1). All five models included pre-treatment body mass and treatment in four of them. Breeding propensity was strongly related to pre-treatment body mass (Table 2; Fig. 1), reaching 50% when individuals were $>$ 2060 g (Fig. 1). The model with a quadratic relationship with body mass was within 2 ΔAICc revealing a threshold value at 2160 g (CI 95%: 2019–2301 g) indicating that only heavier females initiated reproduction. The interaction between VTG and treatment was in the highest ranked model (Table 1) and, based on model averaging, very close to significance (0 was included within 95% CI; Table 2). Vitellogenin was positively related to breeding propensity in control birds ($\beta = 0.34$, CI = (0;0.67); Fig. 2), however this effect was greatly reduced in treatment birds ($\beta = 0.001$ CI = (–0.47;0.47); Fig. 2). In control birds, for a one-unit increase in plasma VTG, there was a 40% increase in the probability of being a breeder. However, in treatment birds, the odds ratio decreased to only 0.092% for a one-unit increase in plasma VTG.

Discussion

Arctic-breeding common eiders are income-capital breeders that feed intensively during the pre-breeding and laying periods, and depend heavily on endogenous stores to produce their eggs and successfully complete their 24 d-long incubation fast (Sénéchal et al. 2011). Our study demonstrates that pre-breeding body condition is a key driver of breeding propensity in this mixed-strategy breeder. This is consistent with other studies on (partial) capital breeding vertebrates (Naulleau and Bonnet 1996, Bêty et al. 2003, Bonenfant et al. 2009) which show that individuals arriving on the breeding grounds in poor condition are more likely to skip reproduction (Chastel 1995). We found that post-treatment body mass alone, rather than treatment with pre-treatment body mass, better explained breeding propensity. Therefore, we speculate that treatment females were responding to the reduction in body condition rather than the stress of captivity. As such, by mimicking a momentary

Table 1. Model selection of the effects of treatment (TRT: 24 h fasting vs control individuals), vitellogenin (VTG), body mass at capture or at release (Mass), and biologically relevant two-way interactions on the breeding propensity of female common eiders nesting on Mitivik Island (Nunavut, Canada) in 2003 and 2004 (n = 222). When an interaction (*) was used, the corresponding fixed effects were also incorporated in the model. All models included year and release date as fixed factors.

		Body mass at capture			Body mass at release		
Model name	*k*	AICc	Δ AICc	w_i	AICc	Δ AICc	w_i
TRT * VTG + Mass	7	**248.07**	**0**	**0.22**	250.81	0.59	0.13
TRT * VTG + Mass^2	7	249.18	1.11	0.13	251.58	1.36	0.09
TRT + Mass + VTG	6	249.44	1.37	0.11	252.23	2.01	0.06
Mass + Mass^2	5	249.45	1.38	0.11	251.41	1.18	0.09
TRT + Mass	5	249.74	1.67	0.1	252.98	2.76	0.04
TRT * VTG^2 + Mass^2	7	250.64	2.57	0.06	253.23	3.01	0.04
TRT * Mass + VTG	7	250.87	2.8	0.06	252.7	2.48	0.05
VTG + Mass	5	251.24	3.17	0.05	250.22	0	0.17
TRT * Mass	6	251.36	3.29	0.04	253.75	3.53	0.03
Mass	4	251.37	3.3	0.04	250.89	0.67	0.12
TRT * Mass^2	6	252.76	4.69	0.02	254.97	4.75	0.02
Mass^2	4	252.82	4.75	0.02	251.94	1.72	0.07
TRT * VTG * Mass	10	253.09	5.02	0.02	255.56	5.34	0.01
VTG * Mass	6	253.33	5.26	0.02	251.66	1.43	0.08
VTG + VTG^2	5	270.79	22.72	0	270.79	20.57	0
TRT * VTG	6	273.68	25.61	0	273.68	23.45	0
TRT + VTG	5	274.98	26.91	0	274.98	24.76	0
VTG	4	278.45	30.38	0	278.45	28.23	0
TRT * VTG^2	6	284.21	36.14	0	284.21	33.99	0
TRT	4	294.45	46.38	0	294.45	44.23	0
Null	3	297.18	49.11	0	297.18	46.96	0

reduction in food availability on the breeding grounds prior to laying, we found that a reduction in pre-breeding condition reduces breeding propensity, regardless of physiological readiness for reproduction (i.e. levels of plasma VTG).

