

Linking pre-laying energy allocation and timing of breeding in a migratory arctic raptor

Vincent Lamarre¹ · Alastair Franke² · Oliver P. Love³ · Pierre Legagneux¹ · Joël Bêty¹

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Abstract For migratory species, acquisition and allocation of energy after arrival on the breeding grounds largely determine reproductive decisions. Few studies have investigated underlying physiological mechanisms driving variation in breeding phenology so far. We linked physiological state to individual timing of breeding in pre-laying arctic-nesting female peregrine falcons (*Falco peregrinus tundrius*). We captured females from two populations 2–20 days before egg-laying to assess plasma concentration of β -hydroxybutyric acid (BUTY) and triglyceride (TRIG), two metabolites known to reflect short-term changes in fasting and fattening rate, respectively. We also assessed baseline corticosterone (CORTb), a hormone that mediates energy allocation, and the scaled mass index (SMI) as an indicator of somatic body reserves. Plasma BUTY was slightly higher during the pre-recruiting period compared to the period of rapid follicular growth, indicating a reduction in catabolism of lipid reserves before investment in follicle development. Conversely, TRIG levels increased in pre-recruiting females, and best-predicted

individual variation in pre-laying interval and lay date. A marked increase in CORTb occurred concomitantly with the onset of rapid follicle growth. SMI was highly variable possibly reflecting variation in food availability or individuals at different stages. Results suggest that (1) lower rates of pre-laying fattening and/or lower mobilization rate of lipoproteins to ovarian follicles delayed laying, and (2) an elevation in pre-laying CORTb may result from, or be required to compensate for, the energetic costs of egg production. Results of this study illustrate how variation in the allocation of energy before laying can influence individual fitness-related reproductive decisions.

Keywords Energy allocation · β -Hydroxybutyric acid · Triglyceride · Corticosterone · Peregrine falcon

Introduction

For animals breeding in seasonal environments the timing of reproduction can strongly influence reproductive success (Meijer et al. 1990; Einum and Fleming 2000; Drent 2006). For migratory species, the capacity to acquire resources soon after arrival on the breeding grounds and to mobilize energetic reserves stored prior to arrival is expected to affect fitness-related parameters by mediating decisions on both the timing of breeding and reproductive investment (Drent and Daan 1980; Rowe et al. 1994). Individuals, thus, face a trade-off between the conflicting advantages associated with early breeding (higher adaptive value of the offspring) and delayed reproduction (improved body condition and hence reproductive investment; Drent and Daan 1980). Furthermore, birds must contend with the energetically demanding process of egg formation (Williams 2005; Nager 2006; Vézina and

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✉ Alastair Franke
alastair.franke@ualberta.ca

✉ Pierre Legagneux
legagneux@gmail.com

¹ Département de biologie, chimie et géographie et Centre d'études nordiques, Université du Québec à Rimouski, 300 allée des Ursulines, Rimouski, QC G5L 3A1, Canada

² Arctic Raptors Project, Box 626, Rankin Inlet, NU X0C 0G0, Canada

³ Department of Biological Sciences and Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON N9B 3P4, Canada

Salvante 2010). Life-history theory predicts that individuals able to concurrently maintain optimal energy allocation for self-maintenance and reproduction should maximize fitness (Stearns 1992).

Empirical studies have shown that pre-breeding body mass, or other indicators of somatic body reserves, can partly explain individual variation in reproductive phenology in arctic (Drent and Daan 1980; Bêty et al. 2003; Nager 2006; Descamps et al. 2011; Hennin et al. 2016) and temperate (Devries et al. 2008) nesting birds that rely in part on stored energetic reserves to support reproduction (i.e., mixed, capital-income breeders). Moreover, experimental reduction of body reserves (Descamps et al. 2011) and food supplementation experiments conducted during the pre-laying period (reviewed by Nager 2006) have provided evidence for a causal relationship between body condition and lay date. Although the influence of pre-laying energetic reserves on reproductive decisions has been investigated, the use of relevant physiological parameters mediating and reflecting energy allocation that explain individual variation in reproductive performance has been poorly investigated in wild animals (Hennin et al. 2016). Indeed, only a few studies have used physiological parameters to investigate either energy allocation during the pre-laying period (Challenger et al. 2001; Gorman et al. 2009; Hennin et al. 2015, 2016) or the relationship between physiological state and reproductive decisions (Goutte et al. 2014).

Relevant indices of physiological state can greatly improve our understanding of individual variation in fitness-related reproductive decisions in species nesting in a seasonally constrained environment (Williams 2012; Love et al. 2014). β -Hydroxybutyric acid (BUTY) and triglyceride (TRIG) can be used to assess pre-laying physiological state because they reflect energy allocation and short-term changes in body condition. In birds, high levels of plasma BUTY, resulting from lipid catabolism, are related to short-term decreases in body condition in birds (Anteau and Afton 2008) and are considered to be indicators of fasting (Jenni-Eiermann and Jenni 1998). During fat deposition, TRIG is transported in the blood as very low density lipoprotein (VLDL), and stored in different tissues (Jenni-Eiermann and Jenni 1998). Plasma levels of TRIG are positively correlated with short-term variation in body mass and, thus, provide reliable estimates of fattening rate in birds captured only once (Jenni-Eiermann and Jenni 1994; Cerasale and Guglielmo 2006; Anteau and Afton 2008; Hennin et al. 2016). Moreover, plasma levels of TRIG increase when it is transported in the form of yolk-targeted VLDL (VLDLy) to growing follicles during rapid follicular growth (RFG; Challenger et al. 2001; Gorman et al. 2009; Williams 2012). RFG precedes egg-laying, and lasts from a few days to a few weeks depending on the species. Furthermore, baseline levels of a glucocorticoid

hormone (corticosterone; CORTb) can be highly indicative of individual physiological state because it plays a key role in mediating energy allocation by adjusting behavior and physiology (Romero 2002; McEwen and Wingfield 2003; Landys et al. 2006; Love et al. 2014; Hennin et al. 2016). Indeed, an increase in CORTb can positively affect energy intake during the pre-laying (Goutte et al. 2014) and chick-rearing periods (Angelier et al. 2007, 2008; Crossin et al. 2012) and has been linked to positive impacts on reproductive decisions (Love et al. 2014; Hennin et al. 2015, 2016). Combining information from a hormone known to play a role in mediating energy intake and two metabolites that are indicators of short-term changes in lipid metabolism can provide insight into the mechanisms underlying the management of the energetically demanding pre-laying period.

Here we use arctic-nesting female peregrine falcons *Falco peregrinus tundrius* to (1) characterize the dynamics of pre-laying physiological parameters that reflect and influence energy allocation (BUTY, TRIG and CORTb) as well as an indicator of somatic reserves (body mass scaled for body size) up to 20 days before the initiation of egg-laying, and (2) examine links between physiological state and SMI following arrival on the breeding grounds and individual variation in the timing of breeding. Raptors are especially good models to investigate these questions because they accumulate somatic energy reserves prior to egg-laying and the amount of stored reserves can affect the timing of breeding (Meijer et al. 1989; Pietiäinen and Kolunen 1993). However, pre-laying dynamics of physiological parameters involved in or reflecting energy allocation have been poorly investigated in this taxonomic group. This contrasts with studies performed on income-strategy breeders that rely on current food intake to develop ovarian follicles (Challenger et al. 2001; Gorman et al. 2008; Stephens et al. 2009) or breeders that strongly rely on endogenous reserves to support reproduction (Hennin et al. 2015, 2016).

