

GPS-loggers influence behaviour and physiology in the black-legged kittiwake *Rissa tridactyla*

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ABSTRACT: In recent decades, data loggers and radio- and satellite transmitters have become an important technological part of research on free living animals. Loggers to track movements and behaviour are especially useful in seabird studies, as seabirds often travel considerable distances at sea where visual observations are challenging. The potential negative effects of these devices on mortality, behaviour and reproduction of birds have received some attention, but few studies have investigated the physiological effects of instrument attachment. In the present study, effects of global positioning system (GPS) loggers on black-legged kittiwakes *Rissa tridactyla* were investigated by obtaining behavioural and physiological parameters of stress (nest attendance, plasma levels of the avian stress hormone corticosterone [CORT], relative leucocyte counts, body mass and reproductive success) during 2 d of GPS-deployment. GPS-equipped kittiwakes had significantly elevated levels of CORT at recapture and also significantly extended the duration of feeding trips compared to controls. Kittiwakes with low body condition index (BCI) attended nests less than controls, and this pattern was more pronounced among GPS-equipped birds. The study underlines the need to take device effects into consideration when instrumenting seabirds. Potentially, effects may become more evident in birds with low body condition or in years where food is limited, and results from GPS-equipped birds should be viewed with this in mind.

KEY WORDS: GPS-loggers · Effects · Physiology · Behaviour · Black-legged kittiwake · *Rissa tridactyla*

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INTRODUCTION

During the last few decades, research on free living animals has benefited from the development of a great diversity of technological devices that enable scientists to track the movements and behaviour of individual animals (Wikelski et al. 2006, Burger & Shaffer 2008, Indermaur et al. 2008, Knapp & Abarca 2009, Janak et al. 2012). Radio transmitters, platform terminal transmitters (PTTs, i.e. satellite transmit-

ters), global location sensing (GLS) loggers, global positioning system (GPS) loggers and time–depth recorders (TDRs) are among the most frequently used types of devices (Burger & Shaffer 2008, Casper 2009).

Tracking and logging approaches are particularly well-suited for seabirds, as they typically travel far from their breeding colonies making visual observation difficult (Vandenabeele et al. 2011). In addition, most seabirds are colony breeders, and can easily be

captured in sufficient numbers at the nest (Burger & Shaffer 2008). Because of their mobility and dependence on the oceans, seabirds are often used as indicators for the state of their environment: usually in terms of prey abundance, but also in relation to climatic changes and pollution (Furness & Camphuysen 1997, Piatt et al. 2007). Loggers and transmitters improve the quality of—and facilitate the progress of obtaining—knowledge about these often extensive and complex ecosystems, e.g. by showing researches where seabirds feed or spend the non-breeding season (and thus where food is abundant), or where seabirds pick up toxic compounds (Burger & Shaffer 2008). Nevertheless, data collected by the use of loggers and transmitters are potentially biased by the possibly negative physiological and behavioural effects of such devices on their bearers. These effects are often poorly considered and frequently not measured at all, in spite of the extensive use of this technology in animal studies (Vandenabeele et al. 2011).

Reproductive performance and behaviour (usually nest attendance) are the parameters most often measured by researchers investigating effects of devices on seabirds (Vandenabeele et al. 2011), but the physiological reason for the observed effects is often poorly considered. Nevertheless, the prolonged foraging trips often observed during chick rearing in device-effect studies on breeding seabirds could be a result of increased stress or energy requirements associated with device deployment, forcing birds to spend more time at sea to maintain their energy reserves (e.g. Weimerskirch et al. 2000, Phillips et al. 2003, Hamel et al. 2004, Barron et al. 2010).

Measuring physiological parameters such as energy expenditure or stress levels may thus help to explain the mechanisms underlying effects previously observed in behavioural or reproductive parameters, and provide insights into the reasons why these devices are detrimental to the birds. Blood levels of the avian stress hormone corticosterone (CORT) is probably the most commonly measured variable in the relatively small number of studies that have investigated effects of devices on the physiology of seabirds (e.g. Tremblay et al. 2003, Takahashi et al. 2008, Elliott et al. 2012, Ludynia et al. 2012, Quillfeldt et al. 2012).

Physiological stress (defined as a state in which homeostasis is threatened or perceived to be threatened; see Charmandari et al. 2005) in birds resembles that of mammals to a large extent (Harvey et al. 1984). Catecholamines (epinephrine and norepinephrine) are released from the adrenal medulla into the general circulation within seconds in response to

a stressor (Wingfield et al. 1997, Charmandari et al. 2005). Simultaneously, corticotropin-releasing hormone (CRH) is released from the hypothalamus. CRH stimulates the release of adrenocorticotrophic hormone (ACTH) into the blood stream, which in turn stimulates the release of glucocorticoids (GCs) from the adrenal cortex, usually within 2 to 3 min of the stressor (Wingfield et al. 1997, Charmandari et al. 2005). Increased blood levels of CORT (the main GC in birds) leads to a number of protective physiological and behavioural responses, such as increased heart and breathing rates, increased alertness and mobilization of stored energy. All these physiological and behavioural responses comprise the acute stress response, and help a bird respond immediately to a threatening situation (Wingfield et al. 1997). Generally, the stress response is time-limited, and the bird will again reach homeostasis within a few hours, when the stressor is no longer present. Chronic exposure to a stressor, on the other hand, could cause an increase in baseline CORT levels, lasting for days or weeks. This may cause a number of detrimental responses, including suppression of the immune and reproductive systems, or inhibition of growth and development (Charmandari et al. 2005).

