



## Demographic, endocrine and behavioral responses to mirex in the South polar skua

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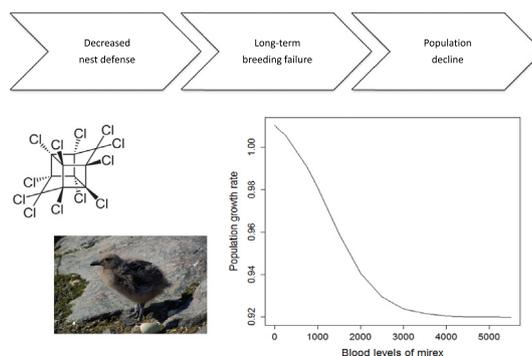
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### HIGHLIGHTS

- Blood levels of POPs did not affect survival rate nor long-term breeding probability.
- Long-term breeding success decreased with increasing mirex and stress levels.
- Stress and parental care hormones were not affected by POP burden.
- Nest defense behavior was weakened in breeders bearing high mirex levels.
- Demographic responses to POP burden were projected using matrix population models.

### GRAPHICAL ABSTRACT



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### ABSTRACT

Population consequences of chronic exposure to multiple pollutants at low environmental doses remain speculative, because of the lack of appropriate long-term monitoring surveys. This study integrates proximate and ultimate aspects of persistent organic pollutants (POP) burden in free-living vertebrates, by coupling hormonal and behavioral endpoints, life-history traits, and population dynamics. Blood samples ( $N = 70$ ) were collected in South polar skuas during two breeding periods, in 2003 and 2005, and individuals were annually monitored until 2011. Multi-state mark recapture models were used to test the effects of POP levels on demographic traits. Survival rate and long-term breeding probability were not related to individual POP levels, whereas long-term breeding success significantly decreased with increasing blood levels of mirex, an organochlorine insecticide. At the proximate level, corticosterone (stress hormone) and prolactin (parental care hormone) levels were not linked to individual POP burden. Nest defense in 2005 was significantly less intensive in chick-rearing skuas bearing higher mirex levels, suggesting reproductive behavioral impairment. Matrix population models were then built to project the rate of population decline according to increasing mirex burden. Although mirex levels were 2.8 times higher in 2003 than in 2005, the population-level effect of mirex was only detected in 2005, the year of higher corticosterone levels. The combination of endocrine traits with demographic analysis thereby enables to provide new support of synergistic interactions between pollutants and stress levels on long-term breeding outputs and population dynamics.

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## 1. Introduction

Environmental chemicals may contribute to wildlife population vulnerabilities, by altering biochemical, genetic, immune, neurological, hormonal and behavioral functions (e.g. Vos et al., 2000). First reports of wildlife population collapses following acute chemical pollution were documented in the late 19th century, after large and intensive spraying of organochlorine pesticides, such as DDT (dichlorodiphenylthichloroethane, Wurster et al., 1965). Poisoning disasters still resonate today, with for instance, the high mortality and population collapses of three *Gyps* vultures' species in South Asia, due to scavenging of domestic livestock carcasses that had been treated with diclofenac (Oaks et al., 2004). Besides these spectacular cases of acute intoxication, wild animals are chronically exposed to complex mixtures of chemical substances at sublethal levels. A large scale experimental manipulation (Kidd et al., 2007) has demonstrated that low doses of a synthetic estrogen, 17 $\alpha$ -ethynylestradiol, may decimate free-living fathead minnow populations *Pimephales promelas*. Long-term effects of such chronic pollution in natural conditions are less readily measurable and remain mainly speculative, because of the dearth of large and longitudinal monitoring data.

Capture-mark-recapture models have shed new light on potential relationships between individuals' pollutant burdens and fitness-related traits. Specifically, recent studies on seabirds have pointed out a decrease in long-term reproductive performances with increasing persistent organic pollutants (POPs) and trace metal elements, such as mercury (Hg) levels in the Brown skua *Catharacta lonnbergi* from the Kerguelen Islands and the South polar skua *C. maccormicki* from Adélie Land, Antarctica (Goutte et al., 2014a) and in the Wandering albatross *Diomedea exulans* in the Crozet Archipelago (Goutte et al., 2014b). A decrease in adult survival rate has been linked to high levels of oxychlorane in the Glaucous gull *Larus hyperboreus* (Erikstad et al., 2013), and to high levels of HCB (hexachlorobenzene) and the chlordan mixture in the Black-legged kittiwakes *Rissa tridactyla* (Goutte et al., 2015). Matrix population models have been built to project demographic responses to pollutant levels in fish species (Miller and Ankley, 2004), amphibians (Willson et al., 2012), reptiles (Salice et al., 2011) and birds (Nakamaru et al., 2003; Goutte et al., 2014a, 2014b). These works support the assumption that pollutant exposure even at low environmental levels may lead to wildlife population decline, by compromising fitness-related traits. Complex issues have also been raised, including species-differences, interrelationships between POP and individual parameters (e.g. sex, previous reproductive state, age, breeding experience and body condition) or environmental factors (e.g. parasite load, food availability, habitat loss; Bustnes et al., 2006a, 2015; Salice et al., 2011).

