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Short-term effects of data loggers on
behaviour and physiology of two species
of seabirds: the black-legged kittiwake
Rissa tridactyla and the common
guillemot *Uria aalge*

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Biology

Submission date: December 2013

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Preface

The Master's thesis has been written at the Department of Biology, Norwegian University of Science and Technology (NTNU), Trondheim. Field work was conducted on the island of Hornøya, Finnmark in June-July 2011 and 2012. Staining of leucocytes and sexing procedures were performed at NTNU laboratories. Corticosterone analyses were carried out at the *Centre National de la Recherche Scientifique* (CNRS) in Chizé, France.

The thesis has been accomplished under supervision of Professor Claus Bech and PhD-student Signe Christensen-Dalsgaard, and was financed by external funding through the SEAPOP project “fine-scale habitat use of seabirds”.

Acknowledgements

I would like to thank my supervisors; Professor Claus Bech and Signe Christensen-Dalsgaard, for their help and guidance through field work and the writing of this thesis. Thanks to Thomas Kvalnes, Johan Henrik Hårdensson Berntsen, and especially Peter Sjolte Ranke for statistical support, and to Elin Noreen for her help with the sexing procedure. I am also very thankful to Dr. Norman Ratcliffe for letting me use some of his guillemot data from the 2011 field season on Hornøya. Thanks to Olivier Chastel and the CNRS for analysing my CORT samples. My fellow students also deserve thanks, and I am especially thankful to Dagfinn Breivik Skomsø, Rosemary Alice Juell and Vegard Sandøy Bråthen for their help, company and support through the work on this thesis.

Finally, I would like to thank Ragnhild for her encouragement, patience, love and support throughout my biology studies.

Trondheim, December 2013

Oddvar Heggøy

Sammendrag

Teknologiske nyvinninger som loggere og sendere har de siste tre tiårene blitt viktige hjelpemidler i forskning på ville dyr og fugler. Loggere er nyttige hjelpemidler i sjøfuglstudier, fordi disse fuglene ofte tilbakelegger store avstander over åpent hav hvor observasjon er vanskelig. Sjøfugler er i tillegg viktige indikatorer på tilstanden i marine økosystemer. Denne type utstyr kan dessverre forårsake negative effekter på studieorganismer. Noen studier har sett nærmere på disse effektene, men få har undersøkt de fysiologiske effektene av instrumentering.

I dette studiet ble effekter av GPS- og TDR-loggere på krykkje *Rissa tridactyla* og lomvi *Uria aalge* undersøkt, ved å se nærmere på adferd og fysiologiske stressparametre. Tilstedeværelse av voksne fugler ved reiret, blodnivåer av stresshormonet corticosterone (CORT), relative antall hvite blodceller, kroppsmasse og hekkesuksess ble målt hos instrumenterte fugler og fugler fra kontrollgrupper. Effekt av plassering av loggere ble undersøkt i et pilotstudie på lomvi og polarlomvi *Uria lomvia*.

Instrumenterte krykkjer hadde økte nivåer av CORT ved gjenfangst, og var borte fra reiret i lenger perioder sammenlignet med kontrollfugler. Krykkjer med dårlig kondisjon tilbragte mer tid borte fra reiret, og dette mønsteret ble forsterket hos instrumenterte fugler. Instrumenterte lomvi hadde en større vektreduksjon i løpet av forsøksperioden enn kontrollfugler. Økte nivåer av CORT og en redusert kroppsmasse ved gjenfangst både hos instrumentert lomvi og kontrollfugler kan imidlertid tyde på negative effekter av håndtering. Alle lomvi som fikk påmontert loggere på mantelen i pilotstudiet viste tegn til ubehag, mens kun små tegn til ubehag ble observert hos lomvi med loggere plassert på overgumpen. Forskjeller i artenes kroppsbygning og biologi forøvrig er foreslått som mulige forklaringer på artsforskjellene som ble funnet i dette studiet. Videre ser festemetode og plassering av loggere ut til å kunne være avgjørende for graden av observerte effekter.

Studiet understreker viktigheten av å ta effekter av instrumentering og håndtering på alvor når loggere av denne størrelsen benyttes på sjøfugler. Dette gjelder også for arter med lav vingebelastning, som krykkje. Effekter kan potensielt bli tydeligere hos fugler med dårlig kondisjon, eller i år med dårlig mattilgang. Effekter av instrumentering bør tas alvorlig både av etiske og bevaringsrelaterte årsaker, men også for å sikre kvaliteten på innsamlet data.

Abstract

New technology, such as loggers and transmitters, has the last three decades become an important part of the research on free-living animals. Loggers are very useful in seabird studies, as seabirds often travel considerable distances at sea where visual observation is difficult, and as they are frequently used as indicators of the state of marine ecosystems. The potential negative effects of devices on birds have received some attention, but few studies have investigated the physiological effects of instrument attachment.

In the present study, effects of GPS-and TDR-loggers on black-legged kittiwakes *Rissa tridactyla* and common guillemots *Uria aalge* were investigated by looking at behavioural and physiological parameters of stress, including nest attendance, plasma levels of the avian stress hormone corticosterone (CORT), relative leucocyte counts, body mass and reproductive success. Equipped groups were compared to control groups for all parameters measured. Effects of placement were investigated in a pilot study on common and Brünnich's guillemots *Uria lomvia*.

Equipped kittiwakes had elevated levels of CORT at recapture and extended the duration of feeding trips compared to controls. Kittiwakes with poor body condition attended nests less than controls, and this pattern was more evident among equipped birds. Equipped common guillemots decreased their body mass more than controls during the experimental period. Both groups of common guillemots showed elevated levels of CORT and a decline in body mass at recapture, suggesting effects of handling. In the pilot study, all guillemots with loggers mounted on the mantle showed signs of discomfort. Only mild discomfort was observed among guillemots with loggers on the rump. Differences in physique and general biology are suggested as possible explanations for the differences between the species in the present study. Placement and method of attachment of loggers seem also to be important aspects related to the level of observed effects.

The study underlines the need to take device effects, as well as handling effects, into consideration when deploying devices on seabirds. This is also important for species with low wing loads, such as the black-legged kittiwake. Potentially, effects may become more pronounced in birds with low body condition or in years where food is limited. Device effects should be considered for ethical and conservational reasons, but also in order to assure the quality of obtained data.

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1. Introduction

1.1 Challenges of field physiology

Since the earliest studies of physiology in free living organisms (i.e. field physiology), there have been considerable advances in the way wildlife are investigated (Costa and Sinervo, 2004). Field physiology and natural behaviour are now usually studied in organisms' natural environment rather than in a laboratory setting (Costa and Sinervo, 2004). Unavoidable though, all research on physiological mechanisms of wild animals potentially causes some kind of stress to the organisms in question. This is also true for all other research that requires handling or result in disturbance of the individuals. When physiological, behavioural or other life-history traits are investigated, such stress may bias sampled data, in the same way as the laboratory setting may bias the physiology of natural behaviour.

1.2 Technological devices in animal studies

During the last three decades the research on free living animals, including birds, mammals, fishes, reptiles, amphibians and even insects, has benefited from the development of a great diversity of technological devices (Burger and Shaffer, 2008; Indermaur et al., 2008; Janak et al., 2012; Knapp and Abarca, 2009; Wikelski et al., 2006). Radio transmitters, platform terminal transmitters (PTTs, i.e. satellite transmitters), global location sensing (GLS) loggers, global positioning system (GPS) loggers and depth loggers are among the most frequently used equipment (Burger and Shaffer, 2008; Casper, 2009). This has revolutionized the way wildlife are investigated, and opened a number of new doors to the science of ecology, conservation biology, physiology and ethology, as well as oceanography and climatology (see Burger and Shaffer, 2008).

Birds, and in particular seabirds, are well suited for tracking and logging studies. Seabirds typically travel far from their breeding colonies where visual observation is difficult (Vandenabeele et al., 2011). At the same time most seabirds are colony breeders, and can easily be captured in sufficient numbers at the nest (Burger and Shaffer, 2008). Because of their mobility and dependence on the oceans, seabirds are often used as indicators on the state of their environment (Furness and Camphuysen, 1997; Piatt et al., 2007). New technology improves the quality and facilitates the progress of obtaining knowledge about these often extensive and complex ecosystems (Burger and Shaffer, 2008).

Nevertheless, data collected by the use of loggers and transmitters are potentially biased by the possible 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).

1.3 Life-history theory

In order to increase overall fitness, life-history theory predicts that long-lived species such as seabirds should minimize reproductive effort during current breeding and prioritize their own survival over that of their offspring (and partner) whenever resources are limited (Stearns, 1992; Williams, 1966). Although foraging decisions may also be influenced by the needs of the chicks (Kilner and Johnstone, 1997; Kitaysky et al., 2001), the body condition of adult birds is likely to play a major role in the allocation of resources during breeding in long-lived species (Drent and Daan, 1980; McNamara and Houston, 1996). Thus, the increased energy requirements associated with device deployment are likely to induce the prolonged foraging trips often observed in device-effect studies (e.g. Hamel et al., 2004; Phillips et al., 2003), as birds are forced to spend more time maintaining their own body condition (Weimerskirch et al., 2000).

1.4 Measurements of device effects

Reproductive performance and behaviour are the parameters most often measured by researchers investigating effects of devices on seabirds (Vandenabeele et al., 2011). However, breeding parameters and behaviour are usually consequences of the physiology of birds, including nutritional status, reproductive status, the state of the immune system and other kinds of stress, as well as interactions between these systems (Charmandari et al., 2005; Costa and Sinervo, 2004; Ricklefs and Wikelski, 2002). Measuring physiological parameters could thus provide valuable information of device effects. Of the small number of device-effect studies measuring physiological parameters, blood levels of the avian stress hormone corticosterone (CORT) is probably the most commonly measured variable (e.g. Elliott et al., 2012; Ludynia et al., 2012; Pereira et al., 2009; Quillfeldt et al., 2012; Takahashi et al., 2008; Tremblay et al., 2003).

1.5 The avian stress response

Physiological stress in birds resembles that of mammals to a large extent (Harvey et al., 1984). Catecholamines (epinephrine and norepinephrine) are released within seconds from the adrenal medulla into the general circulation in response to a stressor (Hill et al., 2008; Wingfield et al.,

1997). At the same time, corticotropin-releasing hormone (CRH) is released from the hypothalamus, which in turn stimulates the release of adrenocorticotrophic hormone (ACTH) into the blood from the pituitary (Hill et al., 2008; Wingfield et al., 1997). Glucocorticoids (GCs), in birds mainly CORT, are released from the adrenal cortex in response to circulating ACTH, usually within two or three minutes of the stressor. CORT ultimately leads to a number of protective physiological and behavioural responses, and exerts its actions both through genomic and more rapid non-genomic membrane actions (Borski, 2000; Hill et al., 2008; Wingfield et al., 1997).

Despite CORT being considered a reliable parameter of stress in birds, many confounding factors may influence blood levels of this hormone, including circadian rhythms (Quillfeldt et al., 2007), nutritional status (Kitaysky et al., 2007; 2010; Williams et al., 2008), breeding stage (Lanctot et al., 2003; Williams et al., 2008), age (Heidinger et al., 2010), gender (Lormée et al., 2003), pollution (Nordstad et al., 2012), habitat condition (Shultz and Kitaysky, 2008), weather condition (Smith et al., 1994; Wingfield and Ramenofsky, 2011) and parasitism (Quillfeldt et al., 2004). In addition, levels of circulating CORT may decrease in response to chronic stress (e.g. Rich and Romero, 2005). Measurements could therefore be somewhat hard to interpret, and comparisons across different populations may prove difficult (Lanctot et al., 2003).

1.6 A complementary measure of stress – leucocyte profiles

The relative percentages of white blood cells (leucocytes), more precisely the ratio between heterophils and lymphocytes (H/L-ratio) in blood, increases with increasing stress levels, and may consequently be used to support measurements of CORT (Davis et al., 2008; Ludynia et al., 2012; Quillfeldt et al., 2012). GCs are probably involved in the redistribution of lymphocytes from blood and into other tissues where they might be needed, as well as in the redistribution of heterophils from bone marrow and into the blood during stress (Bishop et al., 1968; Dhabhar et al., 1994; 1995; 1996).

1.7 Time and methods of deployment

When interpreting results from studies investigating effects of devices on birds, it is important to consider the time aspect, i.e. whether it is a short-term (days-weeks) or a long-term (months-years) study. 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). For instance, plasma levels of CORT may be a more appropriate parameter to measure in

short-term studies, while the H/L-ratio may be more suitable in the long-term (Gross and Siegel, 1983; McFarlane and Curtis, 1989). Moreover, it is important to consider the method of attachment of devices. A number of attachment methods has been tested on seabirds, and the observed effects vary considerably. The most detrimental effects are, however, reported from studies where devices are deployed internally (e.g. Hatch et al., 2000; Meyers et al., 1998). Thus, external attachment is likely to be the better choice.

1.8 Device effect studies

Most of the early studies of instrumental effects on seabirds focused on penguins *Spheniscidae spp.* (e.g. Gales et al., 1990; Wilson and Wilson, 1989; Wilson et al., 1986; 1990), but also members of the *Alcidae*-family (“alcids”), such as guillemots, received some early attention (e.g. Cairns et al., 1987; Wanless et al., 1985; 1988; 1989). Penguins and alcids are suitable for logger deployment because of their large size and robust appearance. As they do not use their legs for underwater propulsion, attachment of devices to leg rings should be more durable than for foot-propelled divers (Elliott et al., 2007). Nevertheless, the small wings and large body size of most alcids, which is likely to be a trade-off between diving and flying performance (Thaxter et al., 2010), results in a particularly high wing load (body mass/wing area), probably making them especially sensitive to instrumentation (Vandenabeele et al., 2012). In addition, alcids forage underwater, and may experience increased drag from externally attached devices (Ackerman et al., 2004). Alcids may also travel long distances to feed, further adding to their susceptibility (Ackerman et al., 2004).

