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## RESEARCH ARTICLE

# Individual quality overwrites carry-over effects across the annual cycle of a long-distance migrant

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## Abstract

1. In seasonal environments, the fitness of animals depends upon the successful integration of life-history stages throughout their annual cycle. Failing to do so can lead to negative carry-over effects where individuals are transitioning into the next season in different states, consequently affecting their future performance. However, carry-over effects can be masked by individual quality when individuals vary in their efficiency at acquiring resources year after year (i.e. 'quality'), leading to cross-seasonal consistency in individual performance.
2. Here we investigated the relative importance of carry-over effects and individual quality in determining cross-seasonal interactions and consequences for breeding success over the full annual cycle of a migratory seabird (black-legged kittiwake *Rissa tridactyla*).
3. We monitored the reproduction and annual movement of kittiwakes over 13 years using geolocators to estimate their breeding success, distribution and winter energy expenditure. We combined this with an experimental approach (clutch removal experiment, 2 years) to manipulate the reproductive effort irrespective of individual quality.
4. Piecewise path analyses showed that successful breeders reproduced earlier and were more likely to breed successfully again the following year. This positive interaction among consecutive breeding stages disappeared after controlling for individual quality, suggesting that quality was dominant in determining seasonal

Pierre Legagneux and Olivier Chastel contributed equally to this work.

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interactions. Moreover, controlling experimentally for individual quality revealed underlying carry-over effects that were otherwise masked by quality, with breeding costs paid in higher energy expenditure and delayed onset of reproduction.

5. We highlight the need to combine an experimental approach along with long-term data while assessing apparent carry-over effects in wild animals, and their potential impact on fitness and population demography.

#### KEYWORDS

corticosterone, energy expenditure, geolocator, kittiwake, reproductive costs, seabird, seasonal interactions, winter distribution

## 1 | INTRODUCTION

Seasonal environments impose strong constraints on animals, often resulting in highly sequential and well-defined life-history stages throughout the annual cycle (Harrison et al., 2011). This is particularly evident in migratory species under a tight schedule to track seasons across time and space and meet their energy requirements throughout the year (Harrison et al., 2011). The fitness of individuals thus relies on successfully integrating these life-history stages in time and failing to do so can lead to carry-over effects, where individuals transition into the next season in different states, affecting their future performance (Norris & Marra, 2007). For instance, limited access to good quality wintering habitat (Marra et al., 1998) and reduced pre-migration nutritional condition (Bêty et al., 2003) can lead to carry-over effects from winter to the breeding season, affecting the timing of arrival at the breeding site, the onset of reproduction, and the reproductive success of individuals. Carry-over effects can also emerge from increased reproductive effort, leading to reduced post-breeding nutritional condition or flight-induced muscle damage (Fowler & Williams, 2017), delayed moult (Langston & Rohwer, 1996) or delayed migration (Fayet, Freeman, Shoji, Kirk, et al., 2016), constraining the ability of migrants to reach optimal winter foraging grounds (Bogdanova et al., 2011; Catry et al., 2013; Whelan et al., 2020).

Reproduction is a particularly demanding life-history stage requiring energy that cannot be allocated into other functions such as self-maintenance (the “resource-allocation trade-offs”, Harshman & Zera, 2007; Stearns, 1992). When resources are limited, life-history theory predicts trade-offs between energetically costly activities with strong potential to create carry-over effects (Williams, 2012). For iteroparous species, such trade-offs lead to conflicts between the allocation in current reproduction, survival and future reproduction (Reznick et al., 2000). Consequently, reproductive allocation may incur lasting costs, manifested as prioritization of somatic maintenance through increased time spent at the wintering site and diminished future reproductive allocation and success (Gatt et al., 2021; Golet et al., 2004; Wernham & Bryant, 1998).

Despite expected trade-offs between current and future reproduction, animals often show a positive correlation between consecutive reproductive attempts (Hamel et al., 2009; Reznick et al., 2000). Some higher quality individuals are indeed more efficient than others in acquiring resources from their environment and will consequently always have more energy to allocate in all functions in a given life-history stage (Hunt et al., 2004; van Noordwijk & de Jong, 1986). Individual quality in this context implies consistency in performance and refers to inter-individual heterogeneity that correlates with fitness traits, usually reproductive success (Bergeron et al., 2011; Forsythe et al., 2021; Wilson & Nussey, 2010). Links between individual quality and life-history decisions can therefore lead to cross-seasonal correlations in breeding and wintering performance with, for instance, better breeders also consistently accessing better quality wintering habitats (e.g. Gunnarsson et al., 2005). This poses the challenging question of differentiating between seasonal interactions arising from genuine carry-over effects and inter-annual consistency in within-individual performance associated with factors such as individual quality (Daunt et al., 2014; Harrison et al., 2011). For example, associations between winter habitat quality, derived from stable isotope analysis, is often associated with breeding parameters, and interpreted as reflecting a carry-over effect (Marra et al., 1998). Experimental approaches are necessary to separate these factors as individuals vary both in their quality and in the environmental conditions they encounter (e.g. Golet et al., 2004). A sound understanding of the relative contribution of carry-over effects and individual quality is essential as they can have different but major repercussions on individual fitness and population dynamics (Harrison et al., 2011).

Carry-over effects occur across taxa (e.g. birds: Catry et al., 2013; mammals: Sanderson et al., 2014; reptiles: Ceriani et al., 2015; amphibians: Cayuela et al., 2014; arthropods: Elliott et al., 2016). However, understanding the mechanisms behind carry-over effects is hindered, particularly in migratory species, by the necessity to track individuals across seasons and sometimes over long distances. While there is strong evidence that energy is a key currency driving such carry-over effects (Harrison et al., 2011), the physiological drivers remain unclear. A growing

literature, however, points towards glucocorticosteroids as potential mediators of carry-over effects (Bonier et al., 2009). Indeed, glucocorticosteroids such as corticosterone in birds modulate energy reserves, allowing organisms to achieve stability in their energy balance throughout their life-history cycle (Angelier & Wingfield, 2013). Secretion of corticosterone is thus considered an adaptive response to variations in seasonal energy demand, but long-term elevated levels or acute stress response induced by environmental stressors or unpredictable events can cause behavioural or physiological changes to redirect energy towards self-feeding and self-maintenance (Wingfield et al., 1998). This can consequently create physiological conflicts with other functions such as feather growth (Romero et al., 2005) and reproduction via inhibition of reproductive behaviour (Goutte et al., 2010; Kitaysky, Wingfield, et al., 2001). For instance, a short-term experimental elevation of corticosterone caused females black-legged kittiwakes (*Rissa tridactyla*) to depart on migration earlier and extend the time spent on the wintering area (Schultner, Moe, Chastel, Tartu, et al., 2014). Moreover, years of late breeding date were associated with high corticosterone levels (Goutte et al., 2010), potentially via inhibition of sex-steroid hormone secretion in females (Goutte et al., 2014). This highlights the potential key role of glucocorticosteroids in mediating environmental conditions and the behavioural response of individuals in the context of carry-over effects (Bonier et al., 2009).