Proximate mechanisms may help understand and better predict the impact of chronic pollution on wildlife population dynamics. Hormone levels play a major role in regulating reproductive phenology and behavior, acquisition and allocation of resources and life-history trade-offs (Kitaysky et al., 2007; Angelier and Chastel, 2009). Hg and POPs can interfere with hormones that trigger the onset of breeding (e.g. luteinizing hormone, sex steroids), the hormone that regulate parental care (prolactin, hereafter referred as PRL; Verreault et al., 2008; Angelier et al., 2016), and with stress hormones (glucocorticoids, such as corticosterone or cortisol, hereafter referred as CORT) (Tyler et al., 1998; Tartu et al., 2015a, 2015b, 2015c, 2016). Such endocrine disruption may result in behavioral impairments during the breeding period. For instance, nest temperature decreased with increasing blood POP levels in incubating Glaucous gulls (Verboven et al., 2009). In female South polar skuas with high blood POP levels, egg hatching was delayed and chicks were in poor body condition (Bustnes et al., 2007).

This study investigates the endocrine, behavioral and demographic consequences of POP burden in a South polar skua population breeding in Antarctica. We are revisiting a long-term data set that was previously used to assess the effect of Hg on vital rates and population dynamics in

this skuas population (Goutte et al., 2014a). In addition, proximate end-points were explored by considering hormone levels and nest defense behavior. The South polar skua is an ideal model for several reasons: (1) polar apex predators are predicted to be highly contaminated, because Arctic and to a lesser extent Antarctic environments are considered as 'sinks' for POPs and because biomagnification of POPs occurs across trophic levels (Bustnes et al., 2006b; Bargagli, 2008), (2) life-history traits could be acquired annually and at the individual level in this long-lived species with high nest fidelity, (3) nest defense behavior is particularly pronounced. The first aim of this study was to investigate whether demographic traits (adult survival rate, breeding probability, probability of raising one or two chicks the following years) are linked with individual POP levels. To do so, we used a 10 year longitudinal monitoring survey and multi-state mark recapture models (MSMR; Lebreton and Pradel, 2002). Because breeding success of long-lived animals has a low elasticity (i.e. has a low importance for population growth rate), we hypothesized that skua with high POP levels will fail to raise their fledglings the following years, as validated for Hg levels in the same skua population (Goutte et al., 2014a). The second goal was to explore whether endocrine and behavioral traits (CORT, PRL and nest defense intensity) the same year were negatively affected by high individual POP levels. The third objective was to project population-level consequences to increasing POP levels, through matrix population modeling (Caswell, 2001).

## 2. Materials and methods

### 2.1. Site and species

South polar skuas were studied in Antarctica, Adélie Land, on the Pointe Géologie Archipelago (66°40' S, 148°01' E), where ~50 pairs of breeders have been checked every year since 1964/1965. This long-lived species reproduces in loose colonies in Antarctica and is highly territorial during breeding with strong site tenacity and mate fidelity (Young, 1963; Jouventin and Guillotin, 1979; Pietz and Parmelee, 1993). Pair formation starts in October, and usually 2 eggs are laid in intervals of 2–4 days in mid-November, hatching of the eggs occurs in late-December and chicks fledge 50 days after (Young, 1963). Parents feed their chicks until they leave the nesting territory between late March and mid-April (Le Morvan et al., 1967). First reproduction can occur at 3-year old at the earliest, but most females start breeding between 5 and 7 years, and a little later for males (Ainley et al., 1990). After the breeding season, adults from Pointe Géologie migrate directly and winter off at the East of Japan (Weimerskirch et al., 2015). Once arrived on the breeding grounds in October, South polar skuas feed regularly on dead Emperor penguin (*Aptenodytes forsteri*) chicks that are available at the surface of sea-ice occupied by the penguin colony (Pryor, 1968). At Pointe Géologie, South polar skuas have been observed feeding on dead chicks of Emperor penguins daily, from their arrival in October until sea-ice breaks up in January or February (C. Barbraud, personal observation). From mid-November until the end of the breeding season South polar skuas feed mainly on eggs and chicks of Adélie penguins (*Pygoscelis adeliae*, Jouventin and Guillotin, 1979; Weimerskirch et al., 2015). All studied skuas were ringed with a stainless steel ring, as well as a plastic ring engraved with a unique alphanumeric code for identification without recapture. Every year, from early November to early February, each individual was identified on its nest or territory during the pre-laying period, incubation, and the chick-rearing period. In addition, groups of non-breeders were observed and ringed birds were identified. Nests and surroundings were monitored for the presence of one or two eggs or chicks.