Device effects on alcids have been investigated in several studies. These have mainly focused on the common guillemot *Uria aalge* (e.g. Elliott et al., 2012; Hamel et al., 2004; Meyers et al., 1998; Tremblay et al., 2003; Wanless et al., 1988) and the closely related Brünnich’s guillemot *Uria lomvia* (e.g. Croll et al., 1992; Elliott et al., 2007; 2008; 2012; Falk et al., 2000; Meyers et al., 1998; Paredes et al., 2005; Takahashi et al., 2008; Watanuki et al., 2001). Changes in foraging behaviour, such as prolonged foraging trips and prey switching, are among the most common effects observed (Elliott et al., 2007; Hamel et al., 2004; Paredes et al., 2005; Wanless et al., 1988; 1989). Mass loss, reduced breeding success and elevated CORT levels have also been reported (Elliott et al., 2007; 2012; Meyers et al., 1998; Paredes et al., 2005; Takahashi et al., 2008; Wanless et al., 1985).

Most gulls *Laridae spp.* 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.

Among gulls, effects of instrument attachment have been poorly investigated. Several authors do, however, address possible device effects when instrumenting gulls, but this typically constitute a minor part of the study (e.g. Bogdanova et al., 2011; Chivers et al., 2012; Daunt et al., 2002; Gabrielsen and Mehlum, 1989; Kotzerka et al., 2010; Paredes et al., 2012). Typically, breeding success and sometimes also nest attendance of study birds relative to control birds are measured. Most studies do not find any effects of their devices (Bogdanova et al., 2011; Chivers et al., 2012; Daunt et al., 2002; Kotzerka et al., 2010; Paredes et al., 2012).

1.9 Aims of study

Of the small amount of data on physiological effects of devices on birds, some studies have been conducted on guillemots (Elliott et al., 2012; Takahashi et al., 2008; Tremblay et al., 2003), but none, or very few, have focused on gulls. GPS-loggers are increasingly being used in seabird studies, and the most frequently used (and least invasive) methods of attachment include external attachment to body feathers using tape or glue (e.g. Guilford et al., 2008; Phillips et al., 2003). However, this usually only allows for short-term studies, as the loggers often fall off after relatively short time. The aim of the present study was to investigate possible short-term effects of GPS-logger deployment on behaviour, physiology and reproduction of black-legged kittiwakes *Rissa tridactyla* (hereafter kittiwake) and common guillemots. Equipped groups were compared to control groups, and differences between species and sex, as well as between different methods of attachment, were investigated.

Effects were predicted to be more pronounced in common guillemots, because of their high wing load and the potentially increased drag and possible buoyancy of devices on diving individuals. Effects were predicted to be more evident for birds with poor body condition. Device effects were also predicted to become more visible during challenging environmental conditions, such as food shortages. Kittiwakes were predicted to be more vulnerable to device effects during early chick rearing, when continuous brooding of chicks was necessary.

2. Material and methods

2.1 Study site

The study was conducted on the island of Hornøya (70°23`N 31°09`E) in the Barents Sea, North-Eastern Norway. Hornøya is designated within the Hornøya and Reinøya Nature Reserve, and a number of colony breeding seabirds are found at the site, including kittiwakes, common guillemots and Brünnich's guillemots, among others. The population of common guillemots is increasing on Hornøya, counting approximately 12 000 pairs in 2012, whereas Brünnich's are less numerous with ca. 300 pairs (Barrett, 2012; Barrett et al., 2013). Between 7000 and 10 000 pairs of kittiwakes breed on Hornøya, but the population trend is negative for this species (Barrett, 2012; Barrett et al., 2013).

2.2 Study species

The kittiwake nests along North Pacific and Atlantic coasts in large and dense colonies (Coulson, 2011; Snow and Perrins, 1998). Adult birds return to the colony in late winter and early spring. The incubation period on Hornøya starts in May or early June, followed by hatching four weeks later. Fledging usually occurs in July (Rob Barrett pers. comm.). On average two eggs are laid, but clutch sizes vary from one to three eggs (del Hoyo et al., 1996). Small chicks are not homeothermic until around sixteen days post-hatching, and are always attended by one adult the first days of their life (Gabrielsen et al., 1992). Later in the chick rearing period they may, however, be left alone at the nest, especially when nutritional conditions are poor (Lanctot et al., 2003; Moe et al., 2002). Kittiwakes are pelagic surface feeders and feed on marine invertebrates, fish and fish entrails from fishing vessels (Coulson, 2011). The species is listed as "Endangered" on the Norwegian 2010 Red List due to a 50-80% decrease in the Norwegian population since 1980 (Kålås et al., 2010). The Norwegian mainland population was estimated to 336 000 pairs in 2006 (Barrett et al., 2006).

The common guillemot has a circumpolar distribution in temperate and colder parts of the Northern Hemisphere (del Hoyo et al., 1996). On Hornøya, common guillemots usually lay their one egg in May. The chick rearing period typically lasts from June until the first couple of weeks of July (Rob Barrett pers. comm.). The single chick is accompanied by a parent while the other is provisioning (Gaston and Jones, 1998). Like razorbills *Alca torda* and Brünnich's guillemots, common guillemots make use of the intermediate chick development strategy, i.e. chicks leave the nest before they are able to fly, and are accompanied by the male bird for several weeks at sea until

fledging (Gaston and Jones, 1998). Common guillemots are pelagic divers, and usually feed on fish species such as capelin *Mallotus villosus*, sandeel *Ammodytidae spp.*, clupeids *Clupeidae spp.* and gadids *Gadidae spp.* on depths from 10-50 meters (Bugge et al., 2011; Gaston and Jones, 1998; Tremblay et al., 2003). The North Atlantic breeding population counts about three million pairs (Harris and Wanless, 2004); only 15 000 of these breed on the Norwegian mainland (Barrett et al., 2006). Dramatic population declines have been documented along the Norwegian coast during the last decades (80% decline in Norwegian population 1962-2009 and a 99% decline in the Norwegian Sea since 1980), and is the reason for the species' status as "Critically Endangered" on the Norwegian 2010 Red List (Kålås et al., 2010).

2.3 Pilot study – testing methods of attachment

A pilot study was conducted during the 2011 field season to test methods of attachment of GPS-loggers on guillemots. The pilot study was carried out in collaboration with Dr. Norman Ratcliffe at the British Antarctic Survey.

Two types of GPS-loggers (I-gotU GT-120, MobileAction Technology, New Taipei, Taiwan and Ecotone Patron (live and dummy), Ecotone Telemetry, Sopot, Poland) were deployed on chick rearing Brünnich's and common guillemots in the course of the pilot study. I-gotU loggers were of dimensions 17 g, 42 x 24 x 8 mm, whereas Ecotone (live/dummy) loggers were of dimensions 12 g, 40 x 21 x 9 mm. GPS-loggers were deployed in an adaptive fashion, i.e. aiming at maximizing recovery rates by minimizing logger effects. During the first part of the study period (20 June-9 July), loggers were predominantly attached to the mantle of both species. Later in the study period (9-14 July) loggers were attached to the rump of the birds, as this seemed to be more tolerated than mantle-attachment. Fourteen Brünnich's guillemots were equipped with GPS-loggers, seven of which had the logger mounted on the mantle. Forty-nine common guillemots were equipped with GPS-loggers and twenty-nine of these had the logger deployed on the mantle. Sixteen GPS-equipped guillemots (nine Brünnich's and seven common guillemots) were also fitted with a cylindrical time-depth recorder (TDR, G5 DST, Cefas Technology Limited, Wales, England; 2.3 g, length: 31 mm, diameter: 8 mm), attached to feathers of the lower breast. Likelihood of recapture was compared between GPS-equipped birds and 32 controls. Twenty-three of the controls (nineteen Brünnich's and four common guillemots) were also equipped with the small TDRs. Probability of recapture and recover of equipment was compared between guillemots with loggers

on the mantle and those with loggers on the rump. Recaptures of all birds were attempted after 2-3 days. All birds were fitted with a small piece of white *Tesa* tape painted with a symbol on their heads (head-flag) for identification. Of the 63 equipped and 32 control guillemots in the pilot study, 51 equipped guillemots and all control birds were recaptured.

2.4 Main study – experimental setup

The main study was conducted during the 2012 field season. Effects of GPS-loggers on kittiwakes and common guillemots were primarily investigated using four different parameters: plasma level of CORT, body mass, nest attendance and reproductive success. Relative leucocyte level in blood was used as a complementary parameter of stress in kittiwakes. Percentage time kittiwake chicks were left unattended in the nest was also calculated.

Kittiwakes (n=50), half of which were controls, were randomly selected from nests containing chicks (from hatching until chicks reached three weeks of age). Common guillemots (n=85), including controls (n=40), were selected at random from the early chick rearing period until chicks left the cliffs (at approximately 21 days of age). 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.

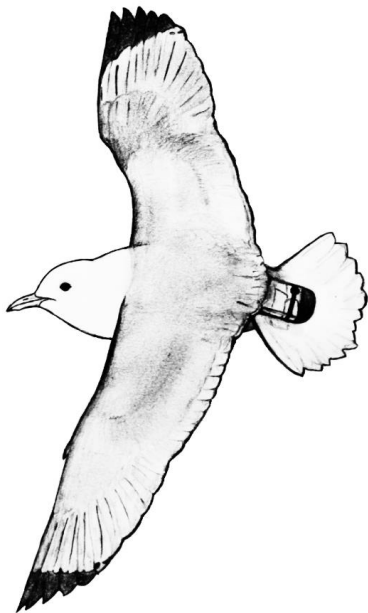


Figure 1. Kittiwake with tail-mounted GPS-logger.

The head of the birds was covered and blood was sampled for sexing, CORT measurement and blood smears. In addition, body mass was measured with a spring balance (Pesola, accuracy to 5.0 g (kittiwake) or 10 g (common guillemot)). Experimental birds were fitted with a GPS-logger either on the tail (kittiwake; figure 1) or on the lower back (common guillemot; figure 2). Most of the equipped common guillemots (n=29) were fitted with a TDR-logger in addition to the GPS. For each of the two species, every second bird captured was usually designated as a control. The neck and breast of equipped kittiwakes was painted blue using Indian ink, while control birds were painted green or black for identification. No banding was applied at 1st capture in order to reduce handling time. Common guillemots were fitted with head-flags for

identification, in addition to green (equipped) and red (control) tape around one leg and white tape with a number on it on the other leg. Handling time from capture to release at 1st capture was ≤ 15 min (equipped: 11.4 ± 0.37 min, control: 6.28 ± 0.29 min) for kittiwakes and ≤ 17 min (equipped: 12.8 ± 0.30 min, control: 5.77 ± 0.27 min) for common guillemots.

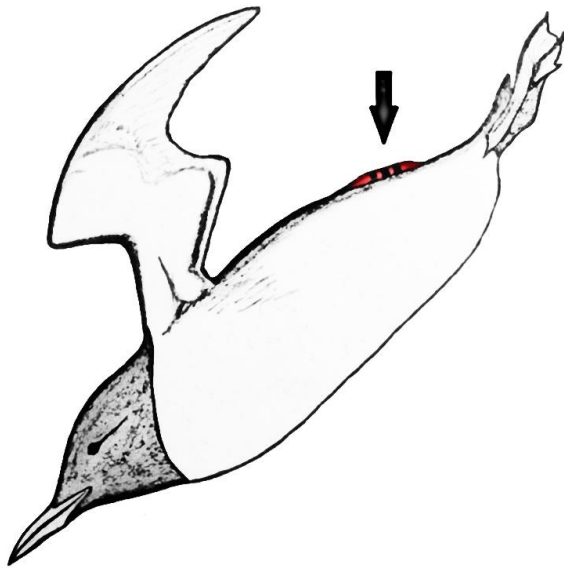


Figure 2. Diving common guillemot with GPS-logger attached to the rump (arrow).

Equipped ($n = 25$) and control ($n = 22$) kittiwakes were recaptured (2nd capture) after approximately two days (1.79 ± 0.21 days (early chick rearing: 1.03 ± 0.02 days, late chick rearing: 2.54 ± 1.73 days)). Most equipped ($n = 42$) and control ($n = 29$) common guillemots were also recaptured two days after 1st capture (2.06 ± 0.10 days). At 2nd capture another blood sample was taken for CORT measurement and blood smears, loggers were removed from equipped birds and tape strips used for the attachment were completely removed. 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). In common guillemots, culmen and gonys length was also measured with the slide calliper. Chick age was recorded at 1st capture, and the number of chicks was recorded both at 1st and 2nd capture.

2.5 Data loggers and method of attachment

GPS-loggers (mGPS-2, earth&Ocean Technologies, Kiel, Germany) deployed on kittiwakes were attached to three to four tail feathers using white *Tesa* tape and a single black strip. These loggers were of dimensions 49 x 24 x 13 mm. GPS-loggers, including *Tesa* tape, weighed 15.5 g, which constituted 3.75% of kittiwake body mass (420 ± 11.3 g).

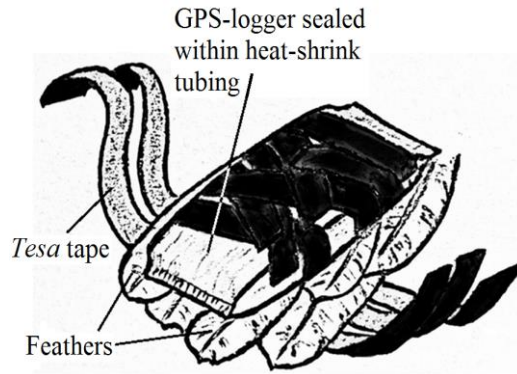


Figure 3. Visual description of how GPS-loggers were attached to the rump of common guillemots using pieces of tape. Method of attachment on kittiwakes was similar.

