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Relationships between POPs and baseline corticosterone levels in black-legged kittiwakes (*Rissa tridactyla*) across their breeding cycle

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ABSTRACT

Chronic exposure to persistent organic pollutants (POPs) in wildlife might alter the response to environmental changes through interference with the regulation of stress hormones. Here, we examined the relationship between blood concentrations of several POPs and baseline plasma corticosterone levels in the black-legged kittiwake (*Rissa tridactyla*) during three distinct periods in the breeding season. The concentrations of POPs and corticosterone increased, whereas body mass decreased progressively from the pre-laying period to the incubation and the chick rearing period. ∑PCB (polychlorinated biphenyls) correlated positively with the baseline corticosterone levels during the pre-laying period, which might suggest that PCBs affect the regulation of corticosterone. However, this relationship was not found during the incubation or the chick rearing period. Possible explanations are discussed with emphasis on how total stress/allostatic load is handled during different periods and conditions.

1. Introduction

Persistent organic pollutants (POPs) are transported by the atmosphere and ocean currents to remote locations, for example the Arctic, where they are biomagnified in the food chain (Borgå et al., 2001; Fisk et al., 2001). Hence, in arctic top predators POPs may reach concentrations which affect their health (AMAP, 1998, 2004; Gabrielsen, 2007). In recent years, the ability of POPs to affect the endocrine system, so-called endocrine disruption, has received increased attention. POPs may interfere with several steps of the endocrine regulation, including hormone synthesis, binding, transport and degradation, but the mechanisms are still poorly understood (Giesy et al., 2003; Odermatt et al., 2006). There has been much focus on POP-induced changes in the regulation of sex hormones and thyroid hormones (Goncharov et al., 2009; Jurgella et al., 2006; Murugesan et al., 2008; Oskam et al., 2003; Rolland, 2000; Verreault et al., 2004, 2006, 2008), but less is known about the potential effects on corticosterone, an important stress hormone in birds. This hormone enables individuals to cope with short- and long-term environmental stress; e.g. food shortage, inclement weather, presence of predators, social aggressive interactions (Wingfield and Sapolsky, 2003). In birds, corticosterone is finely regulated in relation to such stressors and risks. Acute and unpredictable stressors are met with a sharp increase in corticosterone levels within a few minutes, known as the stress response (Romero, 2004). Moreover, on a seasonal time scale, baseline corticosterone levels are primarily regulated in relation to permissive or preparative environmental challenges (Sapolsky et al., 2000), and are responsible for functions such as regulation of foraging activity (Angelier et al., 2007c; Astheimer et al., 1992; Landys et al., 2006), energy allocation between self-maintenance or parental behaviour (Angelier et al., 2007a) and mobilisation of stored reserves (Gray et al., 1990; Sapolsky et al., 2000). The baseline corticosterone level is thus related to the food quality and availability, energy intake and body mass (Angelier et al., 2007c; Kitaysky et al., 1999; Marra and Holberton, 1998), as well as parental effort and investment (Angelier and Chastel, 2009; Angelier et al., 2009a, b).

Contaminants may influence corticosterone regulation (Franceschini et al., 2008; Glennemeier and Denver, 2001; Lorenzen et al., 1999; Love et al., 2003; Verboven et al., 2010), and it is

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important to know how susceptible corticosterone is to alterations in contaminant concentrations. For example in arctic seabirds that are facing both short-term stressors (e.g. inclement weather and food shortage) and long-term challenges (climate change,) which require a finely regulated corticosterone response in order to allow proper adaptations. Although, the mechanisms through which POPs may influence corticosterone regulation are poorly known, it is likely that such compounds disrupt one of the many steps of corticosterone regulation causing dysfunction of the HPA axis (Carsia and Harvey, 2000; Pottinger, 2003). Corticosterone is synthesised, sustained and excreted by numerous mechanisms throughout the body. Particularly the adrenal gland is suspected to be vulnerable to effects of POPs due to its high lipid content and multiple sites for interference (e.g. enzymes and receptors) (Hinson and Raven, 2006; Odermatt et al., 2006). Furthermore, POPs may represent stressors (Bustnes et al., 2001, 2002), because they may impose negative health effects and increase the allostatic load. The allostatic load is the total cost of different stages in life-histories such as reproduction, and allostatic overload results when the available resources are inadequate to meet these costs (McEwen and Wingfield, 2003). As such, the allostatic load may increase when resources are allocated to biotransformation, detoxification and excretion of POPs (Parkinson and Ogilvie, 2008), and to repairing lesions, infections and damage on DNA and other molecules (Preston and Hoffmann, 2008). During reproduction, allostatic overload may lead to cessation of the parental investment, a central prediction of the hypothesis of trade-offs between reproduction and survival in long-lived animals (Kitaysky et al., 1999, 2001; Verboven and Tinbergen, 2002; Wingfield and Kitaysky, 2002).

