

Contribution to the Theme Section 'Tracking fitness in marine vertebrates'

Corticosterone mediates carry-over effects between breeding and migration in the kittiwake *Rissa tridactyla*

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ABSTRACT: Carry-over effects, i.e. when processes in one season influence processes in the next, are believed to have important effects on behavior and fitness in animals. Despite an increasing interest in the identification of carry-over effects, there are few experimental studies of the underlying mechanisms. We investigated how a short-term experimental elevation of the stress hormone corticosterone (CORT) during breeding influences the migratory behavior of black-legged kittiwakes *Rissa tridactyla*. We exposed chick-rearing kittiwakes to a 3 d elevation of CORT, which is usually secreted in response to food shortages. The migratory behavior of CORT-treated kittiwakes and a control group was then tracked using geolocators. We found that CORT treatment affected subsequent autumn migration in a sex-specific manner. CORT-treated females left the breeding grounds earlier and spent a longer period at the wintering grounds than control birds and CORT-treated males. The CORT treatment did not affect the timing of spring arrival or total length of migration. Our findings indicated that physiological stress incurred during breeding can carry over to affect key parameters of migratory behavior in autumn. Identifying carry-over mechanisms, such as those described here, is important to understand how performance and fitness in animals are determined by interactions between different parts of their life cycle.

KEY WORDS: Glucocorticoids · Mechanism · Carry-over effects · Reproduction · Autumn migration · Black-legged kittiwake · *Rissa tridactyla*

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INTRODUCTION

Carry-over effects, which are processes in one life history stage that affect processes in the next stage, are believed to be important determinants of behavior and fitness in animals (Norris 2005, Harrison et al. 2011, Catry et al. 2013). During recent years, carry-over effects have been documented in several species, and usually attributed to habitat or diet quality (Marra et al. 1998, Norris 2005, Sorensen et al. 2009, Bogdanova et al. 2011, Conklin & Battley 2012). At a

proximate level, it has been suggested that physiological stress, acting via the hypothalamic–pituitary–adrenal axis, can result directly in carry-over effects (Legagneux et al. 2012). Other proposed, non-exclusive factors include body condition and the effects of previous breeding outcome (Bogdanova et al. 2011, Klaassen et al. 2012, Legagneux et al. 2012). However, most studies of carry-over effects to date remain correlative, making it difficult to untangle physiological mechanisms from confounding factors such as genetics or different individual quality (Bog-

danova et al. 2011). As, to our knowledge, no experimental manipulations of candidate mediators of carry-over effects have been reported, mechanisms therefore remain essentially unknown (Harrison et al. 2011).

Recently, evidence that indirectly implies glucocorticoid hormones as mediators of carry-over effects has been accumulating (Legagneux et al. 2012, Mark & Rubenstein 2013). Glucocorticoids are physiological mediators of environmental stress (Wingfield 1994, Bonier et al. 2009). In seabirds, secretion of the glucocorticoid hormone corticosterone (CORT) increases with deteriorating food availability, as demonstrated by both experimental and observational studies (e.g. Kitaysky et al. 1999a, Buck et al. 2007, Kitaysky et al. 2007, Kitaysky et al. 2010). Circulating CORT is important for the regulation of stored energy (Wingfield et al. 1998, Sapolsky et al. 2000, Schultner et al. 2013b) and foraging behavior (Wingfield et al. 1998, Sapolsky et al. 2000, Kitaysky et al. 2001, Angelier et al. 2007a,b). However, increases in CORT levels due to stress can also trigger the reduction and abandonment of current reproductive efforts, thereby modulating breeding success (Wingfield et al. 1998, Kitaysky et al. 2001). In summary, CORT has the potential to affect processes previously suggested to be involved in carry-over effects. As well as a modulation of energy stores and breeding success, CORT may also interfere more directly with the preparations for migration. For example, high levels of CORT reduce feather growth (Romero et al. 2005), a potentially important factor in the pre-migratory molt process. Furthermore, it has been demonstrated that chronically increased CORT levels have long-term negative consequences on health, immune and cognitive function, and survival (Wingfield et al. 1998, Sapolsky et al. 2000, Goutte et al. 2010b, Kitaysky et al. 2010), each of these being relevant in the context of carry-over effects. However, no study to date has experimentally tested the specific role of CORT in carry-over effects.