On common guillemots, GPS-loggers (I-gotU GT-120) were attached to feathers on the lower back/rump, just above the uropygial gland, using three to four pieces (cut in half) of black *Tesa* tape (figure 3). These loggers were dismantled from their external protective case to reduce mass, and the battery part of the logger was reinforced with epoxy spatula. To provide waterproofing, loggers were sealed within heat-shrink tubing. Dimensions of the enclosed GPS-loggers were 55 x 26 x 10 mm. Including heat-shrink tubing and *Tesa* tape the mass of a logger was 19.7 g, which constituted 1.84% of common guillemot body mass (1049 ± 11.8 g). In addition to the GPS, TDR-loggers (G5 DST) were attached to colour rings around one leg of most of the equipped common guillemots ($n = 29$) using cable ties. These added 2.7 g to the total instrument mass, and constituted together with GPS-loggers 2.17% of adult body mass. The same method of sealing and attachment of loggers was used on guillemots in the pilot study, except that some epoxy cement and cable ties was used to ensure the GPS-attachment. In addition, TDRs were attached to feathers of the lower breast rather than to colour rings.

2.6 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, Holmen, WI, US). Photos of common guillemot plots were taken every minute, whereas photos of kittiwake plots were taken every five minute. Nest attendance was recorded during the experimental period and during a post-period after 2nd capture (after loggers were removed from equipped birds). The colour on several of the guillemot head-flags faded out after short time, and the breast of the birds were therefore painted blue with Indian ink at 2nd capture for recognition. In order to compare trip duration between birds captured at different occasions, only trips starting within 24 hours post-capture were included in analyses. If any uncertainties prevailed regarding trip duration (e.g. because of poor vision caused by bad weather conditions or other birds walking in front of the camera), minimum trip duration was used. Only trips longer than half an hour were included in analyses, as birds did not seem to feed their chicks following trips of shorter duration. Reliability of

camera photos was confirmed by GPS-data and by direct observations during the photo registration. Even though some time lapse photos made it possible to determine arrivals with or without prey, and even to identify prey species, the time interval between photos was too long to quantify these parameters.

2.7 Reproductive success

Nest content of all kittiwake nests in the study plot was recorded at the beginning of the field season and at (one or) two later occasions during the chick rearing period. Due to colony structure and “jumping activity” (i.e. chicks leaving the breeding shelves) this was not possible for common guillemots. However, nest content was recorded for both species at 1st and 2nd capture.

2.8 Plasma CORT radioimmunoassay

Blood samples were obtained from each bird in the field by brachial vein puncture, using heparinized syringes and capillary tubes, at 1st and 2nd capture. Sampling was completed within three minutes post-capture, and samples were kept on ice until they were centrifuged (6000 rpm for 10 min), usually within four hours post-sampling, to separate erythrocytes from plasma. Plasma was frozen and stored at -20°C until CORT assay. The samples were analysed at the *Centre National de la Recherche Scientifique* (CNRS) in Chizé, France, following the procedure of Lormée et al. (2003). Total plasma CORT (bound and free) was measured in samples by radioimmunoassay. Steroid was extracted by adding 3 mL of diethyl-ether to 100 µL of each sample, followed by vortexing and centrifuging. The diethyl-ether phase containing the steroid was decanted and poured off after snap freezing the tube in an alcohol bath at 38°C. Following evaporation of the resultant, the dried extracts were redissolved in 300 µL of phosphate buffer and CORT was assayed in duplicate. 100 µL of extract was incubated overnight with 5000 cpm of the appropriate ³H-steroid (Perkin Elmer, Waltham, MA, US) and polyclonal rabbit corticosterone-21-thyroglobulin antiserum supplied by Sigma-Aldrich (St. Louis, MO, US). The bound fraction was separated from the free fraction by addition of dextran-coated charcoal and activity was counted on a tri-carb 2810 TR scintillation counter (Perkin Elmer, Waltham, MA, US). Tests were performed to validate the CORT assay on plasma. Inter- and intra-assay variations were 9.99% and 7.07%, respectively. The lowest detectable CORT concentration was 0.14 ng/mL. Two samples were serially diluted in the assay buffer and their displacement curves were parallel to the standard curve. The mean recovery of standard spikes in a sample was 92%.

2.9 H/L-ratio

A small amount of blood was used to make blood smears at 1st and 2nd capture to calculate the H/L-ratio. Blood was fixated with methanol for one minute on microscope slides in the field, and air dried before storing. Blood smears were stained with Giemsa (Sigma-Aldrich, St. Louis, MO, US) in the laboratory at NTNU, Trondheim, within four weeks after 1st capture, following the procedure of Houwen (2000). Stained blood smears were scanned with a light microscope (1000x magnification), and relative percentages of heterophils and lymphocytes were calculated following identification according to the criteria presented by Clark et al. (2009). Minimum 100 leucocytes were identified per slide (if possible), and the H/L-ratio was calculated as the ratio of heterophils to lymphocytes.

2.10 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 at the NTNU according to Griffiths et al. (1998). DNA was extracted from the blood samples using a 5% Chelex 100 resin (Biorad, Hercules, CA, US) procedure. 0.05 µl Taq DNA polymerase, 0.4 µl dNTP Mix, 0.6 µl MgCl₂, 1.0 µl 10xPCR buffer and 2.0 µl Q-solution from Taq PCR Core Kit (Qiagen, West Sussex, UK), 1.95 µl H₂O and 1.0 µl of each of two primers (10 µM, P2 and P8, Invitrogen, Carlsbad, CA, US) was added to the 2.0 µl DNA-template. Exponential amplification of the sex genes was performed by the polymerase chain reaction (PCR). A DNA denaturizing temperature of 94°C for 30 sec started the PCR sequence for the kittiwake DNA, followed by 35 cycles of the subsequent temperatures: 94°C for 30 sec, 46°C for 45 sec and 70°C for 45 sec. The PCR was terminated after 10 min of 70°C, and the products were stored at 4°C until gel electrophoresis. A slightly different PCR was performed for the common guillemot DNA, as the 45 sec of 46°C was replaced by 45 sec of 51°C. PCR products were separated on a 2% agarose gel stained with a non-carcinogenic gel stain (SYBR®Safe DNA gel stain, Invitrogen, Carlsbad, CA, US).

In birds, the female is the heterogametic (ZW) sex, carrying both the CHD-1-Z (chromo-helicase-DNA-binding) and the smaller CHD-1-W gene on the sex chromosome. The homogametic (ZZ) male only carries the small CHD-1-Z gene. Primers added to extracted DNA bind to the start and end of these genes, and help in the PCR amplification process. The gel electrophoresis separates macromolecules based on their size and charge, with smaller molecules

moving more readily in the gel. Thus, visualization of two bands in the gel indicates female DNA, whereas males only display single bands. The DNA bands were visualized under UV light. Four kittiwakes were not successfully sexed by the molecular method, and these were therefore sexed based on morphological measurements following other criteria (Coulson, 2009; Barrett et al., 1985).

2.11 Statistical analysis

Statistical tests were performed using SPSS 21.0 (SPSS Inc. 2013). Graphs were made in SigmaPlot 12.5 (Systat System, Inc. 2013). Variables and residuals were checked for normality (Kolmogorov-Smirnov test, $P \leq 0.05$) and log-transformed when necessary. If transformation failed to produce normally distributed data, nonparametric tests were used. All tests were two-tailed and the significance level was set at $P \leq 0.05$. Tendencies were assumed at $P \leq 0.10$. Pearson correlation analyses were performed to check for 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 the three variables wing length, tarsus length and skull length. The PCA was at first carried out separately for males and females, but for kittiwakes this was not justified by the KMO and Bartlett's Test of sphericity ($KMO < 0.5$, $P = 0.382$). However, when pooling the two sexes, KMO and Bartlett's Test turned out at a significant level, suggesting sample adequacy ($KMO > 0.5$, $P < 0.001$). This was not a problem for common guillemots, and separate PCAs were taken for each sex. 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. Two-sample *t*-tests were used to test for differences between equipped and control birds. Two-sample *t*-tests were also carried out to test for differences between equipped and control groups in all of the other parameters measured (body mass, H/L-ratio, CORT level and chick survival). Paired *t*-tests were performed to check for differences in the measured parameters between 1st and 2nd capture (hereafter referred to as "experimental period") within experimental groups. Separate and combined effects of GPS- and TDR-loggers on common guillemots were not statistically

investigated because of the small sample size of the group that only carried a GPS. Chi-squared (χ^2) tests were used to test whether the character frequencies of equipped birds and controls were different from each other in the pilot study.

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 for kittiwakes (early/late chick rearing). BCI, chick age, time between 1st and 2nd capture and CORT level at 1st capture were included as covariates in common guillemot models when appropriate. CORT level and H/L-ratio at 1st capture, trip duration during the experimental period, time between 1st and 2nd capture and BCI were included as covariates in kittiwake models when appropriate. Interactions between categorical variables were included in all initial models. The linearity of regression slopes assumption was checked graphically as well as statistically. Correlations between all explanatory variables were examined. Common guillemot chick age and date were strongly correlated ($R > 0.5$), but chick age was considered a more informative parameter and date was therefore excluded from further analyses. Similarly, kittiwake chick age, date and the categorical variable “stage of the breeding season” were strongly correlated. However, chick age was not always recorded when capturing a bird, and stage of the breeding season was considered the most informative seasonal parameter due to certain events during the breeding season. Strong correlations were also found between BCI and the body mass parameters for both species. BCI was considered the most illustrative parameter of adult body condition, and thus included in further analyses. Kittiwake BCI correlated strongly with trip durations during the experimental period, and these covariates were therefore included in separate models. Further details on model selection are presented in the appendix. Model selection was performed by excluding non-significant variables from analysis one by one. Final ANCOVAs include only variables with P -values less than 0.1.

2.12 Permissions

The experiment was approved by the Norwegian Animal Research Authority (NARA; ref. 2011-2012/3238). The Norwegian Directorate for Nature Management approved the catching of birds at Hornøya (Norwegian Directorate for Nature Management; ref. 2011/493, 2012/305). Permission to work in the nature reserve was given by the county commissioner (Fylkesmannen i Finnmark; ref. 2011-2012/1272).

3. Results

3.1 Pilot study

Of the 63 guillemots equipped with GPS- and dummy loggers in 2011, 51 (81%) were recaptured, 39 (65%) of which still had their loggers attached (table 1). All control birds were recaptured, and the number of recaptured controls differed significantly from the number of recaptured equipped birds ($\chi^2 = 6.98$, $P = 0.008$).

Ten of the recaptured birds, including eight guillemots with loggers on the mantle and two with loggers on the rump, had plucked the loggers off along with the feathers they were attached to (table 1). Significantly more of the GPS-loggers mounted on the rump were recovered compared to those mounted on the mantle ($\chi^2 = 11.8$, $P = 0.001$). Ten guillemots with loggers on the mantle and two with loggers on the rump were not recaptured (table 1), and at least three of these birds abandoned their chick. The number of recaptured birds with loggers on the rump was significantly higher than the number of recaptured birds with loggers on the mantle ($\chi^2 = 4.15$, $P = 0.042$). Taken together, 47% of loggers mounted on the mantle and 89% of loggers mounted on the rump were recovered. All birds with a logger mounted on the mantle had signs of plucking of feathers under the device. This was less evident on birds with loggers on their rump. No significant difference was found between the number of recaptured guillemots with loggers placed on the rump and the number of recaptured control birds ($\chi^2 = 2.45$, $P = 0.117$). The difference between the number of recaptured guillemots with loggers on the mantle and the number of recaptured controls was strongly significant ($\chi^2 = 10.4$, $P = 0.001$).

Table 1. Number of study birds, recaptures and recovered GPS-loggers, as well as placement of GPS-loggers used in the pilot study.

| Placement | # Deployed | # Recaptured | GPS recovered |
|-----------------------------|------------|--------------|---------------|
| Brünnich's guillemot | | | |
| Mantle | 7 | 6 | 4 |
| Rump | 7 | 6 | 6 |
| Control | 19 | 19 | NA |
| Common guillemot | | | |
| Mantle | 29 | 20 | 13 |
| Rump | 20 | 19 | 18 |
| Control | 13 | 13 | NA |

3.2 Main study

In 2012, the first 24 kittiwakes (12 equipped and 12 controls) were captured 18-24 June (hereafter referred to as “early chick rearing”). During this period kittiwakes appeared to be in good shape, and there were several broods with two or three chicks (figure 4, mean: 1.3 chicks per nest). June 26-29 were characterized by bad weather conditions (wind and heavy rainfall), and the situation seemed to change during this period. Mortality among chicks was high (figure 4), and an extension in length and duration of provisioning trips was observed among adult birds from 29 June and onwards (hereafter referred to as “late chick rearing”). This might have been due to changes in food availability, as birds seemed to bring back smaller amounts of their main prey; spawning capelin, from 29 June until the end of the field season (Thorvaldsen, 2013). In this period, 26 kittiwakes were captured (13 equipped and 13 controls).

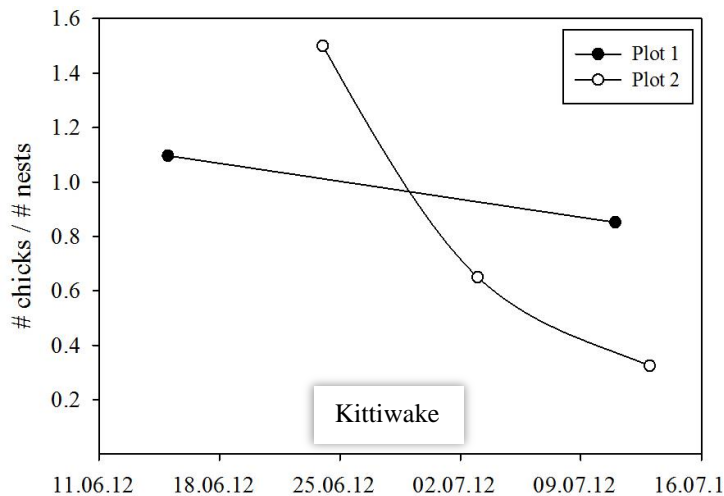


Figure 4. Number of kittiwake chicks per number of nests checked in two working plots in the colony (“Plot 1” and “Plot 2”) throughout the 2012 breeding season.