In particular, arctic-nesting female peregrine falcons are ideal models for examining our research questions for several reasons. First, migratory distance varies considerably across individuals in this long-distant migrant (White et al. 2002) and as such, it is likely that considerable variation in pre-breeding physiological state among individuals exists upon arrival on the breeding grounds. Furthermore, arctic-nesting peregrine falcons are constrained by a short breeding season, and any delay in reproduction can have negative consequences on reproductive success (Anctil et al. 2013). Thus, variation in pre-laying energy allocation is expected to be at the heart of individual reproductive decisions that can impact fitness in our study model.

In the current study, we first predicted that female peregrines would undergo major adjustments of their energy

allocation throughout the pre-laying period. Specifically, we anticipated that plasma BUTY would be relatively high immediately following inward migration, followed by a decline through the pre-laying period, and would be found at low concentrations during the RFG period. Conversely, we expected that TRIG levels would be relatively low immediately after arrival on the breeding grounds, and would increase during the pre-laying period as a result of two distinct mechanisms: (1) the accumulation of lipid reserves (fattening), and (2) the mobilization of lipoproteins to growing follicles during the RFG period. We also predicted that the amount of stored (somatic) reserves would increase during the pre-laying period as predicted by Rowe et al. (1994). Because of the energetic costs associated with the development of ovarian follicles and the role of CORTb in promoting acquisition of resources (i.e., energy intake) during the pre-laying period (see above), we predicted that CORTb would increase in females that were investing in the rapid development of ovarian follicles, and would, thus, be the highest in females immediately prior to laying (Hennin et al. 2015). Secondly, we predicted that physiological state prior to the start of the RFG period would be a reliable indicator of subsequent reproductive phenology (Hennin et al. 2016). Specifically, we anticipated that females in relatively low pre-laying energetic balance (i.e., with relatively high BUTY and low TRIG levels) for a given arrival/capture date during the pre-laying period would have a longer pre-laying interval and would lay later. Finally, we predicted that females with relatively high CORTb levels prior to the start of the RFG period would delay egg-laying (as CORTb should be elevated in females experiencing negative energetic balance at that stage; Hennin et al. 2016).

Materials and methods

Studied populations

We conducted this study in two arctic-breeding peregrine falcons populations. The first population breeds on the west coast of the Hudson Bay near Rankin Inlet, Nunavut, Canada (62°49'N, 92°05'W; Fig. 1). At Rankin Inlet, most pairs arrive during the second and third week of May, and annual median lay date ranges from June 5 to June 13 (Jaffré et al. 2015). The second population breeds approximately 800 km northeast of Rankin Inlet at the northern end of the Melville Peninsula, near the community of Igloolik, Nunavut, Canada (69°53'N, 82°51'W; Fig. 1). In the Igloolik population, annual median lay date of the first egg ranges from June 11 to June 19 (Jaffré et al. 2015). A general description of vegetation, climate and geology of the study areas and nesting activities of peregrine falcons for

both populations can be found in Court et al. (1988), Robinson et al. (2014) and in Jaffré et al. (2015).

Capture and assignment of reproductive status

Data were collected from 2012 to 2015 at Rankin Inlet, and from 2011 to 2013 at Igloolik. Beginning in May, we systematically surveyed all known breeding sites to determine site occupancy. Previously documented nesting sites were visited regularly until occupancy was confirmed or until the breeding season was sufficiently advanced to conclude that a given site was unoccupied (Franke et al. 2010). When site occupancy was confirmed during the pre-laying period, we attempted to capture the individual(s) following non-invasive toe-snare methods outlined in *Wildlife Animal Care Committee Class Protocol #001—Raptor Collection for Falconry* (Government of Alberta). Captured birds were weighed (± 1 g) and unflattened wing chord was measured (± 0.5 mm) to account for variation in body size by calculating scaled mass index (SMI) as a measure of stored somatic reserves. The SMI was calculated following the procedure given in Peig and Green (2009):

$$SMI_i = M_i \left[\frac{WL_0}{WL_i} \right]^{b_{SMA}}$$

where M_i and WL_i indicate body mass and wing length of individual i , respectively; WL_0 is the mean wing length of the sampled females; and b_{SMA} is the scaling exponent of the standardized major axis regression of body mass on wing length.

Additionally, we marked birds using alphanumeric color-coded visual identification band (Acraft, Edmonton, AB, Canada), and United States Fish and Wildlife band. For all surveyed years at Rankin Inlet, captures were conducted over a 3-week period, ranging from May 17 to June 8, although most captures were conducted during the last week of May (median = May 27). Captures were conducted over a period of 2 weeks at Igloolik, ranging from May 28 to June 10. One female captured in 2012 was recaptured in 2014 at Rankin Inlet. Because individual condition measured during the pre-laying period is likely affected by conditions experienced following arrival on the breeding ground, or during life-history stages preceding arrival (Newton 2006), we assumed that these two observations were independent and used the data from both observations in the analyses. The exclusion of either of the two observations did not affect our conclusions (results not shown).

To estimate lay date of the first egg among captured females, we conducted weekly nest visits and deployed motion sensitive cameras (Reconyx models PC85 and PC800 Hyperfire) at nest sites of captured individuals.