Here, we combine longitudinal and experimental approaches to disentangle carry-over effects from inter-annual consistency in individual performance (a proxy of quality, hereafter refer to as 'individual quality') in a migratory seabird, the black-legged kittiwake (hereafter 'kittiwakes'). As long-lived organisms, kittiwakes are expected to modulate their reproductive effort according to environmental conditions, promoting their own survival and future reproduction in years of poor resource availability (Stearns, 1992), a trade-off mediated by glucocorticosteroids (Angelier & Wingfield, 2013). The study site in Svalbard holds the northernmost breeding population of the species, and the short breeding window at such high Arctic latitudes has the potential to impose a strong time constraint on kittiwakes' annual cycle, and delayed laying date is associated with poor breeding outcome in kittiwakes and other Arctic seabirds (de Forest & Gaston, 1996; Goutte et al., 2014; Whelan et al., 2022). These characteristics make this system ideal to investigate carry-over effects affecting individual performances across their annual cycle.

We used 13 years of annual solar geolocation tracking and breeding monitoring of kittiwakes ( $n = 181$ ), including up to 7 years of repeated measurements of the same individuals, therefore encompassing a wide range of variation in environmental conditions. We also measured corticosterone in pre-breeding individuals to explore its potential role in mediating carry-over effects ( $n = 54$ ). To disentangle carry-over effects from individual quality, we manipulated the reproductive effort irrespective of individual quality by removing entire clutches during 2 years, thereby inducing reproductive failure in randomly selected individuals. All individuals were tracked

over the non-breeding stage to determine their winter distribution and daily energy expenditure (DEE) through a time activity budget, and we used piecewise structural equation models (PSEM) to assess direct and indirect causal effects between consecutive breeding stages. If seasonal interactions are dominated by carry-over effects, we expected that controlling for individual quality would show that costs of reproduction are paid in the subsequent year in lower reproductive output and are mediated by the individuals' behaviour and energetic performance during winter, such as delayed migration in fall and higher energy expenditure in winter. Alternatively, if seasonal interactions are dominated by factors related to the individual quality, we expected a positive correlation between consecutive breeding attempts with individuals showing consistency in their breeding performance, but that this correlation would disappear once experimentally controlling for individual quality. We also predicted that carry-over effects from winter into breeding would be mediated by corticosterone levels in pre-laying kittiwakes with, notably, higher levels of corticosterone associated with higher winter energy expenditure and delayed laying date.

## 2 | MATERIALS AND METHODS

### 2.1 | Study system and experimental design

The studied population is a long-term monitored colony of individually marked black-legged kittiwakes situated in Kongsfjorden, Svalbard (High Arctic Norway; 78° 54' N, 12° 12' E). We monitored nest contents from 2008 to 2021 every 2–6 days to determine individual breeding success and phenology. In some years, monitoring of nests had to stop before chicks fledged, thus throughout the study, we used the success of rearing at least one chick for 10 days after hatching (hereafter 'breeding success') as a proxy of the annual reproductive success and expressed as a binary variable (failure = 0, success = 1). We considered this measurement to be representative of reproductive success as three quarters of kittiwake chick mortality occur within 10 days after hatching (Coulson & Porter, 1985). For 15% of the nests, both individuals were tracked. The sex of adults was determined by molecular sexing (following Fridolfsson & Ellegren, 1999) or through behaviour when paired with a known-sex partner.

During summers 2019 and 2020, we conducted a clutch removal manipulation to relieve parents from further reproductive allocation and assess potential carry-over effects while controlling experimentally for individual quality. The full clutch (one or two eggs) was removed to provoke the reproductive failure of 14 nests in 2019 and 12 nests in 2020. The eggs were collected upon laying for a parallel study on contaminants (Jouanneau et al., 2023), and replaced by dummy eggs for 10 days to avoid relaying and minimize the variation in incubation duration among nests. Nests for control and experimental groups were selected randomly, so 'high' and 'low' quality individuals should have been selected in equal proportion to their availability for the study.

## 2.2 | Solar geolocator deployment and processing

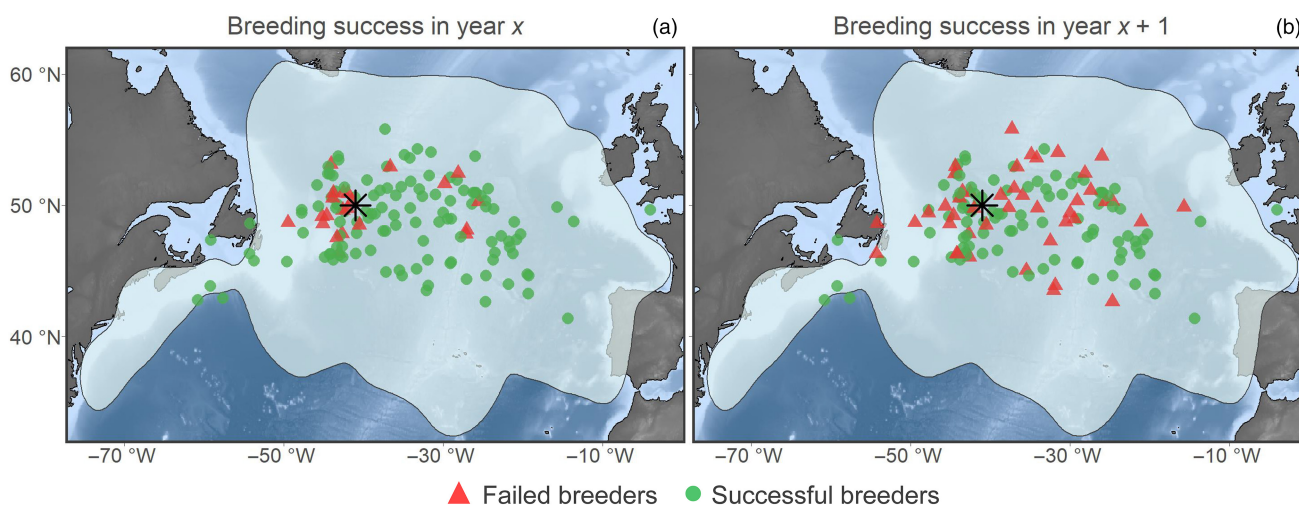
We used geolocators (Lotek: mk18, mk13, mk4083, mk4093; Migrate Technology: Intigeo F100, C65; 3 g=0.7% of average body mass of  $411 \pm 34$ g), mounted on a Darvic leg band, to track the non-breeding movement of kittiwakes. From 2008 and 2020, we deployed 363 geolocators on adults captured at their nest using a noose pole. Devices measured light intensity every minute and recorded the maximum light intensity every 5 or 10 min. They also measured saltwater immersion (whether or not the bird was in contact with the sea water) every 3 or 30s and stored the number of wet measurements within every 10min period. We recaptured 78% of the individuals and retrieved the geolocators. Overall, and after filtering for incomplete tracks, we acquired 277 tracks from 181 different individuals (67 females, 76 males, 38 undetermined) covering 13 non-breeding seasons (fall 2008 to spring 2021, Table S1).