Common guillemots seemed to bring back an equal amount of capelin and sandeel throughout the breeding season (Thorvaldsen, 2013). No extension in provisioning trip duration was observed, and the guillemots did not suffer from any increased chick loss rate late in the breeding season. One common guillemot lost its GPS-logger during the experimental period. Besides this, signs of plucking of feathers under the device were found on one individual. A couple of individuals were seen plucking on the device on camera photos, but with low frequency.

Little signs of discomfort were observed during deployment for any of the species, but some of the guillemots tried to avoid the noose pole at 2nd capture. CORT levels from these birds were excluded from further analyses. A similar behaviour was observed for three control kittiwakes (not recaptured).

CORT

To measure baseline levels of CORT in blood plasma, blood should be sampled within three minutes post-capture to avoid bias caused by the stress response that follows the capture procedure (Romero and Reed, 2005). In the present study a small, although statistically significant, positive relationship was found between baseline level of CORT and time since capture of kittiwakes, even within three minutes post-capture ($R^2 = 0.052$, $P = 0.032$). This was controlled for by using the standardized residuals from the linear regression of handling time on baseline CORT in further analyses. No such relationship was found for the common guillemots ($R^2 = 0.003$, $P = 0.107$). Hence, original CORT data was used in all statistical analyses for this species.

Kittiwake

Baseline CORT levels were not significantly different between equipped and handled control birds at 1st or 2nd capture (table 2). Equipped kittiwakes showed a tendency to increase their CORT levels more than controls during the experimental period (table 2, figure 5). The increase tended to be significant for equipped birds when the groups were treated separately (equipped: $P = 0.097$; control: $P = 0.485$). When separating birds captured during early chick rearing from those captured during late chick rearing, it was evident that these tendencies were due to a significantly larger

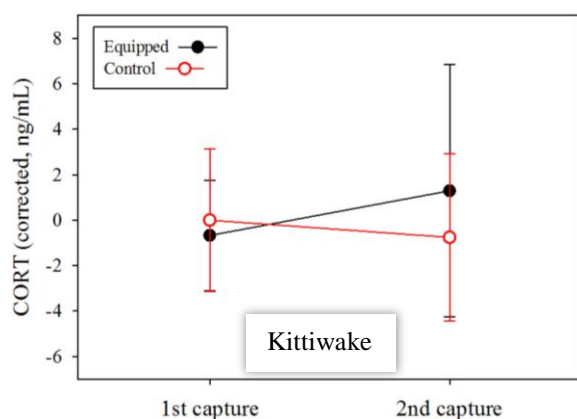


Figure 5. Corrected plasma levels of CORT (\pm SD) in kittiwakes fitted with GPS-loggers (black filled circles) and control birds (red open circles) at 1st and 2nd capture. CORT levels are the standardized residuals from the linear regression of handling time on baseline CORT.

increase in CORT levels of equipped birds compared to controls in the early (equipped: 6.04 ± 1.78 ng/ml, control: -1.23 ± 0.93 ng/ml, $P = 0.003$), rather than in the late (equipped: -1.16 ± 1.19 ng/ml, control: -0.10 ± 1.64 ng/ml, $P = 0.542$) chick rearing period. Thus, the interaction term *treatment*period* explained much (35.4%, $P = 0.001$) of the variation in change in CORT levels during the experimental period (table 3). CORT levels decreased throughout the breeding season, but only for CORT levels at 2nd capture the decrease was significant ($R^2 = 0.112$, $P = 0.033$).

Table 2. Mean (\pm SE) CORT levels of kittiwakes and common guillemots, and H/L ratios of kittiwakes, equipped (E) with logger(s) for approximately 1-2 days and controls (C).

| Species Response variable | n (E, C) | Treatment | | df | t | P |
|-------------------------------|----------|-----------------------|------------------------|----|-------|-------|
| | | Equipped | Control | | | |
| Black-legged kittiwake | | | | | | |
| CORT, 1st capture | 22, 21 | 6.58 \pm 0.52 ng/ml | 7.27 \pm 0.68 ng/ml | 38 | -0.82 | 0.418 |
| CORT, 2nd capture | 21, 20 | 8.85 \pm 1.20 ng/ml | 6.54 \pm 0.84 ng/ml | 35 | 1.57 | 0.125 |
| CORT, difference | 21, 20 | 2.27 \pm 1.30 ng/ml | -0.63 \pm 0.89 ng/ml | 35 | 1.84 | 0.074 |
| H/L, 1 st capture | 20, 17 | 0.64 \pm 0.04 | 0.61 \pm 0.05 | 31 | 0.47 | 0.642 |
| H/L, 2 nd capture | 17, 16 | 0.65 \pm 0.05 | 0.70 \pm 0.04 | 31 | -0.79 | 0.436 |
| H/L, difference | 17, 15 | 0.02 \pm 0.05 | 0.12 \pm 0.06 | 28 | -1.01 | 0.323 |
| Common guillemot | | | | | | |
| CORT, 1st capture | 40, 29 | 3.94 \pm 0.42 ng/ml | 3.66 \pm 0.29 ng/ml | 65 | 0.55 | 0.586 |
| CORT, 2nd capture | 38, 29 | 6.32 \pm 0.59 ng/ml | 5.97 \pm 0.71 ng/ml | 59 | 0.38 | 0.705 |
| CORT, difference | 38, 29 | 2.73 \pm 0.65 ng/ml | 2.31 \pm 0.67 ng/ml | 63 | 0.45 | 0.657 |

Table 3. Summary of final ANCOVA models explaining variation in change in CORT levels, body mass, H/L-ratios, and variation in nest attendance (duration of provisioning trips) of kittiwakes during the experimental period. Details on all explanatory variables included in the initial models are presented in the appendix, table A1-A6.

| Dependent | Explanatory | df | F | P | Estimate \pm SE | r ² |
|-------------------------|-------------------------|----|------|-------|------------------------------------|----------------|
| CORT difference | <i>treatment*period</i> | 33 | 8.22 | 0.001 | | 0.354 |
| | <i>period</i> | 33 | 4.26 | 0.048 | 0.81 \pm 0.39 ng/mL ¹ | 0.124 |
| Body mass change | <i>period</i> | 31 | 9.47 | 0.004 | -20.4 \pm 6.6 g ¹ | 0.240 |
| | Model 1 | | | | | |
| | <i>BCI</i> | 37 | 30.5 | 0.000 | -16.1 \pm 2.9 g | 0.459 |
| Nest attendance | <i>period</i> | 29 | 53.7 | 0.000 | 3.67 \pm 1.19 h ¹ | 0.665 |
| | <i>treatment</i> | 29 | 8.25 | 0.008 | 1.66 \pm 1.19 h ² | 0.234 |
| H/L difference | no significant result | 30 | | | | |

¹ = late compared to early chick rearing period, ² = equipped birds compared to controls

Common guillemot

No significant difference in baseline CORT was found between treatment groups at 1st or 2nd capture (table 2). Both equipped and control common guillemots increased their levels of CORT significantly during the experimental period (equipped: $P < 0.001$, control: $P = 0.002$). The increase was not significantly different between the groups (table 2, figure 6). Of the parameters included in the ANCOVA, CORT level at 1st capture (*cort1*) explained most of the variation in change in CORT levels (table 4). Despite this, only 7.4% of the variation was explained by *cort1* alone. Time between 1st and 2nd capture did not affect the change in CORT levels in the same period (table A7 in the appendix).

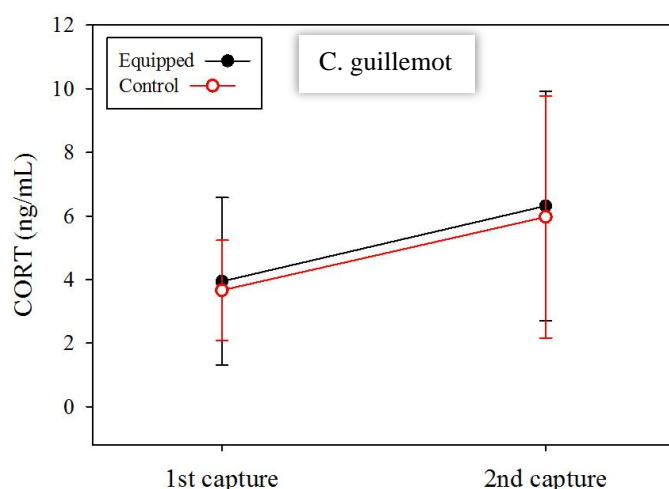


Figure 6. Plasma levels of CORT (\pm SD) in equipped (black filled circles) and control (red open circles) common guillemots at 1st and 2nd capture.

Table 4. Summary of final ANCOVA models explaining variation in change in CORT levels and body mass, and variation in nest attendance (duration of provisioning trips) of common guillemots during the experimental period. Details on all explanatory variables included in the initial models are presented in the appendix, table A7-A10.

| Dependent | Explanatory | df | F | P | Estimate \pm SE | r ² | |
|------------------------------------|--------------------------|--------------------------|---------|----------|--------------------------------|-------------------|-------|
| CORT difference | <i>cort1/no result</i> | 58 | 4.54/NA | 0.037/NA | -0.60 \pm 0.28 ng/mL | 0.074 | |
| Body mass change Model 1 | <i>capture_recapture</i> | 58 | 12.7 | 0.001 | -29.1 \pm 8.2 g | 0.188 | |
| | <i>BCI</i> | 58 | 10.8 | 0.002 | -13.0 \pm 4.0 g | 0.164 | |
| | <i>chick age</i> | 58 | 5.12 | 0.028 | 2.5 \pm 1.1 g | 0.085 | |
| | Model 2 | <i>capture_recapture</i> | 58 | 7.84 | 0.007 | -23.8 \pm 8.5 g | 0.125 |
| | | <i>chick age</i> | 58 | 6.57 | 0.013 | 3.0 \pm 1.2 g | 0.107 |
| | <i>treatment</i> | 58 | 4.07 | 0.048 | -15.3 \pm 8.5 g ¹ | 0.069 | |
| Nest attendance | <i>sex</i> | 34 | 11.8 | 0.002 | 1.86 \pm 1.20 h ² | 0.269 | |
| | <i>chick age</i> | 34 | 4.62 | 0.039 | -0.94 \pm 1.03 h | 0.126 | |

¹ = equipped birds compared to controls, ² = females compared to males

H/L-ratio

Kittiwake

No significant difference was found between H/L-ratios of control and equipped kittiwakes at 1st or 2nd capture (table 2). Neither equipped birds ($P = 0.669$) nor controls ($P = 0.116$) changed their H/L-ratios significantly during the experimental period. There was no significant difference between the groups in change in H/L-ratio during the experimental period (table 2). No significant correlation was found between H/L ratios and CORT levels ($R^2 = 0.032$, $P = 0.145$). No significant differences in H/L-ratio increase were apparent when separating birds captured during early chick rearing (equipped: 0.00 ± 0.06 , control: 0.13 ± 0.06 , $P = 0.142$) from those captured during late chick rearing (equipped: 0.06 ± 0.10 , control: -0.12 ± 0.22 , $P = 0.486$). Finally, no variables turned out at a significant level in the ANCOVA (table A2 and A3 in the appendix).

Body mass

Kittiwake

No significant difference in body mass was found between equipped and control birds at 1st or 2nd capture (table 5, figure 7). When treated separately, none of the groups changed their mass significantly during the experimental period (equipped: $P = 0.312$, control: $P = 0.136$). No significant difference in change in body mass was found between equipped birds and controls (table 5, figure 7). The mean change in body mass of equipped birds was not different from controls, neither during early (equipped: -10.8 ± 8.9 g, control: -19.0 ± 5.1 g, $P = 0.435$) nor during late (equipped: 0.0 ± 5.6 g, control: 9.8 ± 5.1 g, $P = 0.212$) chick rearing.

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 3). When *BCI* was included in the model, this was the only significant parameter (table 3). In general, birds lost more body mass during early than during late chick rearing. A significant negative correlation was found between body mass/*BCI* and date of 1st capture for kittiwakes in general (body mass: $R^2 = 0.372$, $P < 0.001$; *BCI*: $R^2 = 0.341$, $P < 0.001$), corresponding to a mass loss of 7.2 g/day. When graphically investigating the data, a decline in body mass of 4.2 g/day was found between 18 and 23 June. A marked drop in body mass was observed between 23 and 29 June, where kittiwakes lost on average 13.5 g/day. After this the mean body mass stabilized, but a small decline of 1.7 g/day was observed between 29 June and 6 July.

Table 5. Mean (\pm SE) body mass of kittiwakes and common guillemots, equipped (E) with logger(s) for approximately 1-2 days and controls (C). Significant P -values are in bold.

| Species Response variable | n (E, C) | Treatment | | df | t | P |
|------------------------------------|----------|-------------------|-------------------|----|-------|--------------|
| | | Equipped | Control | | | |
| Black-legged kittiwake | | | | | | |
| Body mass, 1 st capture | 25, 24 | 420 \pm 11 g | 415 \pm 13 g | 46 | 0.30 | 0.764 |
| Body mass, 2 nd capture | 24, 20 | 415 \pm 11 g | 417 \pm 11 g | 42 | -0.15 | 0.885 |
| Body mass, difference | 24, 20 | -5.4 \pm 5.2 g | -7.5 \pm 4.8 g | 42 | 0.29 | 0.771 |
| Common guillemot | | | | | | |
| Body mass, 1 st capture | 42, 29 | 1049 \pm 12 g | 1012 \pm 13 g | 65 | 2.14 | 0.036 |
| Body mass, 2 nd capture | 40, 29 | 1015 \pm 11 g | 998 \pm 14 g | 60 | 0.95 | 0.348 |
| Body mass, difference | 40, 29 | -30.1 \pm 4.9 g | -14.1 \pm 5.2 g | 64 | -2.24 | 0.029 |

Common guillemot

Body mass of equipped guillemots decreased significantly more than body mass of controls (table 5), and *treatment*, *chick age* and time between 1st and 2nd capture (*capture_recapture*) explained most of the variation in body mass change during the experimental period (table 4). When *BCI* was included as explanatory variable, *treatment* was not significant in the final model (table 4). Equipped birds had a higher body mass than controls at 1st capture, but the difference was not significant at 2nd capture (table 5, figure 7). Both equipped birds and controls decreased their body mass significantly during the experimental period (equipped: $P < 0.001$, control: $P = 0.010$). This decrease depended on body mass at 1st capture for equipped birds, but not for controls (equipped: $R^2 = 0.112$, $P = 0.035$; control: $R^2 = 0.001$, $P = 0.891$). A negative correlation was found between body mass and date, but the relationship was not statistically significant ($R^2 = 0.037$, $P = 0.077$). The mass decline corresponded to 2.3 g/day.