Our study is one of the first manipulative tests examining whether pre-breeding physiological state influences reproductive decisions (Williams 2012, Crossin et al. 2013). Plasma levels of VTG act as an indicator of follicle recruitment in birds, the final step in the reproductive 'cascade' that marks the decision to initiate a breeding attempt and follicle growth in female birds (Williams 2012). We found that control females with higher plasma VTG had a higher probability of breeding. Previous studies of VTG in the wild have largely used this trait to distinguish between breeding and non-breeding individuals (Vanderkist et al. 2000, Tranquilla et al. 2003) or stages of reproductive readiness (Vezina and Williams 2003, Crossin et al. 2010) largely because VTG production is tightly related to follicle recruitment (Salvante and Williams 2000, Challenger et al. 2001, Gorman et al. 2009). In common eiders, VTG has been found to have a threshold relationship to body mass (Hennin et al. 2015), a key driver of reproductive decisions in these birds (Sénéchal et al. 2011). As such, plasma VTG may play an important role with body mass in predicting the ability

Table 2. Model averaged parameter estimates (Beta) from Table 1 of the effect of body mass at capture (kg), VTG (μg Zn ml^{-1}), treatment and release date (Julian days) on breeding propensity in female common eiders nesting on Mitivik Island (Nunavut, Canada) in 2003 and 2004.

Breeding propensity	Beta	Unconditional SE	95% CI	
(Intercept)	–4.14	16.36	–36.20	27.92
Treatment	0.52	1.92	–3.24	4.28
Mass	5.07	1.05	3.02	7.12
VTG	0.32	0.18	–0.03	0.67
Treatment * VTG	–0.46	0.24	–0.94	0.02
Release date	–0.06	0.03	–0.11	0.00
Year (2004)	–0.68	0.40	–1.46	0.10

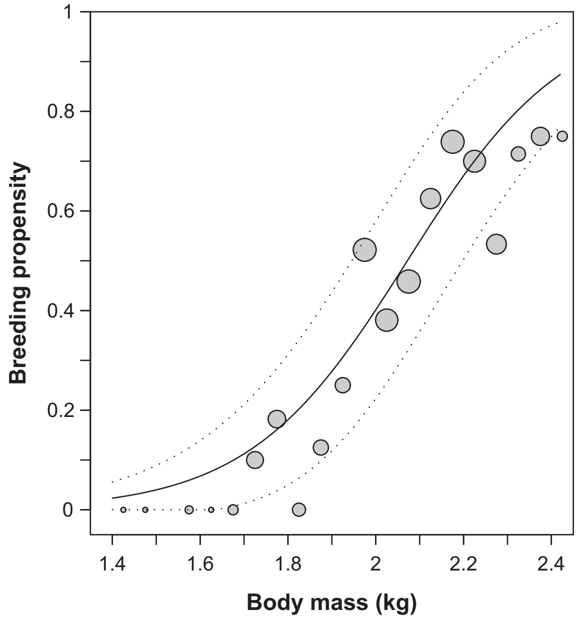

Figure 1. Relationship between breeding propensity (0 = not resighted and 1 = resighted as a breeder) and body mass in pre-breeding female common eiders at Mitivik Island (Nunavut, Canada) in 2003 and 2004. The black line represents the fitted mixed logistic model, and the dotted line its 95% confidence interval. Grey circle sizes are proportional to log (N).