Skull (head and bill) length was measured using a caliper (nearest 0.5 mm) and weight was measured using a spring balance (nearest 2 g). As female skuas are significantly larger than males, we calculated body condition (BC) from a least squares linear regression of weight against skull length for males and females separately.

2.2. Blood sampling and analyses

Skuas were captured in 2003, from 5 January to 7 February (18 males and 18 females, stage: 4 non-breeders, 4 incubating and 28 chick-rearing birds), and in 2004/2005 from 17 December to 19 January (14 males and 20 females, stage: 8 non-breeders, 3 incubating, 23 chick-rearing birds). Among them, nine individuals were sampled during both years. Since POP levels strongly differed between the two years (see Results section), all analyses were conducted for the two years separately. Less than 3 min after capture (Romero and Reed, 2005), blood samples (1 mL) were collected from the alar vein with a 25-gauge needle and a heparinized 5-mL syringe. Blood samples were centrifuged within 3 h (7000 rpm, 6 min at 4 °C). Blood cells were stored at -20 °C until assayed for sex determination as described in Goutte et al. (2014a). Plasmas were used to determine baseline concentrations of CORT and PRL at Chizé laboratory, as described in Lormée et al. (2003) and Angelier and Chastel (2009) respectively. Intra-assay variations (7.4% for CORT and 8.4% for PRL) were measured by including 10 times 4 reference samples. Minimal detection levels were 0.52 ng·mL<sup>-1</sup> for CORT and 19.26 ng·mL<sup>-1</sup> for PRL.

2.3. POPs determination

Levels of polychlorinated biphenyls (PCB) and organochlorine pesticides were determined in 150 µL of plasma at the EPOC/LPTC laboratory, Bordeaux, France as described in Goutte et al. (2014b). In particular, five families of POPs were quantified, using gas chromatography coupled with micro electron capture detector (GC-µECD): ΣPCB congeners (CB- 28, -52, -101, -118, -138, -153 and -180), ΣDDT (2,4' dichlorodiphenyldichloroethylene (DDE), 2,4' dichlorodiphenyltrichloroethane (DDT), 4,4' dichlorodiphenyldichloroethane (DDD), 4,4' DDT, 4,4'-DDE), chlordane mixture (hereafter CHL including cis-chlordane, trans-nonachlor, heptachlore), hexachlorobenzene (HCB) and mirex.

Quality control consisted in the analysis of procedural blanks (clean and empty glass tubes treated like a sample, one blank for 8 samples) and of standard solutions (Standard Reference Material: NIST SRM 2261 and SRM 2262). The most abundant analytes in procedural blanks were PCB-105, -118 and -153. When applicable, analyte levels were blank corrected. Recoveries of compounds for the standard solutions (n = 4) ranged from 80 to 114% with standard deviations lower than 14%. For each analyte, the limit of detection (LoD) was defined as the concentration with a signal to noise ratio of 3. Overall, LoDs ranged from 0.02 to 0.11 ng·g<sup>-1</sup> wet weight. The recovery rates of internal standards were acceptable and were as follows: CB-30: 88 ± 32%, CB-103: 63 ± 12%, CB-155: 72 ± 20%, CB-198: 71 ± 20%; 4,4'-DDT D8: 65 ± 19%. The percentage of total lipids (Table SM1 in Supplementary Material) was measured in 10 µL of plasma by the sulfophosphovanillin (SPV) method for colorimetric determination (Frings et al., 1972). POP results are given in lipid weight (ng·g<sup>-1</sup> lw).

2.4. Territorial behavior

During the breeding season, skuas are highly territorial and emit long calls to advertise territorial ownership (Furness, 1987). Skuas also defend their nests and territory, by flying up above the intruder, and then swooping down at it. In December 2004/January 2005, these two behavioral traits (number of swoops and long calls) were recorded during the intrusion into the territory for captures and blood sampling of incubating and chick-rearing skuas. Behavioral monitoring lasted 10 ± 1 min (mean ± SE) and traits were time corrected (number of swoops per minute and number of long calls per minute).