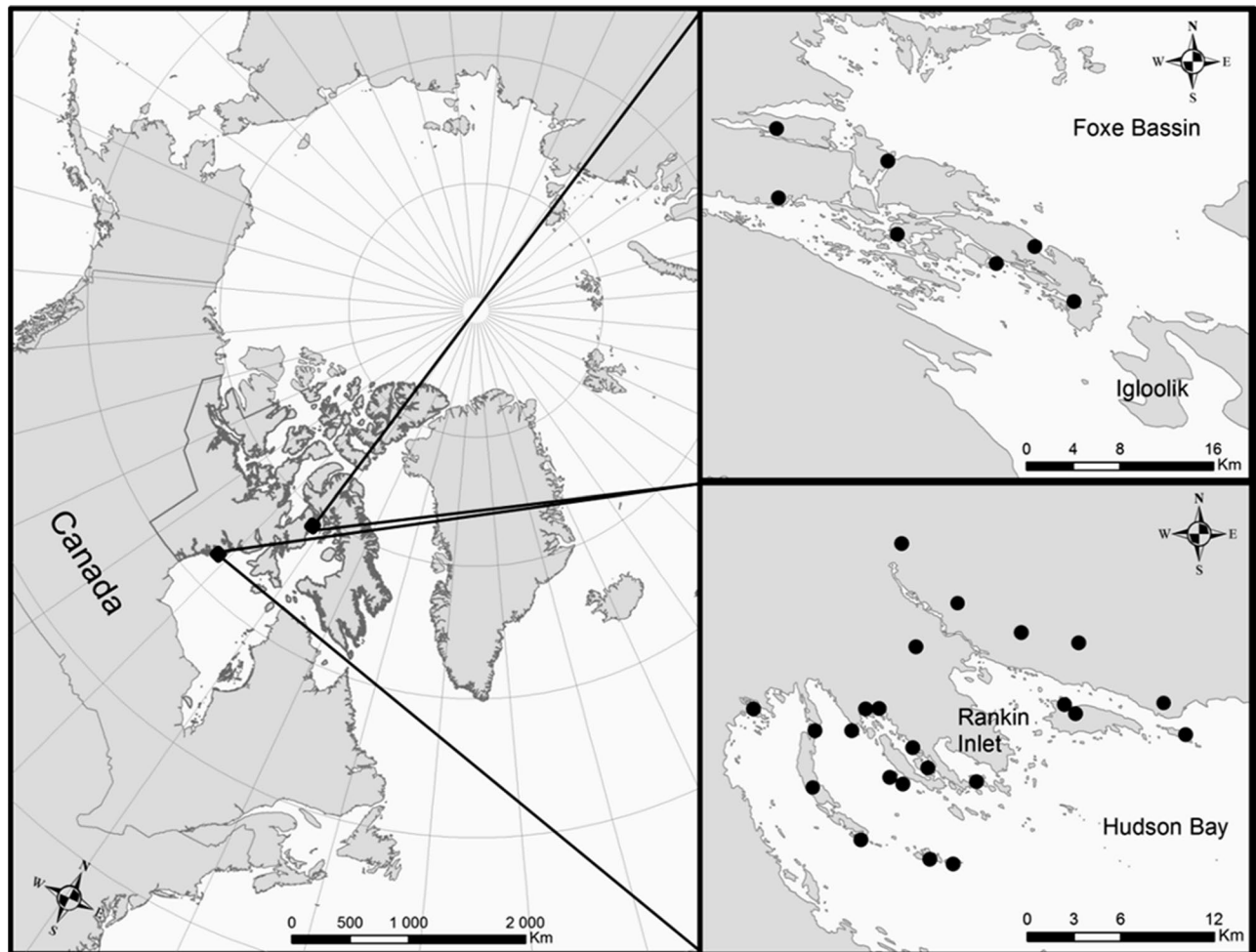


Fig. 1 Locations of monitored populations of arctic-nesting female peregrine falcons near Rankin Inlet and Igloolik, Nunavut, Canada. Circles indicate nest locations of breeding females captured during the pre-laying period and monitored during reproduction over the course of the study

Cameras were programmed to immediately capture one image when triggered by motion, followed by a quiet period of 3 s. In addition, cameras were programmed to collect a single time-lapse image every 15 min. Given that the secretion dynamics of physiological parameters in birds can shift at the RFG period (Challenger et al. 2001; Hennin et al. 2015) we divided the pre-laying period into two stages: the period corresponding to RFG per se, and the period preceding RFG, hereafter called the pre-recruiting period (PR). Females were assigned to one of these two groups based on the number of days from date of capture to lay date (appearance of the first egg). In a closely related species, the common kestrel *Falco tinnunculus*, the duration of rapid follicle growth lasts 7 days with two additional days for albumen and eggshell formation before the egg is laid (Meijer et al. 1989). We, therefore, used 9 days before laying to distinguish between the PR phase and the start of the RFG period. Hence, females captured more than 9 days before egg-laying

were identified as “PR females”, while birds captured after the initiation of rapid follicle growth (≤ 9 days before egg-laying) were identified as “RFG females”. The same procedure was recently conducted in the common eider (*Somateria mollissima*; Hennin et al. 2015).

Blood sample collection

Shortly after capture [mean = 2:55 min \pm 0:13 se; range (1:30–4:12)], we collected up to 1.5 mL of blood from the ulnar vein (26G \times 0.5" needle, 3 mL syringe). Whole blood was immediately transferred to heparinized tubes (4.0 mL, spray-coated with sodium heparin, 68 USP units). Samples were kept cool and at the end of each day blood was centrifuged at 3300 rpm (1380 \times g) for 10 min. Plasma was transferred into microtubes (2.0 mL) and stored at -20 °C until the end of the field season (≈ 90 days) and then stored at -80 °C until analysis.

Physiological assays

Measurement of plasma BUTY (mmol L^{-1}) was completed using a commercially available, previously validated enzymatic, colorimetric assay (Megazyme, Ireland, #K-HDBA; Wagner et al. (2014)). All samples were run in triplicate for 96-well microplate format with a 6-point standard curve on each plate. Plasma was diluted to 1:63 in ultrapure water, and 210 μL of diluted plasma was added to each well. Inter- and intra-assay variation coefficients were 12.2 and 2.74%, respectively, for the 2011–2013 samples. In 2014 and 2015, the intra-assay coefficients of variation were 3.4 and 2.8%, respectively, with only one plate used for each.

Plasma TRIG was quantified using a commercially available and previously validated enzymatic, colorimetric determination kit (Sigma Aldrich, USA, #TR0100-1KT; Williams et al. 2007). Samples were assayed in duplicate with a 5-point standard curve made from a serial dilution of the glycerol standard (2.54 mmol L^{-1}) on each microplate and read at 540 nm with a spectrophotometer plate reader. Plasma was first diluted 1:2 with ultrapure water and rerun at 1:10 if initial levels were found to be too high. The readings from the assay provide the concentration of total and free glycerol which, once subtracted, provides the plasma TRIG concentration (mmol L^{-1}). Inter- and intra-assay coefficients of variation for total TRIG were 9.0 and 5.4%, respectively, for the 2011–2013 samples and 6.8 and 5.8% for 2014 samples. In 2015, the intra-assay coefficient of variation for total TRIG was 3.6%.

Baseline plasma CORT (ng mL^{-1}) was determined using a commercially available enzyme-linked immunosorbent assay (EIA-Assay Designs, Ann Arbor, MI, USA, #ADI-901-097; Hennin et al. 2015) run in triplicate. Plasma was diluted 1:20 using a kit-provided buffer without extraction as serially diluted plasma exhibited parallelism with the standard curve. Inter- and intra-assay coefficients of variation across all plates were 6.3 and 7.4%, respectively, of for 2012–2013 samples and 6.8 and 5.8%, respectively, for the 2014 samples. In 2011 and 2015, the intra-assay coefficients of variation were 5.8 and 13.3%, respectively, for a single assayed plate.

Data analysis

Reproductive phenology and investment

Ancil et al. (2013) showed that the probability of survival of nestlings decreased with hatch date in arctic-nesting peregrine falcons. To further illustrate the effect of timing of breeding on reproductive success of falcons, we investigated the relationships between lay date and clutch size, another fitness-related parameter. We modeled the probability of laying four eggs (typically the maximum clutch

size observed in peregrine falcons; Ratcliffe 1980) according to lay date using a generalized linear mixed effects model and a binomial family with logit link (binomial response: 4 eggs = 1; ≤ 3 eggs = 0). This analysis was performed given that the distribution of clutch sizes were clustered with very few clutches of two (2.6%) or one (1.8%) egg(s). We used the package lme4 version 1.1-5 in R statistical environment version 3.0.2 (R Core Team 2014). We used a larger dataset for these analyses based on long-term population monitoring (Franke et al. 2010; Jaffré et al. 2015) that covered the period from 2008 to 2015 at Rankin Inlet ($n = 218$ clutches) and from 2010 to 2013 at Igloodlik ($n = 34$ clutches). Most nesting territories were occupied in more than 1 year and we, therefore, considered this variable as a random factor for this analysis. In addition, Year and Population were also considered as random factors and we used the following random structure: Territory nested within Year and Population. We used the function predictSE.merMod in the R package AICcmodavg version 2.0-1 to compute predicted values.

