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Higher rates of prebreeding condition gain positively impacts clutch size: A mechanistic test of the condition-dependent individual optimization model

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Abstract

1. A combination of timing of and body condition (i.e., mass) at arrival on the breeding grounds interact to influence the optimal combination of the timing of reproduction and clutch size in migratory species. This relationship has been formalized by Rowe et al. in a condition-dependent individual optimization model (*American Naturalist*, 1994, 143, 689-722), which has been empirically tested and validated in avian species with a capital-based breeding strategy.

2. This model makes a key, but currently untested prediction; that variation in the rate of body condition gain will shift the optimal combination of laying date and clutch size. This prediction is essential because it implies that individuals can compensate for the challenges associated with late timing of arrival or poor body condition at arrival on the breeding grounds through adjustment of their life history investment decisions, in an attempt to maximize fitness.

3. Using an 11-year data set in arctic-nesting common eiders (*Somateria mollissima*), quantification of fattening rates using plasma triglycerides (an energetic metabolite), and a path analysis approach, we test this prediction of this optimization model; controlling for arrival date and body condition, females that fatten more quickly will adjust the optimal combination of lay date and clutch size, in favour of a larger clutch size.

4. As predicted, females fattening at higher rates initiated clutches earlier and produced larger clutch sizes, indicating that fattening rate is an important factor in addition to arrival date and body condition in predicting individual variation in reproductive investment. However, there was no direct effect of fattening rate on clutch size (i.e., birds laying on the same date had similar clutch sizes, independent of their fattening rate). Instead, fattening rate indirectly affected clutch size *via* earlier lay dates, thus not supporting the original predictions of the optimization model.

5. Our results demonstrate that variation in the rate of condition gain allows individuals to shift flexibly along the seasonal decline in clutch size to presumably optimize the combination of laying date and clutch size.

KEYWORDS
clutch size, common eider, condition gain, fattening rate, individual optimization, laying date, path analysis, triglyceride

1 | INTRODUCTION

Trade-offs can be driven by the allocation of limited energy stores to multiple life-history traits, and shape the life-history decisions of individuals (McNamara & Houston, 1996; Stearns, 1989). The allocation of energy stores to multiple life-history traits and biological functions is predicted to occur within an optimality framework in which individuals attempt to minimize the costs and maximize the benefits associated with allocation decisions within the context of a stochastic environment (Brommer, Kokko, & Pietiäinen, 2000). As such, individuals that are better able to overcome extrinsic or intrinsic challenges (i.e., resource availability or assimilation, respectively) to obtain or manage energy stores are predicted to have greater flexibility in mitigating trade-offs associated with fitness-related life history decisions (Kisdi, Meszéna, & Pásztor, 1998; McNamara & Houston, 1996; Rowe, Ludwig, & Schluter, 1994; Stearns, 1989).

Studies across multiple taxa have demonstrated that individuals face a decline in the survival probability of offspring as the breeding season progresses (mammals: e.g., Morris, 1998; insects: e.g., Johansson & Rowe, 1999, reptiles: e.g., Doody, Gorges, & Young, 2003, fish: e.g., Poulos & McCormick, 2015, and birds: e.g., Rowe et al., 1994; Bêty, Gauthier, & Giroux, 2003). For many species breeding in seasonal environments, a critical trade-off occurs between the delay in timing of reproduction in favour of increased body condition and the ability to increase investment in reproduction, against this declining survival probability of the resulting offspring (Bêty et al., 2003; Drent & Daan, 1980; Lepage, Gauthier, & Menu, 2000; Morris, 1998; Rowe & Ludwig, 1991; Rowe et al., 1994). In avian species, particularly those reliant on stored energy for reproduction, the trade-off between offspring survival and female body condition is heavily influenced by the timing of breeding, in which females can delay laying to gain in greater condition (also promoting a greater investment in clutch size); however, as females delay breeding and therefore hatching, offspring have less time to grow and prepare for the upcoming winter; it is this trade-off between female investment in body condition and offspring survival that is thought to underlie the seasonal decline in clutch size seen across many species (Bêty et al., 2003; Drent & Daan, 1980; Rowe et al., 1994). Therefore, females must carefully optimize the allocation of resources between self-maintenance and greater reproductive investment with offspring survival within the context of timing constraints (i.e., timing of arrival, laying, hatching and fledging; McNamara & Houston, 1996; McNamara, 1997).