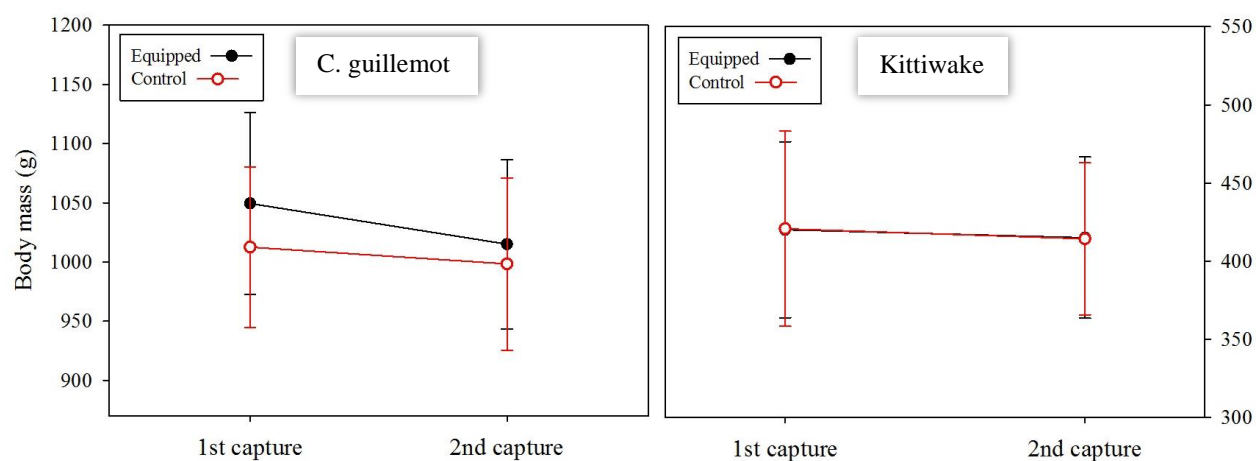


Figure 7. Body mass (\pm SD) of equipped (black filled circles) and control (red open circles) common guillemots (left) and kittiwakes (right) at 1st and 2nd capture. Black filled circles are hidden behind red open circles in the kittiwake figure.

Nest attendance

Kittiwakes

Equipped kittiwakes performed significantly longer feeding trips than control birds during the experimental period (table 6, figure 8 (a)). The longer mean trip duration of equipped birds was much due to the very long feeding trips of five equipped individuals during late chick rearing. Three of these birds had relatively low BCIs at 1st capture (figure 8 (c)), and one of these also had

high levels of CORT in plasma. High CORT levels were found in additionally one bird. The last bird had neither high levels of CORT nor a particularly low BCI. No difference in trip durations was found between equipped birds and controls after 2nd capture, when loggers were removed from equipped birds (table 6, figure 8 (b)). At least four of the five birds performing the longest trips during the experimental period returned to a pattern of trips of shorter duration after 2nd capture (no data on the fifth bird). The difference between equipped and control birds in change in trip durations before and after 2nd capture was not statistically significant (table 6). Nevertheless, equipped birds decreased their trip durations significantly after 2nd capture ($P = 0.049$). This was not observed for control birds (figure 8 (b), $P = 0.841$).

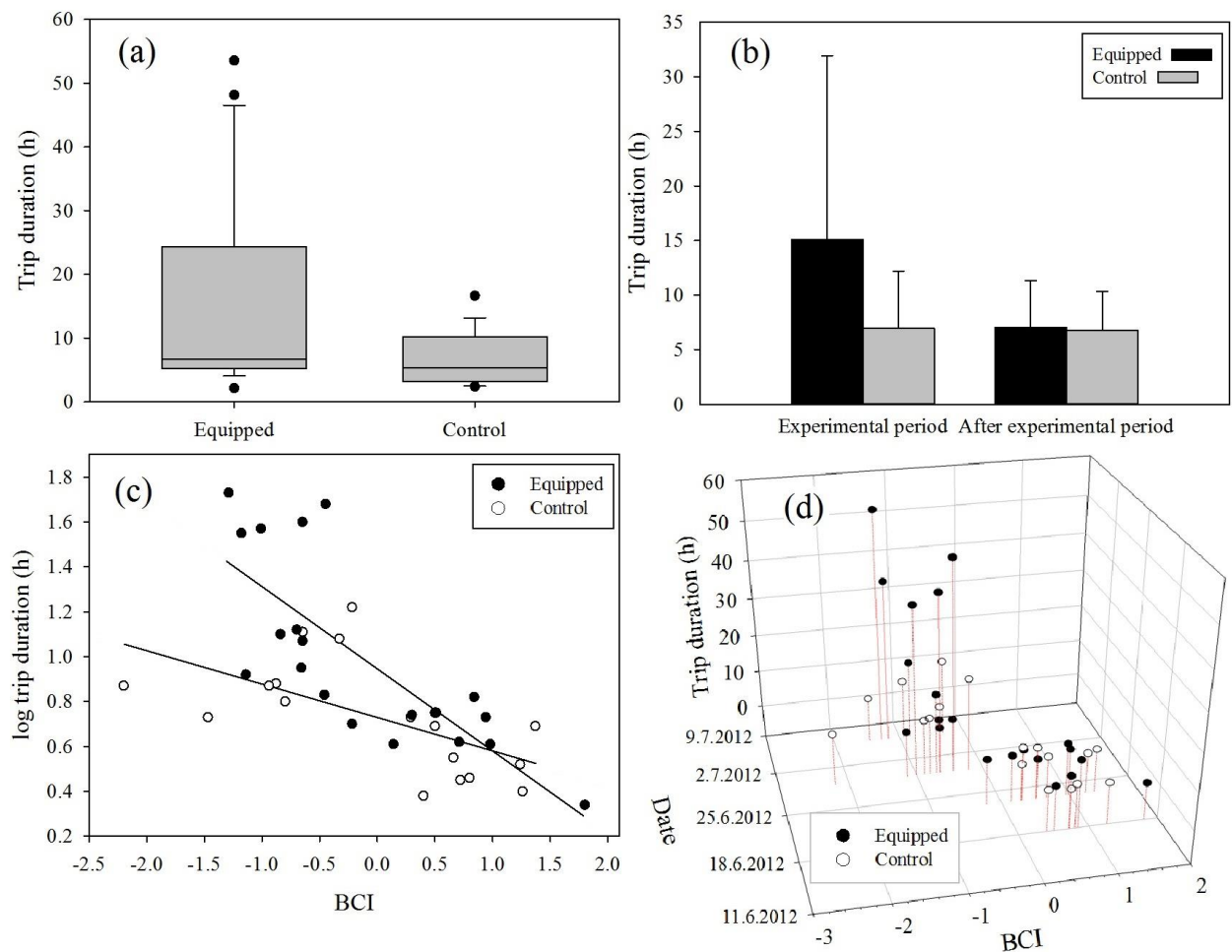


Figure 8. (a): Trip duration of equipped and control kittiwakes during the experimental period. Box plot gives the median (horizontal line inside boxes), interquartile range (boxes), range (bars) and outliers (dots). (b): Mean trip duration of kittiwakes before and after the experimental period. (c): Duration of provisioning trips (logarithmic scale) during experimental period as a function of body condition index (BCI) of equipped (filled circles) and control (open circles) kittiwakes. (d): Trip duration of equipped (filled circles) and control (open circles) kittiwakes in relation to date and BCI.

Equipped kittiwakes tended to perform trips of longer duration (during the experimental period) than controls during early chick rearing (equipped: 4.65 ± 1.10 h, control: 3.48 ± 1.11 h, $P = 0.058$), but performed significantly longer trips during late chick rearing (equipped: 19.2 ± 1.27 h, control: 9.03 ± 1.11 h, $P = 0.008$). Trip durations were significantly longer for all birds, independent of treatment, during late than during early chick rearing (figure 8 (d); early: 4.05 ± 1.08 h, late: 13.18 ± 1.16 h, $P < 0.001$). *Period* and *treatment* thus explained much of the variation in nest attendance (table 3).

No kittiwake chicks were left unattended at the nest during early chick rearing, but most of the chicks were in periods 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 length of provisioning trips during the experimental period for kittiwakes (figure 8 (c), $R^2 = 0.425$, $P < 0.001$). Although the steepness of the slope was affected by the five birds performing trips of very long duration, 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 made longer trips than controls when in poor body condition (figure 8 (c) and (d)). No significant relationships were found between nest attendance during the experimental period and CORT levels at 1st capture ($P = 0.445$), 2nd capture ($P = 0.296$) or the difference in CORT levels between 1st and 2nd capture ($P = 0.560$).

Table 6. Mean (\pm SE) trip duration of kittiwakes and common guillemots, equipped (E) with logger(s) for approximately 1-2 days and controls (C). Transformation of the difference between trip durations during and after the experimental period was not successful, and Mann-Whitney U-test was therefore performed on this variable.

| Species | Response variable | n (E, C) | Treatment | | df | t / Z | P |
|-------------------------------|------------------------------------|----------|-------------------|--------------------|----|-------|--------------|
| | | | Equipped | Control | | | |
| Black-legged kittiwake | | | | | | | |
| | Trip duration, experimental period | 21, 20 | 15.4 ± 3.56 h | 6.88 ± 0.89 h | 39 | 2.08 | 0.045 |
| | Trip duration, after 2nd capture | 18, 14 | 6.91 ± 1.25 h | 6.80 ± 0.94 h | 30 | -0.46 | 0.652 |
| | Trip duration, difference | 18, 14 | 8.17 ± 4.15 h | 0.17 ± 0.71 h | | -1.06 | 0.287 |
| Common guillemot | | | | | | | |
| | Trip duration, experimental period | 31, 16 | 6.05 ± 1.10 h | 5.05 ± 1.18 h | 25 | 0.96 | 0.349 |
| | Trip duration, after 2nd capture | 10, 4 | 5.76 ± 1.31 h | 4.18 ± 1.11 h | 11 | 0.72 | 0.484 |
| | Trip duration, difference | 10, 4 | 0.39 ± 2.26 h | -4.12 ± 2.77 h | 6 | 1.27 | 0.525 |

Common guillemots

The duration of provisioning trips during the experimental period did not differ between equipped and control birds (table 6, figure 9). After 2nd capture, trip durations were also of similar length for both groups (table 6), but this was based on a very low sample size of control birds (n=4). No difference was found between trip durations during and after the experimental period for any of the groups when treated separately (equipped: $P = 0.856$, control: $P = 0.410$), and there was also no between-group difference (table 6).

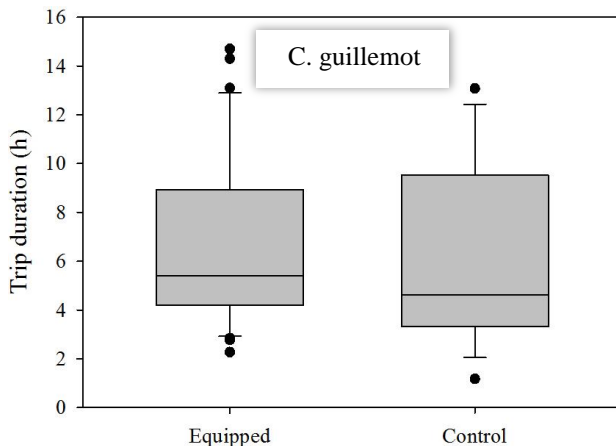


Figure 9. Trip duration of equipped and control common guillemots during the experimental period. Box plot gives the median (horizontal line inside the boxes), interquartile range (boxes), range (bars) and outliers (dots).

Sex and *chick age* explained 26.9% and 12.6%, respectively, of the variation in nest attendance of common guillemots in the final model (table 4). Females spent more time at sea than males during the experimental period (females: 8.38 ± 1.15 h, males: 4.49 ± 1.11 h, $P = 0.002$). As for kittiwakes, no significant relationships were found between nest attendance of common guillemots during the experimental period and CORT levels (1st capture: $P = 0.710$, 2nd capture: $P = 0.318$, CORT difference 1st-2nd capture: $P = 0.206$). In addition, no significant relationship between BCI and nest attendance was found ($R^2 = 0.018$, $P = 0.380$).

Chick survival

No significant difference in chick loss was found between equipped kittiwakes and control birds (equipped: 0.94 ± 0.17 chicks lost/breeding pair, control: 0.79 ± 0.24 chicks lost/breeding pair, $P = 0.593$), and the breeding success was comparable (equipped: 0.50 ± 0.12 large chicks/nest, control: 0.57 ± 0.14 large chicks/nest, $P = 0.699$). No common guillemot chicks were confirmed lost. Nevertheless, some guillemots tried to avoid the noose pole at 2nd capture, and it was difficult to judge whether they still had a chick or not while they were running around on the shelf. Five birds were not seen with their young when recaptured, including three equipped and two control birds.