Pre-laying dynamics of physiological parameters

We examined whether values of physiological parameters (BUTY: $n = 37$, TRIG: $n = 35$, CORTb: $n = 36$) and SMI ($n = 38$) differed among years and between populations using Kruskal–Wallis and Mann–Whitney–Wilcoxon tests, respectively. Following capture, 31 baseline blood samples were collected within 3:00 min or less and eight samples were collected in more than 3:00 min (3:25–4:12 min), which can lead to elevated plasma CORT due to capture stress (Romero and Reed 2005). We, therefore, tested for an effect of duration of blood collection on plasma CORT levels. Results of the linear regression indicated that the duration from time of capture to end of bleeding did not affect plasma CORT ($\beta = 0.90$, $\text{SE} = 1.28$, $r^2 = 0.01$, $P = 0.49$), and as such we are confident that CORT assessed from all samples (performed within 4:12 min) reflected baseline levels (CORTb), and were not related to capture-related stress. We tested for breakpoints in the relationship between physiological parameters (BUTY: $n = 37$, TRIG: $n = 35$, CORTb: $n = 36$) and SMI ($n = 57$) and the pre-laying interval using segmented linear regression (Mugge 2003) using the segmented R package version 0.4-0.0. Using an iterative procedure, this method estimates significant positive or negative changes (breakpoints) in a regression model. This procedure allows for the detection of changes in SMI and the dynamics of physiological parameters during the pre-laying period (Hennin et al. 2015). Because TRIG levels are likely to reflect two distinct mechanisms during the pre-laying period (fattening rate during the PR period and mobilization of lipid reserves during the RFG period), we used absolute

values to represent pre-laying dynamics of this physiological parameter. To represent variation in SMI during the pre-laying period, we took advantage of additional data collected at Rankin Inlet from 2009 to 2015 [pre-laying interval range: (2–21 days)]. Finally, we performed Mann–Whitney–Wilcoxon tests to compare TRIG, BUTY, CORTb and SMI in female peregrines captured in the PR (BUTY: $n = 25$, TRIG: $n = 25$, CORTb: $n = 24$, SMI: $n = 44$) and RFG (BUTY: $n = 12$, TRIG: $n = 10$, CORTb: $n = 12$, SMI: $n = 13$) phases.

Linking pre-laying physiological state to breeding phenology

We used linear mixed models in R package nlme version 3.1-111 to examine the relationships between pre-laying physiological state (including SMI) and the pre-laying interval as well as lay date. Only PR females with a complete profiles (i.e., simultaneous measurement of BUTY, TRIG, CORTb and SMI: $n = 23$) were included in the analyses. To examine the relationship between individual state and lay date, we included the standardized date of capture (difference between individual capture date and the median capture date for each year and each population) as a covariate in the models. Such standardization takes into account inter-site variation in the timing of capture of female peregrine falcons with captures occurring approx. 1 week later at Igloodik compared to Rankin Inlet. We used absolute TRIG concentrations rather than the residuals of a linear regression between TRIG and body mass (Williams et al. 1999) to estimate physiological fattening rate in PR females because plasma TRIG and body mass were poorly correlated ($r^2 = 0.06$, $P = 0.82$) and hence, residual TRIG was highly correlated to absolute TRIG values ($r^2 = 0.99$, $P < 0.001$). Using absolute or residual TRIG values did not affect model selection (results not shown). Plasma BUTY was log-transformed to meet the assumptions of normal distribution and of the homoscedasticity of the variances. Because of our limited sample size, we restricted physiological covariates to two per model. All covariates were standardized using the scale function in R or using relative capture dates (see above). To avoid multicollinearity, all pair of covariates showing a Pearson $r > 0.5$ were not included in the same model. Ten different candidate models were selected a priori to examine the relationship between individual state and the pre-laying interval, and 11 candidate models were selected to examine the relationship between individual state and lay date. Models were ranked based on second-order Akaike's information criterion (AICc) to control for small sample size (Burnham and Anderson 2002) using the aictab function in the AICcmodavg R package

version 2.0-1. Models with $\Delta\text{AICc} < 2$ were selected as the most parsimonious (Burnham and Anderson 2002). We also calculated the proportion of variance explained by the fixed factors (marginal r^2) of linear mixed models with the r-squaredGLM function in the R package MuMin version 1.9.13. We tested different combinations of random effects for Population and Year (Population, Year and Year nested within Population) for both pre-laying interval and lay date. For each dependant variables, we ranked three null models with three different random factors. For the pre-laying interval analyses, models with a random effect of Population had the lowest AICc and models with other combinations of random effects had $\Delta\text{AICc} > 2$. We, thus, retained Population as a random factor for this specific analysis. For lay date, models with a random effect of Year had the lowest AICc but models with a random effect of Population had a ΔAICc lower than 2 and were, thus, equivalent. However, retaining both random effects in the analysis translates into an increase in AICc. We, thus, performed model ranking using Year as a random effect and we repeated the ranking using Population as a random effect, which did not affect model ranking of the most parsimonious models (i.e., models with $\Delta\text{AICc} < 2$). Hence, Year was retained as a random effect in structure of the models for this analysis. For this specific analysis, the territory was not considered in the random structure of the candidate models because only four territories were used in more than 1 year. Data in the text, figures and tables are presented as mean \pm standard error of the mean (SE).

Results

Capture and assignment of reproductive phenology and investment

Of 38 breeding females captured during the pre-laying period at Rankin Inlet and Igloodik, 26 were captured during the PR period (10–20 days before laying) and 12 were captured during the RFG period (2–9 days before laying; Table 1). Of the females captured during the PR period, we were able to obtain a complete physiological profile on 23 (Table 1). The pre-laying interval of all breeding females ranged from 2 to 20 days and did not differ between populations ($U = 150$, $P = 0.51$); however, lay date of the first egg was 6 days earlier in the Rankin Inlet population (mean lay date: June 8 \pm 0.9) than in the Igloodik population (mean lay date: June 14 \pm 0.7; $U = 17.5$, $P = 0.0003$). We found that the probability of laying a clutch of four eggs decreased with lay date in both populations (fixed effects: $\beta = -0.27 \pm 0.06$, $P < 0.0001$; Fig. 2).