Seabirds in general, and kittiwakes in particular, represent a unique system to study mechanisms of carry-over effects on migration. Not only have kittiwakes been a focal species in much of the work on glucocorticoid hormones, meaning that the birds' hormonal profiles, the environmental influence on these, and behavioral and physiological effects of hormones, are relatively well known (e.g. Kitaysky et al. 2001, Angelier et al. 2007a, Buck et al. 2007, Kitaysky et al. 2010). Kittiwakes and many other seabirds are also large enough that they can be fitted with small tracking devices. Furthermore, the annual migration of seabirds is usually large scale, which

makes it possible to track the animals through low-cost, but coarse-resolution devices such as geolocators (relative to, for example, GPS-based technology). Many kittiwakes in the Atlantic, for example, migrate a distance of several thousand kilometers twice annually between their breeding colonies and wintering grounds (Frederiksen et al. 2012).

In the present study, we examined whether physiological stress during breeding carries over to affect migration patterns in arctic-breeding kittiwakes. As a proxy of physiological stress, we increased the CORT levels in chick-rearing kittiwakes for a short-term period through CORT implants. Subsequently, we tracked individual migration patterns with geolocators that were recovered during the following breeding season.

MATERIALS AND METHODS

Corticosterone treatment

Kittiwakes are cliff-nesting, medium-sized gulls with a northern circumpolar distribution. Both partners on a nest share parental duties about equally, typically raising 1 or 2 chicks. The breeding season lasts from April or May to August or September, with chicks hatching around 10 July (Moe et al. 2009). Kittiwakes can molt their primary feathers from May to December, with most feathers being replaced before arrival at the wintering areas in November (Olsen & Larsson 2004, González-Solís et al. 2011). During July to August 2011, we performed a short-term stress experiment in a colony of chick-rearing kittiwakes in Kongsfjorden, Svalbard, Norway. Briefly, when chicks were about 10 d old, we implanted one parent subcutaneously with a CORT-filled silastic tube (CORT treatment: 'CORT', $n = 13$; $n_{\text{male}} = 5$, $n_{\text{female}} = 8$). Small incisions were made at both ends of the implant to facilitate a rapid hormone release, effectively replicating earlier studies in which 2 implants with single incisions were used. The implants produce a peak in baseline CORT levels before returning to pre- or slightly below pre-implantation levels 2 to 3 d later (Kitaysky et al. 2001, Angelier et al. 2009, Goutte et al. 2010a, Schultner et al. 2013a). The disinfected implant was inserted under the skin between the shoulders through a small incision and the incision closed with tissue glue. A control group of individuals received an empty implant (CORT treatment: 'control', $n = 12$; $n_{\text{male}} = 6$, $n_{\text{female}} = 6$). Implants were given while birds were held for a different purpose (equilibration period of doubly labeled water for measuring energy expendi-

ture) for ~1 h, and handling times (\pm SE) were almost identical for both treatments (CORT = 1 h 15 min \pm 1 min, control = 1 h 17 min \pm 2 min). At implantation, males were heavier than females (linear model: $F_{1,16} = 42.880$, $p < 0.001$), as expected (Moe et al. 2002), but body mass did not differ among the treatments in either sex (CORT treatment: $F_{1,16} = 1.556$, $p = 0.230$; CORT treatment \times sex: $F_{1,16} = 2.652$, $p = 0.123$). Also baseline CORT levels were similar between treatment groups ($F_{1,15} = 0.218$, $p = 0.648$), but elevated in males compared with females ($F_{1,15} = 23.033$, $p < 0.001$). There was no significant interaction between CORT treatment and sex before the experiment ($F = 1.445$, $p = 0.248$; control females = 5.4 ± 1.2 ng ml⁻¹, CORT females = 6.3 ± 0.4 ng ml⁻¹, control males 11.8 ± 1.5 ng ml⁻¹, CORT males = 10.2 ± 1.1 ng ml⁻¹). Initial conditions for the implant treatment were also similar with respect to clutch size (Pearson's chi-squared test: $\chi^2 = 0.008$, $p = 0.927$) and timing of implantation (t -test: $t_{16,746} = 0.147$, $p = 0.885$). We recaptured the birds and removed the implants after the peak in CORT levels was produced, i.e. after a 3 d period. Consequently, there was no difference in baseline CORT levels at recapture between implant treatments ($F_{1,14} = 0.120$, $p = 0.735$) or sexes ($F_{1,14} < 0.001$, $p = 0.993$), and no significant interaction between implant and sex ($F_{1,14} = 0.273$, $p = 0.609$; control females = 6.9 ± 1.7 ng ml⁻¹, control males = 8.1 ± 1.9 ng ml⁻¹, CORT females = 7.1 ± 0.8 ng ml⁻¹, CORT males = 6.3 ± 2.7 ng ml⁻¹). For a more detailed description of the CORT experiment, see Schultner et al. (2013a).