The relationships between individual condition, timing of arrival on the breeding grounds, timing of reproduction and investment in clutch size have been formalized in a condition-dependent individual optimization model (hereafter "optimization model") proposed by Rowe et al. (1994; figure 1). The optimization model predicts that females arriving on the breeding grounds earlier and in greater condition will meet the condition threshold for breeding earlier, thereby allowing for an earlier lay date and investment in a larger clutch (Rowe et al., 1994). Although this component of the optimization
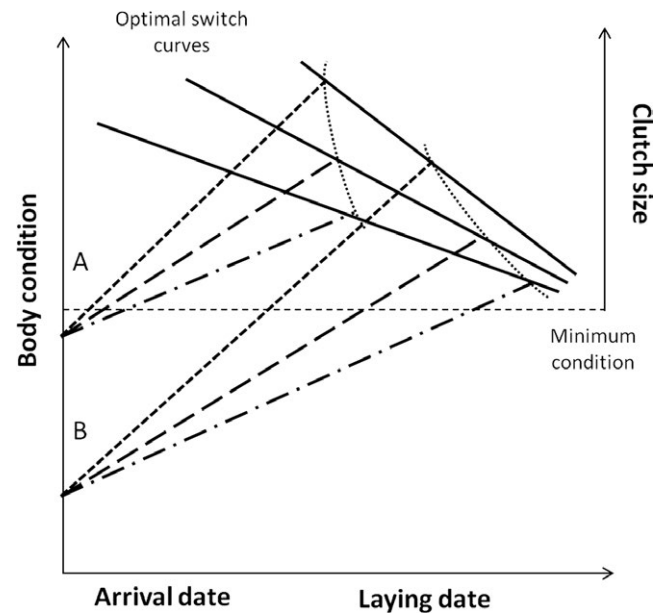
FIGURE 1 The condition-dependent individual optimization model explaining the seasonal decline in clutch size, accounting for differences in rate of condition gain (adapted from Rowe et al., 1994; figure 5). The horizontal dashed line indicates the minimum body condition threshold required to invest in reproduction. The short-dashed, long-dashed and dashed-dotted slanted lines represent females with high, medium and low fattening rates, respectively. The bold slanted lines represent the optimal switch curves for laying date and clutch size; females with higher fattening rates have steeper optimal switch curves. The curved dotted lines connect the optimal lay date and clutch sizes of females with differing fattening rates and similar arrival body condition. Females with similar fattening rates are found along the same switch curve, regardless of initial body condition. Group "A" represents females arriving in good body condition, and "B" represents females in poor arrival body condition. When comparing females with similar arrival body conditions (within A or within B), those with higher fattening rates lay earlier and invest in a higher clutch size compared to females with lower fattening rates

model has been tested empirically and demonstrated previously (Bêty et al., 2003; Descamps, Bêty, Love, & Gilchrist, 2011; Hennin, Bêty, et al., 2016), the model makes an additional set of important predictions about the impact of the rate of condition gain on clutch size (Rowe et al., 1994). In a specific manner, a female with a high fattening rate is predicted to meet the condition threshold for breeding earlier, allowing for an earlier lay date and investment in a larger clutch compared to if she had a slower fattening rate (Figure 1). Moreover, the benefit of delaying laying (i.e., increased body condition) would increase for a female with a higher fattening rate, generating a different optimal switch curve (slope of relationship outlining the seasonal decline in clutch size) for lay date and clutch size (Figure 1; short-dashed vs. long-dashed lines, or dashed-dotted line in A and B). Hence, a female with a slower fattening rate would have a different optimal switch curve and would meet the condition threshold for breeding later, resulting in a later lay date and a smaller clutch size (Figure 1; dashed-dotted lines). In an interesting manner,

within this framework, a female arriving in lower condition or at a later date, but capable of a higher fattening rate, may be able to lay earlier and invest in a larger clutch size compared to females that arrived earlier or in better condition, but with a lower fattening rate.

There is a substantial amount of variation in the ability of females to gain in condition, resulting in different delays prior to laying. For example, in arctic-nesting common eiders (*Somateria mollissima*), a migratory species with a partly capital-based breeding strategy, females take up to 30 days to initiate laying postarrival at the breeding colony (Descamps et al., 2011; Hennin, Bêty, et al., 2016), indicating that they have the opportunity to fatten prior to breeding and demonstrating that the Rowe et al. model (1994) regarding gain in condition is ecologically realistic. Further, fattening rate has been shown to play a role in influencing this variation, where hens with higher fattening rates are capable of laying within a shorter period of time (Hennin, Bêty, et al., 2016). Although some studies have used supplemental feeding to test predictions of the optimization model experimentally (Schoech & Hahn, 2007), supplemental feeding can simultaneously alter several parameters (e.g., perception of habitat quality), potentially artificially impacting timing of laying and clutch size by attracting higher quality individuals to food-supplemented territories, or acting as an environmental cue of food abundance (Davies & Deviche, 2014; Nager, 2006; Williams, 2012). In an important way, these studies have not quantified traits such as fattening rate to relate to investment in clutch size per se. As such, despite the significant impact fattening rate is predicted to have on fitness-related metrics, few studies have been able to empirically test this component of the optimization model.