Table 1 Sample size of breeding arctic-nesting female peregrine falcons captured during the pre-recruiting (PR) and rapid follicle growth (RFG) periods between 2012 and 2015 at Rankin Inlet and between 2011 and 2013 at Igloolik with numbers in square brackets indicating sample size for females with complete profile (i.e., simultaneous measure of β -hydroxybutyrate, triglyceride, baseline CORT and scaled mass index—see “Materials and methods”)

Population	Year	PR	RFG	Total	Pre-laying interval (days)			Lay date (Julian date)		
					Min	Max	Mean (SE)	Min	Max	Mean (SE)
Rankin Inlet	2012	4 [4]	2 [2]	6 [6]	2	18	11 (1.1)	158	171	163 (1.9)
	2013	7 [5]	4 [4]	11 [9]	8	17	12 (1.1)	155	164	158 (0.7)
	2014	5 [5]	1 [1]	6 [6]	9	15	13 (0.9)	152	158	155 (0.9)
	2015	5 [5]	1 [1]	6 [6]	8	18	15 (1.5)	156	164	159 (1.2)
	2012–2015	21 [19]	8 [8]	29 [27]	2	18	13 (0.8)	152	171	159 (0.9)
Igloolik	2011	3 [2]	3 [1]	6 [3]	4	16	10 (2.0)	161	166	164 (0.8)
	2012	–	1 [1]	1 [1]	8	–	–	164	–	–
	2013	2 [2]	–	2 [2]	16	20	–	167	168	–
	2011–2013	5 [4]	4 [2]	9 [6]	4	20	11 (1.8)	161	168	165 (0.7)
	Total	26 [23]	12 [10]	38 [33]						

Pre-laying interval (number of days between capture and lay date), lay date (Julian date) are shown

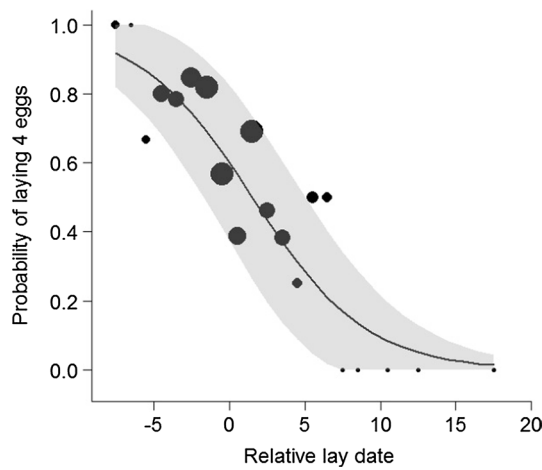


Fig. 2 Probability of laying a clutch of four eggs in arctic-nesting female peregrine falcons in relation to relative lay date with values standardized relative to the yearly median. The solid black line represents fitted logistic regression and its 95% confidence interval is represented by the shaded area. Symbols represent the mean proportion of four-egg clutches grouped by similar lay date (symbol size is proportional to the $(\log + 1)$ number of clutches)

Pre-laying dynamics of physiological parameters

With the exception of plasma BUTY, physiological parameters and SMI did not differ between populations or among years (Table 2). Plasma BUTY levels were slightly higher in 2014 in the Rankin Inlet population. SMI was similar during the RFG and PR periods (PR 1006 ± 17 g, RFG 1050 ± 23 g, $U = 219$, $P = 0.21$; Fig. 3a). However, a breakpoint in the relationship between SMI and the pre-laying interval was detected at 17.0 ± 0.8 days prior to egg-laying (Fig. 3a). Females with a pre-laying interval >17 days presented lower SMIs than females with a pre-laying interval ≤ 17 days (mean = $901 \text{ g} \pm 26$,

$n = 8$ and mean = $1035 \text{ g} \pm 14$, $n = 49$, respectively; $U = 53$, $P < 0.001$). Plasma concentrations of BUTY were higher during the PR period compared to the RFG period (Fig. 3b; PR $1.46 \pm 0.15 \text{ mmol L}^{-1}$, RFG $0.95 \pm 0.16 \text{ mmol L}^{-1}$, $U = 218$, $P = 0.03$); however, no breakpoints in the concentration of plasma BUTY were detected during the pre-laying phase. Conversely, plasma TRIG increased during the PR period (slope: $\beta = 1.41 \pm 0.31$, $t = 4.53$, $P < 0.0001$) and reached the highest values at approximately 8 days prior to egg-laying (breakpoint value: 7.8 ± 2.1 days; Fig. 3c), likely indicating a combination of fattening and mobilization of lipid reserves. Plasma TRIG remained stable after reaching the breakpoint (slope: $\beta = -0.85 \pm 1.77$, $t = -0.48$, $P = 0.64$). Plasma TRIG concentration doubled in the RFG phase when compared to the PR period (PR $8.00 \pm 1.41 \text{ mmol L}^{-1}$, RFG $16.63 \pm 2.06 \text{ mmol L}^{-1}$,

Table 2 Effect of the Population and Year on physiological parameters and the scaled mass index (SMI) assessed in arctic-nesting female peregrine falcons between 2012 and 2015 at Rankin Inlet and between 2011 and 2013 at Igloolik using, respectively, Mann–Whitney–Wilcoxon and Kruskal–Wallis tests (see “Materials and methods”)

Parameter	Population		Year	
	<i>U</i> value (<i>df</i> = 1)	<i>P</i> value	<i>H</i> value (<i>df</i> = 3)	<i>P</i> value
BUTY [37]	181	0.05	11.61	0.02
TRIG [35]	85.5	0.97	1.78	0.78
CORTb [36]	147	0.36	0.72	0.95
SMI [38]	166	0.23	1.54	0.82