White blood cells (leucocytes) are an essential part of the immune system and the defence against infections. The relative percentage of leucocytes, more precisely the ratio between heterophils and lymphocytes (H/L ratio), is increasingly being used as an additional measure of stress (Davis et al. 2008, Ludynia et al. 2012, Quillfeldt et al. 2012). GCs are probably involved in the redistribution of lymphocytes from blood into other tissues where they might be needed, as well as in the redistribution of heterophils from bone marrow into the blood during stress, causing the H/L ratio to increase (Bishop et al. 1968, Dhabhar et al. 1994, 1995, 1996). Despite the connection between the H/L ratio and plasma levels of CORT, these measures are not always correlated, and may respond differently to stressors (Müller et al. 2011, Vleck et al. 2000).

Most of the early studies of device effects on seabirds focused on penguins *Spheniscidae* spp. (e.g. Wilson et al. 1986, 1990, Wilson & Wilson 1989, Gales et al. 1990), but members of the *Alcidae* family ('alcids') and the order Procellariiformes also received some early attention (e.g. Wanless et al. 1985, 1988, 1989, Cairns et al. 1987, Phillips et al. 2003). Many of these studies found negative effects on nest attendance and reproductive success, although devices were much heavier than the ones that are usually used now. Similarly, most of the studies investigating

physiological effects of devices have been conducted on diving seabirds (Tremblay et al. 2003, Takahashi et al. 2008, Elliott et al. 2012). Although frequently used in tracking studies, effects of instrument attachment on gulls *Laridae* spp. have been poorly investigated. The studies that do exist typically measure breeding success and occasionally nest attendance of study birds relative to control birds, but most of these do not report any effects of their devices (e.g. Daunt et al. 2002, Kotzerka et al. 2010, Bogdanova et al. 2011, Chivers et al. 2012, Paredes et al. 2012). Most gulls have a relatively low wing load, and are thus likely to experience less constraint in mass-specific mechanical power output relative to payload mass compared to species with higher wing loads (Vandenabeele et al. 2012). In addition, gulls are surface feeders and do not face the problem of increased hydrodynamic drag caused by devices during underwater movements (Vandenabeele et al. 2012). This may lead researchers to consider device effects unlikely or insignificant. Nevertheless, gulls rely heavily on flying skill and manoeuvrability, and tracking devices could potentially influence the efficiency of feeding and provisioning, and increase flight costs.

The aim of the present study was to investigate possible short-term effects of GPS-logger deployment on behaviour, physiology and reproduction in the black-legged kittiwake *Rissa tridactyla* (hereafter 'kittiwake'). The effects of GPS-logger deployment on kittiwakes were investigated using 5 different parameters: plasma level of CORT, H/L ratio, body mass, nest attendance and reproductive success. The percentage of time that kittiwake chicks were left unattended in the nest was also calculated. Effects of loggers were expected to be seen as an increase in CORT levels and H/L ratio, and a decrease in body mass, nest attendance and reproductive success.

MATERIALS AND METHODS

Study site and species

The study was conducted on the island of Hornøya (70° 23' N, 31° 09' E) in the southern Barents Sea, northeastern Norway, where approximately 10 000 pairs of kittiwakes nested in 2012 (R. Barrett unpubl. data). Kittiwakes usually lay 2 eggs, but clutch sizes vary from 1 to 3 eggs (Coulson 2011). The chicks are not homeothermic until around 16 d post-hatching, and are always attended by one adult in the first days

of their life (Gabrielsen et al. 1992). Later in the chick rearing period they may be left alone at the nest, especially when nutritional conditions are poor (Moe et al. 2002, Lanctot et al. 2003). Kittiwakes are pelagic surface feeders, and the birds nesting on Hornøya feed primarily on Atlantic herring *Clupea harengus* and capelin *Mallotus villosus* (Furness & Barrett 1985, Barrett 2007).

Experimental setup

The study was conducted between 18 June and 9 July 2012. Kittiwakes ($n = 50$, half of which were controls), were randomly selected from nests containing chicks (from hatching until chicks reached 3 wk of age). Only one member of the pair was caught. Birds were captured (1st capture) on the nest using a noose-pole, and handling occurred out of sight of conspecifics when this was practically possible. The head of the birds was covered and blood was sampled for sexing, CORT measurement and blood smears. Blood samples were obtained from each bird during 1st and 2nd capture by brachial vein puncture using heparinized 1 ml syringes and capillary tubes. Sampling was completed within 3 min post-capture in order to obtain baseline CORT (hereafter 'CORT') levels, both at 1st and 2nd capture. In addition, body mass was measured with a spring balance (Pesola, read to the nearest g). GPS-loggers (mGPS-2, earth&OCEAN Technologies) were attached to 3 or 4 feathers on the rump of equipped birds using white Tesa tape and a single black cable tie. These loggers were of dimensions $49 \times 24 \times 13$ mm; including Tesa tape, loggers weighed 15.5 g, which comprised $3.75 \pm 0.10\%$ of kittiwake body mass (420 ± 11.3 g). Every second bird captured was designated as a control. The neck and breast of GPS-equipped (hereafter 'equipped') kittiwakes was painted blue using a permanent marker, while control birds were painted green or black for identification. The birds were not banded at 1st capture in order to reduce handling time. Handling time from capture to release at 1st capture was ≤ 15 min (equipped: 11.4 ± 0.37 min, control: 6.28 ± 0.29 min, $p < 0.001$).