Physiological traits are prime candidates for enhancing the predictive capacity of theoretical models because they can represent the collective result of individual phenotypes responding to environmental variables (Ricklefs & Wikelski, 2002), and a single sample can often be used as a proxy for variation in individual condition (Zera & Harshman, 2001). Plasma triglycerides are intermediate metabolites assembled in the liver which increase in the body following foraging (Gibbons, Wiggins, Brown, & Hebbachi, 2004), and have been used by physiological ecologists to measure the fattening rate of individuals, particularly during hyperphagic life-history stages (Williams, Warnock, Takekawa, & Bishop, 2007). Triglycerides are positively related to the rate of condition gain (i.e., fattening rate) within an individual, which has been validated experimentally in several vertebrates including bats (McGuire, Fenton, Faur, & Guglielmo, 2009), turtles (Price, Jones, Wallace, & Guglielmo, 2013) and many avian species (Cerasale & Guglielmo, 2006; Jenni-Eiermann & Jenni, 1994; Williams et al., 2007) including ducks (Anteau & Afton, 2008). The consistency in the interpretation of this trait within and across taxa makes it a useful and reliable metric to apply to other systems in which these relationships have yet to be tested, or that are too challenging to test in a wild system. Furthermore, in common eiders, triglycerides have been shown to not only increase in relation to increasing energetic demands prior to growing follicles, and influence body mass thresholds required to initiate reproduction (Hennin et al., 2015), but also interact with signals of energetic demand to

predict the timing of reproduction (Hennin, Bêty, et al., 2016). Taken together, these results provide confidence that triglycerides can be employed as a useful physiological mechanism to quantify fattening rate and its downstream impacts on reproductive investment decisions.

Combining a 10-year dataset of more than 120 arctic-nesting common eiders with a path analysis approach, we test the influence of variation in fattening rates on laying date and clutch size within the framework of the condition-dependent individual optimization model (Bêty et al., 2003; Descamps et al., 2011; Hennin, Bêty, et al., 2016; Rowe et al., 1994). Common eiders are a circumpolar breeding species and an ideal system to test the predictions of this model because: (a) eiders use a mixed (i.e., both capital and income resources) breeding strategy for reproduction and must meet a minimum body mass threshold to invest in reproduction (Legagneux et al., 2016; Sénéchal, Bêty, Gilchrist, Hobson, & Jamieson, 2011), (b) triglycerides appear to influence the body mass threshold and the transition from the prerecruiting to the follicle growth stage (Hennin et al., 2015), (c) prior to reproductive investment (i.e., follicle recruitment) females are in a hyperphagic life-history stage and must acquire enough endogenous fat stores to both fuel follicle growth and complete their 24-day incubation period in which they fast (Bottitta, Nol, & Gilchrist, 2003), and (d) they reproduce within an extreme seasonal environment and must therefore optimally time their reproduction to maximize both within year reproductive productivity and future offspring survival (Love, Gilchrist, Descamps, Semeniuk, & Bêty, 2010). Based on the optimization model, we predict that individuals with higher rates of condition gain (i.e., higher fattening rates/triglycerides) will have earlier timing of laying and larger clutch sizes compared to females with lower rates of condition gain (Figure 1).

2 | MATERIALS AND METHODS

2.1 | General field methods and study site

This study was conducted from 2003 to 2014 (excluding 2005 as blood samples were not collected in this year) in the Canadian low Arctic at Mitivik Island in the East Bay Migratory Bird Sanctuary, Nunavut (64°02′N, 81°47′W). Females arrive from their wintering grounds to Mitivik Island in early June and lay between mid-June to early July (Mosbech et al., 2006). At this time, females begin foraging to gain in body condition to invest in reproduction, largely eating molluscs, bivalves and amphipods (Sénéchal et al., 2011). We initiate captures when eiders are first seen flying around the colony in mid-June until early July, annually (Love et al., 2010). We therefore use capture date as a proxy for individual arrival date at the colony (Descamps et al., 2011; Hennin, Bêty, et al., 2016).

Birds were captured passively as they flew over the colony using large flight nets. As birds hit the net, they were extracted and blood sampled from the tarsus within 10 min of capture using 26 G needles with heparinized 75-μl capillary tubes (2003), heparinized vacutainers with a 26 G butterfly needle (2004), or 23 G thin-wall, 1-inch

needles attached to a heparinized 1-ml syringe (2006–2014). After collection, blood samples were transferred to a 1.5-ml heparinized tube, kept cool (~4°C) and centrifuged at 2,000 *g* within 6 hr of collection to separate plasma and red blood cells. Samples were stored at −80°C until further analysis.