Numbers in square brackets indicate sample size for each physiological parameter

BUTY β -hydroxybutyrate, TRIG triglyceride, CORTb baseline corticosterone

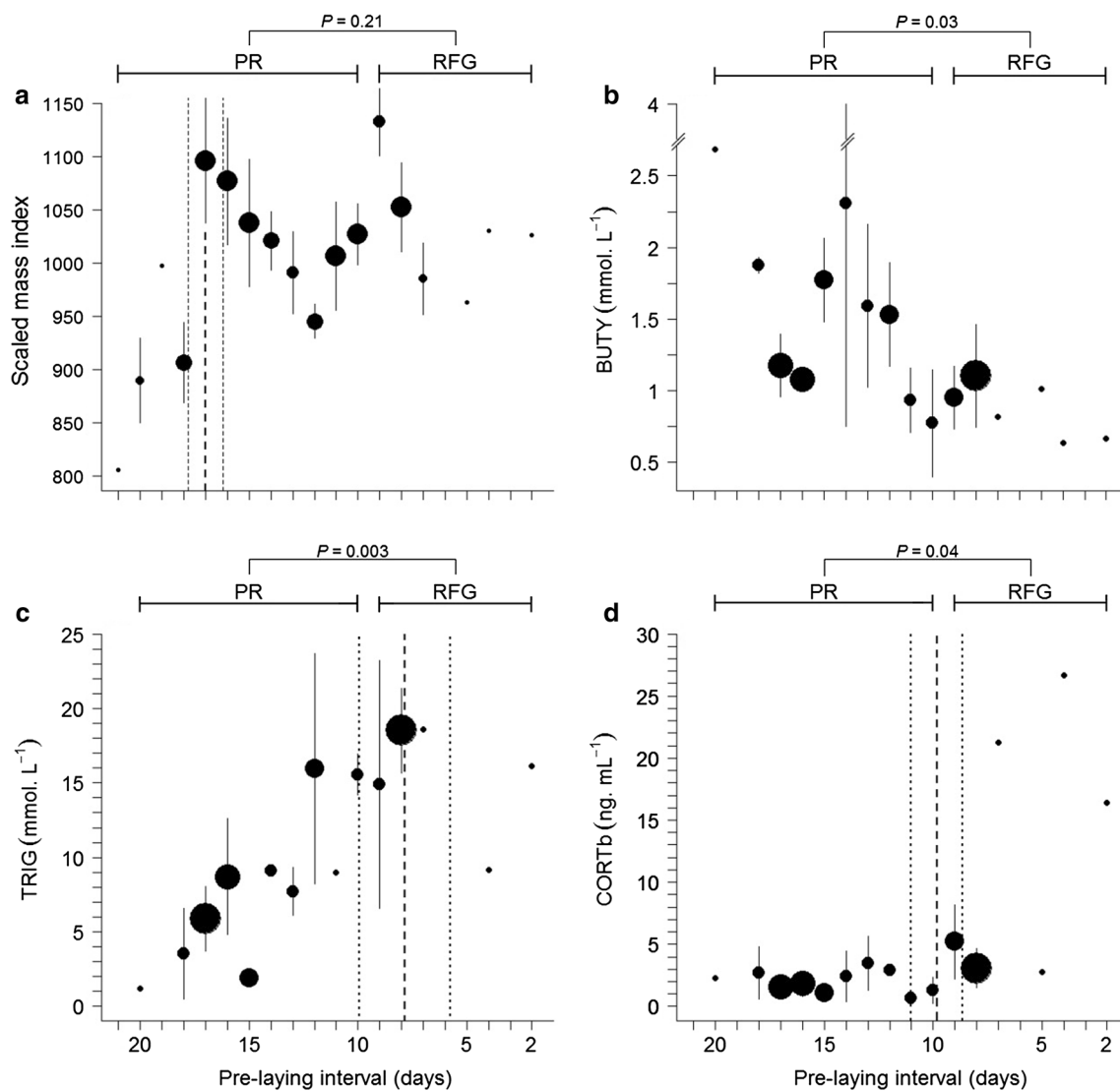


Fig. 3 Variation in **a** scaled mass index (SMI) and dynamics of **b** β -hydroxybutyrate (BUTY), **c** triglycerides (TRIG) and **d** baseline CORT during the pre-recruiting (PR) and rapid follicle growth (RFG) periods in arctic-nesting female peregrine falcons. Mean values are shown for each day during the pre-laying period with symbol size

proportional to sample size and SE are indicated by *filled vertical lines*. *Dashed vertical lines* indicate breakpoints with SE indicated by *dotted lines*. The duration of the PR and RFG periods are indicated by *horizontal bars* and result of the Mann–Whitney–Wilcoxon test is provided

$U = 42$, $P = 0.003$; Fig. 3c). Plasma CORTb was relatively low and stable during the PR period (slope: $\beta = -0.04 \pm 0.34$, $t = -0.12$, $P = 0.91$), but increased (slope: $\beta = 2.35 \pm 0.60$, $t = 3.92$, $P = 0.0004$) approximately 1 day prior to the start of the estimated RFG period (breakpoint value: 9.8 ± 1.2 ; Fig. 3d). Following this increase, CORTb levels remained relatively high and were significantly higher than during the PR period (PR 1.92 ± 0.34 ng mL⁻¹, RFG 8.17 ± 2.57 ng mL⁻¹, $U = 81.5$, $P = 0.04$; Fig. 3d).

Linking pre-laying physiological state to breeding phenology

Candidate models explaining variation in the pre-laying interval and lay date are shown in Tables 3 and 4, respectively. In PR females, CORTb and BUTY were positively correlated ($r = 0.49$; $df = 21$, $P = 0.02$) and, therefore, were not included in the same model. No other significant correlations were detected among physiological parameters, or between physiological parameters and SMI

Table 3 Candidate models, sign of the relationship (+, -), number of parameters (*k*), second-order Akaike’s information criterion (AICc), ΔAICc, Akaike weights (ω_i), log-likelihood (LL) and marginal r^2 of the candidate models linking physiological state to the pre-

laying interval (i.e., number of days between capture and lay date) of pre-recruiting arctic-nesting female peregrine falcons with Population as a random factor (see “Materials and methods” for details)

Candidate models	<i>k</i>	AICc	ΔAICc	ω_i	LL	Marginal r^2
–TRIG	4	70.19	0.00	0.54	–29.98	0.21
NULL	3	72.60	2.41	0.16	–32.67	–
–TRIG + SMI	5	73.79	3.60	0.09	–30.13	0.22
–TRIG + log(BUTY)	5	74.72	4.53	0.06	–30.60	0.21
log(BUTY)	4	75.00	4.81	0.05	–32.39	0.07
–TRIG – CORTb	5	75.00	4.81	0.05	–30.74	0.21
CORTb	4	76.73	6.54	0.02	–33.25	0.00
–SMI	4	76.75	6.56	0.02	–33.26	0.00
SMI + log(BUTY)	5	79.57	9.38	0.00	–33.02	0.07
–SMI + CORTb	5	81.04	10.85	0.00	–33.76	0.00

Parameters	TRIG	Intercept
<i>B</i>	–0.26	17.30
SE	0.09	1.30
Lower CI	–0.45	14.74
Upper CI	–0.08	19.85

Bold values represent the most parsimonious models (delta AICc < 2)

Estimated parameters for the most parsimonious model (ΔAIC < 2), SE and 95% confidence intervals (lower and upper CI) are also shown

Table 4 Candidate models, sign of the relationship (+, -), number of parameters (*k*), second-order Akaike’s information criterion (AICc), ΔAICc, Akaike weights (ω_i), log-likelihood (LL) and mar-

ginal r^2 of the candidate models linking physiological state to lay date of pre-recruiting arctic-nesting female peregrine falcons with Year as a random factor (see “Materials and methods” for more details)

Candidate models	<i>k</i>	AICc	ΔAICc	ω_i	LL	marginal r^2
–TRIG + capture date	5	66.88	0.00	0.59	–26.67	0.41
Capture date	4	69.39	2.51	0.17	–29.58	–
–TRIG + BUTY + capture date	6	71.95	5.08	0.05	–27.35	0.40
–TRIG + SMI + capture date	6	72.16	5.28	0.04	–27.45	0.41
BUTY + capture date	5	72.31	5.44	0.04	–29.39	0.31
–TRIG – CORTb + capture date	6	72.52	5.64	0.04	–27.63	0.41
NULL	3	72.72	5.84	0.03	–32.73	–
–SMI + capture date	5	73.40	6.52	0.01	–29.94	0.29
CORTb + capture date	5	74.35	7.47	0.01	–30.41	0.27
–SMI + BUTY + capture date	6	77.17	10.30	0.00	–29.96	0.31
–SMI – CORTb + capture date	6	78.41	11.54	0.00	–30.58	0.29

Parameters	TRIG	Capture date	Intercept
<i>B</i>	–0.28	0.93	4.25
SE	0.09	0.19	1.29
Lower CI	–0.46	0.55	1.72
Upper CI	–0.11	1.30	6.78

Bold values represent the most parsimonious models (delta AICc < 2)

Estimated parameters of the most parsimonious model (ΔAIC < 2), SE and 95% confidence intervals (lower and upper CI) are also shown

($r < 0.40$, $P > 0.06$). Regardless of capture date, females with lower fattening rates (i.e. low TRIG) during the PR period had a longer pre-laying interval (Table 3; Fig. 4a) and laid later in the season compared to females with higher rates of fattening (Table 4; Fig. 4b).