2.5. Estimating the effects of POPs on hormones, behavior and current breeding success

Circulating levels of POP families (ΣPCB, ΣDDT, CHL, HCB and Mirex) were compared between the two sampling years (2002/2003 and 2004/2005) using Welch's t-tests. Because POP levels strongly differed between the two years (see Results section and Table S1, S1), we conducted subsequent analyses, by considering the two years separately. Ln-transformed variables were used if necessary to meet the assumptions of parametric statistical tests. Since stage (non-breeding, incubating, chick-rearing) and sampling date were correlated, they were not included in the same model. The additive effects of sex, sampling date (or stage) and body condition (BC) on the levels of POP families (ln-transformed) or baseline CORT (ln-transformed) were tested using GLMs (general linear models) with an identity link function and a normal error distribution. Similarly, effects of sex, sampling date, BC and brood size on baseline PRL levels and on nest defense behaviors (number of long calls and swoops per minute) were tested in chick-rearing skuas. After model selection, the effects of ln-transformed levels of ΣPCB, ΣDDT, CHL, HCB or Mirex on ln-transformed levels of CORT, PRL, number of long calls per minute and number of swoops per minute were tested using GLMs with normal error distribution and an identity link function. Success of the current reproductive attempt was coded as 1 and failure as 0. The effects of ln-transformed levels of each POP family on current breeding success were tested using GLMs with a logit link function and binomial error distribution. Akaike's Information Criterion adjusted for small sample sized (AICc) was used for model selection through the R package 'AICcmodavg' (Mazerolle, 2017; R Development Core Team, 2015).

2.6. Estimating the effect of POP families on demographic parameters

We used the same MSMR model that was previously described in Goutte et al. (2014a) to evaluate the demographic consequences of blood POP concentrations in skuas that were sampled in 2003 or 2005 and annually monitored until 2011. Five states were defined: nonbreeder (NB); failed breeder (FB); successful breeder with one chick (SB1); successful breeder with two chicks (SB2); and dead. This last state refers to permanent emigration from the study site or death. Demographic parameters were the probability of survival (S), the probability of breeding (β), the probability of breeding successfully (γ), the probability of successfully raising two chicks (δ), and the detection probability (p). This MSMR model was parameterized by the survival-transition probabilities matrix:

$$\begin{matrix}
 & \text{NB} & \text{FB} & \text{SB1} & \text{SB2} & \dagger \\
 \text{NB} & \left[ \begin{matrix} S(1-\beta) & S\beta(1-\gamma) & S\beta\gamma(1-\delta) & S\beta\gamma\delta & * \\ S(1-\beta) & S\beta(1-\gamma) & S\beta\gamma(1-\delta) & S\beta\gamma\delta & * \\ S(1-\beta) & S\beta(1-\gamma) & S\beta\gamma(1-\delta) & S\beta\gamma\delta & * \\ S(1-\beta) & S\beta(1-\gamma) & S\beta\gamma(1-\delta) & S\beta\gamma\delta & * \\ \dagger & - & - & - & - \end{matrix} \right] & & & & & \\
 \text{FB} & & & & & & & & & \\
 \text{SB1} & & & & & & & & & \\
 \text{SB2} & & & & & & & & & \\
 \dagger & & & & & & & & & 
 \end{matrix}$$

Asterisks in the column for dead birds represent the complementary parameter (complement of the sum of positive row entries). Further details are provided in Goutte et al. (2014a). We used the same initial model than the one validated in Goutte et al. (2014a): apparent survival rates, breeding probabilities, and detection probabilities the following years were higher in individuals captured as breeders in year t than non-breeders, and breeding success probabilities did not differ between individual previously observed as breeder or as non-breeders. An effect of POP families (ΣPCB, ΣDDT, CHL, HCB, Mirex), with or without an interaction with sex was tested separately on each demographic parameter (S, β, γ, δ). Levels of each POP family were standardized for 2003 and 2005 separately. Each demographic

parameter ( $\theta$ ) was included in the MSMR models as a function of  $POP_i$  that was the standardized concentration of a POP family for individual  $i$ :  $\text{logit}(\theta) = a + b \times POP_i$ , with the intercept  $a$  and the slope  $b$ . A demographic effect of  $POP_i$  was validated, when the 95% Confidence Interval (CI) of the mean of  $b$  did not contain 0 (Grosbois et al., 2008). The goodness of fit was tested using U-CARE (Choquet et al., 2009a) and models were run under E-SURGE 1.8.5 (Choquet et al., 2009b).