4. Discussion

4.1 Measurements of stress and behaviour

The aim of the present study was to investigate potential short-term effects of device deployment on kittiwakes and common guillemots, by comparing physiological and behavioural parameters of stress between equipped birds and controls. Physiological stress in organisms is typically measured by blood levels of glucocorticoids (Wingfield et al., 1997). This may not, however, be sufficient to evaluate the effects of experimental treatment, given the complexity of the stress response (reviewed by Charmandari et al., 2005). Stress hormone levels is the ultimate result of a variety of interactions between an organism and its environment, and interactions between the stress system and other systems such as the immune system, digestive system and the reproductive system further adds to the complexity (Costa and Sinervo, 2004). As an attempt to complement measurements of CORT, H/L-ratio was measured in the present study. The BCI calculated also gives clues of the nutritional status of individuals. Factors such as age, body condition of the chick, prey availability, diet and predation are also measurable parameters that would provide a more complete picture of the challenges faced by individuals in the present study. Given the limited time available, and the potential disturbing effects of multiple measurements, CORT and H/L-ratio determined from a single blood sample from each capture, and the monitoring of individual behaviour through time lapse photo registration, may still prove effective measures of individual condition.

A weak, but significant, positive correlation between CORT levels and time of blood sampling was found within three minutes post-capture in the present study. Thus, it is appropriate to question if the “three minute rule” is valid in order to evaluate levels of baseline CORT in kittiwakes. No significant correlation was found within *two* minutes post-capture of kittiwakes in the present study, and some authors actually conform to a “two minute rule” (e.g. Navarro et al., 2008; Quillfeldt et al., 2012). However, in most species, blood samples taken within three minutes post-capture are considered likely to reflect baseline or near-baseline CORT levels (Romero and Reed, 2005). Regardless of this, correcting for an increase will usually solve potential problems associated with time of sampling, as long as the relationship is not too complex.

4.2 Physiological parameters

Equipped kittiwakes tended to increase their CORT levels more than controls during the experimental period, mainly due to a significantly larger increase in CORT levels of equipped birds during early chick rearing. The energy requirement per hour spent off the nest for breeding kittiwakes is probably highest during the first part of the chick rearing period (Moe et al., 2002), when chicks are not fully homeothermic and require brooding of one adult (Gabrielsen et al., 1992). This seems also to be the case in the present study, as kittiwakes decreased their body mass more during early than during late chick rearing (excluding the marked drop in body mass 24-29 June). As CORT levels often reflect changes in individual body condition, CORT levels are also expected to be at their highest during early chick rearing (e.g. Kitaysky et al., 1999; Williams et al., 2008). Data from the present study partly support this. Given the already high energy requirements of adults during early chick rearing, birds are probably more vulnerable to the additional demands of carrying a logger during this period. This could be the reason why effects of loggers on CORT levels were more pronounced in early compared to late chick rearing.

No correlation between H/L-ratio and CORT levels was found in kittiwakes, despite the fact that both parameters are considered reliable measures of stress (Davis et al., 2008; Wingfield et al., 1997). The H/L-ratio is expected to increase within only a couple of hours of a stressor (D. B. Skomsø unpublished data; Davis et al., 2008), i.e. well below the duration of deployment in the present study. However, Ludynia et al. (2012) found no effect of 1-3 days deployment of GPS-loggers on the H/L-ratio of southern rockhopper penguins *Eudyptes chrysocome*. Significantly elevated levels of CORT were found in equipped birds in the same study (Ludynia et al., 2012). Conversely, Quillfeldt et al. (2012) reported elevated H/L-ratio of thin-billed prions *Pachyptila belcheri* fitted with GLS-loggers for one year. An increased hormonal response to stress among equipped birds was found in the study, but baseline CORT levels were not influenced (Quillfeldt et al., 2012). These data are consistent with the suggestion that 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 and Siegel, 1983; McFarlane and Curtis, 1989; Müller et al., 2011; Rich and Romero, 2005; Vleck et al., 2000).

Both equipped and control common guillemots increased their levels of CORT between 1st and 2nd capture significantly, but no significant difference was found between the two groups. No

corresponding increase in CORT levels was observed throughout the breeding season. Thus, elevated CORT levels at 2nd capture may be a capture and/or handling effect rather than a seasonal effect, or an effect of the loggers. Learned behaviour may also have made birds more stressed by human presence at the nesting site, causing CORT levels to increase *prior to* recapture (Schwartzkopf-Genswein et al., 1997, Wilson and McMahon, 2006).

4.3 Nest attendance

Equipped kittiwakes performed trips of longer duration than controls during the experimental period. The difference was most evident during late chick rearing, and was no longer present when loggers were removed. It may seem contradictory 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. Still, the two groups tended to differ in nest attendance also during early chick rearing, suggesting compensatory behaviour from partners of equipped birds. When chicks become homeothermic at an age of approximately sixteen days, adults may leave them without compromising their own reproductive success (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., 2007b). Equipped birds may as well *need* to increase their trip durations to be able to deal with the higher energetic demands, reduced flight efficiency or simply the extra distraction caused by the device. The fact that nest attendance of equipped birds and controls did not differ significantly when loggers were removed strongly suggests that the longer trips of equipped birds were indeed a result of the device rather than a handling effect.

Mean trip duration of equipped kittiwakes during late chick rearing was strongly influenced by the very long trips performed by five individuals. Such long trips were also observed following satellite transmitter deployment on white-chinned petrels *Procellaria aequinoctialis* (Catard et al., 2000). Four of the five kittiwakes performing long trips in the present study had low BCIs and/or high levels of CORT at 1st capture, and may thus have been particularly vulnerable to device deployment. It is, however, worth to notice that several equipped birds with similar BCIs and CORT levels did not respond in this way, suggesting the response to device deployment to vary considerably between individuals. All five birds were recaptured following the single long trip,

subsequently returning to a pattern of shorter trip durations. Patterns of short and long trips were observed both among equipped and control birds. Typically, the long trips were far from as long as those observed among the five mentioned birds, and were not exclusively observed immediately after capture. This may suggest that the alternating short and long trips found for several seabirds (e.g. Catard et al., 2000; Chaurand and Weimerskirch, 1994; Phillips et al., 2003; Weimerskirch et al., 2000) is a strategy also utilized by the kittiwake, as already reported by Paredes et al. (2012). BCI (and body mass at 1st capture) correlated negatively with the duration of the following provisioning trips, as previously reported for other seabirds (e.g. Catard et al., 2000; Chaurand and Weimerskirch, 1994; Weimerskirch et al., 2000). This, combined with the observed pattern of short and long trips, may indicate that adult kittiwakes regulate provisioning according to their own body condition. 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 (Chaurand and 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 and control kittiwakes in the amount of time chicks spent alone in the nest, the reduced parental care of equipped birds may have been partly compensated for by their partners.

No difference in nest attendance was observed between common guillemot treatment groups. However, as long as the provisioning of chicks was not quantified, differences in provisioning between the groups may have existed, as parents do not necessarily bring back food every time they return from a trip (Paredes et al., 2005).

4.4 Body mass

No difference in change in body mass was observed between equipped kittiwakes and controls during the experimental period. This may suggest that the duration of deployment was not sufficient for kittiwakes to adjust their body mass. Kittiwakes in general experienced a significant decrease in body mass throughout the breeding season, which is a normal response to the energetic challenges of breeding (Moe et al., 2002). 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 (Moe et al., 2002).

Body mass of equipped common guillemots declined significantly more than the mass of control birds during the experimental period. In 2012, this was the only effect of logger deployment found in this species. Many seabird studies report mass reductions of equipped birds following instrument attachment, including several studies on alcids (e.g. Croll et al., 1992; Elliott et al., 2007; 2012; Falk et al., 2000; Paredes et al., 2005). This may be attributed to the extra stress and energetic demands of carrying devices, e.g. combined with a reduced feeding efficiency caused by buoyancy and drag of loggers when diving. In the present study, equipped birds lost on average almost 16 g more than control birds during the experimental period, i.e. almost corresponding to the mass of the device(s). The mass reduction may therefore as well be a method of adjusting for an increased wing load, e.g. to improve flight efficiency (see Vandenabeele et al., 2012). Control birds lost on average 6.8 g/day, which is a bit more than the average mass loss throughout the breeding season (2.7 g/day). The difference is small, but may indicate effects of handling on body mass.

Equipped common guillemots had a higher body mass compared to controls at 1st capture. Thus, the difference in mass loss between equipped and control birds could potentially be a result of a higher tendency of heavier birds to lose mass. This could be expected from the tendency of extreme measurements to be closer to the mean on the subsequent measurement (regression toward the mean). However, no significant relationship was found between body mass at 1st capture and mass loss for control birds. In contrast, this relationship was highly significant for equipped birds. This may be attributed to a higher capability of heavy birds to reduce fat stores and thereby to adjust for the extra mass of a logger (e.g. to improve flight efficiency). The reason for a higher mass of equipped birds compared to controls at 1st capture may be that, despite the intention of random selection, the most nervous birds were more likely to be designated as controls because of the higher probability of recovering expensive equipment. It is likely that these birds also were those with the lowest body mass.

4.5 Reproductive success

No difference in reproductive success was found between equipped birds and controls for any of the species. The duration of deployment was relatively short for both species, and may not have been sufficient to transfer effects of devices from adults to the chicks. Partners of equipped birds

may also have compensated for a decreased parental performance of their mates (Paredes et al., 2005; Wanless et al., 1988). Effects on partners of equipped birds are normally difficult to measure (Ballard et al., 2001), and no attempts were made on 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). Although depending on the specific aim of the study, parameters other than reproductive success could often be more appropriate in order to investigate effects of device deployment on seabirds.

4.6 Effects of identification marks

The different colours of the Indian ink used to recognize birds in the field and on cameras might have had influences on behaviour and stress. Wilson et al. (1990) found the reaction of breeding adélie penguins *Pygoscelis adeliae* to back-mounted peck recorders to vary depending on the colour of the recorders, with devices resembling the colour of the birds' plumage (black) receiving less high pressure pecks than devices of other colours (blue, yellow and white). Colour is an important part of bird ecology, and camouflage (both related to predators and prey) and social signalling are factors that may have been influenced in the present study (Baker and Parker, 1979). The colours used in the present study (blue, green and black) were not dramatically different from the normal plumage colour of the birds, and probably did not affect measured parameters to a large extent. However, since effects of colour were not measured, this may be difficult to elucidate. Similar effects could be relevant in relation to the head flags used to recognize guillemots in the field. In addition to the possible effects of flag coloration, head flags may also have caused some discomfort to the birds, and could potentially be responsible for some of the apparent changes in CORT levels and body mass of both equipped and control birds. Future studies using similar tags on guillemots should therefore keep this in mind. However, as both equipped birds and controls in the present study were fitted with head-flags, effects of GPS-loggers should still be possible to elucidate.

4.7 Difference between species

Kittiwakes and common guillemots responded differently to the deployment of loggers. Equipped kittiwakes had elevated CORT levels at recapture, and a lower nest attendance compared to control birds during the experimental period. Conversely, equipped common guillemots experienced an increased mass loss compared to controls, but no device effect on CORT or nest attendance was

seen. This was somewhat unexpected, as guillemots face the problem of buoyancy and drag from loggers when diving, in addition to the higher wing load and thus higher energetic demands of flight for this species compared to kittiwakes (Ackerman et al., 2004; Vandenabeele et al., 2012). Accordingly, several studies on alcids report some effects of devices (see Ackerman et al., 2004), whereas device effects are rarely reported from gull studies (e.g. Chivers et al., 2012; Wanless, 1992). Moreover, heavy birds are expected to be more affected by devices than smaller species when devices account for a similar fraction of body mass, as large birds are expected to have less power surplus (Caccamise and Hedin, 1985; Vandenabeele et al., 2012).

GPS-loggers constituted 3.8% of mean kittiwake body mass in the present study, whereas GPS-loggers and the combined instrumental mass of GPS-loggers and TDRs constituted 1.8% and 2.2%, respectively, of mean common guillemot body mass. Kittiwakes stay more airborne while feeding than guillemots, and the larger fraction of body mass constituted by the loggers may in itself be one reason why logger effects on foraging and stress seemed more pronounced for this species. Several authors suggest that instruments deployed on seabirds (and other birds) should not exceed a given fraction (usually 3-5%) of body mass (Caccamise and Hedin, 1985; Cochran, 1980; Phillips et al., 2003). Despite this, a number of studies report effects of loggers of even smaller body mass fractions than this (e.g. Ackerman et al., 2004; Adams et al., 2009; Elliott et al., 2012; Wanless et al., 1988; Whidden et al., 2007). Hence, it is evident that most kinds of devices may influence behaviour and physiology of birds. Weimerskirch et al. (2000) pointed out that the average food loads carried by yellow-nosed albatrosses *Thalassarche chlororhynchos* were much heavier (20% of adult body mass) than the loggers used in the study, and if mass of devices should be a problem, it had to be due to a reduced foraging ability. Similarly, the mean and maximum regurgitate mass of kittiwakes breeding on the Isle of May, Scotland, was 41 g and 68 g, respectively, i.e. 11% and 18% of adult body mass in the study (Galbraith, 1983). Other factors, such as method of attachment, shape, positioning, colour and streamlining may therefore be more important to consider than the pure mass of the equipment when deploying devices on birds (Vandenabeele et al., 2012).

4.8 Placement of loggers

In the pilot study, the number of recaptured guillemots and recovered GPS-loggers was significantly lower when loggers were mounted on the mantle rather than on the rump of the birds.