Discussion

The main goals of our study were to investigate the pre-laying dynamics of physiological parameters involved in, and reflecting energy allocation to ultimately examine trade-offs in reproductive decisions. We found a strong relationship between timing of breeding, a key parameter directly related with nestling survival (Ancil et al. 2013), and reproductive investment (clutch size). We also found evidence that female peregrine falcons underwent major physiological adjustments over the course of the pre-laying period, and that pre-laying energy allocation (fattening rate and rate of lipid mobilization) impacts the timing of breeding. These results illustrate the interplay between pre-laying individual state and the timing of breeding, ultimately determining reproductive investment. Delaying timing of breeding can produce advantages by increasing individual state and hence clutch size while potentially decreasing juvenile survival prospect illustrating the cost of delaying reproduction (Drent and Daan 1980). Such a trade-off is predicted by a theoretical condition-dependant model of laying date and clutch size (Rowe et al. 1994) and assessing physiological parameters involved in energy allocation improved our ability to investigate such trade-offs (Hennin et al. 2015, 2016, this study). Body condition (measured through a scaled mass index—SMI) was found to be highly variable during the pre-laying period possibly reflecting variation in food availability or individuals at different pre-laying stages. Investigating variation in body condition during this critical life-history stage deserves more attention in future studies and would ideally require repeated intra-annual recaptures of the same individuals.

Physiological state during the pre-recruiting period was instrumental to predict the timing of breeding, a result similar to what has been reported recently in a species that largely rely on endogenous reserves (Hennin et al. 2015, 2016). The current work represents one of the first investigations in the dynamics of physiological metrics and individual drivers of pre-breeding investment in an avian top predator.

Pre-laying dynamics of plasma metabolites

β -Hydroxybutyrate (BUTY) is an energetic metabolite negatively related to daily body mass change (Jenni-Eiermann and Jenni 1994; Anteau and Afton 2008) and is elevated in

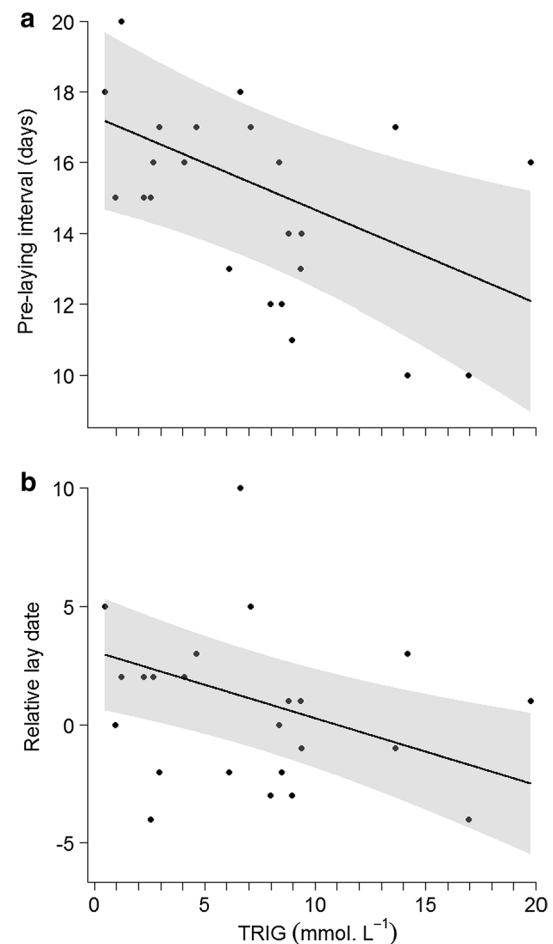


Fig. 4 Relationship between plasma TRIG and **a** the pre-laying interval (number of days between capture and lay date) and **b** the relative lay date (i.e., lay date standardized to the yearly median of each population) in pre-recruiting arctic-nesting female peregrine falcons (i.e., females captured between 10 and 20 days before egg-laying) at Rankin Inlet and Igloolik. The shaded gray area represents 95% confidence interval

fasting birds (Cherel et al. 1988; Jenni-Eiermann and Jenni 1998; Boismenu et al. 1992). Early in the pre-recruiting period, plasma BUTY levels observed in female peregrines were similar to levels found in wild birds after 1.5–3 days of experimental fasting (1.3–3.1 mmol L⁻¹ in Boismenu et al. 1992; and 4 mmol L⁻¹ in Totzke et al. 1999), and likely indicated that female peregrines were likely fasting as they arrived at their breeding sites. As predicted, BUTY levels declined during the period of rapid follicle growth period (RFG) compared to the pre-recruiting (PR) period. During the RFG period, BUTY levels were similar to those measured in captive birds that had been fed prior to fasting experiments (Boismenu et al. 1992; Swain 1992; Totzke et al. 1999). However, we did not find relationship between BUTY and pre-laying interval likely because BUTY levels were relatively low, possibly reflecting only short periods

of fasting. Longer periods of fasting would likely increase pre-laying interval or reduce breeding propensity (Legagneux et al. 2016). Plasma triglyceride (TRIG), an indicator of physiological fattening rate (Jenni-Eiermann and Jenni 1994; Anteau and Afton 2008; Hennin et al. 2015, 2016), was relatively low in females at the onset of the PR period. However, consistent with our predictions, the fattening rate of females increased rapidly throughout the PR period (up to 8 days prior to egg-laying) as did body condition (SMI), indicating that females accumulated lipid reserves throughout this period.

Relatively high concentrations of BUTY early in the PR period likely resulted from food restriction associated with low prey abundance in the final stages of inward migration and immediately after arriving at breeding sites. Indeed, avian preys are scarce when peregrines arrive on their arctic-breeding grounds in May (Court et al. 1988) and snow cover can limit availability of small rodents to raptors (Sonerud 1986). Arctic-nesting peregrine falcons regularly consume mammalian prey species (i.e., lemmings and ground squirrels), especially in years when they are abundant (Court et al. 1988; Bradley and Oliphant 1991; L'Hérault et al. 2013). The low availability of food resources likely led to the use of stored lipids as a main source of energy, indirectly leading to the release of BUTY in line with previous work in fasting migratory birds (Jenni-Eiermann and Jenni 1998).

Pre-recruiting mobilization of follicle precursors

When female birds enter the final stage of follicle growth during vitellogenesis there is a shift from the synthesis of generic very low density lipoproteins to yolk-targeted very low density lipoprotein (VLDL_y) in the liver (Walzem et al. 1999; Williams 2012). Following this shift, TRIG is transported in the blood stream in the form of VLDL_y for the development of growing follicles. In our study, plasma TRIG increased steadily over the course of the pre-recruiting phase (8–12 days before egg-laying), from a minimum of 5 mmol L⁻¹ to a maximum of 19 mmol L⁻¹. At this time, TRIG levels measured in peregrines during the PR period were similar to levels observed in free-living starlings *Sturnus vulgaris* (range 11–54 mmol L⁻¹; Challenger et al. 2001) when a full follicle hierarchy was established, i.e., immediately before the initiation of egg-laying (Challenger et al. 2001). In peregrines, the increase in TRIG well before laying suggests that the mobilization of lipid resources to early developing ovarian follicles may be initiated prior to rapid follicle growth and is consistent with results reported in Hennin et al. (2015) for common eiders (a mixed capital-income breeding bird). The authors of that study indicated that mobilization of follicle precursors appeared to take place well before the expected initiation

of rapid follicle growth. The early mobilization of follicle constituents observed in common eiders has been proposed as a reproductive strategy for species that have evolved in environments characterized by a short breeding seasons (Hennin et al. 2015), such as the arctic. Based on our results, we suggest that a similar mechanism likely exists in female arctic-nesting peregrine falcons.