Geolocator deployment

Birds were equipped with light-level geolocators mounted on a leg band ($n = 25$, Mk18L and Mk18H, 1.5 and 1.9 g, British Antarctic Survey) later in the breeding season, when their chicks were ~25 d old. In July 2012, we recovered 22 and successfully extracted data from 20 geolocators, 12 of which were from CORT-treated individuals ($n_{\text{females}} = 7$, $n_{\text{males}} = 5$) and 8 from controls ($n_{\text{females}} = 4$, $n_{\text{males}} = 4$). One data-extracted geolocator from a CORT-treated male only held data up to 26 December 2011.

Geolocator analyses

Geolocator data were analyzed with BASTrak software (British Antarctic Survey). Following Frederiksen et al. (2012), we used a light threshold level of

10 and a sun elevation angle of -3° to estimate 2 daily positions. Estimates of latitude were unreliable around the equinoxes, and the periods 7 September to 19 October and 24 February to 5 April were consequently removed. We estimated timing of autumn departure and spring arrival as the date when the birds crossed 70° N (see 'Migration analyses' below). This parameter was used instead of departure and arrival at the colony (79° N) because geolocators cannot provide positions under constant daylight, which occurs from end of April to end of August at the colony. In contrast, positions (and timing) could be determined for all birds when they crossed 70° N. At this point, all birds were in rapid transit towards or away from the wintering areas, which we regard as a useful benchmark for inter-individual comparison of timing of migration.

Migration analyses

Geolocator positions have an average error of ~185 km (Phillips et al. 2004). To reduce the influence of outliers and errors, we smoothed positions using a 3-position moving average based on spherical trigonometry. Distances between successive smoothed positions and between positions and the colony were calculated as great circle distances assuming a spherical Earth. We analyzed 3 main parameters of migration timing: (1) autumn departure from the breeding region, defined as the date an individual crossed latitude 70° N in southward direction; (2) time spent at the wintering grounds, defined as the number of days an individual spent south of 70° N; and (3) spring arrival, defined as the date an individual crossed 70° N in northward direction. We also analyzed the median distance to the colony for each individual in each month, and the time spent in the west versus the east Atlantic sectors. Based on spatial rather than biological considerations, we used 35° W to separate west and east Atlantic into roughly similar-sized sectors.

Effects of corticosterone treatment on migration

For each of the 3 migration parameters, we fitted linear models with migration behavior as response and the factors CORT treatment (CT; control or CORT) and sex (S; female or male), along with the interaction between CT and S, as explanatory variables. Median monthly distance to the colony was analyzed with linear mixed-effect models, with treat-

Table 1. Effects of CORT treatment during breeding (CT: CORT or control) and sex (S: female or male) on autumn departure, time spent south of 70° N and spring arrival in kittiwakes *Rissa tridactyla*. Autumn departure and spring arrival were defined as the date when crossing 70° N during southward and northward migration, respectively. Statistically significant p-values (<0.05) are in bold

	df	F	p
Autumn departure (cross 70° N southbound)			
CT	1,16	2.2	0.155
S	1,16	5.0	0.039
CT × S	1,16	11.5	0.004
Time spent south of 70° N			
CT	1,15	0.6	0.449
S	1,15	0.3	0.593
CT × S	1,15	5.9	0.028
Spring arrival (cross 70° N northbound)			
CT	1,15	0.1	0.705
S	1,15	1.2	0.283
CT × S	1,15	0.7	0.428