To infer geographic positions, geolocator light data were processed according to the procedure based on the threshold method to estimate twilight events and developed for the SEATRACK international initiative (Bråthen et al., 2021), a collaborative project focused on tracking North Atlantic seabird wintering movements, of which this study is part. Geolocation-based-tracking is inherently prone to create lower accuracy locations in latitudes around equinox periods and cannot be used over periods of continuous daylight (or continuous night) at high latitudes. To fill these gaps in the tracks, and to reduce biases along the trajectories, missing locations were re-estimated by interpolation between known locations using an algorithm specifically developed for SEATRACK (Fauchald et al., 2019) and recently applied in kittiwakes (Léandri-Breton et al., 2021; detailed methods in Supporting Information). This “informed random movement algorithm” is based on the determination of space-time

prisms following the method first proposed by Technitis et al. (2015) to generate plausible locations using additional information available: (1) immersion data to determine colony attendance, (2) land masks (land filters) to constrain positions over the ocean, (3) longitudes (obtained from the geolocator data, as longitude can still be estimated during the equinoxes) and (4) light levels to determine whether the new position was north of the latitudinal limit of the polar day in summer or night in winter (Fauchald et al., 2019).

## 2.3 | Breeding phenology and winter distribution

The timing of departure from the colony area in fall and return to the colony area in spring were estimated using Lavielle partitioning algorithm (see Léandri-Breton et al., 2021 and Supporting Information). This was done over a 5-day running maximum of the saltwater immersion data indicating a behavioural transition between land use (dry) and continuously pelagic behaviour (wet). The foraging trips after the first visit to the colony area in spring were excluded, as individuals start to display a central-place foraging behaviour with long pre-laying trips as far as Iceland (Bogdanova et al., 2011). The wintering stage was defined for each track as the last date in fall and the first date in spring the individual crossed the 60°N, corresponding to the northernmost extent of the winter distribution (Léandri-Breton et al., 2021). The centre of the population's winter range was defined as the centroid of the 95% utilization distribution kernel (UD), estimated over the population's winter positions (from all tracks,  $n=38,900$  positions) and projected using a Lambert Azimuthal Equal Area coordinate system (Figure 1,  $h=200$  km,  $50 \times 50$  km grid cells). Similarly, the centroid of each individual's track was calculated from a 95% UD over the individual's winter position. The distance from the



**FIGURE 1** Centroids of each individual winter track ( $n=141$ ) showing the winter distribution of successful and failed breeders during consecutive breeding stages. (a) Reproductive success during the previous breeding stage (year  $x$ ), with failed breeders clustered near the population's range centre (black star \*). (b) Reproductive success during the following breeding stage (year  $x+1$ ), with failed breeders spread across the population's winter distribution. The grey polygon illustrates the 95% utilization distribution kernel of the population ( $n=38,900$  positions).



population's range was defined as the orthodromic distance between the population's winter centroid and the centroid of each individual's winter track.

## 2.4 | Daily energy expenditure in winter

We used the standardized saltwater immersion data (SSI) to build a time-activity budget based on the identification of three behaviours for each 10-min periods: sustained flying (SSI=0%), resting on water (SSI ≥98%) and active foraging (0% < SSI < 98%), which is characterized by a succession of short flights and short swimming or shallow diving bouts (Jodice et al., 2003). To estimate the DEE during the wintering stage, we combined the time-activity budget with the population-specific resting metabolic rate (Gabrielsen et al., 1988) and the activity-specific field metabolic rates for the kittiwake flying and foraging behaviours (Jodice et al., 2003; detailed methods in [Supporting Information](#)).

## 2.5 | Blood sampling and hormone assays

From 2019 to 2021, 92 kittiwakes (21 females, 41 males and 30 undetermined) previously equipped with a geolocator were recaptured during the pre-laying stage and sampled within 3 min (average sampling time:  $129 \pm 29$  s, range: 72–180 s) for 2 mL of blood from the brachial vein. The time before sampling had no effect on the corticosterone levels (beta regression,  $coef=0.044$ ,  $SE=0.053$ ,  $df=55$ ,  $p=0.41$ , [Supporting Information](#)). Total baseline corticosterone concentrations (bound and free fractions) were measured in plasma via radioimmunoassay following the method validated by Lormée et al. (2003). The corticosterone was extracted from each 40 µL plasma sample by adding 3 mL of diethyl-ether. It was vortexed, centrifuged and frozen at  $-20^{\circ}\text{C}$  to separate the diethyl-ether phase containing the hormone from the plasma. The solvent was evaporated in a  $40^{\circ}\text{C}$  bain-marie. The extract was then re-dissolved in a phosphate buffer and incubated overnight at  $4^{\circ}\text{C}$  with 4000 CPM of  $\text{H}^3$ -corticosterone (Perkin, Elmer, US) and a polyclonal antiserum (anti-corticosterone antibody provided by Merck, Sigma Aldrich, France). The bound and free fractions were separated using dextran-coated charcoal and the activity of the bound fraction was counted in a Tri-carb liquid scintillation counter 2810TR (Perkin, Elmer, US). All samples were assayed in duplicates. Intra- and inter-assay coefficients of variability were 11.13% and 16.88%, respectively. The lowest detectable concentration was 0.28 ng/mL.

## 2.6 | Path analyses

We used PSEM to assess direct and indirect causal effects between consecutive breeding stages. We formulated potential pathways based on the theoretical framework and chronology of stages of

the annual cycle of the species ([Figure 2](#)) to fit linear mixed-effects (LME) and generalized linear mixed-effects models (GLME). These models were incorporated into three different PSEM using the package 'piecewiseSEM' (Lefcheck, 2016). They incorporated both the direct pathway between consecutive breeding stages and the indirect pathways through intermediate parameters associated to the wintering and migratory stages ([Figure 2](#)). The dataset for the first model ( $n=141$  tracks) included all individual tracks from the 13 years of the study, but excluding the individuals from experimental nests ([Figure 2](#)). Therefore, with this first model we adopted a longitudinal approach with the objective of determining seasonal interactions among breeding in year  $x$ , non-breeding and breeding in year  $x+1$ , whether they arise from potential carry-over effects or from individual quality.