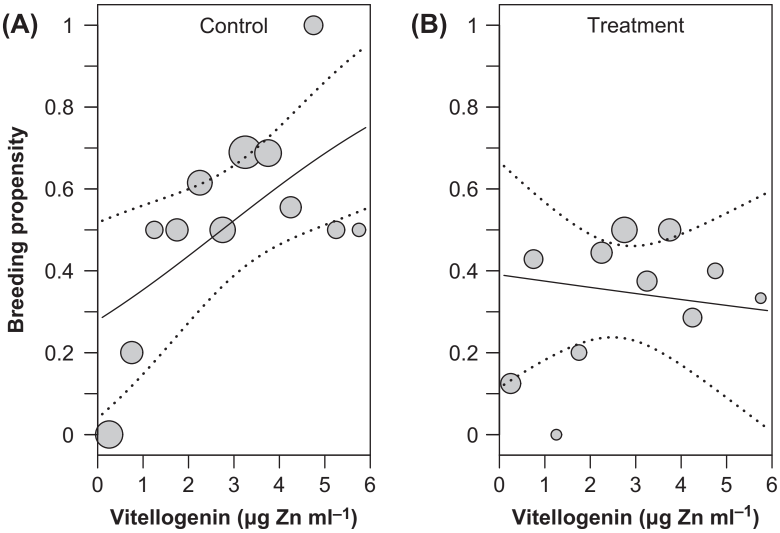

Figure 2. Relationship between breeding propensity (0 = not resighted and 1 = resighted as breeder in the colony) and vitellogenin for control (A) and treatment (B) common eider females controlling for date of and body mass at release. The fitted mixed logistic model (black line) and its 95% confidence interval (dotted line) are shown. Grey circle sizes are proportional to log (N).

of common eider females to commit to reproduction within a breeding season.

Although females with higher plasma VTG had a higher probability of breeding, importantly, we found that after females underwent the body mass reduction treatment, this relationship disappeared. The dissolution of this relationship may have resulted from two possibilities. First, despite a higher level of reproductive readiness (sensu Crossin et al. 2013) with initiation of vitellogenesis and follicle development (Williams et al. 2004), if a female drops below the theoretical mass threshold required for breeding, the likelihood of foregoing reproduction that year is very high because of the short period of time in which they have to reproduce and re-accumulate the needed fat stores in order to fast through their incubation period (Bêty et al. 2003, Descamps et al. 2011). In addition to the presence of a mass threshold to invest in reproduction, common eiders have previously been shown to demonstrate a negative relationship between both egg value (i.e. the probability that an egg survives until recruitment) and reproductive success with laying date (see Fig. 3 in Descamps et al. 2011). Further, to compensate for the loss of endogenous resources during holding, our experiment could also have induced follicle atresia to supplement the females energetically (Challenger et al. 2001). Therefore, it is likely that our experiment reduced female condition below the mass threshold needed to reproduce, thereby causing females to resorb follicles they may have already produced, and delaying them in laying date to the point where females abandoned reproduction for the year.

Secondly, we cannot entirely rule-out the possibility that our treatment effect was due to the stress experienced in captivity. Indeed, while reduced, compared to the model selection based on pre-treatment body mass, the treatment effect was not totally removed when post-treatment body mass was used. Previous research has shown that food shortage itself can induce a physiological stress (Wingfield and Ramenofsky 1999), and that stressful events can jeopardize reproductive decisions in several avian species (Wingfield and Sapolsky 2003, Breuner et al. 2008, Dickens and Bentley 2014). We were currently unable to quantify the level of stress individuals may have undergone, largely due to our inability to include a 'proper' control group (i.e. held females that ate and did not lose body mass; Descamps et al. 2011). Therefore to determine driving mechanisms or the relative impact of food shortage and stress involved though our manipulation would require further examinations. Regardless, in most birds, the time and effort it would take to regain lost condition for reproduction or regrow follicles after an environmental perturbation (mimicked though our experiment) would likely be too long or costly to outweigh the minimal potential fitness benefits of reproducing later that year (Lepage et al. 2000, Bêty et al. 2003, Descamps et al. 2011). The decision to invest in or skip reproduction can thus depend on external environmental conditions such as food shortage or any situations of environmental stress experience prior laying. This is consistent with studies on arctic greater snow geese *Chen caerulescens* where breeding propensity depended to spring environmental conditions on the breeding grounds (Reed et al. 2004, Dickey et al. 2008).

Skipping reproduction is considered as an evolutionary stable strategy in long-lived species facing unstable environments (Shaw and Levin 2013). Our study empirically tests the potential underlying intrinsic and environmental mechanisms driving breeding propensity, an important reproductive decision, in a partial capital breeding species. Our experimental approach demonstrates how a natural perturbation, such a food shortage during critical pre-breeding period, can affect breeding decisions independent of the degree of physiological reproductive readiness (plasma VTG titres). In a global change context, unpredictable events prior to the reproductive period such as food shortages (e.g. spring storms) are likely to increase (Visser et al. 2009), especially in polar regions where abiotic conditions are undergoing rapid and pronounced change (Post 2013). Future studies should aim to test the potential, mechanistic links between pre-breeding environmental conditions (spring storms, timing of ice breakup) and breeding propensity to understand how increasingly variable climate will impact key reproductive factors affecting demographic parameters.

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Supplementary material (Appendix JAV-00824 at <www.avianbiology.org/appendix/jav-00824>). Appendix 1.