The baseline corticosterone level is at its peaks during sustained breeding activities (Kitaysky et al., 1999; Landys et al., 2006; Chastel et al., 2005), e.g. during parental food provisioning (Fyhn et al., 2001). In birds, the high baseline corticosterone level during breeding promotes metabolism and loss of body mass (Landys et al., 2006; Kitaysky et al., 1999; Moe et al., 2002). This again leads to re-mobilisation and increased concentrations of circulating lipophilic POPs (Bustnes et al., 2010; Henriksen et al., 1996; Wiemeyer and Cromartie, 1981). Hence, POPs may exert their highest effect potential in the reproductive periods (Bustnes et al., 2010; Verreault et al., 2004). In breeding glaucous gulls (*Larus hyperboreus*), a gull species known for carrying high POP loads (Borgå et al., 2001; Bustnes et al., 2003a,b), Verboven et al. (2010) recently found that high POP levels were related to elevated baseline and a lower stress induced levels of corticosterone. Moreover, positive relationships have been reported in herring gulls (*Larus argentatus*) and black guillemots (*Cepphus grylle*) (Peakall et al., 1981). However, other studies in herring gulls and tree swallows (*Tachycineta bicolor*) have reported negative relationships (Lorenzen et al., 1999; Martinovic et al., 2003; Mayne et al., 2004). Consequently, it is not well understood how POPs may affect corticosterone levels in birds.

The aim of the present study was to examine relationships between POPs and baseline corticosterone level of an arctic seabird, the black-legged kittiwakes (*Rissa tridactyla*, hereafter 'kittiwake') in Svalbard. Specifically, we focused on the dynamics of both POPs (PCBs, *p,p'*-DDE, HCB and oxychlordane) and baseline corticosterone in adult kittiwake across the main stages of reproduction (pre-breeding, incubation and chick rearing). POPs concentrations in the blood are known to increase with decreasing body mass (Henriksen et al., 1996; Bustnes et al., 2010) and kittiwake are known to lose body mass from the pre-breeding to the chick rearing stage (Moe et al., 2002). Hence, we expected the blood concentrations of lipid soluble POPs to increase from the pre-breeding to the incubation and chick rearing periods as the loss of body mass progressed, and that the potential effects of POPs on corticosterone levels should be strongest during the incubation and chick rearing periods. Secondly, we hypothesized that individuals with high blood concentrations of POPs would show elevated baseline levels of corticosterone (Verboven et al., 2010).

2. Materials and methods

2.1. Study species and field procedures

The kittiwake is a long-lived gull, with a circumpolar distribution, breeding in colonies on cliffs (Cullen, 1957). In Svalbard, it normally lays two eggs (1–3) and feed mainly on capelin (*Mallotus villosus*), polar cod (*Boreogadus saida*) and amphipods (Mehlum and Gabrielsen, 1993; Strøm, 2005). The study area was Krykkjefjellet, a seabird cliff located 6 km southeast of Ny-Ålesund in Kongsfjorden, Svalbard (78°54′N, 12°13′E, Fig. 1). The kittiwakes were caught on their nest with a snare on a long fishing rod. All birds were in adult breeding plumage; i.e. no dark patches on their heads or black fields on their outer primaries (Cramp and Simmons, 1983), and were potential breeders. In Svalbard, kittiwakes breed during continuous daylight and monthly average air temperatures are −11.1, −4, 1.5 and 4.9 °C in April, May, June and July, respectively (Ny-Ålesund 1961–1990, Norwegian Meteorological Institute, Oslo, Norway; http://www.eklima.met.no).

Blood samples for hormone and contaminant analyses were taken from free-living, adult birds of both sexes during the pre-breeding (April 26–29, $n = 35$), incubation (June 26–July 05, $n = 14$) and chick rearing period (July 23–27, $n = 16$) in 2007. Mean air temperatures were −8.7, 5.9 and 7.9 during those three periods, respectively (Norwegian Meteorological Institute, Oslo, Norway; http://www.eklima.met.no). Median hatching date in 2007 was July 12, but it may vary from