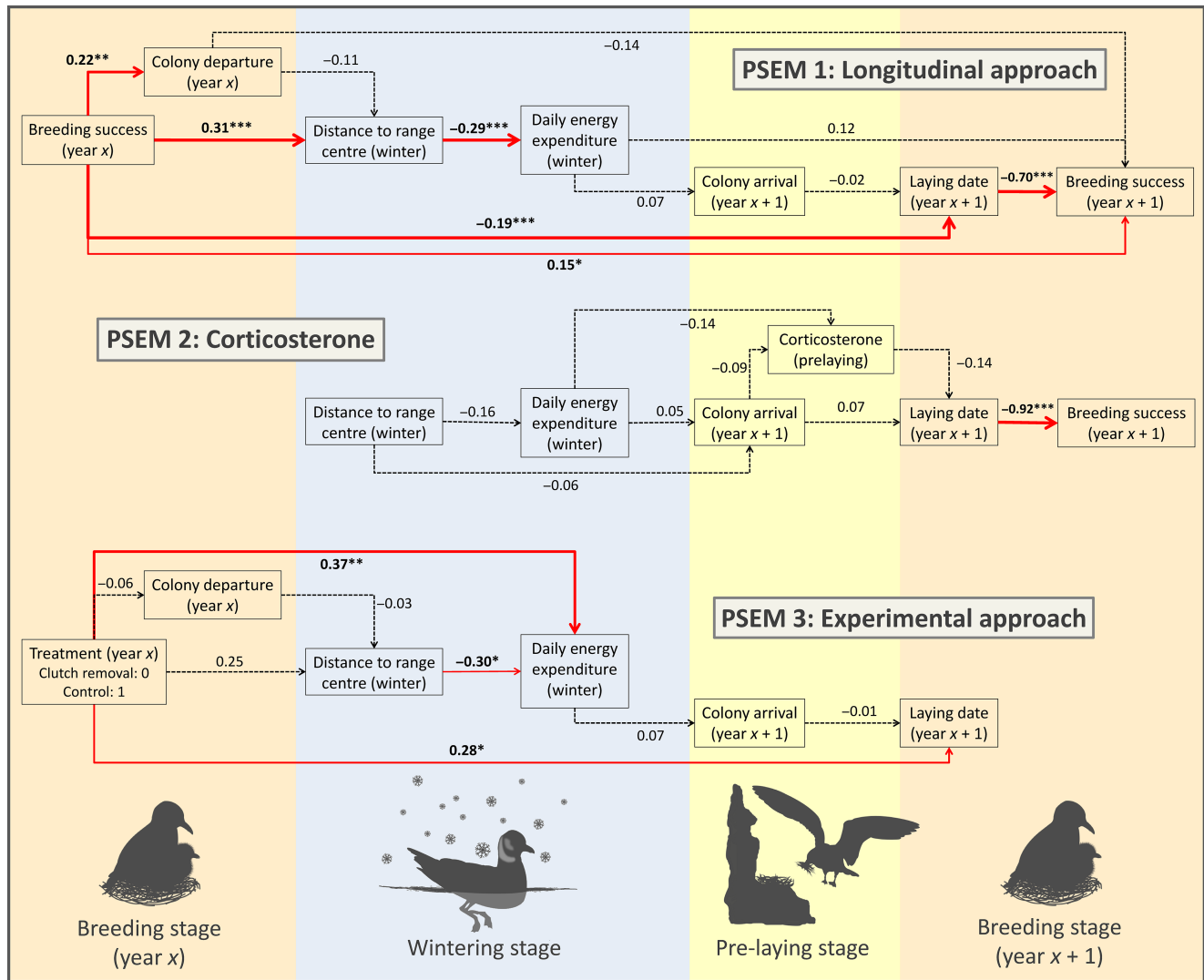
A second PSEM was fitted to test the role of corticosterone during pre-laying as a potential mediator of carry-over effects. We used a subset of the dataset with individuals blood-sampled during the pre-laying stage and excluding individuals from experimental nests in year  $x+1$  ( $n=54$  sampled from 2019 to 2021, [Figure 2](#)).

We fitted a third PSEM to assess carry-over effects arising from breeding costs by manipulating the reproductive effort irrespectively of individual quality. This third PSEM was thus based on an experimental approach including experimental individuals ( $n=26$ ) and control individuals ( $n=44$ ) from the clutch removal experiment carried out in 2019 and 2020 ([Figure 2](#)). The breeding success during the recapture year was excluded from the pathways of this model since not enough nests were monitored until breeding success in 2021. However, later laying reduces breeding success (LME,  $coef=-0.042$  per day,  $SE=0.005$ ,  $df=43$ ,  $p<0.0001$ ,  $R^2=0.47$ ), and the results from this model are thus still reflective of the interactions from one breeding stage to the next.

In all PSEMs, 'nest' was included as random factors as well as, for the first PSEM, 'year' and 'nest' in year  $x$  and year  $x+1$  (as both pair members were included). The goodness-of-fit of each PSEM was evaluated from the Fisher's  $C$ -value test of conditional independencies ( $d$ -separation, Shipley, 2009). The  $d$ -separation test failed in the third PSEM indicating the path directly linking the treatment to the winter DEE was missing. This path was thus added to the final model. The global fit for all three final PSEM was good, and the  $d$ -separation test indicated that no further paths were missing (PSEM 1:  $C=13.6$ ,  $df=20$ ,  $p=0.9$ ; PSEM 2:  $C=19.4$ ,  $df=14$ ,  $p=0.2$ ; PSEM 3:  $C=15.4$ ,  $df=14$ ,  $p=0.3$ ). To achieve normality, the distance to the population's range centre was log-transformed in all models. Model predictions were reported with their standard error. The output of each PSEM is reported in [Supporting Information \(Table S2\)](#).

## 2.7 | Individual repeatability

To further investigate whether individuals showed interannual consistency in their behavioural traits, we estimated the individual repeatability  $r$  (intra-class correlation) of each behavioural parameter by calculating the proportion of intra-individual variance



**FIGURE 2** Directed acyclic graphs (DAG), showing the direct and indirect causal pathways tested in each three piecewise structural equation models (PSEM), with standardized coefficients. Arrows show the predicted directions between behavioural parameters associated to each stage of the annual cycle of the species. Dotted arrows indicate not statistically significant pathways. Solid red arrows, bold values and stars (\*) next to the coefficients indicate statistically significant pathways.

while accounting for differences among individuals. This was done using the function 'rpt' (R package 'rptR', Stoffel et al., 2017) and only individuals with multiple years of measurements. Among those, 58 individuals were tracked multiple years allowing estimation of repeatability in movement behaviour ( $n=58$  individuals tracked up to 7 years,  $2.7 \pm 1.1$  years in average, Table S3). Repeated tracking of individuals was not necessarily done over consecutive years, with an average interval between first and last measurement of  $3.5 \pm 1.7$  years (range 2–9 years, Table S3). The distance to the population's range centre was log-transformed to improve normality and models were fitted over a Gaussian distribution, with the exception of the breeding success for which we used a binary distribution. All analyses were carried out in R version 4.3.2 (R Core Team, 2023).