Following blood sampling, females were banded with one full and one half alpha-numeric darvic band, and a metal band. Body mass was measured (g), and then, females were given a set of uniquely shaped and coloured nasal tags for ease of identification in the colony postrelease. Nasal tags were attached using UV degradable monofilament and fall off prior to fall migration. Using the nasal tags to identify individuals, females were monitored using spotting scopes from seven permanent blinds along the periphery of the colony using standardized behavioural observations from trained observers (Descamps et al., 2011; Hennin, Bêty, et al., 2016; Love et al., 2010). Based on direct monitoring or candling of eggs during nest visits, we determined Julian lay date. Clutch size was determined either by counting eggs during nest visits, or by posthatching nest visits to count the number of hatched eggs membranes. To minimize disturbance and possible predation events, we only entered the colony to candle nests when laying dates were uncertain, opportunistically recording clutch size of other nasal-tagged hens nesting en route to the focal nest to be candled.

Only prerecruiting females (i.e., uncommitted to reproduction at the time of capture and far from laying; N = 127; see Supporting Information Table S1) were included in our analyses. Females were classified as prerecruiting if they were 8 days or longer prior to laying at capture (Hennin et al., 2015), as it takes approximately 6 days to completely grow a follicle (Alisauskas & Ankney, 1992), and approximately 28 hr to complete egg formation (Watson, Robertson, & Cooke, 1993). Females that were 7 days or less away from laying were considered to be in rapid follicle growth (RFG; Challenger, Williams, Christians, & Vézina, 2001; Salvante & Williams, 2002; Hennin et al., 2015) and therefore excluded. We excluded RFG females because they no longer produce generic triglycerides for somatic fattening, but begin producing yolk-targeted very low-density lipoprotein (VLDLy) for fat deposition into yolks exclusively (Salvante, Lin, Walzem, & Williams, 2007; Salvante & Williams, 2002; Williams, 2012), meaning that our total triglyceride measure no longer represents a metric of fattening.

2.2 | Plasma triglyceride assays

Triglycerides were quantified using a commercially available enzyme immunoassay kit (Sigma Aldrich, U.S.A., #TR0100-1KT), previously validated in common eiders (Hennin et al., 2015). After dilution, samples were added to a 96-well plate with 240 μl of Reagent A (measures free glycerol), followed by the addition of 60 μl of Reagent B (measures total glycerol). After the addition of each reagent, the plate was agitated and incubated at 37°C then read in a spectrophotometer plate reader (Biotek Synergy H1, Biotek, USA) at 540 nm. To obtain final triglyceride values, the free glycerol values were subtracted from the total glycerol values.

We regressed triglycerides against body mass to obtain the residuals to obtain fattening rates for further analyses (Williams et al., 2007). Inter- and intra-assay coefficients of variation for total triglycerides were 11.27% and 4.42%, respectively, and 5.51% and 6.29% for free glycerol, respectively.