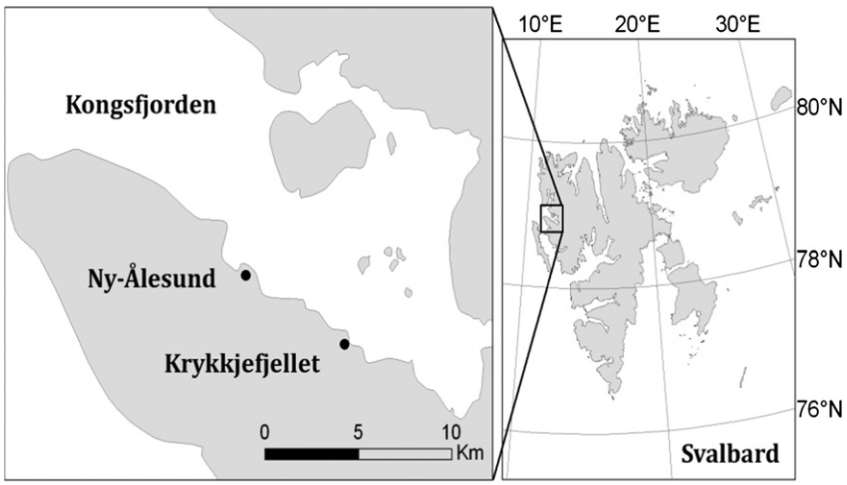

Fig. 1. Location of the study colony Krykkjefjellet in Kongsfjorden, Svalbard.

July 1 to 25 between years (Moe et al., 2009). The blood samples were taken from the alar vein using a heparin treated 5 mL syringe and a 23G needle. We included blood samples taken within 5 min (range 2:57–5:00 min) for baseline corticosterone, following previous studies of the same population (Angelier et al., 2007b; Chastel et al., 2005). There was no effect of sampling time on levels of corticosterone during this time interval ($F = 0.09$, df = 63, $P = 0.77$), so the data were considered to reflect baseline levels. In field, the samples were immediately stored in darkness at ambient temperatures in June and July. In April, the samples were kept from freezing. When returning from the field, after 1–5 h, about 0.5 ml blood from each bird was centrifuged to separate blood plasma for hormone analyses, before all the samples were frozen at −20 °C.

Body mass and skull length (head and bill) were measured with an accuracy of 5 g and 0.1 mm, respectively and the birds were banded with a metal and a colour ring. Finally, the birds were marked on the head with a water resistant pen, to avoid recaptures. Permissions to work in the area were granted by the Governor of Svalbard.

2.2. POPs analyses

The concentrations of POPs in the blood samples were analyzed at the Norwegian Institute for Air Research (NILU) in Tromsø. The following compounds were analysed: the PCBs (CB-28, -31, -33, -37, -47/49, -52, -99, -101, -105, -118, -123, -128, -138/-163, -141, -149, -153, -156, -157, -167, -170, -180, -183, -187, - 189 and -194), DDTs and metabolites (DDE and DDD), HCB, α-, β-, γ-HCH, heptachlor, heptachlor epoxide, trans-, cis-, and oxychlordane, mirex and trans- and cisnonachlor. The compounds chosen for further investigation was the ∑PCBs (CB-28, -99, -105, -118, -138/-163, -153, -170, -180, -183 and -187), HCB, *p,p′*-DDE and oxychlordane.

To a whole-blood sample of 0.9–2.0 ml, a 100 μL internal standard solution was added (^{13}C-labelled compounds [α-, β-, γ-HCH, HCB, DDT, DDE, PCB-28, -52,-101, -105, -118, -123, -138, -153, -180] from Cambridge Isotope Laboratories: Woburn, MA, USA). The sample was extracted twice with 6 ml of n-hexane, after denaturation with ethanol and a saturated solution of ammonium sulphate in water. Matrix removal on florisil columns, separation on an Agilent Technology 7890 GC and detection on an Agilent Technology 5975C MSD were performed as described by Herzke et al. (2009). The limit for detection was threefold the signal-to-noise ratio, and for the compounds investigated the limit ranged from 0.4 to 122 pg/g wet weights (ww). For validation of the results, blanks (clean and empty glass tubes treated like a sample, 13 in total) were run for every tenth sample, while standard reference material (9 in total, 1589a human serum from NIST) was run for every 14 samples. There was no contamination of the blank samples, and the accuracy of the method was within the 20% range.

2.3. Sexing procedure and hormone level analyses

The hormone levels and the sex of the birds were determined at the Centre d'Etudes Biologiques de Chizé (CEBC), France. To sex the birds, DNA was extracted from red blood cells and the CHD gene was amplified in a PCR procedure, as described by Weimerskirch et al. (2005). Total (free plus bound) plasma corticosterone levels were determined by radioimmunoassay (RIA) as described by Lormee et al. (2003), following the procedure for steroid hormones by Mauget et al. (1994). Minimal detectable corticosterone levels were 0.5 ng/mL (lowest measurement: 2.9 ng/mL). The samples ($n = 65$) were run in three assays; the coefficients of intra- and inter assay variation were assessed using several reference plasma samples within each and separate assays, and were 10.1 and 8.3%, respectively.