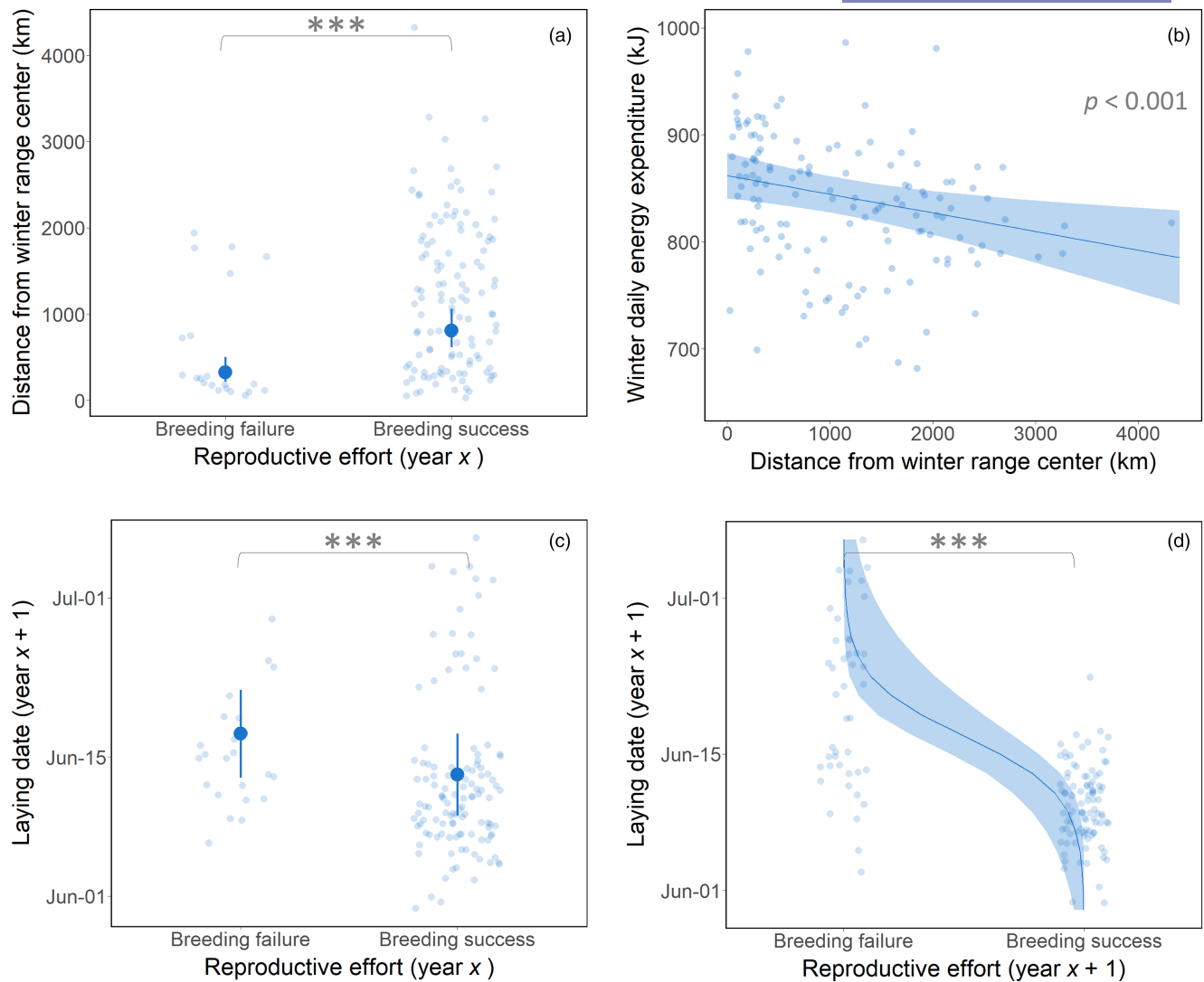
This study was approved by the Norwegian Food Safety Authority (FOTS ID 2086, 3319, 4169, 6291, 6348, 8482, 15603,

15611, 19970, 23259, 23877, 27564), the Governor of Svalbard and the McGill University Animal Care Committee.

### 3 | RESULTS

#### 3.1 | Longitudinal approach (PSEM 1 and 2)

Consecutive breeding stages were linked by direct pathways, indicating that the breeding effort in a given year  $x$  can have direct positive effects on the reproduction in the subsequent year  $x+1$  (see Figure 2). Indeed, the breeding success in year  $x$  had a strong effect on the timing of laying and the breeding success in year  $x+1$ , with successful breeders laying 5 days earlier (laying date  $163 \pm 4$  days versus  $168 \pm 4$  days, Figure 3c) and having 20% higher breeding success than failed breeders during year  $x+1$  (breeding success of  $0.54 \pm 0.09$  versus



**FIGURE 3** Partial residual effects of four pathways from the first PSEM (longitudinal approach) showing direct and indirect causal effects between consecutive breeding stages arising either from carry-over effects or individual quality. The pathways show the interactions between (a) the reproductive effort and the subsequent winter distribution (i.e. distance from the population's winter range centre); (b) the winter distribution and the winter daily energy expenditure; (c) the reproductive effort and the subsequent breeding phenology (i.e. laying date); and (d) the reproductive effort and the breeding phenology on the same year. Plots show model predictions, with their 95% confidence intervals, over the jittered raw data. Models with log transformed predictors are plotted on the original scale.

$0.74 \pm 0.06$ ). Furthermore, the timing of laying in year  $x+1$  explained the breeding success that same year, with successful breeders laying 11 days earlier than failed breeders (averaged laying date  $161 \pm 0.4$  days versus  $172 \pm 1.3$  days, [Figure 3d](#)). Therefore, the strongest path based on the standard coefficients linked the breeding success in year  $x$  to the breeding success in year  $x+1$  via the timing of laying ([Figure 2](#)).

This first PSEM also revealed indirect pathways, but none of these had cascading effects persisting into the subsequent breeding stage (see [Figure 2](#)). Successful breeders in year  $x$  left the colony 7 days later than failed breeders (departure date  $249.8 \pm 2.4$  days versus  $242.5 \pm 3.1$  days), but this difference had no detectable effects on the winter distribution. However, the breeding success in year  $x$  was strongly correlated with the winter distribution of individuals, with failed breeders wintering 40% closer to the population's range

centre than successful breeders ( $327 \pm 143$  km versus  $810 \pm 220$  km, [Figure 3a](#)). Furthermore, there was a decrease in DEE of 11.0% ( $94.7$  kJ/day) over the distance from the centre to the edge of the population's winter range ( $4293$  km, [Figure 3b](#)).

The standard coefficients from the second PSEM did not reveal any path connecting the baseline corticosterone levels of pre-laying individuals to behavioural parameters during the previous winter or the following breeding stage (see [Figure 2](#)). The only statistically significant path in this model was the effect of the timing of laying on the breeding success in year  $x+1$ , with successful breeders laying 14 days earlier than failed breeders (lay date:  $160.5 \pm 0.7$  days versus  $174.4 \pm 1.5$  days). Body condition index (i.e. residuals of the linear correlation between the skull length and the body mass) did not improve the model fit ([Table S4](#)).