### 2.7. Matrix population models

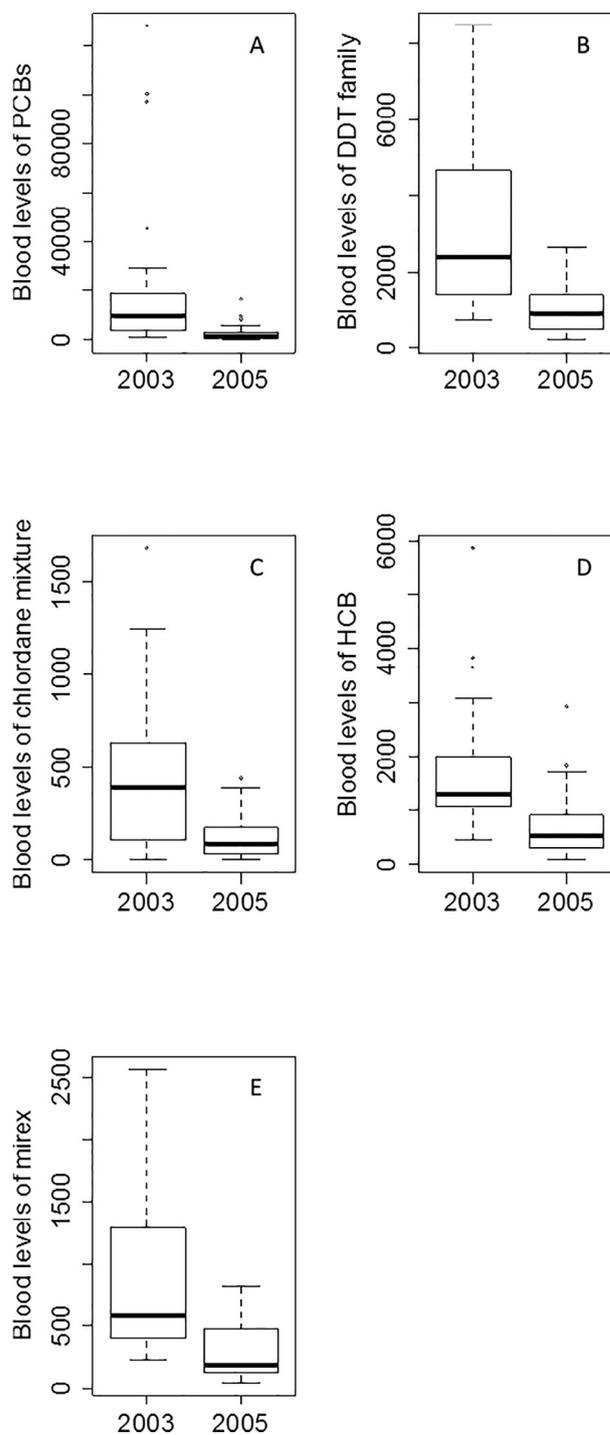
To assess the population-level effects of POP, specifically of mirex in 2005 (see Results section), population models were built through pre-breeding matrices that were structured by reproductive status classes and age (Caswell, 2001) as previously described in Goutte et al. (2014a) for the same population of South polar skuas. This model is structured into 9 classes, including 4 sexually-immature age classes; 5 pre-breeder classes and 2 stage classes (breeder and non-breeder). Model parameters were survival rate of adult breeders and non-breeders; survival rate of immatures during the 2nd and the 3rd year; the proportion of juveniles trying to breed for the first time, breeding probability of breeders and non-breeders, the proportion of immigrants and fecundity (i.e. the product of clutch size (2), the probability of successfully breeding, the probability of successfully raising two chicks, the survival probability during the first year). The deterministic growth rate ( $\lambda$ , Caswell, 2001) was calculated with deterministic models without stochasticity (Goutte et al., 2014a). The stochastic growth rate  $\lambda_{sto}$  was then estimated using stochastic matrix models. The yearly value of a vital rate that was not correlated with POP levels was sampled from a beta distribution (Morris and Doak, 2002) with variance and mean estimated from the selected MSMR model (Goutte et al., 2014a) or from Ainley et al. (1990). The value at year  $t$  of a vital rate that was significantly correlated with POP levels ( $\theta^t$ ) was calculated as  $\theta^t = \text{logit}^{-1}(a + b \times POP^t)$  with  $POP^t$ : the mean POP value sampled from a lognormal distribution. Population-level consequences of mirex concentrations (see Results section) were evaluated by changing mirex levels within the range of observed values (from 0 to 5000  $\text{ng} \cdot \text{g}^{-1}$  lw) and by estimating the corresponding  $\lambda_{sto}$  through Monte Carlo simulations (R-package *popbio*, Stubben and Milligan, 2007, R Development Core Team, 2015).