Birds were recaptured (2nd capture) after approximately 2 d (equipped: 1.86 ± 0.28 d, control: 1.70 ± 0.32 d, $p = 0.720$). During 2nd capture, another blood sample was taken for CORT measurement and blood smears, and loggers and tape strips used for the attachment were removed from equipped birds. Biometric measurements were obtained, including body mass, tarsus and skull length (head and bill; using a

slide calliper, accuracy to 0.01 mm) and wing length (flattened, measured with a ruler to the nearest 1.0 mm). The number of chicks in the nest of the focal individuals was recorded both at 1st and 2nd capture. In addition, nest content of all nests was recorded at the beginning (15 June) and at the end (13 July) of the field season. For some of the birds, blood samples, nest attendance or biometric measurements were not successfully obtained, resulting in lower sample sizes for some parameters.

Nest attendance

Nest attendance of focal birds and their partners was monitored by time lapse photo registration of the study plots using scouting cameras (HC500/PC800 HyperFire, Reconyx). Photos were taken every 5 min. Nest attendance was recorded between 1st and 2nd capture (hereafter referred to as the 'experimental period'), i.e. the period the focal bird carried a GPS-logger, and during a period after 2nd capture (after loggers were removed from equipped birds). In order to compare trip duration between birds captured on different occasions, only trips starting within 24 h post-capture were included in the analyses. Only trips longer than 30 min were included in the analyses, as birds did not seem to feed their chicks following trips of shorter duration. Reliability of the information from the camera photos was confirmed by GPS data.

Plasma CORT radioimmunoassay

Blood samples were kept on ice in the field until they were centrifuged ($2600 \times g$ for 10 min), usually within 4 h post-sampling, to separate erythrocytes from plasma. Plasma was frozen and stored at -20°C until CORT assay. The samples were analysed following the procedure of Lormée et al. (2003). Total plasma CORT (bound and free) was measured in samples in one radioimmunoassay at the UMR 7372. Intra-assay variation was 7.07% ($n = 6$ duplicates). The lowest detectable CORT concentration was 0.14 ng ml^{-1} .

H/L ratio

A small amount of blood was used to make blood smears during 1st and 2nd capture. Blood was fixed with methanol for 1 min on microscope slides in the

field, and air dried before storing. Blood smears were stained with Giemsa (Sigma-Aldrich) within 4 wk after 1st capture, following the procedure of Houwen (2000). Stained blood smears were scanned with a light microscope (1000 \times magnification), and relative percentages of heterophils and lymphocytes were calculated following identification according to the criteria presented by Clark et al. (2009). A minimum of 100 leucocytes were identified on each slide (if possible), and the H/L ratio was calculated as the ratio of heterophils to lymphocytes.

Molecular sexing

A small drop of blood for sexing was obtained from each individual bird in the field and stored on 70% ethanol. Sexing was performed according to Griffiths et al. (1998). Four kittiwakes were not successfully sexed by the molecular method, and were therefore sexed based on morphological measurements (Coulson 2009, Barrett et al. 1985).

Statistical analyses

Statistical tests were performed using SPSS v.21.0 (SPSS 2012). Variables and residuals were checked for normality (Kolmogorov-Smirnov test, $p \leq 0.05$) and log-transformed when necessary. All tests were 2-tailed and results were considered significant at $p \leq 0.05$. Tendencies were assumed at $p \leq 0.10$. Pearson correlation analyses were performed to determine relationships between continuous variables. Means and parameter estimates are given with standard error (\pm SE).

A body condition index (BCI) was calculated for the individuals included in the study. Principal component analysis (PCA) was performed on 3 biometric variables: wing length, tarsus length and skull length. The PCA was first carried out separately for males and females, but this was not justified by the Kaiser-Meyer-Olkin measure of sampling adequacy (KMO) and Bartlett's Test of sphericity (KMO < 0.5, $p = 0.382$). However, when the 2 sexes were pooled, the KMO and Bartlett's Test were significant, suggesting sample adequacy (KMO > 0.5, $p < 0.001$). PCA variables were set as covariates in general linear models, with body mass at 1st capture as the dependent variable. Standardized residuals from these models were used as BCIs in further analyses.

Trip durations before and after 2nd capture were averaged for each individual, and *t*-tests were used

to test for differences in nest attendance between equipped and control birds. In addition, *t*-tests were used to check for differences between and within experimental groups for all other parameters measured (body mass, H/L ratio, CORT level and chick survival).