ment, month and sex as fixed factors and individual identity as a random factor (random intercept). The number of birds and observations were 20 and 137, respectively. The random term remained constant in all candidate models, while the fixed-effect terms were changed. We thus fitted the models with maximum likelihood (Pinheiro & Bates 2000, Zuur et al. 2009). We selected the best model for inference using an information theoretic approach with Akaike's information criterion corrected for small sample size (AIC_c). The relative likelihoods of candidate models

were expressed with AIC_c weights (Burnham & Anderson 2002). As month (M) is a strong predictor of distance to colony (Frederiksen et al. 2012), we included M in each candidate model. The set of candidate models was then designed to include all combinations with CT and S, along with the interactions. Intercept was included in all the models, and we also included a model with intercept only. The intercept-only model has no biological meaning, but is useful as a statistical null model. All analyses were carried out in R v2.15.2 (R Core Team 2012), including packages 'nlme' (Pinheiro et al. 2013) and 'AICcmodavg' (Mazerolle 2013). We report means ± standard errors throughout.

RESULTS

Autumn departure of kittiwakes was affected by the CORT treatment in a sex-specific manner ($p = 0.004$ for CT × S, Table 1). When treatments were pooled, female kittiwakes departed earlier than males (24 October ± 3 d and 30 October ± 2 d, respectively; S, $p = 0.039$, Table 1). However, CORT-treated females departed for autumn migration on 19 October ± 3 d, whereas CORT-treated males departed 2 wk later (2 November ± 2 d, Fig. 1). Control females and males departed on 1 November ± 3 d and 27 October ± 3 d, respectively (Fig. 1).

CORT treatment also affected the total time spent in the wintering areas in a sex-specific manner (CT × S, $p = 0.028$, Table 1). CORT-treated females spent 13 d more at the wintering grounds than

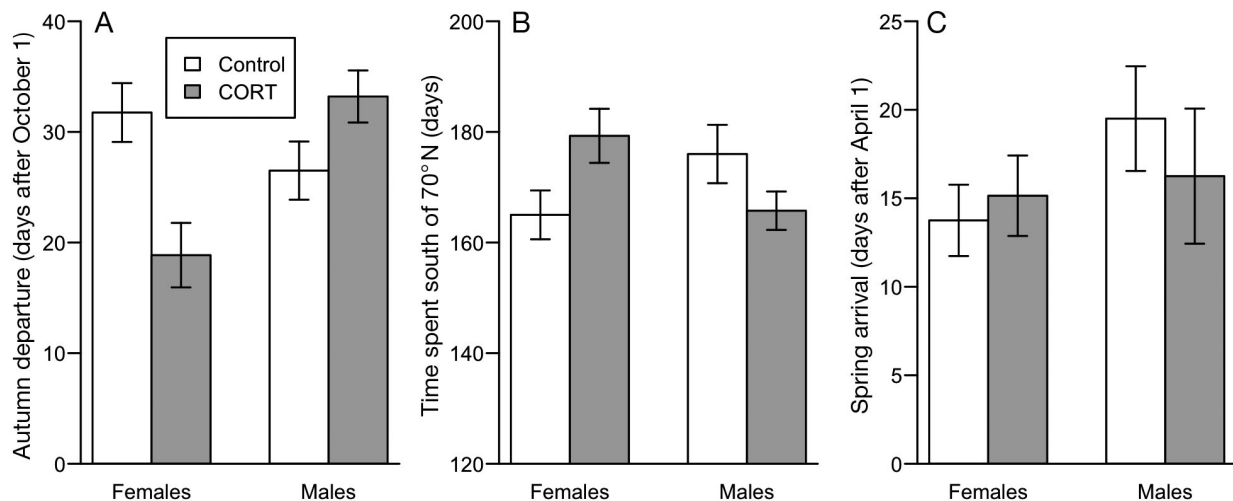


Fig. 1. *Rissa tridactyla*. (A) Autumn departure (days after October 1, 2011), (B) time spent south of 70° N, and (C) spring arrival (days after April 1, 2012) for male and female individuals. Birds were either CORT (grey bars, $n_{\text{male}} = 5$, $n_{\text{female}} = 7$) or control (white bars, $n_{\text{male}} = 4$, $n_{\text{female}} = 4$) treated while breeding (July 2011). Autumn departure and spring arrival refer to timing of crossing 70° N during southbound and northbound migration, respectively. Displayed are means ± SE