2.4. Statistical analyses

All the statistics were done in *R* (v2.11.1; R, 2010). Samples with POP concentrations below the detection limit (DL) were assigned to 0.5 × DL. This included 5 samples for oxychlordane, 1 for HCB and 2 for DDE. Boxplots were used in initial explanatory analyses, and these samples at 0.5 × DL were identified as outliers ($n = 8$), with large gaps to the lower 95% confidence limits. Furthermore, model diagnostics (QQ-plots, residuals versus fitted, residuals versus leverage, scale-location) were used to ensure that the assumptions of linear models were adequately met (linearity, independence, constant variance and normality). Accordingly, all POPs and corticosterone samples were $\log_e$ transformed, and the 8 samples identified as outliers were excluded from the final analyses.

We used linear models (lm) to test how corticosterone levels were related to POPs, breeding period, sex, body mass, head length and the interactions 'POP × period' and 'body mass × period'. The lipid soluble POPs are highly intercorrelated, and each POP was consequently analyzed in separate linear models. Many models can be formed with different combinations of these explanatory variables, and we used a model selection approach with Akaike's information criteria corrected for small sample size (AICc) to obtain the best balance between bias and precision. Models were ranked after their AICc values, and the model with lowest AICc was the highest ranked model (Anderson, 2008; Burnham and Anderson, 2002). To test the strength of the variables, each variable's relative importance (VI) was calculated by summing up the AICc weights of all models which included a certain variable (Burnham and Anderson, 2002). In this way, the strength of the model selection procedure could be controlled (Anderson, 2008), since important variables will be included in many models with high AICc weights, and thus gain a high VI.

Linear models require independent data, and 28 samples were excluded from birds that were sampled more than once, giving a final sample of 65 kittiwakes. Excluded samples were selected from the period with highest sample size. We also performed mixed-effects linear models (lme) on the larger dataset ($n = 93$) where individuals also were represented more than once. These results did not change the conclusions, but some models did not converge, probably because too few individuals were sampled more than once. Hence, a complete model selection procedure could not be performed with this approach, and we chose to present the linear models with independent data.

ANOVAs were used in the linear models to compare body mass and levels of hormone and POPs in different periods among the sexes, and *t*-tests were used for pair-wise post hoc comparisons of means. Significance level was 0.05, and means are reported with ±1 standard error.

3. Results

3.1. Levels and dynamics in body mass, POPs and hormones

Body mass of female kittiwakes was on average 57 ± 9.0 g lower than males (469 ± 6.3 g, $F_{1,\ 59} = 65.7$, $P < 0.001$) in all periods (*sex* × *period*, $F_{2,\ 59} = 0.6$, $P = 0.54$, Fig. 2). Body mass was on average significantly lower (5.6%) in the pre-breeding period (PB) compared to the incubation (INC) period when sexes were pooled ($t = 2.38$, df = 33.5 $P = 0.023$, Table 1, Fig. 2), and the difference was 8.8% from the PB to the chick rearing (CR) period ($t = 3.50$, df = 34.0, $P = 0.023$). ∑PCB concentration in the blood (ww) increased significantly from the PB period to the INC period ($t = -3.10$, df = 14.4 $P = 0.008$, Table 1, Fig. 2), and the CR period ($t = -5.21$, df = 17.7, $P < 0.001$). The mean concentrations increased by 113 and 150% (*period*, $F_{2,\ 59} = 20.4$, $P < 0.001$, Fig. 2), respectively, when sexes were pooled (*sex*, $F_{1,\ 59} = 0.4$, $P = 0.52$; *sex*period*, $F_{2,\ 59} = 0.4$, $P = 0.69$, Fig. 2). Oxychlordane showed a similar increase in mean concentrations; 119 and 103% for PB–INC ($t = -4.12$, df = 14.5, $P < 0.001$) and PB–CR ($t = -3.37$, df = 15.5, $P = 0.004$), respectively. HCB increased significantly only from the PB to the CR ($t = -2.41$,