Analysis of covariance (ANCOVA) was used to investigate variation in change in CORT levels, body mass and H/L ratio, as well as variation in trip durations during the experimental period. Categorical variables included treatment and sex, as well as stage of the breeding season (early or late chick rearing). CORT level and H/L ratio at 1st capture, trip duration during the experimental period, duration of experimental period and BCI were included as covariates when appropriate. Interactions between categorical variables were included in all initial models. The assumption of linearity of regression slopes was checked graphically as well as statistically. Correlations between all explanatory variables were examined. Date and the categorical variable 'stage of the breeding season' were strongly correlated. Stage of the breeding season was considered the most informative seasonal parameter due to weather events during the breeding season (see 'Results'). Strong correlations were also found between BCI and the body mass parameters. BCI was considered the most illustrative parameter of adult body condition, and thus included in further analyses. BCI also strongly correlated with trip durations during the experimental period, and these covariates were therefore included in separate models. Model selection was performed by excluding non-significant variables from the analysis one by one. Final ANCOVAs include only variables with *p*-values less than 0.1.

RESULTS

A total of 24 kittiwakes were captured between 18 and 24 June (hereafter referred to as 'early chick rearing'). The corresponding chick age in this period was generally between 0 and 2 wk old. The remaining 26 birds were captured after 29 June (hereafter referred to as 'late chick rearing'), when most of the chicks were >2 wk old. All but 3 control birds were successfully recaptured.

Plasma CORT levels

A small, although statistically significant, positive relationship was found between baseline level of CORT and time since capture, even within 3 min post-capture ($R^2 = 0.052$, $p = 0.032$). This was controlled for by using the standardized residuals from a linear regression of plasma CORT on handling time as a measure of baseline CORT in all further analyses.

The results showed that there was a strong effect of treatment on CORT levels when controlling for the covariance with period. The interaction term treatment \times period (early/late chick rearing) explained 35.4 % ($p = 0.001$) of the variation in change in CORT levels (i.e. difference between CORT at initial capture and recapture) during the experimental period (Table 1). Equipped birds increased their baseline CORT levels significantly more than controls during the experimental period in early chick rearing ($p = 0.003$), but not in late chick rearing ($p = 0.542$, Table 2). Combining the 2 periods showed that overall, the equipped birds tended ($p = 0.074$) to increase their CORT levels more than controls during the

Table 1. Summary of final ANCOVA models explaining variation in change in corticosterone (CORT) levels, body mass, heterophils and lymphocytes (H/L) ratios, and variation in nest attendance (duration of provisioning trips) of kittiwakes *Rissa tridactyla* during the experimental period

Dependent	Explanatory	df	<i>F</i>	<i>p</i>	Estimate \pm SE	r^2
CORT change	Treatment \times Period	33	8.22	0.001		
	Period	33	4.26	0.048	0.81 \pm 0.39 ng ml ^{-1a}	0.124
Body mass change	Model 1	31	9.47	0.004	-20.4 \pm 6.6 g ^a	0.240
	Model 2	37	30.5	<0.001	-16.1 \pm 2.9 g	0.459
Nest attendance	Period	29	53.7	<0.001	3.67 \pm 1.19 h ^a	0.665
	Treatment	29	8.25	0.008	1.66 \pm 1.19 h ^b	0.234
H/L difference	No significant result	30				

^aLate compared to early chick rearing period
^bEquipped birds compared to controls

Table 2. Mean (\pm SE) corticosterone (CORT) levels, heterophils and lymphocytes (H/L) ratios, body mass and trip durations of kittiwakes *Rissa tridactyla* either equipped with a GPS logger (E) or having no device attached (control, C). For some of the birds, blood samples, nest attendance or biometric measurements were not successfully obtained, resulting in variable sample sizes. Significant p-values are shown in **bold**. ECR: early chick rearing; LCR: late chick rearing

Response variable	n (E, C)	Treatment		t/Z	p
		Equipped	Control		
CORT 1st capture	21, 20	6.58 \pm 0.52 ng ml ⁻¹	7.27 \pm 0.68 ng ml ⁻¹	-0.67	0.509
CORT 2nd capture	21, 20	8.85 \pm 1.20 ng ml ⁻¹	6.54 \pm 0.84 ng ml ⁻¹	1.57	0.125
CORT, change	21, 20	2.27 \pm 1.30 ng ml ⁻¹	-0.63 \pm 0.89 ng ml ⁻¹	1.84	0.074
CORT, change ECR	10, 11	6.04 \pm 1.78 ng ml ⁻¹	-1.23 \pm 0.93 ng ml ⁻¹	3.63	0.003
CORT, change LCR	11, 9	-1.16 \pm 1.19 ng ml ⁻¹	-0.10 \pm 1.64 ng ml ⁻¹	-0.62	0.542
H/L 1st capture	17, 15	0.63 \pm 0.03	0.58 \pm 0.05	0.74	0.466
H/L 2nd capture	17, 15	0.65 \pm 0.05	0.69 \pm 0.05	-0.61	0.550
H/L, change	17, 15	0.02 \pm 0.05	0.12 \pm 0.06	-1.01	0.323
H/L, change ECR	10, 10	0.00 \pm 0.06	0.13 \pm 0.06	-1.54	0.142
H/L, change LCR	7, 5	0.06 \pm 0.10	-0.12 \pm 0.22	0.73	0.486
Body mass 1st capture	24, 20	421 \pm 12 g	425 \pm 14 g	-0.24	0.813
Body mass 2nd capture	24, 20	415 \pm 11 g	417 \pm 11 g	-0.15	0.885
Body mass, change	24, 20	-5.4 \pm 5.2 g	-7.5 \pm 4.8 g	0.29	0.771
Body mass, change ECR	12, 12	-10.8 \pm 8.9 g	-19.0 \pm 5.1 g	0.80	0.435
Body mass, change LCR	12, 8	0.0 \pm 5.6 g	9.8 \pm 5.1 g	-1.29	0.212
Trip duration, exp. period	21, 20	15.4 \pm 3.56 h	6.88 \pm 0.89 h	2.08	0.045
Trip duration, exp. period ECR	10, 9	4.65 \pm 1.10 h	3.48 \pm 1.11 h	2.04	0.058
Trip duration, exp. period LCR	11, 11	19.2 \pm 1.27 h	9.03 \pm 1.11 h	2.93	0.008
Trip duration, after 2nd capture	18, 14	6.91 \pm 1.25 h	6.80 \pm 0.94 h	-0.46	0.652
Trip duration, change	18, 14	-8.17 \pm 4.15 h	0.17 \pm 0.71 h	-1.06	0.287