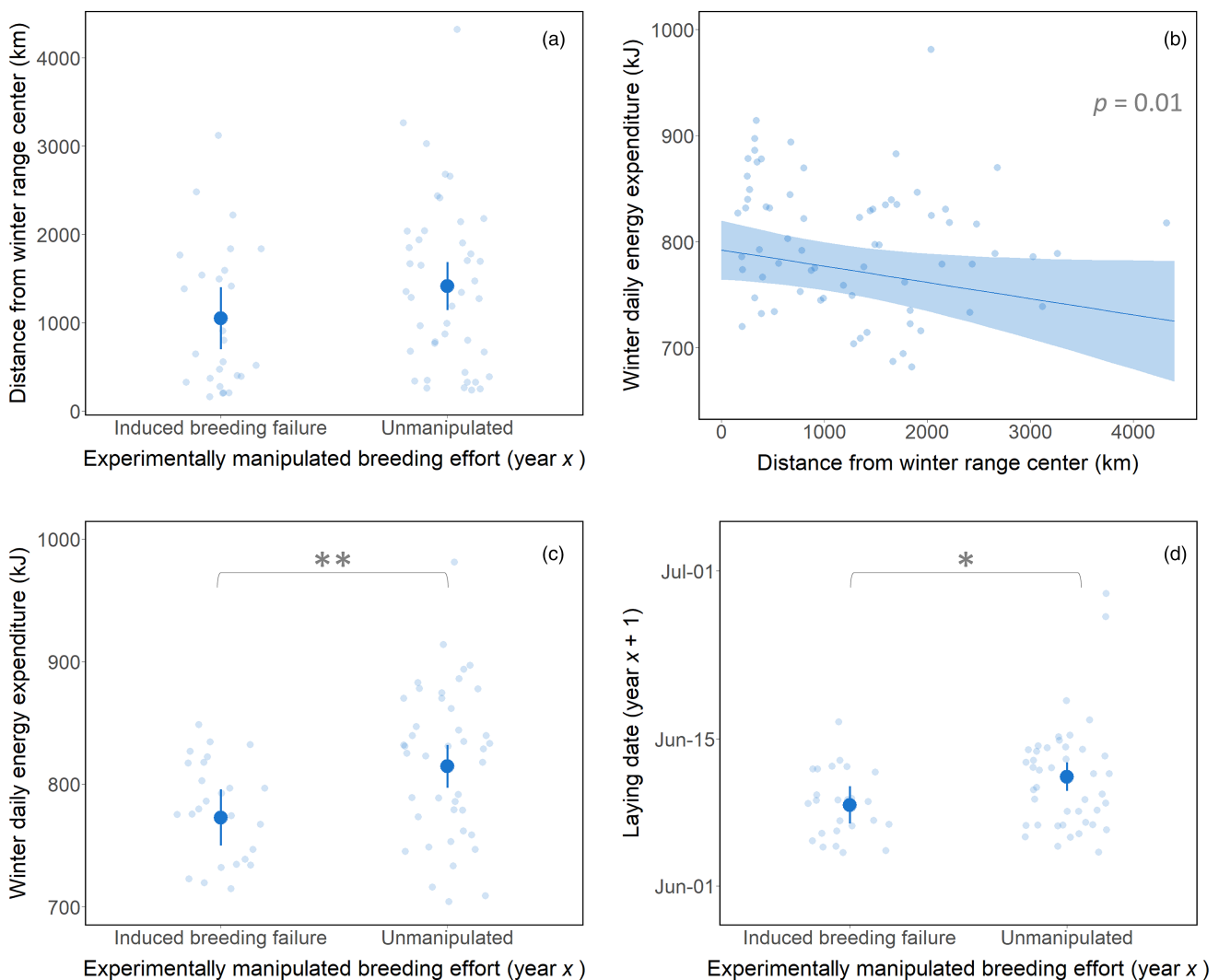
### 3.2 | Experimental approach (PSEM 3)

By using data from the clutch removal experiment, hence manipulating the reproductive effort irrespectively of individual quality, the results of the third PSEM revealed paths expected to indicate true carry-over effects (see Figure 2). With this third PSEM, the path linking the breeding success in year  $x$  to the winter DEE was no longer mediated by the winter distribution (distance to the population's range centre) as found with the first PSEM (Figure 4a,b). Instead, the breeding effort treatment had a small but direct effect on the DEE in winter, with control individuals spending 6% more energy in winter than experimental individuals ( $816.5 \pm 9.1$  kJ vs.  $770.7 \pm 12.4$  kJ, Figure 4c). The treatment also directly affected the breeding stage in the following year, with control individuals

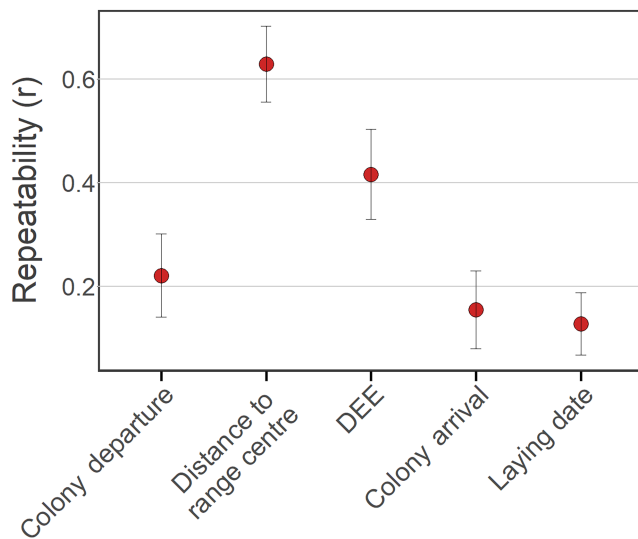
laying 2.7 days later than induced failed breeders (average laying date  $162.4 \pm 0.7$  days vs.  $159.7 \pm 0.9$  days, Figure 4d). Such delay corresponds to a decrease of 11.9% in the breeding success probability (based on population-wide breeding success, LME,  $coef = 0.044$  per day,  $SE = 0.006$ ,  $df = 43$ ,  $p < 0.0001$ ).

### 3.3 | Individual repeatability in behaviour

Behavioural parameters associated with the winter distribution and energy expenditure were moderately to highly repeatable (Figure 5), with 63% repeatability in the distance at which each individual is wintering to the population's range centre ( $r = 0.63$ , 95% CI [0.47; 0.76],  $SE = 0.07$ ,  $p < 0.0001$ ) and 42% repeatability



**FIGURE 4** Partial residual effects of four pathways from the third PSEM (experimental approach) showing potential carry-over effects arising from the breeding effort while experimentally controlling for differences in individual quality. The pathways show the interactions between (a) the experimentally manipulated reproductive effort and the subsequent wintering distribution (i.e. distance from the population's winter range centre); (b) the winter distribution and the winter daily energy expenditure; the manipulated reproductive effort and (c) the subsequent winter daily energy expenditure as well as (d) the breeding phenology (i.e. laying date) in the following year. Plots show model predictions, with their 95% confidence intervals, over the jittered raw data. Models with log transformed predictors are plotted on the original scale.



**FIGURE 5** Individual repeatability ( $r$ ) in behavioural parameters associated with different stages of the annual cycle of black-legged kittiwakes with standard errors, where 0=no repeatability and 1=high repeatability.

in the DEE in winter ( $r=0.42$ , 95% CI [0.24; 0.57],  $SE=0.09$ ,  $p<0.0001$ ). This suggests that variations in these parameters are partly driven by inter-annual consistency in individuals' winter behaviour. Repeatability was, however, low for parameters associated with breeding phenology (Figure 5): colony departure in fall ( $r=0.22$ , CI [0.07; 0.38],  $SE=0.08$ ,  $p<0.0001$ ), colony arrival in spring ( $r=0.16$ , CI [0.02; 0.32],  $SE=0.07$ ,  $p<0.0001$ ) and timing of egg laying ( $r=0.13$ , CI [0.02; 0.25],  $SE=0.06$ ,  $p<0.05$ ). Breeding success had low repeatability ( $r=0.22$ , CI [0.05; 0.41],  $p<0.001$ ), but was associated with high variability ( $SE=0.24$ ). We did not include this parameter in Figure 5 because it is the only binary variable not directly comparable with other parameters. Overall, the breeding success in our dataset is relatively high, with 64% of the pairs successfully raising at least one chick to 10 days old (272 successful attempts, 97 failed attempts).