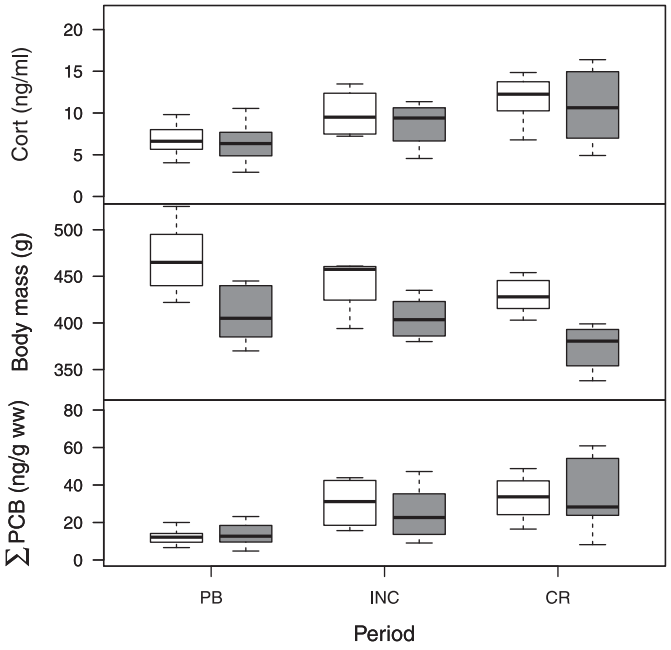

Fig. 2. Box plot of corticosterone (Cort), body mass and ∑PCB for male (white) and female (grey) kittiwakes during the pre-breeding (PB), incubation (INC) and chick rearing (CR) periods. Shown are median value (thick line) along interquartile range (IQR, top and bottom of box), and maximum- and minimum values within 1.5 IQR (whiskers).

df = 18.7, $P = 0.03$), with a change in mean concentrations of 29%. Finally, there was no significant change in mean *p,p′*-DDE concentrations (PB–INC: −11%, $t = 0.49$, df = 15.6, $P = 0.63$).

There was a marginally significant increase in corticosterone level from the PB to the INC period ($t = -1.99$, df = 20.3, $P = 0.06$, see Table 1, Fig. 2), whereas the increase from the PB to the CR period was significant ($t = -3.92$, df = 25.9, $P < 0.001$). The mean concentrations increased 33 and 58%, respectively (period, $F_{2, 59} = 8.1$, $P < 0.001$, Fig. 2), with no significant differences between the sexes (*sex*, $F_{1, 59} = 0.0$, $P = 0.90$, Fig. 2) and no significant interaction between sex and period (*sex* × *period*, $F_{2, 59} = 0.1$, $P = 0.88$, Fig. 2).

3.2. Relationships between POPs and hormones

The five best ranked models explaining variation in corticosterone levels in relation to each of the investigated POPs are presented in Table 2. Breeding period was included in all the best models (Table 2) and was a strong predictor with high variable importance (VI &gt ;0.99, Table 3). Body mass, sex and head showed overall low variable importance, and no estimates were presented for these variables. ∑PCB and HCB were the only POPs included in the best models (Table 2). ∑PCB showed a strong variable importance (VI = 0.88, Table 3), while HCB did not (VI = 0.32, Table 3). Hence, ∑PCB was the only class of POPs with a significant relationship to corticosterone. Furthermore, the interaction between period and ∑PCB was important (Table 2, Table 3). The estimates showed that ∑PCB was significant and positively related to corticosterone during the pre-breeding period (estimate: 0.42, df = 59, $P = 0.008$, Table 4, Fig. 3), but not during the incubation or chick rearing period (Table 4). None of the other POPs (HCB, *p,p′*-DDE, oxychlordane) were significantly related to corticosterone.

4. Discussion

As predicted, all POPs except *p,p′*-DDE, increased from the pre-breeding to the incubation and chick rearing period (Table 1). Compared to previous studies of kittiwakes, the loss of body mass was, however, lower in the present study (e.g. Henriksen et al., 1996; −18%, here; −8.8%), so in a more stressful year, the POP concentrations may be higher (Bustnes et al., 2010; Wiemeyer and Cromartie, 1981). Baseline corticosterone levels were not correlated with blood concentrations of POPs during the incubation and chick rearing periods, contrary to our prediction, in neither sex. However, there was a significant positive correlation between baseline corticosterone and ∑PCB levels during the pre-breeding period (Fig. 3). This relationship might result from direct effects, alternatively from co-variation between the two traits.

If PCB impact upon corticosterone levels during pre-breeding period, it may have negative consequences for the breeding success and fitness of the kittiwake. A high baseline corticosterone level in pre-breeding kittiwakes have been shown to increase the propensity for non-breeding (Goutte et al., 2010b), lower the nest attendance (Angelier et al., 2009a) and delayed breeding (Goutte et al., 2010a, 2011). In addition, energy costs related to e.g. detoxification of POPs (Parkinson and Ogilvie, 2008; Preston and Hoffman, 2008) might elevate the baseline corticosterone level by increasing the allostatic load (McEwen and Wingfield, 2003). Under stressed conditions, this might trigger allostatic overloads, forcing birds to cease reproduction in accordance with current life history theory; i.e. trade-offs between reproduction and survival in long-lived animals (Kitaysky et al., 1999, 2001; Verboven and Tinbergen, 2002; Wingfield and Kitaysky, 2002). However, the dynamics between POPs and corticosterone is hard to predict. For example, studies of herring gulls (Peakall et al., 1981) and glaucous gulls (Verboven et al., 2010) have shown positive relationships between POPs and corticosterone levels, whereas studies on tree swallows (Martinovic et al., 2003; Mayne et al., 2004) and herring gull embryos (Lorenzen et al., 1999) reported negative relationships between the two parameters. However, the relationship between POPs and corticosterone levels could therefore depend on species, life history stage, concentrations and contaminants studied. Our study highlights that the effect may also depend on the period of sampling.