Table 2. Comparison of linear mixed-effect models (individual identity was entered as a random effect) analyzing median distance to colony of individual kittiwakes *Rissa tridactyla* in relation to CORT treatment (CT), month (M) and sex (S) based on Akaike's information criterion corrected for finite sample size (AIC_c) and weights (AIC_c weights). K denotes the number of parameters in each model and models are ranked according to their ΔAIC_c . Number of individuals = 20, observations = 137

Rank	Model	K	AIC_c	ΔAIC_c	AIC_c weights
1	CT + M + S + 'CT × M' + 'CT × S' + 'M × S' + 'CT × M × S'	30	2186.3	0.0	0.99
2	M + S	10	2198.9	12.6	<0.01
3	M	9	2199.0	12.8	<0.01
4	M + S + 'M × S'	16	2200.3	14.0	<0.01
5	CT + M	10	2201.2	14.9	<0.01
6	CT + M + S	11	2201.2	14.9	<0.01
7	CT + M + S + 'CT × S'	12	2201.8	15.6	<0.01
8	CT + M + S + 'M × S'	17	2202.8	16.5	<0.01
9	CT + M + 'CT × M'	16	2206.3	20.0	<0.01
10	CT + M + S + 'CT × M'	17	2206.4	20.2	<0.01
11	Intercept only	3	2417.3	231.1	<0.01

CORT-treated males (179 ± 5 d and 166 ± 3 d, respectively, Fig. 1). In contrast, control females spent 11 d less at the wintering grounds than males (165 ± 4 d and 176 ± 5 d, respectively, Fig. 1). These effects on time spent at the wintering grounds were mainly driven by the timing of autumn departure, as there was no effect of CORT treatment and sex on timing of spring arrival (CT × S, $p = 0.428$, Table 1, Fig. 1). On average, CORT-treated females and males arrived (i.e. crossed 70° N, see 'Materials and methods') on 15 April ± 2 d and 16 April ± 4 d, respectively, whereas control females and males arrived on 14 April ± 2 d and 20 April ± 3 d, respectively (Fig. 1).

In line with these differences in migratory behavior, distance to colony was best explained by the full model including the 3-way interaction CT × M × S compared with other candidate models (AIC_c weight = 0.99, Table 2). Thus, CORT treatment affected the birds' distance to the colony, and this effect depended on month and sex. In October, during the time of autumn migration, CORT-treated females were distributed further south than CORT-treated males and control females, which remained at higher latitudes and closer to the colony (Figs. 2 & 3). Overall, distance from colony was similar during the winter months December, January and February in control and CORT-treated birds (Fig. 3, Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m496/p125_supp.pdf). All birds visited both the west and the east Atlantic sectors during winter (Fig. S1 in the supplement), and time spent in the different sectors was not affected by the CORT treatment (for time in the west Atlantic: $F_{1,15} = 1.821$, $p = 0.197$) or sex ($F_{1,15} = 0.948$, $p = 0.346$) after controlling for time spent south of 70° N ($F_{1,15} = 4.566$, $p = 0.050$). Total

distance travelled during the migration period was not affected by the CORT treatment ($F_{1,16} = 0.031$, $p = 0.863$) or sex ($F_{1,9} < 0.001$, $p = 0.988$).

DISCUSSION

We demonstrated experimentally that physiological stress during breeding has a carry-over effect that modifies migratory behavior in a long-lived seabird. Female kittiwakes that were CORT-treated during the chick-rearing period departed from their breeding grounds early, compared with kittiwakes in other years and nearby colonies (Frederiksen et al. 2012), whereas similarly stressed males left later. This resulted in ~2 wk longer residence of CORT-treated females at the wintering grounds (south of 70° N) compared with controls. CORT-treated males, in contrast, spent an average of 10 d less at the wintering grounds than control males. Later migratory behavior, i.e. total distance travelled, time spent in different sectors of the Atlantic or spring arrival at the breeding grounds, was not affected and thus confirms results from earlier studies that carry-over effects across multiple seasons may be difficult to detect (Bogdanova et al. 2011).