2.3 | Statistical analyses

As some variables required in this study (arrival date, body mass, fattening rate, laying date and clutch size) may be intercorrelated, we used *d*-separation path analysis (Shipley, 2000, 2009) to determine the most likely casual relationships among variables in the dataset. This method allowed us to test for the potential direct and indirect (i.e., mediated through other variables) relationships of fattening rate on clutch size as outlined in the condition-dependent individual optimization model. We first derived 10 conceptual models of hypothesized direct and indirect relationships among the variables of interest, based on previous literature (Bêty et al., 2003; Descamps et al., 2011; Hennin, Bêty, et al., 2016; figure 2). The full test of Rowe et al.'s (1994) model is Model A where fattening rate directly impacts both lay date and clutch size. We excluded linkages between fattening rate, body mass or arrival date because the optimization model predicts that there is no covariance between body mass and arrival date (Bêty et al., 2003; Descamps et al., 2011; Rowe et al., 1994), nor do we predict that fattening rate should covary with arrival date. In addition, as fattening rate is calculated from body mass, including linkages between these variables may result in spurious relationships. We also tested additional plausible direct and indirect effects of fattening rate on laying date and clutch size (Figure 2). Although not a direct prediction of the optimization model, we tested for potential direct effects of body mass on clutch size as body mass can represent a reserve of potential resources (fat stores) which can be allocated towards the production and growth of eggs in common eiders. In previous tests of this model (Hennin, Bêty, et al., 2016), we included baseline corticosterone (i.e., energetic demand at arrival); however, as sampling for corticosterone began in 2006, we did not have enough females with both corticosterone and clutch sizes quantified to include this trait in the current analyses. The conceptual acyclic models were then converted to a set of conditional independencies (see Shipley, 2000 for details) and tested using GLMMs. In each of these statistical models, we included Year as a random intercept (to account for shared variance among individuals captured in the same year; Shipley, 2009). Although we had low sample sizes in some years due to manipulative experiments in the colony (see Supporting Information Table S1), results were consistent when these years were included and excluded; we have therefore kept years with smaller sample sizes in our analyses. Body mass and fattening rate were coded as continuous data, and dates as ordinal. We used either a Gaussian model with an identity function (normally distributed data; lay date) or Poisson model with a log link function (Poisson distributed data; clutch size). Using these statistical models, we then calculated Fisher's *C* statistic (which is equivalent to a maximum-likelihood
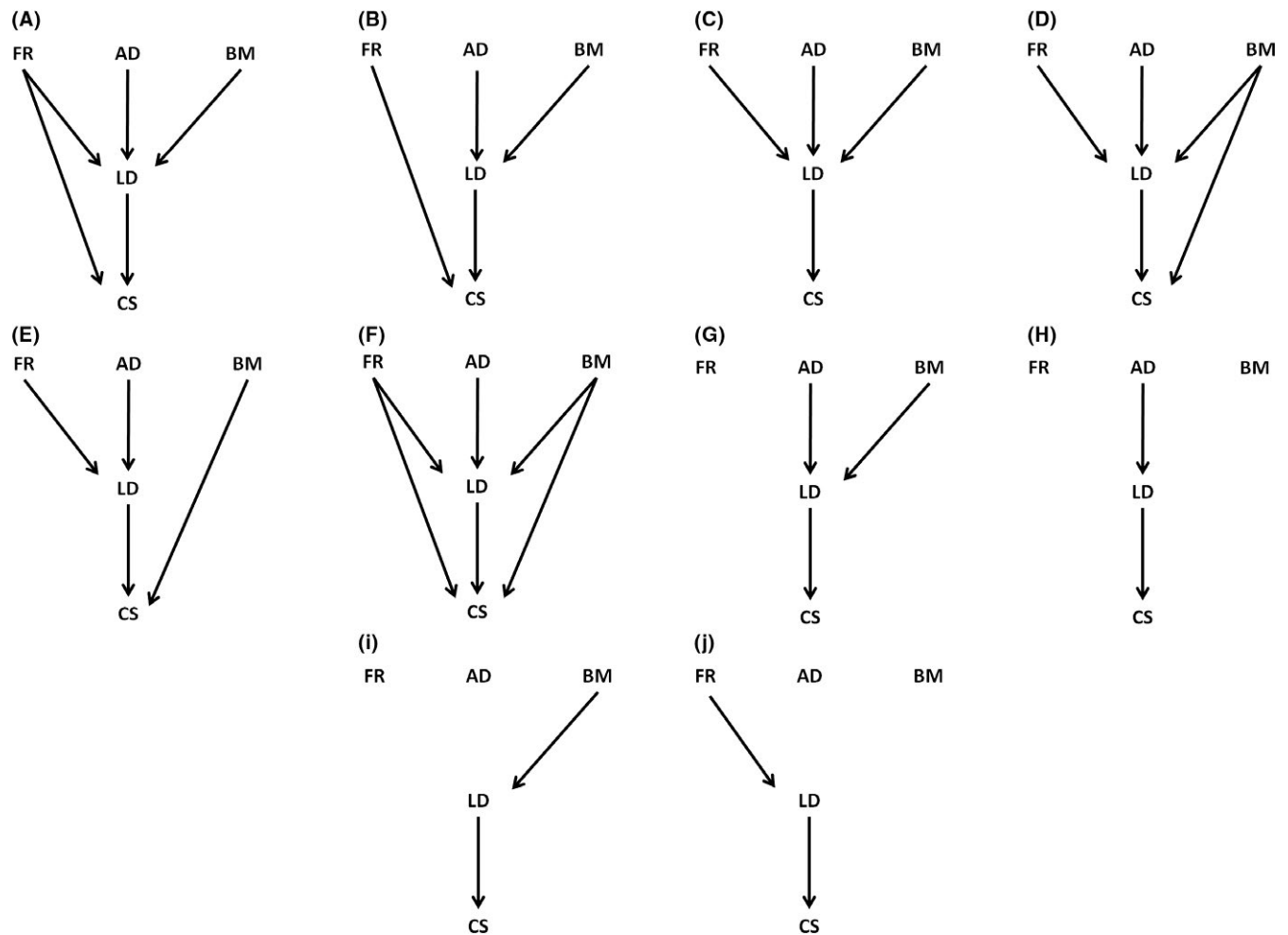
FIGURE 2 Hypothesized path diagrams linking fattening rates to clutch size in prerecruiting female common eiders at East Bay. Arrows indicate the causal relationships among variables. The variables included in each model are fattening rate (FR), body mass (BM), arrival date (AD), laying date (LD) and clutch size (CS)

estimate) and the *C*-statistic Information Criterion (CICc) for each conceptual model (Shipley, 2013).

For the four most competitive models (A, C, D and F), we calculated path coefficients using GLMMs (Figure 3) calculate from standardized and centred data (Schielzeth, 2010) and are therefore comparable within and between models. Analyses were run in R version 3.3.0 (R Core Team, 2016) using the LME4 (Bates, Maechler, Bolker, & Walker, 2015) and IGRAPH (Csardi & Nepusz, 2006) packages.