TRIG dynamics during the rapid follicle growth period

We detected a breakpoint in the plasma concentration of TRIG in female peregrine falcons. TRIG concentration increase during the PR period until approximately 1 day following the beginning of the estimated period of RFG. These results are in sharp contrast with observations in European starlings in which very low density lipoprotein (VLDL) increased during RFG and peaked on the last day of follicle development (when only one follicle remained; Challenger et al. 2001). However, Hennin et al. (2015) indicated that VLDL in arctic-nesting common eiders peaked approximately 5 days before the start of egg-laying and hypothesized that female eiders forage at lower rates once sufficient endogenous reserves for egg production have been accumulated, therefore, leading to decreased plasma VLDL. Although males are known to provision females during the pre-laying period, female falcons are known to reduce their own foraging rates prior to egg-laying (Meijer et al. 1989). For example, female common kestrels only capture approximately 5% of their food requirements during the RFG period (Meijer et al. 1989). The mobilization of energetic resources coincident with energetic requirements for follicle development may be an adaptation for species breeding in unpredictable environments (Hennin et al. 2015), and may explain why plasma concentration of precursors in arctic-nesting female peregrines increased well before the final day of follicle development in contrast to that reported in starlings. Repeated physiological measurements on the same individual during the pre-laying period would help to confirm our interpretation.

Pre-laying dynamics of baseline corticosterone

Plasma CORT_b levels were relatively low during the pre-recruiting period and increased significantly during the period of rapid follicle growth. It is well established across multiple vertebrate taxa that CORT_b is generally elevated during reproduction (Romero 2002), and is thought to facilitate the energetic demands of breeding (Love et al. 2004, 2014). However, few studies have compared CORT_b levels in the pre-recruiting and rapid follicle growth stages in female birds (but see Hennin et al. 2015). Similar to our results, an increase in CORT_b was observed prior to the predicted period of rapid follicle growth in common eiders

nesting in the Arctic (Hennin et al. 2015). In this mixed capital-income breeder (Sénéchal et al. 2011), a positive relationship between CORTb and body mass was observed during the pre-laying period, and suggests that an increase in CORTb to intermediate levels stimulates foraging and resource acquisition during energetically demanding life-history stages (Hennin et al. 2015). In avian predators, including the peregrine falcon, the male assumes the major proportion of the food provisioning to the female during a period of 6–7 weeks from the pre-laying to the chick-rearing period (Cade 1960; Carlier and Gallo 1995). As with Eurasian kestrels (Meijer et al. 1989), female peregrines become lethargic (i.e., non-active) prior to egg-laying. A moderate elevation in corticosterone can promote food begging (Kitaysky et al. 2001). In female peregrines, an increase in food begging could indirectly facilitate energy demand associated with the development of ovarian follicles by promoting increased foraging in males. Interestingly, CORTb was positively correlated with plasma BUTY during the pre-recruiting period, suggesting that a negative energetic balance may result in an increase of glucocorticoid hormones. Plasma CORTb could, thus, be an indirect indicator of nutritional state in pre-recruiting female peregrine falcons, something that has been reported in multiple species at multiple life-history stages (see Love et al. 2005). Despite higher CORTb levels during the period of rapid follicle growth, BUTY levels were very low (discussed above), indicating that females maintained a positive energetic balance during egg production, most likely due to provisioning by males.

Although Hennin et al. (2015) found that CORTb in pre-recruiting common eiders increased before laying, we found little support for this in pre-recruiting female peregrine falcons. Compared to Hennin et al. (2015), our sample size was reduced which may prevent robust comparisons. This type of pre-laying data is difficult to obtain and studies have reported both significant and non-significant relationships between pre-laying CORTb and reproductive decisions. In black-legged kittiwakes *Rissa tridactyla*, pre-laying CORTb was not related to lay date, although pre-laying body condition was (Goutte et al. 2014). Moreover, an experimental reduction in the secretion of pre-laying corticosterone in this species resulted in earlier lay dates (Goutte et al. 2011). In pre-laying snow petrels *Pagodroma nivea*, higher CORTb was correlated with a higher probability of skipping or delay in reproduction (Goutte et al. 2010). Plasma CORTb levels can also be negatively associated with baseline levels of luteinizing hormone and the capacity to release this hormone, which is involved in the maturation of reproductive organs (Goutte et al. 2010). A reduction in CORTb may, thus, promote gonadal development and affect breeding decisions (Goutte et al. 2010, 2011). It appears, therefore, that complex, potentially

context-dependent and species-specific interacting mechanisms involving CORTb may mediate breeding decisions in pre-laying individuals (Goutte et al. 2014).

Given the extreme difficulty of capturing free-living birds during the pre-laying period, few studies have investigated the link between physiological parameters and reproductive decisions and, other than work by Hennin and colleagues (2015, 2016) none have distinguished between individuals captured during the pre-recruiting and rapid follicle growth periods. Although Love et al. (2014) showed that elevated CORTb can prepare individuals for predictable increases in reproductive investment using experimental manipulations of reproductive investment in a passerine species; the role of baseline glucocorticoids during the pre-laying period deserves further attention. Experimental investigations into the effects of a moderate elevation of pre-laying CORTb on behavior (food intake), and ultimately breeding decisions will be necessary to improve our understandings of the actions of glucocorticoids hormones in birds (Hennin et al. 2016). Because of the prominent role of males in provisioning food to their mate during the pre-laying period in raptors, a similar manipulation would be useful in males.

Linking pre-laying physiological state and timing of breeding

Physiological fattening rate of individual females measured during the pre-recruiting period (i.e., 10–20 days prior to egg-laying) best-predicted individual variation in breeding phenology. Regardless of capture date, females with an elevated physiological fattening rate had a shorter pre-laying interval and initiated reproduction earlier. Energy balance during the pre-recruiting period, thus, appears to have an impact on individual-based decisions regarding the timing of breeding, a parameter known to ultimately affect nestling survival (Ancil et al. 2013). Theoretical optimization models predict that breeding investment and timing of breeding are based on a combination of body condition, condition gain and arrival date on the breeding site (Rowe et al. 1994) and a recent empirical test of this model in eiders confirmed that higher fattening rates in the PR stage lead to shorter pre-laying intervals and earlier laying dates (Hennin et al. 2016). Our results also support predictions from these theoretical models where we found that condition gain (fattening rate) appeared to be a key driver of breeding decisions regarding timing of breeding in peregrine falcons. Investigating physiological adjustments prior laying compared to body mass alone can, thus, better reflect trade-offs that a female must face during this crucial period. We also recommend that studies investigating links between body condition and reproductive decisions use additional physiological parameters that specifically reflect and mediate energy allocation.

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Author contribution statement JB and AF originally formulated the idea. VL, JB and AF developed methodology. OPL advised on the choice of relevant physiological parameters and supervised laboratory analyses. AF and VL conducted fieldwork. VL, JB and PL performed statistical analyses. VL wrote the manuscript with the input of all co-authors.

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