experimental period (Table 2, Fig. 1). CORT levels decreased throughout the breeding season, but the relationship between date and CORT levels at 1st capture was not significant ($R^2 = 0.045$, $p = 0.175$). No significant difference was found in the change in H/L ratio between equipped birds and controls (Table 2),

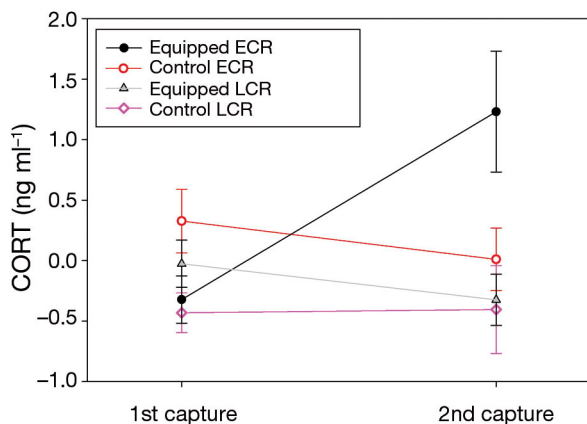


Fig. 1. Corrected plasma levels (\pm SE) of baseline corticosterone (CORT) in kittiwakes *Rissa tridactyla* fitted with GPS loggers ($n = 10$ in early chick rearing, ECR; $n = 11$ in late chick rearing, LCR) and control birds ($n = 11$ in ECR, $n = 9$ in LCR) at 1st and 2nd capture. CORT levels are presented separately for each group in ECR and LCR. CORT levels are expressed as the standardized residuals from the linear regression of plasma CORT levels (ng ml⁻¹) on handling time

and no significant correlation was found between H/L ratios and CORT levels ($R^2 = 0.032$, $p = 0.145$).

Body mass and body condition

No significant difference in body mass change was found between the groups (Table 2), and period of the breeding season explained most of the variation in change in body mass during the experimental period when included in the ANCOVA (Table 1). A significant negative correlation was found between BCI (and also body mass) and date of 1st capture (BCI: $R^2 = 0.341$, $p < 0.001$; body mass: $R^2 = 0.372$, $p < 0.001$). This was seen as a corresponding mass loss of 7.2 g d⁻¹. Between 18 and 23 June, birds lost on average 4.2 g of body mass d⁻¹. A marked drop in body mass was observed between 23 and 29 June, where birds lost on average 13.5 g d⁻¹. After this, the mean body mass stabilized, but a small decline of 1.7 g d⁻¹ was observed between 29 June and 6 July.

Behavioural changes

Equipped kittiwakes performed feeding trips of significantly longer duration than control birds during the experimental period (Table 2). When sepa-

rated by early or late chick rearing, this tendency was near-significant during early chick rearing ($p = 0.058$), while the trips were significantly longer during late chick rearing ($p = 0.008$; Table 2). No difference in trip duration was found between equipped birds and controls when loggers were removed from equipped birds (Table 2, Fig. 2). Equipped birds decreased their trip durations significantly after 2nd capture ($p = 0.049$). This was not observed for control birds ($p = 0.841$). GPS-data showed that equipped birds were provisioning very far from the colony. The birds with the longest trip durations also seemed to be moving farthest from the colony (431 km at most). Unfortunately, data was too deficient to evaluate whether birds were feeding or just sitting on the sea. Trip durations were significantly longer for all birds, independent of treatment, during late than during early chick rearing (Fig. 3; early: 4.05 ± 1.08 h, late: 13.18 ± 1.16 h, $p < 0.001$). Period and treatment explained much of the variation in nest attendance (Table 1). No chicks were left unattended at the nest during early chick rearing, but most of the chicks (90%) were left unattended during late chick rearing. No difference was found between the amount of time chicks of equipped birds and chicks of controls were left alone at the nest (equipped: $9.5 \pm 3.3\%$, control: $7.1 \pm 2.7\%$, $p = 0.549$). A significant negative correlation was found between BCI (and body mass at 1st capture) and the duration of provisioning trips for all focal birds during the experimental period ($R^2 = 0.425$, $p < 0.001$). Although the slope was affected by 5 birds performing trips of very long dura-