3 | RESULTS

Comparison of models based on CICc values indicated that model A was the highest ranked model and competitive with models C, D and E (Table 1). All four models had similar structures suggesting a direct effect of fattening rate, body mass and arrival date on laying date, and indirect effects of all three on clutch size mediated through laying date (Figure 3). In essence, higher fattening rate, earlier arrival and heavier body mass predicted earlier laying (Figure 3). At last, there was a direct, negative effect of the timing of laying

on clutch size (Figure 3); individuals that initiated laying earlier had larger clutch sizes. Models without a direct effect of fattening rate on laying date (models B, G, H, I and J) performed poorly, indicating strong support for the hypothesis that accounting for fattening rate (i.e., triglycerides) enhances our ability to explain individual variation in lay date and clutch size.

The highest ranked model included a direct relationship between fattening rate and clutch size (Model A; Figure 3a), and two of our other competitive models included a direct effect of body mass (Model D; Figure 3c), or body mass and fattening rate (Model F; Figure 3d) on clutch size. However, the path coefficients for these direct links to clutch size were low (i.e., weak effects) and highly nonsignificant (Figure 3a,c,d), suggesting these relationships are not biologically important.

4 | DISCUSSION

Using a 10-year dataset across an 11-year period in arctic-nesting common eiders, we tested an important prediction of the
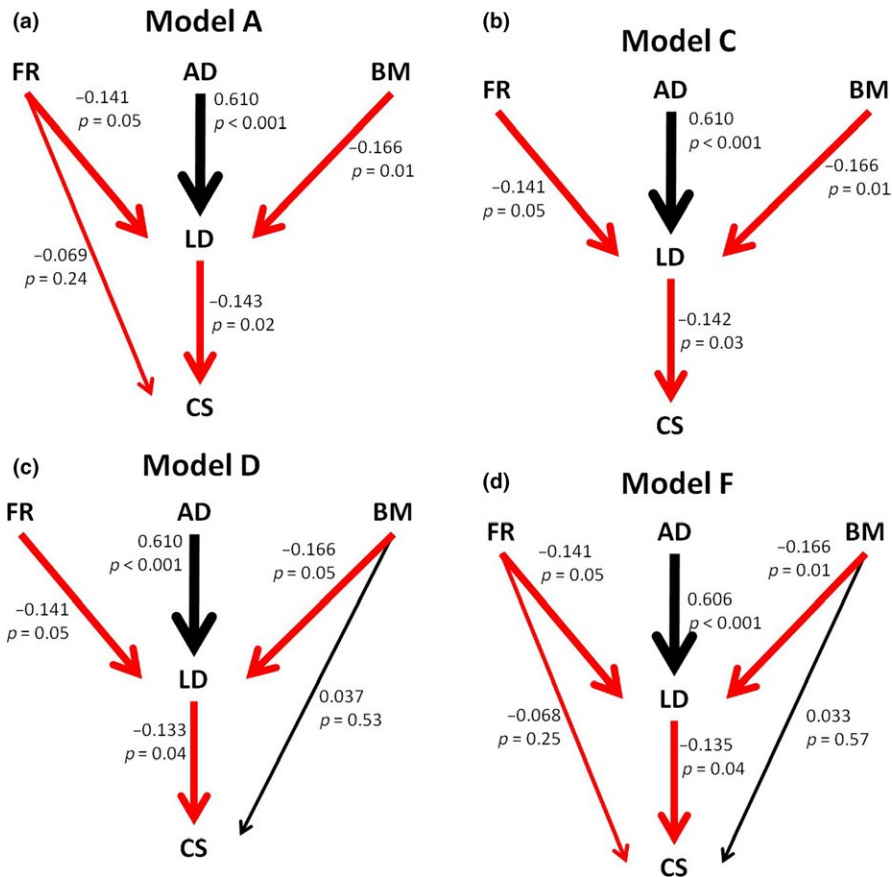
FIGURE 3 Final path diagrams in order of CIC rank for competing paths linking fattening rate to clutch size in prerecruiting female common eiders at East Bay. Arrows are coloured according to whether the causal relationship is positive (black) or negative (red), and arrow size is proportional to the strength of the effect. The values listed beside each arrow are the standardized path coefficients, and the p-value, respectively. The variables included in each model are fattening rate (FR), body mass (BM), Julian arrival date (AD), Julian laying date (LD) and clutch size (CS)

TABLE 1 Comparison of models linking fattening rate to clutch size using confirmatory path analysis. Model letters correspond with the hypothesized directed acyclic models presented in Figure 2