Several of the guillemots which were not recaptured probably abandoned their chicks. Although signs of plucking of feathers under the devices were observed in some of the guillemots with loggers on the rump, this was far more evident in birds with mantle-mounted loggers. Equipped Brünnich's guillemots (50% with loggers on the mantle) also had a significantly lower nest attendance than control birds during the experimental period (Norman Ratcliffe, unpublished data). These results clearly suggest that the rump/lower back is the best placement of GPS-loggers on guillemots. This is consistent with findings from penguin studies, suggesting this positioning to minimize drag caused by the device (Bannasch et al., 1994). Despite some differences in morphology and physiology, alcids such as guillemots are similar to penguins in shape, and members of both groups use wing propulsion for underwater movement (Gaston and Jones, 1998). However, animals are expected to carry loads with more ease when attached close to their centre of gravity rather than on extremities (Adams et al., 2009; Caccamise and Hedin, 1985; Casper, 2009). Thus, it has been questioned whether attachment to the lower back could affect balancing and swimming during dives, as this is not the closest point to the bird's centre of gravity. Results from penguin studies are, however, somewhat ambiguous (Chiaradia et al., 2005; Healy et al., 2004). Nevertheless, streamlining and shape of devices seem to be more crucial points for diving species (Bannasch et al., 1994; Culik et al., 1994), consistent with the findings from the pilot study. Still, both balance and streamlining are issues that should be considered (Healy et al., 2004).

Compared to alcids, gulls rely heavily on flying skill and manoeuvrability, and may thus be more vulnerable to negative effects of device deployment away from their centre of gravity. Potentially, this could influence efficiency of feeding and provisioning, and increase energetic demands (Adams et al., 2009). Device attachment to the back of birds rather than to the tail may thus reduce the problem, 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. Paredes et al., 2012; Wanless, 1992), as in the present study, but several also deploy loggers on the bird's back, usually reporting no negative effects (Chivers et al., 2012; Daunt et al., 2002; Kotzerka et al., 2010). Parameters measured in these logger-effect studies are typically activity patterns, nest attendance, chick mass and reproductive success (Chivers et al., 2012; Daunt et al., 2002; Kotzerka et al., 2010). In the study by Kotzerka et al. (2010) two birds shed the logger by pulling out feathers to which it was attached, which may indicate some discomfort. No signs of this were seen in the present study. Wanless (1992) found no evidence of negative effects of

tail-mounted devices on kittiwake behavioural parameters and nest attendance. Devices in this study constituted < 1% of adult body mass (Wanless, 1992), i.e. less than in the present study. Paredes et al. (2012) found no increase in CORT levels following two days deployment of GPS-loggers mounted on the tail of kittiwakes. They did not compare this with CORT levels of control birds (Paredes et al., 2012). Hence, some data exist on logger effects on kittiwakes, but very few authors report any negative effects. However, parameters used to evaluate this are generally few and often not very sensitive. Whether placement of loggers on the back would be a better solution in the present study is therefore difficult to judge. This issue clearly requires further investigation.

4.9 Device effects – their measures and consequences

Only small signs of discomfort caused by loggers were observed in the field in the present study, despite apparent effects of loggers on nest attendance and CORT levels of kittiwakes and on mass loss of guillemots. Moreover, no obvious relationships were found between measured behavioural and physiological parameters for any of the species. Evidently, physiological changes may not be reflected in observable behaviour, which underlines the importance of measuring more than one parameter when device effects are investigated.

CORT level has in the present study proved to be a usable measure of short-term effects of logger deployment in kittiwakes. In addition, CORT levels in guillemots may have been affected by the capture and handling procedure. This contradicts the suggestion by Elliott et al. (2012) that CORT is a more appropriate measure of long-term effects of devices. CORT levels did not correlate with H/L-ratios of kittiwakes, despite the fact that these systems are thought to influence each other directly (Dhabhar et al., 1994; 1995; 1996). This supports the hypothesis that H/L-ratio could be a more appropriate measure of stress in the long-term (Gross and Siegel, 1983; McFarlane and Curtis, 1989).

Device effects observed in the present study could cause a number of unfavourable responses in experimental birds. Connections between CORT and the pituitary hormone prolactin, involved in parental behaviour, are thought to mediate the reduced nest attendance and increased daily distance travelled often observed among parental birds with elevated levels of CORT (Angelier et al., 2007b; 2009, Kitaysky et al., 2001). Especially in birds with poor body condition resources may be shifted away from reproduction and towards self-maintenance (Angelier et al., 2007a). Lowered

nest attendance of adult kittiwakes in the present study may have caused lower chick feeding rates, which could be critical during periods of low food availability. Ultimately, this could lead to reduced breeding success and thereby lower fitness. Although no correlation was found between CORT levels and nest attendance in the present study, elevated CORT levels may still be a problem in this concern, as stress may manifest long after stressful events have passed (Kitaysky et al., 2001). In principle, activation of the stress system is an adaptive and time limited response to a stressor (Charmandari et al., 2005). However, redistribution of resources towards self-maintenance during periods of reproduction would, if the stress response is caused by device deployment, be maladaptive. Reduced body mass may be beneficial for equipped guillemots in order to decrease energy requirements of flight during the experimental period, but would also pose an additional cost when devices are removed, as storages must be restored. Finally, common for all device effects are the potential bias of scientific data. In the case of logger-studies, the majority addresses feeding patterns and distribution of individuals. Changes in normal behaviour caused by loggers may thus lead to wrong conclusions.

Results from the present study suggest that method of attachment, placement of the device and device shape and size are more important than mass of the equipment, although mass may also be an issue if foraging efficiency is reduced. Species differences in response may come as consequences of different placement of loggers, as well as the different biology of guillemots and kittiwakes. The pilot study was crucial to determine optimal placement of loggers on guillemots, and should preferably also have been performed on kittiwakes prior to the main study. TDR-loggers or other salt water recorders could preferably have been deployed on kittiwakes, to provide a more complete picture of the activity pattern of this species. Additional parameters could have been measured to investigate logger effects on guillemots (and kittiwakes), including provisioning of chicks. Effects of tagging (especially head-flags) and handling should also be given more attention. To investigate possible long-term effects of device deployment in the present study, comparisons of return rate and reproductive success of experimental birds in later breeding seasons could have been performed. Measurements of device effects during later breeding seasons would also have made it possible to investigate how effects change according to year and environmental conditions.

5. Concluding remarks

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 where environmental conditions are unsatisfactory. Body condition, physiological condition, breeding stage and the duration of deployment need also to be taken into consideration. Placement, colour and shape of devices should be evaluated according to the biology of the species in question. Finally, one should always evaluate whether the risks and impacts of instrument deployment on the organism in question justify benefits and gains of the experiment.

Recent studies on instrumental effects on birds show that this still is a major issue, despite the wide use and small size of technological devices today. Researchers are urged to always keep this in mind when deploying devices on birds, and to measure their effects, not only by monitoring chick survival and body mass, but also by measuring behavioural and physiological parameters. These are parameters that always will be affected when capturing birds, and in fact by researchers' pure presence at a breeding site. Nevertheless, it is the researchers' responsibility to minimize their own influence on the study organisms in question, in order to promote rather than oppose conservation of vulnerable species, for ethical reasons, but also in order to assure the quality of their own research.

6. References

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7. Appendix

7.1 Kittiwake ANCOVAs

Different ANCOVAs on the different periods of the breeding season were considered because of the contrasting nutritional conditions between early and late chick rearing. This would, however, result in small sample sizes, and it was therefore decided to perform common ANCOVAs on all variables.

Sex, *treatment* and *period* (of the breeding season) were included as fixed factors in all of the models, as well as the interactions between *sex* and *treatment*, *sex* and *period*, *treatment* and *period* and between *sex*, *treatment* and *period*. Covariates in each model were chosen based on careful evaluation of which parameters were biologically the most reasonable to include.

Chick age was strongly correlated with period ($R^2 = 0.701$, $P < 0.001$) and date ($R^2 = 0.618$, $P < 0.001$). The age of chicks was, however, not registered for every adult bird captured. As the changing nutritional conditions in the middle of the breeding season were expected to affect the measured stress and behavioural parameters more than simply the date, period was used as a seasonal, bimodal categorical parameter in all of the kittiwake models. Furthermore, *BCI* was considered more likely to reflect true body condition of an individual than just the body mass, and was therefore included as covariate in models where appropriate. In addition, *BCI* and the logarithm of trip durations during the experimental period (*trip1log*) were strongly negatively correlated ($R^2 = 0.425$, $P < 0.001$), and could not be included in the same models if assumptions should be met. Therefore, separate analyses were performed when appropriate. Handling time of individual birds could potentially affect parameters of stress also in kittiwakes, but was very similar among both controls and equipped birds, and would therefore have a limited explanatory power. CORT levels, H/L-ratio and body mass at 1st capture were exclusively included as explanatory variables, instead of levels at 2nd capture or the change in levels during the experimental period. This was because these variables were expected to have the highest predictive power on dependent variables.

CORT difference

Kolmogorov-Smirnov tests revealed departures from normality for the H/L-ratio at 1st capture (*H/L 1*) and the standardized residuals from the linear regression of handling time on baseline CORT at 1st capture (*cort1_res*). *H/L 1* data was symmetric, and therefore not transformed. *Cort1_res* was negatively skewed and excluded from further analysis (because it was already transformed).

H/L 1, *trip1log*, time between 1st and 2nd capture (*capture_recapture*) and *BCI* were proposed as likely to explain some of the variation in CORT difference between 1st and 2nd capture. *capture_recapture*, *trip1log* and *BCI* were not statistically independent variables (significant interactions with *treatment*), thus violating the homogeneity of regression slopes assumption. No tendencies or significant relationships were found between these covariates and the CORT difference during the experimental period in models where treatment was excluded as explanatory variable. The covariates were therefore excluded from further analyses (table A1).

Table A1. Results of an ANCOVA explaining variation in change in CORT levels of black-legged kittiwakes during the experimental period, in relation to the explanatory variables treatment, sex, period of the breeding season (period), H/L-ratio at 1st capture (H/L 1) and the interactions between treatment and sex, treatment and period, period and sex and between period, treatment and sex. Rejected variables are presented with their values before being excluded from the models.

| <i>Final model</i> | df | F | P | R² | Estimate ± SE | r² |
|---------------------------|-----------|----------|----------|----------------------|----------------------|----------------------|
| treatment*period | 33 | 8.22 | 0.001 | 0.420 | | 0.354 |
| period | 33 | 4.26 | 0.048 | 0.420 | -0.68 ± 0.58 | 0.124 |
| <i>Rejected variables</i> | | | | | | |
| sex*period | 33 | 1.28 | 0.295 | 0.468 | | 0.083 |
| H/L 1 | 33 | 1.24 | 0.275 | 0.492 | 1.32 ± 1.19 | 0.044 |
| sex*treatment | 33 | 1.16 | 0.291 | 0.513 | | 0.043 |
| treatment | 33 | 0.25 | 0.619 | 0.513 | -0.63 ± 0.75 | 0.010 |
| sex | 33 | 0.80 | 0.381 | 0.513 | -0.57 ± 0.76 | 0.030 |
| sex*treatment*period | 33 | 0.00 | 0.981 | 0.514 | 0.04 ± 1.73 | 0.000 |

H/L-ratio difference

Kolmogorov-Smirnov tests revealed departures from normality for *H/L 1*, and data seemed to be scattered. No successful transformation was achieved, and the parameter was therefore excluded from further analysis.

Cort1_res, *BCI*, *trip1log*, *capture_recapture* and *chick age* were considered likely to explain some of the variation in the change in H/L-ratio between 1st and 2nd capture. Two separate analyses were performed: one with *BCI* (model 1: table A2) and one with *trip1log* (model 2: table A3) as explanatory variables. *Capture_recapture* was not statistically independent (significant interaction with *sex*) in model 2, thus violating the homogeneity of regression slopes assumption. This variable was therefore excluded from further analyses.

Table A2. Model 1: Results of an ANCOVA explaining variation in change in H/L-ratio of black-legged kittiwakes during the experimental period, in relation to the explanatory variables treatment, sex, period of the breeding season (period), adult body condition index (BCI), time between 1st and 2nd capture (capture_recapture), levels of CORT at 1st capture (cort1_res) and the interactions between treatment and sex, treatment and period, period and sex and between period, treatment and sex. Rejected variables are presented with their values before being excluded from the models.

| <i>Rejected variables</i> | df | F | P | R² | Estimate ± SE | r² |
|---------------------------|-----------|----------|----------|----------------------|----------------------|----------------------|
| capture_recapture | 30 | 0.86 | 0.361 | 0.029 | 0.08 ± 0.09 | 0.029 |
| treatment | 30 | 1.13 | 0.296 | 0.067 | -0.09 ± 0.09 | 0.039 |
| sex*period | 30 | 1.89 | 0.157 | 0.239 | | 0.185 |
| treatment*sex*period | 30 | 1.01 | 0.409 | 0.331 | | 0.121 |
| sex*treatment | 30 | 0.92 | 0.347 | 0.331 | | 0.040 |
| period | 30 | 0.79 | 0.383 | 0.331 | -0.11 ± 0.24 | 0.035 |
| sex | 30 | 0.71 | 0.409 | 0.331 | -0.45 ± 0.21 | 0.031 |
| BCI | 30 | 0.28 | 0.601 | 0.340 | -0.04 ± 0.07 | 0.013 |
| treatment*period | 30 | 0.02 | 0.905 | 0.340 | | 0.001 |
| cort1_res | 30 | 0.00 | 0.996 | 0.340 | 0.00 ± 0.08 | 0.000 |

Table A3. Model 2: Results of an ANCOVA explaining variation in change in H/L-ratio of black-legged kittiwakes during the experimental period, in relation to the explanatory variables treatment, sex, period of the breeding season (period), nest attendance (trip1log), levels of CORT at 1st capture (cort1_res) and the interactions between treatment and sex, treatment and period, period and sex and between period, treatment and sex. Rejected variables are presented with their values before being excluded from the models.

| <i>Rejected variables</i> | df | F | P | R² | Estimate ± SE | r² |
|---------------------------|-----------|----------|----------|----------------------|----------------------|----------------------|
| sex*period | 25 | 1.45 | 0.257 | 0.172 | | 0.172 |
| treatment*sex*period | 25 | 1.26 | 0.323 | 0.361 | | 0.229 |
| sex | 25 | 1.02 | 0.327 | 0.361 | -0.55 ± 0.23 | 0.056 |
| sex*treatment | 25 | 0.39 | 0.686 | 0.380 | | 0.046 |
| cort1_res | 25 | 0.50 | 0.492 | 0.380 | 0.06 ± 0.09 | 0.030 |
| treatment*period | 25 | 0.36 | 0.555 | 0.380 | 0.21 ± 0.29 | 0.022 |
| period | 25 | 0.22 | 0.644 | 0.380 | -0.38 ± 0.22 | 0.014 |
| trip1log | 25 | 0.19 | 0.670 | 0.388 | -0.13 ± 0.30 | 0.012 |
| treatment | 25 | 0.10 | 0.760 | 0.388 | -0.23 ± 0.24 | 0.006 |

Body mass change

BCI, *H/L 1*, *capture_recapture*, *chick age*, *trip1log* and *cort1_res* were proposed as likely to explain some of the variation in change in body mass during the experimental period. *H/L 1* limited the total sample size when included in the model, and was therefore excluded as covariate. Two separate analyses were performed: one with *BCI* (model 1: table A4) and one with *trip1log* (model 2: table A5) as explanatory variables.