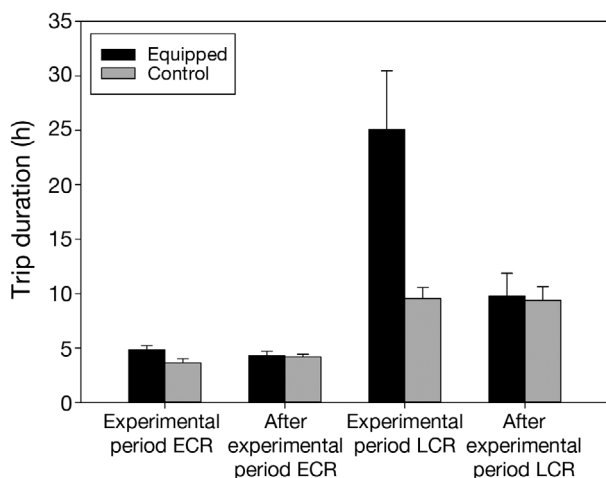


Fig. 2. Mean trip duration (+SE) of equipped (black bars, $n = 10$ in early chick rearing, ECR; $n = 11$ in late chick rearing, LCR) and control (grey bars, $n = 9$ in ECR, $n = 11$ in LCR) kittiwakes *Rissa tridactyla* during and after the experimental period in ECR and LCR

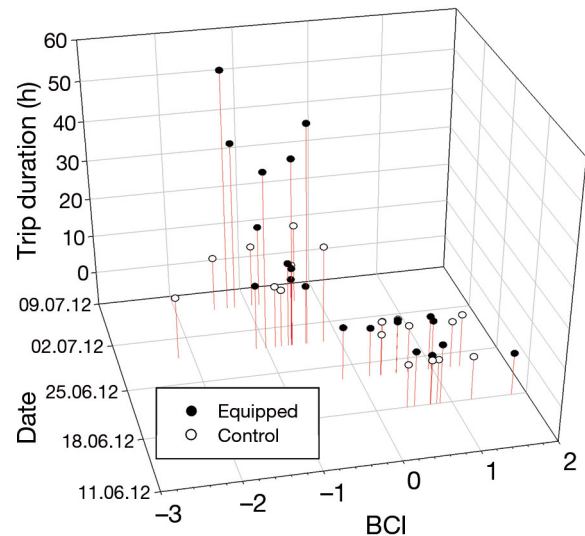


Fig. 3. Trip duration of equipped (filled circles; $n = 20$) and control (open circles; $n = 18$, where 2 of these are obscured by filled circles) kittiwakes *Rissa tridactyla* during the experimental period in relation to date and body condition index (BCI)

tion (Fig. 3), the relationship was still highly significant when these trips were excluded ($R^2 = 0.450$, $p < 0.001$). A significant difference was found between the regression slopes of equipped and control birds ($p = 0.016$), as equipped birds with a low value BCI made longer trips than controls (Fig. 3). No significant relationships were found between nest attendance and CORT levels. Although nest attendance was the only measured behavioural parameter, equipped birds seemed to behave similarly to control birds when at the nest, as no obvious signs of increased preening or restlessness was observed in the field or on camera photos among equipped birds.

Breeding success

No significant difference in chick loss was found between equipped and control birds (equipped: 0.94 ± 0.17 chicks lost breeding pair⁻¹, control: 0.79 ± 0.24 ; $p = 0.593$). Breeding success was also not affected by logger deployment (equipped: 0.50 ± 0.12 large chicks nest⁻¹, control: 0.57 ± 0.14 ; $p = 0.699$).

DISCUSSION

Our results clearly suggest that both behaviour and physiology of the kittiwakes were affected by GPS-logger deployment. CORT levels of GPS-equipped birds were higher than controls during the experi-

mental period in early chick rearing, but not in late chick rearing. During the first part of the chick rearing period, kittiwake chicks are not fully homeothermic and require brooding by one of the adults (Gabrielsen et al. 1992). This is also the part of the chick rearing period when the energy requirement for adult birds is suggested to be highest, during the time when they are not sitting on the nest (Moe et al. 2002). Brooding of the chicks leaves adults with a time constraint, as they have less time both for provisioning and feeding. Given the already high energy requirements of the provisioning adults during early chick rearing, they are probably more vulnerable to the additional demands of carrying a logger during this period. As CORT levels mirror activity (Astheimer et al. 1992, Angelier et al. 2007), this could be one of the reasons why effects of loggers on CORT levels were significant during early chick rearing but not during late chick rearing. A study conducted on Hornøya in 2011 identified a break point in breeding success on 19 June, after which breeding failure increased abruptly, and which was related to a marked increase in foraging effort (Ponchon et al. 2014). In 2012, a similar break point appeared to be reached between 26 and 29 June, during a period characterized by bad weather conditions with wind and heavy rainfall. Although breeding success was not monitored on a daily basis in the present study, mortality among chicks appeared to be high during this period. During the later stages of the breeding season, adults also brought back fewer spawning capelin than they did during the early chick rearing period (Thorvaldsen 2013). Apart from this, the 2012 breeding season was a moderate one on Hornøya with just below 30% successful pairs (Ponchon et al. 2014). This could also explain some of the differences in observed logger effects on CORT levels between early and late chick rearing, indicating a shift in resource allocation away from reproduction and towards self-maintenance.