Table 1
Summary statistics for body measurements, hormones and POPs in kittiwakes from Kongsfjorden, Svalbard. "ww": wet weight.

Variable	Males				Females			
	N	Mean	Std. error	Median	*N*	Mean	Std. error	Median
Pre-breeding:								
Body mass (g)	18	469	7.5	465	17	411	6.4	405
Scull (mm)	18	94.1	0.5	94.3	17	90.1	0.4	89.8
Corticosterone (ng/ml)	18	7.1	0.5	6.6	17	7.2	1.0	6.3
∑PCB (ng/g ww)	18	12.5	1.1	12.2	17	14.9	2.0	12.7
p,p′-DDE (ng/g ww)	18	3.6	0.5	3.0	17	3.3	0.5	2.9
HCB (ng/g ww)	18	1.3	0.1	1.2	17	1.6	0.1	1.6
Oxychlordane (ng/g ww)	16	0.8	0.1	0.7	15	0.9	0.1	0.9
Incubation:								
Body mass (g)	4	443	16.2	458	10	405	6.7	404
Scull (mm)	4	94.2	0.8	94.4	10	90.6	0.5	90.8
Corticosterone (ng/ml)	4	9.9	1.5	9.5	10	9.3	1.4	9.4
∑PCB (ng/g ww)	4	30.5	7.0	31.2	10	28.7	6.4	22.7
p,p′-DDE (ng/g ww)	3	4.9	1.9	3.8	9	2.5	0.7	2.0
HCB (ng/g ww)	4	1.6	0.3	1.6	10	1.7	0.2	1.7
Oxychlordane (ng/g ww)	4	1.8	0.3	1.7	10	1.8	0.3	1.6
Chick rearing:								
Body mass (g)	8	429	6.5	428	8	374	8.1	381
Scull (mm)	8	94.7	0.4	94.8	8	89.4	0.9	89.5
Corticosterone (ng/ml)	8	11.8	1.0	12.3	8	10.8	1.6	10.6
∑PCB (ng/g ww)	8	33.2	4.0	33.7	8	35.2	6.7	28.3
p,p′-DDE (ng/g ww)	8	2.5	0.9	1.3	8	3.7	1.0	2.6
HCB (ng/g ww)	8	1.7	0.1	1.7	7	2.2	0.3	2.2
Oxychlordane (ng/g ww)	8	1.4	0.2	1.3	7	1.9	0.4	1.6

Table 2
Model selection table showing the five best models explaining variation in corticosterone levels in kittiwakes in relation to each of the POPs (∑PCB, HCB, *p,p′*-DDE and oxychlordane) and the other explanatory variables (head, sex, breeding period, body mass and the interactions 'POP × period' and 'body mass × period'). Log_e transformed values have been used for corticosterone and the POPs. The number of parameters in each model is given by "*k*". and the difference in AICc between the best model and the other models are given by ΔAICc.

Models	AICc	ΔAICc	AICc weights	*k*
Corticosterone – ∑PCB				
1. ∑PCB. Period. ∑PCB × Period	66.24	0	0.220	7
2. ∑PCB. Period. ∑PCB × Period. Sex	66.55	0.312	0.188	8
3. ∑PCB. Period. ∑PCB × Period. Body mass	66.96	0.715	0.154	8
4. ∑PCB. Period. ∑PCB × Period. Head	68.06	1.819	0.089	8
5. ∑PCB. Period. ∑PCB × Period. Sex. Body mass	69.08	2.840	0.053	9
Corticosterone – HCB				
1. Period. HCB	67.46	0	0.262	4
2. Period	68.94	1.480	0.125	5
3. Period. Sex	69.07	1.609	0.117	5
4. Period. Body mass	69.46	1.998	0.097	5
5. Period. Head	69.71	2.243	0.085	5
Corticosterone – *p,p′*-DDE				
1. Period	68.70	0	0.246	4
2. Period. Sex	69.84	1.139	0.139	5
3. Period. Body mass	70.13	1.429	0.120	5
4. Period. Head	70.31	1.601	0.110	5
5. Period. *p.p′*-DDE	71.05	2.344	0.076	5
Corticosterone – Oxychlordane				
1. Period	57.86	0	0.260	4
2. Period. Oxy.	59.25	1.385	0.130	5
3. Period. Sex	59.81	1.947	0.098	5
4. Period. Body mass	59.85	1.982	0.096	5
5. Period. Head	60.23	2.368	0.079	5