## 3. Results

### 3.1. Levels of POP families in the South polar skua

The two years strongly differed in the plasma levels of POP in skuas, with POP levels 5.5 times higher in 2003 compared to 2005 (from 2.3 times for HCB to 8.3 times for PCB, all Welch's  $t$ -tests,  $p < 0.001$ , Fig. 1, Table SM1 in Supplementary Material). These changes are also observed at the individual level for the nine skuas that were sampled in 2003 and in 2005 (Fig. SM1 in Supplementary Material).

Ln-transformed blood levels of  $\Sigma$ PCB were unrelated to sex, BC, stage or sampling date in 2003 (Table SM2A in Supplementary Material), whereas they decreased with sampling date (slope estimate  $\pm$  SE:  $-0.09 \pm 0.04$ ) in 2005, tended to be higher in males than in females and to be related to BC, but the 95% CI of the mean of the slope contains 0 [ $-0.87$ ;  $0.55$ ] (Table SM2B in Supplementary Material). Ln-transformed  $\Sigma$ DDT levels were unrelated to sex, BC, stage or sampling date in 2005, whereas they increased with date in 2003 ( $0.04 \pm 0.01$ ) and were slightly higher in males than in females (Table SM2 in Supplementary Material). CHL levels decreased with BC in 2003 ( $-0.41 \pm 0.31$ ) and with sampling date in 2005 ( $-0.08 \pm 0.02$ , Table SM2 in Supplementary Material). HCB levels were higher in males than in females in 2003. The relationship between HCB and date in 2005 was not supported by the 95% CI of the mean of the slope that contains 0 [ $-0.38$ ;  $0.20$ ] (Table SM2 in Supplementary



**Fig. 1.** Blood levels of POP families (A:  $\Sigma$ PCB (sum of chlorinated biphenyl - 28, -52, -101, -118, -138, -153 and -180), B:  $\Sigma$ DDT (sum of 2,4'-DDE (dichlorodiphenyldichloroethylene), 2,4'-DDT (dichlorodiphenyltrichloroethane), 4,4'-DDD (dichlorodiphenyldichloroethane), 4,4'-DDT, 4,4'-DDE), C: CHL (sum of cis-chlordane, trans-nonachlor, heptachlore), D: HCB (hexachlorobenzene), E: Mirex,  $\text{ng} \cdot \text{g}^{-1}$  lw) in 2003 and 2005 in South polar skuas.

Material). Mirex levels in 2003 were higher in males than in females. The negative relationship between mirex levels in 2003 and date was not supported by the 95% CI of the mean of the slope that contains 0 [ $-0.00$ ;  $0.05$ ]. Mirex levels were unrelated to individual parameters in 2005 (Table SM2 in Supplementary Material).

3.2. Relationships between POP levels and demographic traits

Current reproduction success of breeders did not significantly differ between 2003 (84.4%) and 2005 (96.2%,  $p = 0.209$ ) and was not correlated to POP levels in any year (Table SM3 in Supplementary Material).

The goodness of fit was overall not significant in 2003 (males:  $df = 26$ ,  $\chi^2 = 8.26$ ,  $p = 1$ , females:  $df = 24$ ,  $\chi^2 = 4.22$ ,  $p = 1$ ) nor in 2005 (males:  $df = 14$ ,  $\chi^2 = 3.74$ ,  $p = 1$ , females:  $df = 20$ ,  $\chi^2 = 3.76$ ,  $p = 1$ ). Of the set of candidate models describing demographic parameters, the selected model ( $\Delta AICc < 2$ ) was the effect of high mirex levels in 2005 on long-term reproductive failure (Table 1B, Fig. 2). The levels of other POP families in 2003 or in 2005 were not related to adult survival rate, the long-term probability of breeding, and of raising one or two chicks (Table 1A, B). For the effect of CHL levels in 2005 on adult survival rate, although the model was supported by the  $\Delta AICc$  (Table 1B), the model was not approved since 0 was included in the confidence interval  $[-0.72; 0.96]$ . The effect of HCB levels in 2003 on survival rate of adult

skuas was not supported by the  $\Delta AICc$  lower than 2 for the intercept model (Table 1A).