Model	Fisher's C	CICc	ΔCICc	Likelihood	w_i
A	8.43	30.56	0	1	0.30
C	10.92	30.65	0.09	0.96	0.29
D	9.43	31.57	1.01	0.61	0.18
F	7.16	31.75	1.19	0.55	0.17
B	14.70	34.43	3.87	0.15	0.04
G	20.47	37.84	7.28	0.03	0.01
E	18.49	38.22	7.66	0.02	0.01
H	29.65	44.71	14.14	0.001	0
I	75.42	90.48	59.92	0	0
J	84.58	99.64	69.08	0	0

condition-dependent individual optimization model as outlined by Rowe et al. (1994); that rates of condition gain (i.e., fattening rate) will influence the optimal combination of laying date and clutch size. After controlling for the effect of arrival date and body condition, we demonstrate that fattening rate plays a significant role in influencing the timing of laying and has an indirect, downstream impact on clutch size; females with higher fattening rates have earlier laying dates and larger clutch sizes. Although intuitive, these results are

compelling because they demonstrate that a physiological component of fattening rate impacts the investment decisions underlying reproductive trade-offs, and that some females have the flexibility to mitigate the potential fitness costs (i.e., reduced clutch size) generated by the constraints of late arrival and/or poor condition on arrival at the breeding grounds.

Our four best models all suggest that fattening rate, arrival date and body mass have strong direct effects on laying date, while laying date has a strong effect on clutch size (representing the shift in the optimal combination curve, i.e., higher clutch size for a given lay date; Figure 1). While these four models differed slightly in the additional variables with direct effects on clutch size, these additional links among models had low path coefficients and were nonsignificant (Figure 3). When using information-theoretic approaches, the inclusion of an additional, uninformative parameter can create an apparently competitive model via small changes in CICc values and some have argued that the simpler model should be preferred in such situations (Arnold, 2010; Burnham & Anderson, 2002).

We may not have found strong support for the predicted direct linkage between physiological fattening rate and clutch size for a few reasons. First, our captured individuals were already optimized for their current level of investment within their environmental context and often it is not until individuals are pushed outside their optimum via a manipulation that causal relationships become evident and the associated trade-offs become more clear (Ketterson, Nolan, Cawthorn, Parker, & Ziegenfus, 1996; Williams, 2008). Instead, our

signal of fattening rate may be taken too early in the season and, although capable of predicting timing of investment, may not be strong enough to predict overall investment (clutch size), or perhaps instead influenced other clutch-based metrics (e.g., egg size). At last, we may have not found support for the full Rowe et al. (1994) model because it may not account for all parameters, relationships among parameters may be more complex in nature, or there may be sources of imprecision in the trait measurements (e.g., missed predation events resulting in underestimates of clutch size, candling nests to obtain lay date estimates) reducing the strength of relationships among variables. Future studies aiming to test this theoretical model and further validate this prediction may better clarify these relationships by manipulating individual rate of condition gain outside of their current optimum (e.g., manipulating foraging rates *via* elevations of baseline glucocorticoids; Hennin, Wells-Berlin, & Love, 2016), without impacting other relevant ecological parameters (e.g., habitat quality).

The optimal combination of timing of laying and clutch size is driven largely by the trade-off between delaying laying to gain in body condition and invest in a larger clutch size against the declining value of offspring as the breeding season progresses (Bêty et al., 2003; Drent & Daan, 1980; Lepage et al., 2000; Rowe et al., 1994). A potential physiological mechanism underlying this trade-off is the shift in lipoprotein metabolism in females prior to the onset of rapid follicle growth. At the physiological level, females face a trade-off between the costs and benefits of meeting their own energetic needs (maintaining larger generic very low-density lipoprotein (VLDL) particles for triglyceride transport to adipose tissue and fattening) and the allocation of resources to eggs/offspring (increased, smaller-particle, yolk-targeted VLDL or VLDLy production for triglyceride transport). Although domesticated species show a complete shift from generic VLDL to VLDLy production (Salvante, Lin, et al., 2007; Walzem, 1996), it is unlikely that free-living birds would exhibit such an abrupt shift as egg production must occur in less favourable environmental conditions (e.g., very low ambient temperatures), particularly early in the breeding season. Nevertheless, at some point females must physiologically switch from generic VLDL to initiate synthesis of VLDLy, decreasing the ability to allocate generic VLDL production to self-maintenance and fattening. Our study highlights that the costs and benefits, and therefore the resolution, of this trade-off between self-maintenance and investment in eggs should be related to both the timing of laying, and the relative importance of maintaining a sufficient supply of generic VLDL for self-maintenance. In income-breeding species, the costs of initiating the production of VLDLy too early should be relatively low because they do not rely on accumulated somatic stores for reproduction. However, in species with a capital or partly capital-based strategy, like common eiders, females must maintain or even accumulate, fat stores during the prelaying period and face a greater cost to switching to producing VLDLy at the onset of RFG. An earlier or a more complete shift towards VLDLy production may compromise the condition of laying females that rely on stored reserves during subsequent life-history stages (e.g., incubation), which may negatively impact subsequent breeding performance (Salvante, Walzem,