Table A4. Model 1: Results of an ANCOVA explaining variation in change in body mass of black-legged kittiwakes during the experimental period, in relation to the explanatory variables treatment, sex, period of the breeding season (period), adult body condition index (BCI), time between 1st and 2nd capture (capture_recapture), levels of CORT at 1st capture (cort1_res) and the interactions between treatment and sex, treatment and period, period and sex and between period, treatment and sex. Rejected variables are presented with their values before being excluded from the models.

| <i>Final model</i> | df | F | P | R² | Estimate ± SE | r² |
|---------------------------|-----------|----------|----------|----------------------|----------------------|----------------------|
| BCI | 37 | 30.5 | 0.000 | 0.459 | -16.1 ± 2.92 | 0.459 |
| <i>Rejected variables</i> | | | | | | |
| sex | 37 | 2.32 | 0.137 | 0.517 | -8.55 ± 5.61 | 0.064 |
| cort1_res | 37 | 1.70 | 0.201 | 0.540 | -5.62 ± 4.31 | 0.049 |
| capture_recapture | 37 | 1.67 | 0.205 | 0.484 | -8.27 ± 6.41 | 0.045 |
| treatment*sex | 37 | 0.98 | 0.385 | 0.568 | | 0.060 |
| treatment | 37 | 0.20 | 0.656 | 0.568 | 4.37 ± 8.43 | 0.006 |
| period*treatment*sex | 37 | 0.67 | 0.616 | 0.607 | | 0.091 |
| treatment*period | 37 | 0.43 | 0.657 | 0.607 | | 0.031 |
| period | 37 | 0.19 | 0.666 | 0.607 | -8.36 ± 18.9 | 0.007 |
| period*sex | 37 | 0.01 | 0.919 | 0.607 | 17.5 ± 18.0 | 0.000 |

Table A5. Model 2: Results of an ANCOVA explaining variation in change in body mass of black-legged kittiwakes during the experimental period, in relation to the explanatory variables treatment, sex, period of the breeding season (period), nest attendance (trip1log), time between 1st and 2nd capture (capture_recapture), levels of CORT at 1st capture (cort1_res) and the interactions between treatment and sex, treatment and period, period and sex and between period, treatment and sex. Rejected variables are presented with their values before being excluded from the models.

| <i>Final model</i> | df | F | P | R² | Estimate ± SE | r² |
|---------------------------|-----------|----------|----------|----------------------|----------------------|----------------------|
| period | 31 | 9.47 | 0.004 | 0.240 | -20.4 ± 6.62 | 0.240 |
| <i>Rejected variables</i> | | | | | | |
| treatment*period | 31 | 1.39 | 0.267 | 0.308 | | 0.090 |
| treatment | 31 | 0.07 | 0.799 | 0.308 | -12.5 ± 9.32 | 0.002 |
| sex | 31 | 0.15 | 0.704 | 0.352 | -10.9 ± 16.2 | 0.006 |
| period*treatment*sex | 31 | 0.41 | 0.803 | 0.352 | | 0.063 |
| cort1_res | 31 | 0.08 | 0.786 | 0.354 | -1.73 ± 6.29 | 0.003 |
| trip1log | 31 | 0.03 | 0.865 | 0.355 | 2.81 ± 16.3 | 0.001 |
| treatment*sex | 31 | 0.02 | 0.893 | 0.355 | | 0.001 |
| period*sex | 31 | 0.00 | 0.975 | 0.355 | | 0.000 |
| capture_recapture | 31 | 0.00 | 0.977 | 0.355 | -0.44 ± 15.2 | 0.000 |

Nest attendance

BCI, *chick age*, *cort1res* and *H/L 1* were proposed as likely to explain some of the variation in trip durations, and included in the model (table A6).

Table A6. Results of an ANCOVA explaining variation in nest attendance (trip durations) of black-legged kittiwakes during the experimental period, in relation to the explanatory variables treatment, sex, period of the breeding season (period), adult body condition index (BCI), levels of CORT at 1st capture (*cort1_res*), H/L-ratio at 1st capture (H/L 1) and the interactions between treatment and sex, treatment and period, period and sex and between period, treatment and sex. Rejected variables are presented with their values before being excluded from the models.

| <i>Final model</i> | df | F | P | R² | Estimate ± SE | r² |
|---------------------------|-----------|----------|----------|----------------------|----------------------|----------------------|
| period | 29 | 53.7 | 0.000 | 0.707 | -0.57 ± 0.08 | 0.665 |
| treatment | 29 | 8.25 | 0.008 | 0.707 | 0.22 ± 0.08 | 0.234 |
| <i>Rejected variables</i> | | | | | | |
| treatment*period | 29 | 1.33 | 0.259 | 0.722 | -0.18 ± 0.15 | 0.049 |
| H/L 1 | 29 | 1.78 | 0.194 | 0.740 | 0.30 ± 0.22 | 0.067 |
| sex | 29 | 0.36 | 0.555 | 0.744 | 0.05 ± 0.08 | 0.015 |
| BCI | 29 | 0.30 | 0.592 | 0.747 | -0.05 ± 0.09 | 0.013 |
| <i>cort1_res</i> | 29 | 0.04 | 0.838 | 0.748 | -0.01 ± 0.06 | 0.002 |
| treatment*sex | 29 | 0.63 | 0.438 | 0.765 | 0.32 ± 0.28 | 0.032 |
| period*sex | 29 | 0.31 | 0.585 | 0.765 | 0.27 ± 0.28 | 0.016 |
| period*treatment*sex | 29 | 0.85 | 0.367 | 0.765 | | 0.043 |

7.2 Common guillemot ANCOVAs

Sex and *treatment* were included as fixed factors in all of the models, as well as the interaction between *sex* and *treatment*. Covariates in each model were chosen based on careful evaluation of which parameters were biologically the most reasonable to include.

A significant correlation was found between chick age and date of capture ($R^2 = 0.209$, $P < 0.001$). Chick age was considered a more likely parameter to affect adult physiology and behaviour than simply the date of capture. Therefore chick age was included as covariate in all common guillemot models. Similarly, BCI was used as a measure of body condition rather than body mass at first capture, as this parameter was considered more likely to reflect true body condition of an individual. Handling time of individual birds could potentially affect parameters of stress, but was very similar among both controls and equipped birds, and therefore had a limited explanatory power. CORT levels and body mass at 1st capture were exclusively included as explanatory variables, instead of levels at 2nd capture or the change in levels during the experimental period. This was because these variables were expected to have the highest predictive power on dependent variables.

CORT difference

BCI, *chick age*, *trip1log*, *capture_recapture* and CORT level at 1st capture (*cort1*) were proposed as likely to explain some of the variation in CORT difference between 1st and 2nd capture. *Trip1log* limited the total sample size when included in the model, and was therefore excluded as covariate. Two ANCOVAs were performed, one with (table A7) and one without *cort1* (since including *cort1* could potentially mask other significant relationships because of its relation to the dependent variable).

Cort1 was finally the only parameter explaining the variation in CORT difference significantly ($P = 0.037$). When *cort1* was removed from the model, no significant relationships were found.

Table A7. Results of an ANCOVA explaining variation in change in CORT levels of common guillemots during the experimental period, in relation to the explanatory variables treatment, sex, chick age, time between 1st and 2nd capture (*capture_recapture*), adult body condition index (*BCI*), levels of CORT at 1st capture (*cort1*) and the interaction between treatment and sex. Rejected variables are presented with their values before being excluded from the models.

| <i>Final model</i> | df | F | P | R² | Estimate ± SE | r² |
|---------------------------|-----------|----------|----------|----------------------|----------------------|----------------------|
| <i>cort 1</i> | 58 | 4.54 | 0.037 | 0.074 | -0.60 ± 0.28 | 0.074 |
| <i>Rejected variables</i> | | | | | | |
| <i>BCI</i> | 58 | 2.48 | 0.121 | 0.113 | -0.84 ± 0.53 | 0.042 |
| <i>treatment</i> | 58 | 0.77 | 0.383 | 0.125 | 0.89 ± 1.01 | 0.014 |
| <i>sex</i> | 58 | 0.52 | 0.476 | 0.134 | -0.74 ± 1.03 | 0.009 |
| <i>chick age</i> | 58 | 0.23 | 0.635 | 0.137 | 0.07 ± 0.15 | 0.004 |
| <i>capture_recapture</i> | 58 | 0.48 | 0.493 | 0.145 | -0.81 ± 1.18 | 0.009 |
| <i>treatment*sex</i> | 58 | 0.08 | 0.786 | 0.146 | | 0.001 |

Body mass change

BCI, *chick age*, *trip1log*, *capture_recapture* and *cort1* were proposed as likely to explain some of the variation in body mass change during the experimental period. *Trip1log* limited the total sample size when included in the model, and was therefore excluded as covariate. Two ANCOVAs were performed, one with (model 1: table A8) and one without (model 2: table A9) *BCI* as explanatory variable (since including *BCI* could potentially mask other significant relationships because of its relation to the dependent variable).

Table A8. Model 1: Results of an ANCOVA explaining variation in body mass change of common guillemots during the experimental period, in relation to the explanatory variables treatment, sex, chick age, adult body condition index (BCI), time between 1st and 2nd capture (capture_recapture), levels of CORT at 1st capture (cort1) and the interaction between treatment and sex. Rejected variables are presented with their values before being excluded from the models.

| <i>Final model</i> | df | F | P | R² | Estimate ± SE | r² |
|---------------------------|-----------|----------|----------|----------------------|----------------------|----------------------|
| capture_recapture | 58 | 12.7 | 0.001 | 0.298 | -29.1 ± 8.16 | 0.188 |
| BCI | 58 | 10.8 | 0.002 | 0.298 | -13.0 ± 3.97 | 0.164 |
| chick age | 58 | 5.12 | 0.028 | 0.298 | 2.53 ± 1.12 | 0.085 |
| <i>Rejected variables</i> | | | | | | |
| treatment | 58 | 2.73 | 0.105 | 0.332 | -11.8 ± 7.15 | 0.048 |
| cort1 | 58 | 0.95 | 0.335 | 0.344 | 1.98 ± 2.03 | 0.018 |
| treatment*sex | 58 | 0.04 | 0.958 | 0.345 | | 0.002 |
| sex | 58 | 0.00 | 0.974 | 0.345 | -1.99 ± 11.6 | 0.000 |

Table A9. Model 2: Results of an ANCOVA explaining variation in change in body mass of common guillemots during the experimental period, in relation to the explanatory variables treatment, sex, chick age, time between 1st and 2nd capture (capture_recapture), levels of CORT at 1st capture (cort1) and the interaction between treatment and sex. Rejected variables are presented with their values before being excluded from the models.

| <i>Final model</i> | df | F | P | R² | Estimate ± SE | r² |
|---------------------------|-----------|----------|----------|----------------------|----------------------|----------------------|
| capture_recapture | 58 | 7.84 | 0.007 | 0.219 | -23.8 ± 8.51 | 0.125 |
| chick age | 58 | 6.57 | 0.013 | 0.219 | 3.00 ± 1.17 | 0.107 |
| treatment | 58 | 4.07 | 0.048 | 0.219 | -15.3 ± 8.51 | 0.069 |
| <i>Rejected variables</i> | | | | | | |
| cort1 | 58 | 1.65 | 0.204 | 0.242 | 2.76 ± 2.15 | 0.030 |
| treatment*sex | 58 | 0.03 | 0.971 | 0.243 | | 0.001 |
| sex | 58 | 0.01 | 0.941 | 0.243 | -2.59 ± 12.4 | 0.000 |

Nest attendance

BCI, *chick age*, and *cort1* were proposed as likely to explain some of the variation in *trip1log*, and included as explanatory variable in the model (table A10).

Table A10. Results of an ANCOVA explaining variation in nest attendance (trip durations) of common guillemots during the experimental period, in relation to the explanatory variables treatment, sex, chick age, adult body condition index (BCI), levels of CORT at 1st capture (cort1) and the interaction between treatment and sex. Rejected variables are presented with their values before being excluded from the models.

| <i>Final model</i> | df | F | P | R² | Estimate ± SE | r² |
|---------------------------|-----------|----------|----------|----------------------|----------------------|----------------------|
| sex | 34 | 11.8 | 0.002 | 0.281 | 0.27 ± 0.08 | 0.269 |
| chick age | 34 | 4.62 | 0.039 | 0.281 | -0.02 ± 0.01 | 0.126 |
| <i>Rejected variables</i> | | | | | | |
| BCI | 34 | 1.11 | 0.300 | 0.306 | -0.05 ± 0.05 | 0.035 |
| treatment | 34 | 1.90 | 0.178 | 0.347 | 0.12 ± 0.08 | 0.060 |
| cort1 | 34 | 0.19 | 0.668 | 0.351 | 0.01 ± 0.03 | 0.006 |
| treatment*sex | 34 | 0.35 | 0.558 | 0.359 | | 0.012 |