3.3. Relationships between POP levels, hormones and territorial behavior

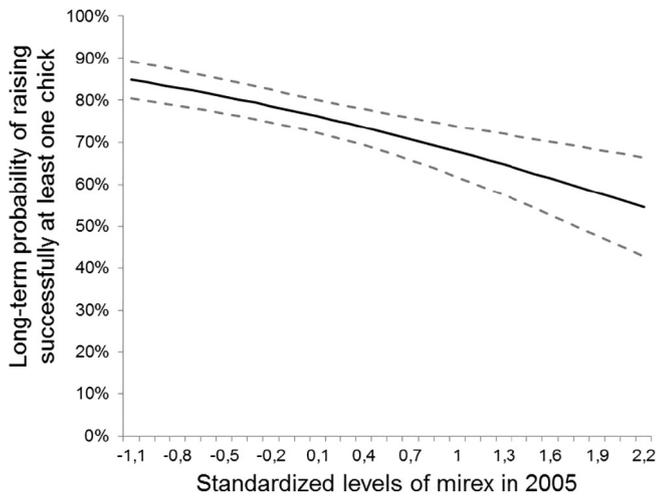
Baseline CORT levels were lower in 2003 (mean  $\pm$  SE:  $8.91 \pm 1.10$  ng·mL<sup>-1</sup>) than in 2005 ( $15.16 \pm 1.49$  ng·mL<sup>-1</sup>,  $W = 318$ ,  $p = 0.001$ ) for all skuas and for breeders only ( $W = 270$ ,  $p = 0.022$ ). Males tended to exhibit higher CORT levels compared to female skuas in 2003 (Tables SM1 and SM4 in Supplementary Material). CORT levels were higher in incubating skuas and tended to decrease with increasing BC in 2005, although the 95% CI contains 0  $[-0.43; 0.04]$  (Table SM4 in Supplementary Material). No correlation was found between ln-transformed levels of baseline CORT and POP families during both years (Tables SM6A and B in Supplementary Material).

PRL levels in 2003 did not differ between chick-rearing males and females, between skuas brooding one or two chicks, and were unrelated

Table 1

Modeling the effects of standardized blood levels of  $\Sigma$ PCB (sum of chlorinated biphenyl - 28, -52, -101, -118, -138, -153 and -180),  $\Sigma$ DDT (sum of 2,4'-DDE (dichlorodiphenyldichloroethylene), 2,4'-DDT (dichlorodiphenyltrichloroethane), 4,4'-DDD (dichlorodiphenyldichloroethane), 4,4'-DDT, 4,4'-DDE), CHL (sum of cis-chlordane, trans-nonachlor, heptachlore), HCB (hexachlorobenzene), Mirex in 2003 (A) and 2005 (B) on demographic parameters ( $S$ : probability of survival,  $\beta$ : the probability of breeding,  $\gamma$ : the probability of breeding successfully,  $\delta$ : the probability of successfully raising two chicks), of South Polar Skuas; effects are ranked from lowest to highest  $\Delta AICc$ .  $\Delta AICc$  is the difference in AICc (Akaike's Information Criteria adjusted for small sample-sizes) between the current and the most appropriate model.