& Williams, 2007). Within the context of the optimization model, we found that females with higher fattening rates had earlier lay dates, thus initiating the production of VLDLy to invest in reproduction earlier, and thereby having the ability to invest in a larger clutch size. Considering the importance of prelaying fattening and maintaining somatic resources for subsequent life-history stages in this species, faster fattening females may be more physiologically and energetically prepared to mitigate the cost of reduced investment in self-maintenance in favour of initiating the allocation of resources towards follicle growth at an earlier time.

Although females can theoretically benefit from fattening quickly, not all females appear to do so, which may stem from several factors, including: (a) physiological/behavioural capability to gain in condition, (b) resource availability and (c) mate quality. First, individuals demonstrate a substantial amount of variation in foraging behaviour (Rigou & Guillemette, 2010; Woo, Elliott, Davidson, Gaston, & Davoren, 2008), prey selection (Smith, Miller, Merchant, & Sankoh, 2015), metabolic or physiological limitations in mass gain (Cornelius, Boswell, Jenni-Eiermann, Breuner, & Ramenofsky, 2013; Dierschke, Delingat, & Schmaljohann, 2003), and digestion or assimilation efficiency (Bond & Esler, 2006; McWilliams & Carasov, 2001), many of which have been shown to change with age (Angelier, Schaffer, Weimerskirch, & Chastel, 2006; Desrochers, 1993; Elliott et al., 2014; Zimmer, Ropert-Coudert, Kato, Ancel, & Chiaradi, 2011). Although our current techniques for ageing (e.g., Carney, 1992) in our colony are unreliable (H. G. Gilchrist, unpublished data), and instances of recapturing known-age individuals are rare, higher fattening females may represent an age class that is more experienced in foraging, reproducing and more invested in reproduction (Froy, Phillips, Wood, Nussey, & Lewis, 2013; Martin, 1995). Second, as a gregarious-feeding seaduck species (Guillemette & Himmelman, 1996) breeding in the Arctic, sea ice plays an important role throughout common eider life-history stages (Love et al., 2010; Mallory, Gaston, Gilchrist, Robertson, & Braune, 2010) and often restricts the availability of foraging locations, increasing competition for resources and potentially reducing fattening rates (e.g., Moore & Yong, 1991). Lower fattening females may therefore represent a group of less dominant females that may have shifted their diet to lower quality prey items (Clark & Ekman, 1995; Witter & Swaddle, 1995), affecting their fattening rates (Seaman, Guglielmo, & Williams, 2005; Smith, McWilliams, & Guglielmo, 2007). At last, in species with little to no male parental investment, females will often invest in larger clutch sizes (Harris & Uller, 2009; Horváthová, Nakagawa, & Uller, 2011; Sheldon, 2000) or in greater egg quality (Cunningham & Russell, 2000) when paired to a high-quality male. As an iteroparous, long-lived species with female-biased offspring incubation and guarding (Coulson, 1984), lower fattening common eider females may be paired to a lower quality mate, investing more in self-maintenance by reducing the costs of increased foraging workloads (e.g., increased oxidative damage; Bize, Devevey, Monaghan, Doligez, & Christe, 2008).

Despite being published more than 20 years ago, no studies have yet tested the impact of fattening rate *per se*, in the context of the condition-dependent individual optimization model to explain the seasonal decline

in clutch size. We demonstrate that there is variation in the rate of condition gain in prerecruiting female common eiders, a capital-income-breeding species, and that this variation impacts both the timing of reproduction and clutch size. Although fattening rate did indirectly influence clutch size through changes in laying date, birds laying on the same date had similar clutch sizes, independent of their fattening rate. Hence, we did not detect a change in the optimal shift curves for timing of laying and clutch size, and therefore, this specific prediction of the condition-dependent individual model has yet to be confirmed. Overall, our results are novel because they illustrate that females with a higher fattening rate could overcome late timing of arrival or poor arrival body condition to achieve a similar clutch size of females arriving earlier or in greater condition. It is currently unknown whether these high fattening females represent a specific phenotype; however, future studies may be able to discern this by examining the behavioural and physiological traits of the same females over multiple breeding seasons.

AUTHORS' CONTRIBUTIONS

H.L.H., J.B., T.D.W. and O.P.L. conceived the ideas and designed methodology; all authors collected the data; H.L.H. and C.J.D. analysed the data with input from O.P.L.; H.L.H. led the writing of the manuscript with input from all authors.

DATA ACCESSIBILITY

Data deposited in the Dryad repository: https://doi.org/10.5061/dryad.5n42p7t (Hennin et al., 2018).

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