We found carry-over effects of elevated CORT levels in kittiwakes to be sex specific. This is in line with earlier studies in which breeding success carried over to migration in a sex-specific way, with female but not male kittiwakes spending longer time in the west Atlantic sector after a failed breeding attempt (Bogdanova et al. 2011). However, whether the sex specificity of carry-over effects can be attributed to contrasting parental investment before winter migra-

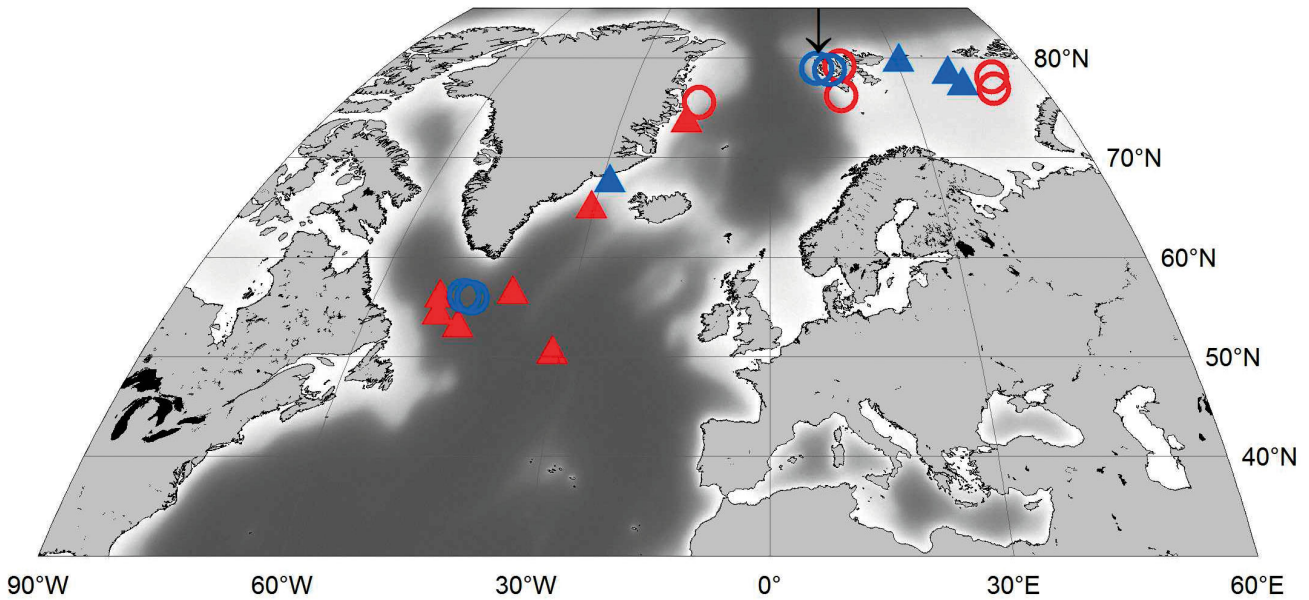


Fig. 2. *Rissa tridactyla*. Median positions in October for male (circles) and female (triangles) individuals from Kongsfjorden, Svalbard, Norway (79° N, 12° E). Red symbols: CORT-treated kittiwakes ($n_{\text{male}} = 5$, $n_{\text{female}} = 7$); blue symbols: controls ($n_{\text{male}} = 4$, $n_{\text{female}} = 4$); arrow: position of breeding colony

tion, to the need of females to attain energy for egg production in the following breeding period, or to differential roles in the establishment and defense of breeding sites remains an interesting question for future research.

Earlier observational studies have shown that habitat and diet quality or quantity, the intrinsic state of animals and reproductive success can lead to carry-over effects in animals (e.g. Norris 2005, Bogdanova et al. 2011, Harrison et al. 2011). However, proximate mechanisms remain largely elusive in these studies.