To our knowledge this is the first study to investigate the relationship between POPs and corticosterone levels across several breeding stages in birds, including the pre-breeding, incubation and chick rearing periods. The relationship between ∑PCB levels and corticosterone levels during the pre-breeding period, but not during incubation or the chick rearing period, did not support our predictions. However, there was no indication that the relationship could be confounded with body condition, which is known to affect both baseline corticosterone (Kitaysky et al., 1999) and POP levels (Bustnes et al., 2010), and ∑PCB showed a relatively strong variable importance (Table 3). However, caution is needed in the interpretation since we do not know how well body mass reflects the true body condition (Langseth et al., 2000; Jacobs et al., 2011). Thus, we suggest the following post hoc explanations for relationship between PCBs and baseline corticosterone found in the pre-breeding period.

Firstly, PCBs/POPs might impact upon CORT levels during incubation and chick rearing, but this could be masked by the strong influence of natural factors on the baseline corticosterone level during these periods. These factors, including breeding duties, food availability and energy balance (Angelier et al., 2007a, c, 2009a; Landys et al., 2006; Marra and Holberton, 1998), are known to cause a strong increase in the baseline corticosterone level (Kitaysky et al., 1999; Romero, 2002). The sample size in the pre-breeding period (35) was higher than during incubation (14) and chick rearing (16). Thus, the resolution was lower in the latter periods, and a higher resolution may be needed in order to avoid the possibly masking effect of naturally elevated corticosterone levels. Furthermore, in species with a higher contaminant burden, the causal effect of POPs on stress hormones is stronger, as seen in glaucous gulls during the demanding incubation period (Verboven et al., 2010). Glaucous gulls are at a higher trophic level and their contaminant burden is almost ten times higher than in kittiwakes (Borgå et al., 2001; Bustnes et al., 2003b). The baseline corticosterone levels in kittiwakes may relate to POPs if the concentrations are higher than in the present study, e.g. due to harsher conditions in which body mass loss is higher and concentration of POPs

Table 3
Variable importance (VI) of different parameters explaining corticosterone concentration in kittiwakes. The values were obtained from the model selection procedure in Table 2. Separate model selections were performed for each of the persistent organic pollutants (POPs) ∑PCB, HCB, *p,p′*-DDE and oxychlordane. Variables with a high VI (>0.8) are marked in bold.

Variable	POP included in the model selection			
	∑PCB	HCB	*p,p′*-DDE	Oxy-CD
POP	**0.88**	0.32	0.24	0.33
Period	**0.99**	**1.00**	**1.00**	**0.99**
Period × POP	**0.83**	0.03	0.02	0.03
Body mass	0.35	0.27	0.30	0.28
Sex	0.36	0.29	0.31	0.28
Head	0.24	0.24	0.26	0.26
Period × Body mass	0.05	0.03	0.03	0.03

Table 4
Estimates, standard errors (SE) and significance levels (*p*) for the best model explaining corticosterone concentration in kittiwakes when ∑PCB was included as the focal POP. These values are not presented for the other POPs, as they had low VI and clearly had no impact on the level of corticosterone. The estimates for the terms log(∑PCB) and intercept represent the slope estimates and the intercept for log(∑PCB) during the pre-breeding (PB) period. The slopes and intercepts for the incubation (INC) and chick rearing (CR) period are found by adding the respective estimates of the terms log (∑PCB) × Period and Period. Note that PCB is given in pg/g in this table.

Variable	Estimate	SE	*p*
Intercept	−2.03	1.43	0.16
log (∑PCB)	0.42	0.15	0.008
Period: INC–PB	6.27	2.20	0.006
Period: CR–PB	6.60	2.40	0.008
log (∑PCB): Period: INC–PB	−0.62	0.22	0.008
log (∑PCB): Period: CR–PB	−0.63	0.24	0.011