## 4 | DISCUSSION

Using a long-term dataset of a well-studied avian migrant combined with an experimental approach, we investigated the relative importance of carry-over effects and individual quality in determining cross-seasonal interactions and breeding success consequences. From the longitudinal approach spanning 13 consecutive years, the breeding success was connected to the distribution of individuals during the following wintering stage, which, in turn, was connected to the energy expenditure of individuals in winter. This effect, however, did not cascade into the subsequent breeding stage. The strongest pathway directly linked consecutive breeding stages, with the breeding success in a given year resulting in an earlier onset of breeding (egg laying) the following year, which led to a 20% higher breeding success. However, when

experimentally manipulating the reproductive effort irrespective of individual quality, this positive interaction between successive breeding stages disappeared. Instead, the breeding effort led to reproductive costs paid in elevated energy expenditure in winter, likely to recuperate from these costs, and a later onset of reproduction the following year associated with a 12% lower breeding success the following year (based on population-wide breeding success). The experimental approach also revealed that quality and area fidelity, rather than reproductive costs, were dominant in driving the winter distribution of individuals, masking underlying carry-over effects into the winter energy expenditure of individuals. Thus, individual quality overwrote carry-over effects, although both were present.

### 4.1 | Individual quality

Although life-history theory is predicated on the idea that reproduction is costly, individuals often show positive correlations between current and future reproduction (Hamel et al., 2009; Reznick et al., 2000). This is what we observed in the study population with the individual breeding performance in a given year positively associated with the onset and success of reproduction the following year. Similarly to this, and despite the fact that breeding kittiwakes are operating close to their metabolic ceiling (Welcker et al., 2010), breeders from another study had higher probability of breeding again the subsequent year compared to individuals that skipped reproduction (Cam et al., 1998). Such absence of apparent allocation trade-offs between traits in a given population can arise when there is high variance in resource acquisition among individuals, with higher quality individuals being more efficient in extracting resources from their environment, consequently having more energy to allocate in all functions in a given life-history stage without impacting their future reproduction and survival (Hunt et al., 2004; van Noordwijk & de Jong, 1986). Notably, in Adélie penguins (*Pygoscelis adeliae*), successful breeders exhibited no apparent reproductive costs as they displayed higher survival and future breeding potential than unsuccessful breeders (Lescroël et al., 2009). Heterogeneity in individual quality can have a genetic basis, but may also arise for instance from cohort or maternal effects which can have irreversible, long-lasting impacts on the fitness of individuals later in life ('silver spoon effect', Grafen, 1988; Wilson & Nussey, 2010). We found strong effects of individual quality in our system that could notably arise from larger individuals being able to better compete for resources (Ronconi & Burger, 2011). Age can also be a source of differences in individual apparent quality, especially in long-lived species, with survival and reproductive output typically peaking in more experienced, mid-aged individuals, before declining with senescence (Forslund & Pärt, 1995). More experienced adults may indeed be better able to acquire resources from the environment, having refined their foraging behaviour and locations over the years ('exploration-refinement hypothesis', Guilford et al., 2011). Age is indeed likely associated to consistency in behaviour (i.e. winter distribution) and breeding

performance in our study, since all birds were adults and those tracked over a longer period were likely older individuals. Overall, differences in apparent quality would lead to individuals also varying in their ability to cope with resource limitations, resulting in differential breeding costs, as observed in our study population.

## 4.2 | Consistency in spatial movement

Breeding allocation can also lead to carry-over effects influencing subsequent spatial behaviour of individuals, as shown in a few experimental studies on migratory seabirds. For instance, inducing breeding failure in male Cory's shearwater (*Calonectris borealis*) decreased their propensity in engaging in long-distance migration compared to successful breeders (Catry et al., 2013). Pacific kittiwakes that were supplementary fed during breeding travelled shorter distances and contracted their winter distribution compared to unfed individuals (Whelan et al., 2020). Similarly to these studies, we found a correlation between the breeding effort and the winter distribution of individuals, which in turn was connected to the energy expenditures of individuals during winter: failed breeders (reduced breeding effort) wintered closer to the population's range centre compared to successful breeders (Figure 1a). However, this link disappeared after manipulating the breeding effort irrespectively of individual quality, indicating that the winter distribution was more determined by factors related to individual quality than by carry-over effects. In line with this, individuals from the study population show high area fidelity in winter as indicated by the repeatability in the position of the distribution centroid of individuals (>60%, Figure 5) and the consistency in their overall movement in winter (mean nearest neighbour distance of 260km between tracks; Léandri-Breton et al., 2021). Site fidelity is commonly found across taxa (Piper, 2011), suggesting that within-individual spatial consistency is likely a widespread factor masking underlying carry-over effects and needs to be taken into account.

Similarly, Bogdanova et al. (2011) found that kittiwakes failing reproduction left their colony in Scotland earlier and travelled over 3000km to reach the same wintering area as failed breeders in our study, while most successful breeders departed later and wintered closer to the colony along the European coasts. Failed breeders may have more time and energy to engage in a long-distance migration to reach profitable winter locations (Bogdanova et al., 2011), but our results suggest that such spatial differences may also result from differences in individual quality. In line with this, fidelity to wintering areas in a population of Atlantic puffins (*Fratercula arctica*) was associated with significant differences in breeding success, indicating that individual of different quality may visit different areas (Fayet, Freeman, Shoji, Boyle, et al., 2016). Overall, we suggest that higher quality individuals with higher breeding performances are also performing better in winter as they use areas allowing them to maintain better energy performances (lower energy expenditures) throughout the wintering stage.