Our results showed that the glucocorticoid hormone CORT can be a mediator of carry-over effects between the reproductive and migratory life history stages. Theoretically, the stress hormone CORT itself could have directly triggered differences in migratory behavior. This would support one of the few experimental studies on carry-over effects, in which stress during migration—induced by captivity—was suggested to carry over to reproduction in wild geese (Legagneux et al. 2012). As physiological stress in that particular study was not manipulated or meas-

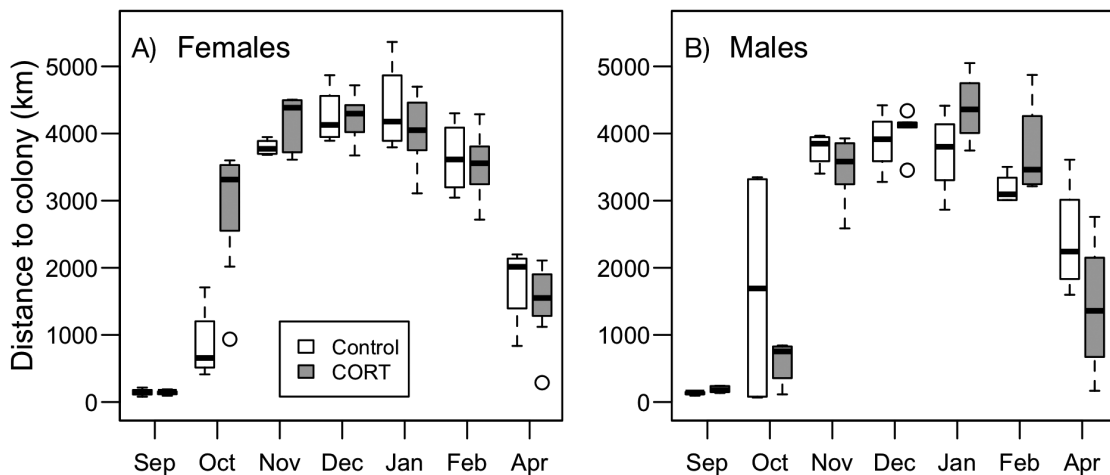


Fig. 3. *Rissa tridactyla*. Monthly median distance to colony (km) during the non-breeding period (September 2011 to April 2012) of (A) female or (B) male kittiwakes that were either CORT (grey boxes, $n_{\text{male}} = 5$, $n_{\text{female}} = 7$) or control (white boxes, $n_{\text{male}} = 4$, $n_{\text{female}} = 4$) treated while breeding (July 2011). Boxes around the median represent the first and third quartiles, whiskers the largest and smallest value within 1.5× the interquartile range from the box, and points outside this range are plotted as outliers

ured at the proximate level, an involvement of stress hormones remained speculative. However, other studies have established that elevated levels of CORT affect foraging and cognitive capabilities, and can impact immunocompetence and post-reproductive survival (Sapolsky et al. 2000, Romero 2004, Bonier et al. 2009, Goutte et al. 2010b, Kitaysky et al. 2010). There is also evidence that CORT is directly involved in processes important for molt (Romero 2002, Romero et al. 2005, DesRochers et al. 2009) and migration (Piersma et al. 2000, Landys-Ciannelli et al. 2002, Reenerkens et al. 2002, Landys et al. 2004). Thus, CORT could have been a direct causal determinant of the changes in migratory behavior that we observed in this study. However, firstly, CORT is suggested to delay rather than advance molt, as it may decrease feather protein deposition (Romero et al. 2005). As kittiwakes usually molt most of their primary feathers before autumn migration (Olsen & Larsson 2004, González-Solís et al. 2011), CORT-treated birds would be expected to migrate later. Secondly, in our study the exposure of breeding birds to elevated levels of CORT was only short term (less than 3 d) and CORT returned to baseline levels after this increase. Therefore, it would be surprising if such a transient increase in stress hormones would have a long-lasting direct effect. Thirdly, we only observed an advance in the migration schedule of CORT-treated females, and not in males. The direct effects of CORT would therefore be sex specific, in that they would cause an advance of migration in one but not the other sex. At the moment, there is no physiological evidence that would support such a notion, e.g. a largely different CORT-receptor distribution between sexes. Finally, evidence against a consistent proximate effect of circulating CORT on migration schedules is derived from an examination of the hypothalamic-pituitary-adrenal (HPA) axis function during mid- to late chick rearing: baseline total and free CORT levels a few weeks before departure were lower in CORT-treated, early departing females than in controls (potentially reflecting a 'better' physiological state as discussed below; see Fig. S2 in the Supplement for mid- to late-season CORT levels), but within each treatment group, lower CORT levels tended to be associated with later departure. CORT consequently does not seem to be a convincing proximate mechanism to determine departure, and the relationship between HPA axis function and migration appears to be context dependent. To conclude thus far, we did not find indications for a direct proximate effect of CORT (CORT treatment or mid- to late-season CORT levels) on molt and/or migration.