No correlation between H/L ratio and CORT levels was found, despite the fact that both parameters are considered reliable measures of stress (Wingfield et al. 1997, Davis et al. 2008). The H/L ratio of kittiwakes is expected to increase within only 1 or 2 h of the onset of a stressor (Davis et al. 2008, D. B. Skomsø unpubl. data), i.e. well below the duration of deployment in the present study. However, Ludynia et al. (2012) found no effect of a 1 to 3 d deployment of GPS-loggers on the H/L ratio of southern rockhopper penguins *Eudyptes chrysocome*, although significantly elevated levels of CORT were found from before to after foraging in the GPS-equipped birds in

the same study. Conversely, Quillfeldt et al. (2012) reported elevated H/L ratios of thin-billed prions *Pachyptila belcheri* fitted with GLS-loggers for 1 yr. An increased hormonal response to stress among equipped birds was also found in that study, but baseline CORT levels were not influenced (Quillfeldt et al. 2012). These data are consistent with the suggestion that the H/L ratio may be a more appropriate parameter when evaluating long-term effects of stress in birds, whereas CORT levels are more reliable as a short-term measure (Gross & Siegel 1983, McFarlane & Curtis 1989, Vleck et al. 2000, Rich & Romero 2005, Müller et al. 2011). Nonetheless, several studies have found no difference in CORT following short-term GPS-attachment, and one found a long-term effect (Tremblay et al. 2003, Takahashi et al. 2008, Elliott et al. 2012).

Equipped kittiwakes performed trips of longer duration than controls during the experimental period. This difference was most evident during late chick rearing, and was no longer present after the loggers were removed. It may seem inconsistent that the effect of loggers on nest attendance was most pronounced during late chick rearing, while the effect on CORT levels was most evident during early chick rearing. However, the ability to increase duration of provisioning trips during early chick rearing may be limited by the need of chicks to receive body heat from their parents. Reduced food availability may also have made differences between the groups more apparent, e.g. as loggers may have altered the feeding efficiency of equipped birds. Still, the 2 groups also tended to differ in nest attendance during early chick rearing, suggesting compensatory behaviour from partners of equipped birds. If predator pressure is low, adults may leave their chicks without compromising reproductive success when the chicks become homeothermic at an age of approximately 16 d (Gabrielsen et al. 1992). Thus, they can prioritize their own body condition by performing longer feeding trips, and as a consequence, stress levels are expected to decrease (Angelier et al. 2007). Equipped birds may also need to increase their trip durations to be able to deal with the possibly higher flight costs and reduced flight efficiency caused by the attached device. The observed increase in CORT levels and the longer trip durations of equipped birds during the experimental period could potentially be a result of the longer handling time of this group. However, the fact that nest attendance of equipped birds and controls did not differ significantly when loggers were removed strongly suggests that at least the longer trips of equipped

birds were indeed a result of the devices rather than a handling effect. The duration of deployment of loggers in this study was fairly short and one can thus argue whether or not the observed effects were physiologically detrimental to the birds. We consider this unlikely, as the CORT levels recorded were considered within the naturally occurring range of baseline values for the species (Lanctot et al. 2003, Schultner et al. 2013).

BCI (and body mass at 1st capture) correlated negatively with the duration of the subsequent provisioning trips, as previously reported for other seabirds (e.g. Chaurand & Weimerskirch 1994, Catard et al. 2000, Weimerskirch et al. 2000). This may suggest that adult kittiwakes regulate provisioning according to their own body condition, and could indicate a shift away from reproduction and towards self-maintenance. Stored energy reserves allow birds to maximize provisioning of their chicks by performing short trips, at the expense of their own body condition (Weimerskirch et al. 2003). However, if energy reserves are depleted, e.g. by the scarcity of available prey, long-lived species such as kittiwakes will, according to life-history theory, prioritize maintenance of their own body condition over that of their offspring and partner (Williams 1966, Stearns 1992, Chaurand & Weimerskirch 1994, Weimerskirch et al. 2000). Equipped birds made longer trips than controls when in poor body condition, suggesting that kittiwakes are more likely to be negatively affected by devices when energy reserves are depleted, e.g. during challenging environmental conditions. As no difference was found between equipped birds and controls in the amount of time chicks spent alone at the nest, reduced parental care of equipped birds may have been partly compensated for by their partners.

No difference in body mass change during the experimental period was observed between equipped kittiwakes and controls. This could be a result of the relatively short duration of logger-deployment, but may also be a result of equipped birds prioritizing maintenance of their own body condition over that of their chicks. Focal birds in the present study experienced a significant decrease in body mass throughout the breeding season. The marked drop in body mass between 23 and 29 June may, according to the reproductive stress hypothesis, be attributed to the challenging weather conditions during this period, as well as a decrease in the availability of prey (Moe et al. 2002).