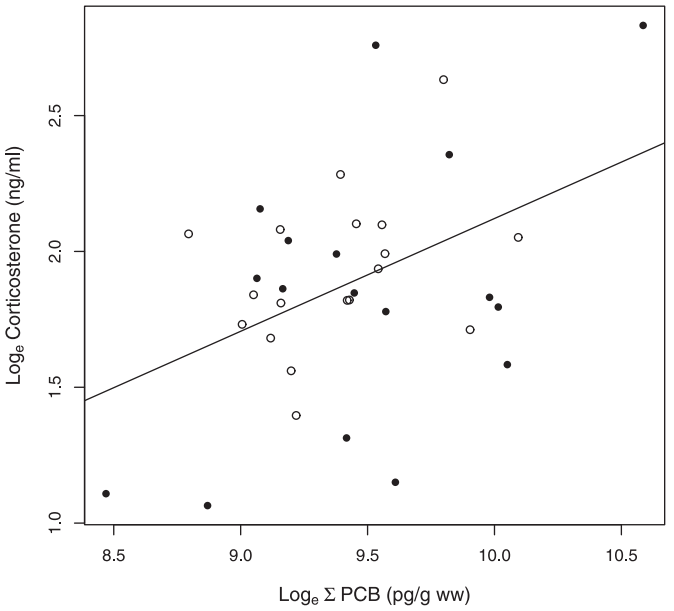

Fig. 3. The relationship between corticosterone concentration and ∑PCBs in male (open circles) and female (filled circles) kittiwakes during the pre-breeding period ($n = 35$). Linear regression: $\log_e\text{Cort} = 0.42\ (\pm 0.15) \times \log_e\sum\text{PCB} - 2.03\ (\pm 1.43)$ ($P = 0.008$, $r^2 = 0.19$).

increase more, as seen in other bird studies (e.g. Bustnes et al., 2010; Henriksen et al., 1996; Wiemeyer and Cromartie, 1981).

Secondly, during the different breeding stages we may have sampled birds of different age, experience and individual quality. Indeed, during pre-breeding it is possible that we included both birds that bred later and birds that did not breed, whereas only birds with eggs or chicks were sampled in the latter periods. As birds of poor body condition tend to allocate resources from breeding to self-maintenance (Angelier et al., 2007a, 2009a), the birds sampled during pre-breeding might on average have been of lower quality compared to the other seasons, which might explain the observed correlation between PCBs and baseline corticosterone during this period.

Finally, 2007 was a year with favourable conditions for the kittiwakes, as indicated by the high production of chicks compared to previous seasons (Moe et al., 2009). Hence, we would expect good body condition (Moe et al., 2002) and low levels of both baseline corticosterone (Kitaysky et al., 1999; Lanctot et al., 2003; Welcker et al., 2009) and POPs (Bustnes et al., 2005b). However, in poor years, the kittiwake will experience a larger loss of body mass followed by remobilazation of POPs (Bustnes et al., 2005b), which might result in similar relationships as seen in the glaucous gulls (Verboven et al., 2010). Paradoxically, as the baseline corticosterone level is responsible for adaptations to natural variations and man-made changes in the environment, potential effects of POPs on corticosterone might inhibit the ability to adapt to the environment (Jenssen, 2006; Verboven et al., 2010; Wingfield and Sapolsky, 2003). This implies that an animal's response to a normal stressor may be affected by POPs and vice versa (Pottinger, 2003). Such effects might be more pronounced under stressful conditions, e.g. during large changes in the environment, when the ability to adapt is most crucial. This highlights the importance of investigating POPs not *per se*, but in context with other factors affecting the allostatic load, such as environmental, ecological and physiological stressors (Bustnes et al., 2006; Letcher et al., 2010).

In the present study, the ∑PCB levels (mean values: 12.5–35.5 ng/g, Table 1) were far higher than the levels of other compounds (HCB, *p,p′*-DDE, oxychlordane; mean values: 0.7–4.9 ng/g, Table 1), possibly explaining why only PCBs alone were significantly related to the baseline corticosterone levels. As lipophilic POPs are closely inter-correlated (Bustnes, 2006), it is difficult to assign an effect to a specific PCB congener, a mix of congeners or even a mix of PCBs and other compounds. Thus, despite the fact that PCBs alone show a relationship to the corticosterone level, other POPs might also affect baseline corticosterone level in pre-breeding kittiwakes. The results from the present study are supported by various findings of PCB-related effects in other seabird species, particularly the glaucous gull from the same area and food web (Bjørnøya, Svalbard). For example, POPs affect immune function (Bustnes et al., 2004) and the survival of adult gulls (Bustnes et al., 2003b); i.e. heavily contaminated gulls have been found dead (Gabrielsen et al., 1995). Other effects, such as reduced chick growth (Bustnes et al., 2005a) and chick immunity (Sagerup et al., 2009) have also been reported. However, since glaucous gulls are at a higher trophic level, have higher POP concentrations (mean blood-values of PCB-153 alone: 106–237 ng/g (ww) (Bustnes et al., 2004), compared to ∑PCB 12.5–35 ng/g (ww) in the present study) and are known to metabolise POPs poorly compared to kittiwakes (Borgå et al., 2007; Henriksen et al., 2000), such effects may not be expected in kittiwakes.

In conclusion, baseline corticosterone and POP levels increased throughout the investigated periods, as expected, but significant relationships between POPs and baseline corticosterone was only found for PCB in the pre-breeding period, despite the relatively low POP levels in this period. Hence, this study highlights the needs for further studies on effects from POPs during the reproductive season and the necessity of assessing not only POPs *per se*, but together with other factors affecting the allostatic load, such as physiological, ecological and environmental factors. Notably, we would like to suggest experimental approaches to unravel the true mechanisms.

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