Although our study identified CORT as an important mediator of carry-over effects between breeding and migration, the exact pathways that lead to changes in migration schedules in response to a short-term physiological stress remain to be established. Theoretically, CORT may carry over to migration by affecting 2 non-exclusive factors: reproductive performance or the pre-migratory state of individuals. Reproductive performance has been proposed as a major link between breeding and migration (Bogdanova et al. 2011, Catry et al. 2013), and CORT (or its major underlying factor in kittiwakes, food availability) is a known modulator of reproductive success (Wingfield et al. 1998, Kitaysky et al. 1999b, 2001). However, kittiwakes in our study maintained relatively high parental care and had increased reproductive success in response to the CORT treatment (Schultner et al. 2013a). Although we did not observe predation on study nests during our daily presence in the colony, CORT-mediated changes in parental behavior may have interacted unnoticed with predation events to modify breeding success. But as the timing of autumn departure from the breeding grounds of CORT-treated females was similar for unsuccessful and successful breeders in this study (Table S1 in the Supplement), breeding success overall did not seem to have a strong influence on observed differences in migratory behavior. CORT may alternatively have contributed to individual differences in energy stores at the end of the breeding season. Reproduction is a costly activity and often leads to a depletion of energy stores (e.g. Drent & Daan 1980, Golet & Irons 1999) and can reduce future survival (e.g. Stearns 1989, Golet et al. 1998). Elevated levels of CORT, on the other hand, can stimulate food acquisition and intake (Sapolsky et al. 2000, Angelier et al. 2007a), potentially leading to larger energy stores at the end of the season, which would then allow an earlier migration. Similarly, as molt is energetically costly (Portugal et al. 2007, Fox et al. 2013), early or rapid completion of molt due to available stored energy may have contributed to an advancement of migration timing (González-Solís et al. 2011, Fox et al. 2013). However, although CORT-treated females in our study tended to gain body mass through the breeding season, compared with control females (Table S2, Fig. S3 in the Supplement), differences were subtle (about 7% change relative to initial body mass) and statistically insignificant (Table S2 in the supplement). Furthermore, as mass change and departure from breeding grounds in CORT-treated males were similar to control males, we could not conclusively

assess the role of energy stores. In summary, although we could not rule out a direct effect of CORT on migratory behavior, a possible link between physiological stress experienced during reproduction and migratory behavior is the dynamics of energy stores. However, sample sizes in our study were limited and future studies are clearly needed to investigate the interactive effects of hormones, behavior, energy balance and reproductive success in detail.

In conclusion, this is the first study that demonstrates a link between physiological stress during reproduction, mediated by CORT, and migratory behavior. We were not able to quantify other important aspects of pre- and post-breeding ecology that are linked to breeding performance, such as prospecting on other colonies (Ponchon et al. 2013) and dispersal (Danchin et al. 1998), owing to the continuous light conditions in Arctic summer; however, they should be explored in the future. Another intriguing question that deserves more attention is whether and how stress during reproduction and resulting changes in migration behavior translate into individual fitness (Plot et al. 2012). Larger-scale studies that investigate proximate factors and deploy tracking devices are needed, to avoid the limitations of small sample sizes in current experimental carry-over studies. However, with our study, we demonstrated the significance of an experimental approach to advance our understanding of carry-over effects.

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