## 4.3 | Underlying carry-over effects

After controlling for individual quality, the breeding allocation directly determined the activity budget in winter, with individuals experimentally relieved from breeding costs experiencing reduced energy expenditure on the wintering site compared to control individuals. Control individuals may have increased their activity to compensate for poor foraging conditions on their wintering grounds, although this seems unlikely considering that wintering area selection is in great part determined by site fidelity in our study (>60% repeatability). More likely, this difference in energy expenditure suggests that control individuals increased their activity to regain condition following their higher breeding allocation, while experimental individuals were able to 'take it easy' the winter following the manipulation. Likewise, chick cross-fostering in Manx shearwaters (*Puffinus puffinus*) showed that increased breeding effort led to elevated activity in winter and lower reproductive success the following year, although such differences were not apparent for individuals with reduced breeding effort (Fayet, Freeman, Shoji, Kirk, et al., 2016). Moreover, elevated winter energy expenditure was associated with lower reproductive performances in European shags (*Gulosus aristotelis*) and Manx shearwaters, suggesting that individuals adjusted their activity in response to their own immediate condition rather than in anticipation of future breeding costs (Daunt et al., 2014; Shoji et al., 2015). In our study, however, differences in energy expenditure between experimental and control birds did not persist into the next breeding stage, potentially because individuals were successful in adjusting their activity to compensate for breeding costs. Consequences of breeding allocation can indeed weaken over the course of the non-breeding stage, a period in the annual cycle potentially less time-constrained, allowing breeding costs to be buffered rather than accumulated when conditions are favourable (Bogdanova et al., 2017; Briedis et al., 2018; Ramos et al., 2018). For instance, previous studies on kittiwakes showed that longer time spent on the wintering site was associated with reduced telomere shortening (Schultner, Moe, Chastel, Bech, & Kitaysky, 2014) while higher energy expenditure during breeding had no detrimental effect on the return rate of individuals the following year (Welcker et al., 2010). In another clutch removal experiment, consequences of breeding costs on the following breeding propensity were buffered during winter in most years of the study, although survival costs were still entailed (Golet et al., 2004). However, breeding costs in our study were not entirely buffered by the wintering stage as controlling for individual quality revealed underlying carry-over effects paid in a delayed onset of breeding the following year, with control individuals (higher breeding allocation) laying 2.7 days later compared to individuals experimentally relieved of further breeding allocation. Although this difference in the breeding phenology appears small, it corresponds to a 12% decrease in breeding success (at the population level) and has the opposite direction than what was found before controlling for individual quality (i.e. breeding success in

a given year positively associated to 20% increased success the following year). This indicates that controlling for individual quality revealed a potential cost of reproduction lasting into the following breeding stage. Thus, the experimental approach provided evidence that, although they are masked by individual quality and site fidelity, carry-over effects exist in the study population, with reproductive costs resulting in an elevated energy budget in winter and a delayed onset of breeding, a parameter strongly related to breeding success in our study and in birds in general (Goutte et al., 2010; Perrins, 1970).

#### 4.4 | Pre-laying corticosterone levels

We did not find a relation between baseline corticosterone levels measured in pre-laying individuals and the previous wintering stage nor with the subsequent breeding output (i.e. reproduction onset and success). Other studies have shown either negative effects (Harms et al., 2015), no effects (Bourgeon et al., 2014) or even positive effects (Pérez et al., 2016) of corticosterone levels measured in winter-grown feathers into the subsequent reproductive output. These mixed results likely reflect variations in the strength and persistence of carry-over effects in relation to conditions experienced during previous stages (Ramos et al., 2018). In our study population, the effects of the wintering behaviour did not carry into the breeding stage, and potential carry-over effects into the hormonal stress response of pre-laying birds were likely buffered as well. Moreover, kittiwakes could not be sampled immediately after their return from the wintering stage, and their blood corticosterone levels may thus reflect the foraging conditions experienced in the past weeks at the breeding colony more than those experienced on the wintering site (Kitaysky, Kitaiskaia, et al., 2001). In line with this, Goutte et al. (2014) found that corticosterone levels of pre-laying kittiwakes varied among years and were lower in years of earlier breeding onset when local foraging conditions are favourable. How corticosterone varies according to local environmental conditions and foraging activity of pre-laying individuals remains unclear and would require further investigation. Measuring the corticosteroid binding globulin (CBG), rather than the total plasma concentration, would improve understanding of changes in the circulating, active proportion of corticosterone in relation to environmental conditions experienced (Desantis et al., 2013).

## 5 | CONCLUSIONS

Overall, variations in individual quality associated to breeding performances and repeatability in behaviour were dominant in determining seasonal interactions in behaviour and performance of the study population. We found that individuals with better breeding performance (successful breeders) were also performing better in winter (lower energy expenditure), leading to positive correlations

across seasons between current reproduction, winter distribution and future reproduction. It is only after controlling experimentally for consistency in breeding performance (individual quality) that we could conclude these correlations were attributed to differences in individual quality, and also reveal underlying carry-over effects that were otherwise masked by quality. Because variations in costs and in quality are likely both present in a population, it is not possible to predict the sign of the covariance between traits (Wilson & Nussey, 2010). Moreover, it is not possible to assess the strength of carry-over effects if the covariance is negative, nor to conclude that underlying costs are absent if the covariance is positive (Wilson & Nussey, 2010). An experimental approach is required to separate costs and quality effects as they can both have important, but different, evolutionary and demographic consequences on animal populations (Harrison et al., 2011).

#### AUTHOR CONTRIBUTIONS

D.-J. Léandri-Breton, K. H. Elliott, O. Chastel and P. Legagneux conceived the ideas and designed methodology. D.-J. Léandri-Breton, W. Jouanneau, F. Amélineau, F. Angelier, P. Blévin, A. Goutte and S. Tartu collected the data. A. Tarroux, P. Fauchald, V. S. Bråthen and B. Moe carried out geolocation preliminary analyses and data management. C. Parenteau and W. Jouanneau conducted hormone radioimmunoassay. G. W. Gabrielsen provided expert advice. D.-J. Léandri-Breton led the analyses and the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing or conflict of interests.

## DATA AVAILABILITY STATEMENT

Data supporting this study are available from the Norwegian Polar Data Centre: <https://doi.org/10.21334/npolar.2024.e7e71c1c> (Léandri-Breton et al., 2024).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Figure S1.** Example of sun elevation angle selection from Bråthen et al. (2021) for a black-legged kittiwake track (June 2011 to June 2012).

**Figure S2.** Example of sun elevation angle selection from Bråthen et al. (2021) for a black-legged kittiwake track (same track as in Figure S1).

**Figure S3.** Frequency distribution of daily locations of black-legged kittiwakes estimated from the geolocation data only and those re-estimated with the algorithm IRMA developed for the SEATRACK program, over the tracking period.

**Figure S4.** Movement rate plotted against time elapsed between two locations, for black-legged kittiwakes.

**Figure S5.** Distribution of standard conductivity counts during nighttime showing very high standard saltwater immersions associated to resting behaviour on water.

**Figure S6.** Levels of corticosterone in plasma of black-legged kittiwakes (*Rissa tridactyla*) over the time before blood sampling (in seconds).

**Table S1.** Number of non-breeding tracks per year of tracking and per sex determined by molecular sexing (following Fridolfsson & Ellegren, 1999) or through behaviour when paired with a known-sex partner.

**Table S2.** Pathways included in each three piecewise structural equation models (PSEM) fitted to test direct and indirect causal effects between consecutive breeding stages of the annual life cycle of black-legged kittiwakes (*Rissa tridactyla*).

**Table S3.** Distribution of individuals per number of years of

non-breeding movement tracking and over the time interval between first and last year of tracking, as well as the total numbers of individuals included in path analyses ( $n = 181$  individuals tracked) and in repeatability estimates of non-breeding behavioural parameters ( $n = 58$  individuals tracked multiple years).

**Table S4.** Pathways of an additional piecewise structural equation model (PSEM) fitted to test the role of body condition index during pre-laying (instead of corticosterone level) as a potential mediator of carry-over effects ( $n = 54$ ) in black-legged kittiwakes (*Rissa tridactyla*).

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