No difference in reproductive success was found between equipped birds and controls, but this may

also be a result of the short duration of device deployment. Partners of equipped birds may also have compensated for a decreased parental performance of their mates (Wanless et al. 1988, Paredes et al. 2005). Effects on partners of equipped birds are normally difficult to measure (Ballard et al. 2001), and no attempts were made to investigate this in the present study. Despite some studies reporting nest abandonments following device deployment, the number of studies reporting decreased breeding success for equipped seabirds is relatively low (e.g. Phillips et al. 2003). Nonetheless, if the birds had been equipped with loggers for extended periods of time, the detrimental effects of the loggers might have been much larger (especially during periods with low prey availability), possibly affecting the breeding success of the birds. Ponchon et al. (2014) showed how abruptly the number of successful breeding pairs dropped when the birds had to spend too much time and energy foraging. One could hypothesise that a break point similar to this could occur if birds were equipped for longer periods when already struggling to find sufficient amounts of food.

The results of the present study were somewhat unexpected, given that kittiwakes mainly feed on the sea surface and have a low wing load compared to other seabirds such as alcid. Despite this, they rely heavily on flying skill and manoeuvrability, and may thus be vulnerable to negative effects of device deployment. Potentially, loggers and transmitters could influence efficiency of feeding and provisioning, and increase flight costs (Adams et al. 2009). Device attachment to the back of birds rather than to the tail may reduce this problem (Vandenabeele et al. 2014), despite a possible increase in aerodynamic drag. Unfortunately, optimal placement of loggers on gulls has received little attention. Researchers often attach loggers to the tail of kittiwakes (e.g. Wanless 1992, Paredes et al. 2012), as in the present study, but several have also deployed loggers on the bird's back, usually reporting no negative effects (Daunt et al. 2002, Kotzerka et al. 2010, Chivers et al. 2012). Parameters measured in these logger-effect studies are typically activity patterns, nest attendance, chick mass and reproductive success (Daunt et al. 2002, Kotzerka et al. 2010, Chivers et al. 2012). Paredes et al. (2012) also measured CORT levels of kittiwakes equipped with GPS-loggers mounted on the tail for 2 d and reported no negative effects; however, they did not compare their results with CORT levels of control birds. In a study by Kotzerka et al. (2010), 2 birds shed their back-mounted loggers by pulling out the feathers to which they were attached, which may

indicate some discomfort. No signs of this were seen in the present study. Whether placement of loggers on the back would be a better solution is therefore difficult to judge. This issue clearly requires further investigation.

Our GPS-loggers constituted 3.8% of the mean kittiwake body mass in the present study. Several authors suggest that instruments deployed on seabirds (and other birds) should not exceed a given percentage (usually 3 to 5%) of body mass (Cochran 1980, Caccamise & Hedin 1985, Phillips et al. 2003). Despite this, a number of studies have reported negative effects of loggers of even smaller body mass percentages than this recommended level (e.g. Wanless et al. 1988, Ackerman et al. 2004, Whidden et al. 2007, Adams et al. 2009, Elliott et al. 2012). Weimerskirch et al. (2000) pointed out that the average food loads carried by yellow-nosed albatrosses *Thalasarche chlororhynchos* were much heavier (20% of adult body mass) than the weight loads used in their study, and that the marked response to the addition of loads may have been due to a reduced foraging ability or a displacement of weight. Similarly, the mean and maximum regurgitate mass of kittiwakes breeding on the Isle of May, Scotland, was found to be 41 and 68 g, respectively, which corresponded to 11 and 18% of adult body mass in that particular study (Galbraith 1983). Other factors, such as method of attachment, shape, positioning, colour and streamlining may therefore be equally important to consider as the mass of the equipment when deploying devices on birds (Vandenabeele et al. 2012).

No visible signs of discomfort caused by loggers, such as increased preening or restlessness, were observed in the field in the present study, despite the apparent effects of loggers on both nest attendance and CORT levels. Moreover, no clear-cut relationships were found between measured behavioural and physiological parameters. Evidently, physiological changes may not be reflected in observable behaviour, which underlines the importance of measuring more than one parameter when effects of devices are investigated. The overall effect on plasma CORT levels in equipped kittiwakes may not in itself be triggering behavioural changes, but merely indicate a slightly higher stress level in the birds.

In conclusion, the present study underlines the need to take the potentially disturbing effects of instrument deployment on behaviour and physiology into consideration when interpreting results from logger studies, even when working with species with low wing loads such as gulls. Effects may be more

noticeable when birds are faced with a challenging environment, and one should therefore be especially careful when evaluating logger data from studies in which environmental conditions are sub-optimal. Body condition, physiological condition, breeding stage and the duration of deployment also need to be taken into consideration, and risks and impacts should be evaluated against benefits and gains of the experiment. Recent studies on device effects on birds have shown that this is still a major issue, despite the wide usage and small size of technological devices currently available. Researchers may neglect their own influence on their study organisms, but effects of devices should be measured on all occasions. These measurements should be done not only by monitoring chick survival and body mass, but also by measuring behavioural and physiological parameters. This is important for ethical reasons, but also in order to avoid results being affected by the devices used in a study.

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