A. 2003				B. 2005			
Hypothesis	Rank	Deviance	$\Delta AICc$	Model	# Id. par.	Deviance	$\Delta AICc$
Intercept model	11	762.542	0	Intercept model	11	576.258	0
Effect of [ $\Sigma$ PCBs] on $\gamma$	12	762.275	1.976	Effect of [ $\Sigma$ PCBs] on $S$	13	572.836	1.215
Effect of [ $\Sigma$ PCBs] on $\delta$	12	762.485	2.186	Effect of [ $\Sigma$ PCBs] on $\delta$	12	575.213	1.259
Effect of [ $\Sigma$ PCBs] on $S$	13	760.505	2.471	Effect of [ $\Sigma$ PCBs] and sex on $\delta$	14	571.575	2.316
Effect of [ $\Sigma$ PCBs] on $\beta$	13	761.673	3.639	Effect of [ $\Sigma$ PCBs] on $\gamma$	12	576.235	2.281
Effect of [ $\Sigma$ PCBs] and sex on $\gamma$	14	760.278	4.531	Effect of [ $\Sigma$ PCBs] on $\beta$	13	575.653	4.032
Effect of [ $\Sigma$ PCBs] and sex on $\delta$	14	761.985	6.239	Effect of [ $\Sigma$ PCBs] and sex on $\gamma$	14	573.839	4.579
Effect of [ $\Sigma$ PCBs] and sex on $S$	17	758.170	9.424	Effect of [ $\Sigma$ PCBs] and sex on $S$	17	569.034	7.039
Effect of [ $\Sigma$ PCBs] and sex on $\beta$	17	759.726	10.980	Effect of [ $\Sigma$ PCBs] and sex on $\beta$	17	571.284	9.289
Effect of [ $\Sigma$ DDT] on $\beta$	13	758.889	0.855	Effect of [ $\Sigma$ DDT] and sex on $\gamma$	14	570.093	0.833
Effect of [ $\Sigma$ DDT] on $\gamma$	12	761.476	1.176	Effect of [ $\Sigma$ DDT] on $\delta$	12	576.126	2.172
Effect of [ $\Sigma$ DDT] on $\delta$	12	762.521	2.222	Effect of [ $\Sigma$ DDT] on $\gamma$	12	576.257	2.303
Effect of [ $\Sigma$ DDT] on $S$	13	760.905	2.870	Effect of [ $\Sigma$ DDT] on $S$	13	574.791	3.170
Effect of [ $\Sigma$ DDT] and sex on $\gamma$	14	759.911	4.164	Effect of [ $\Sigma$ DDT] on $\beta$	13	575.484	3.862
Effect of [ $\Sigma$ DDT] and sex on $\delta$	17	755.583	6.837	Effect of [ $\Sigma$ DDT] and sex on $\delta$	14	574.884	5.625
Effect of [ $\Sigma$ DDT] and sex on $\beta$	14	762.294	6.548	Effect of [ $\Sigma$ DDT] and sex on $\beta$	17	569.111	7.116
Effect of [ $\Sigma$ DDT] and sex on $S$	17	758.969	10.224	Effect of [ $\Sigma$ DDT] and sex on $S$	17	571.102	9.107
Intercept model	11	762.542	0	Effect of [CHL] on $S$	13	569.411	0
Effect of [CHL] on $\delta$	12	761.904	1.605	Intercept model	11	576.258	2.210
Effect of [CHL] on $\gamma$	12	762.507	2.207	Effect of [CHL] on $\gamma$	12	575.081	3.337
Effect of [CHL] and sex on $\delta$	14	758.858	3.111	Effect of [CHL] on $\delta$	12	575.539	3.795
Effect of [CHL] on $\beta$	13	761.162	3.128	Effect of [CHL] and sex on $S$	17	566.041	6.256
Effect of [CHL] on $S$	13	761.316	3.281	Effect of [CHL] on $\beta$	13	575.118	5.707
Effect of [CHL] and sex on $\gamma$	14	761.862	6.116	Effect of [CHL] and sex on $\gamma$	14	573.734	6.685
Effect of [CHL] and sex on $\beta$	17	758.200	9.454	Effect of [CHL] and sex on $\delta$	14	574.811	7.762
Effect of [CHL] and sex on $S$	17	759.072	10.326	Effect of [CHL] and sex on $\beta$	17	569.857	10.072
Effect of [HCB] on $S$	13	757.825	0	Intercept model	11	576.258	0
Intercept model	11	762.542	0.209	Effect of [HCB] on $\beta$	13	572.314	0.693
Effect of [HCB] and sex on $\gamma$	14	757.499	1.962	Effect of [HCB] on $\gamma$	12	575.628	1.674
Effect of [HCB] on $\gamma$	12	762.004	1.914	Effect of [HCB] and sex on $\gamma$	14	571.993	2.733
Effect of [HCB] on $\delta$	12	762.492	2.402	Effect of [HCB] on $\delta$	12	576.088	2.134
Effect of [HCB] on $\beta$	13	760.615	2.790	Effect of [HCB] on $S$	13	576.197	4.576
Effect of [HCB] and sex on $\delta$	14	762.125	6.588	Effect of [HCB] and sex on $\beta$	17	568.597	6.602
Effect of [HCB] and sex on $S$	17	756.252	7.716	Effect of [HCB] and sex on $\delta$	14	575.070	5.811
Effect of [HCB] and sex on $\beta$	17	757.089	8.553	Effect of [HCB] and sex on $S$	17	570.515	8.520
Intercept model	11	762.542	0	Effect of [Mirex] on $\gamma$	12	571.264	0
Effect of [Mirex] on $\beta$	13	759.539	1.505	Effect of [Mirex] and sex on $\gamma$	14	569.236	2.666
Effect of [Mirex] on $S$	13	760.015	1.981	Intercept model	11	576.258	2.690
Effect of [Mirex] on $\gamma$	12	762.126	1.827	Effect of [Mirex] and sex on $S$	17	564.398	5.093
Effect of [Mirex] on $\delta$	12	762.530	2.231	Effect of [Mirex] on $\delta$	12	575.643	4.378
Effect of [Mirex] and sex on $\gamma$	14	759.831	4.084	Effect of [Mirex] on $S$	13	574.545	5.613
Effect of [Mirex] and sex on $\beta$	17	754.524	5.779	Effect of [Mirex] and sex on $\delta$	14	572.840	6.270
Effect of [CHL] and sex on $\delta$	14	761.884	6.138	Effect of [Mirex] on $\beta$	13	574.982	6.051
Effect of [Mirex] and sex on $S$	17	758.277	9.532	Effect of [Mirex] and sex on $\beta$	17	571.434	12.129



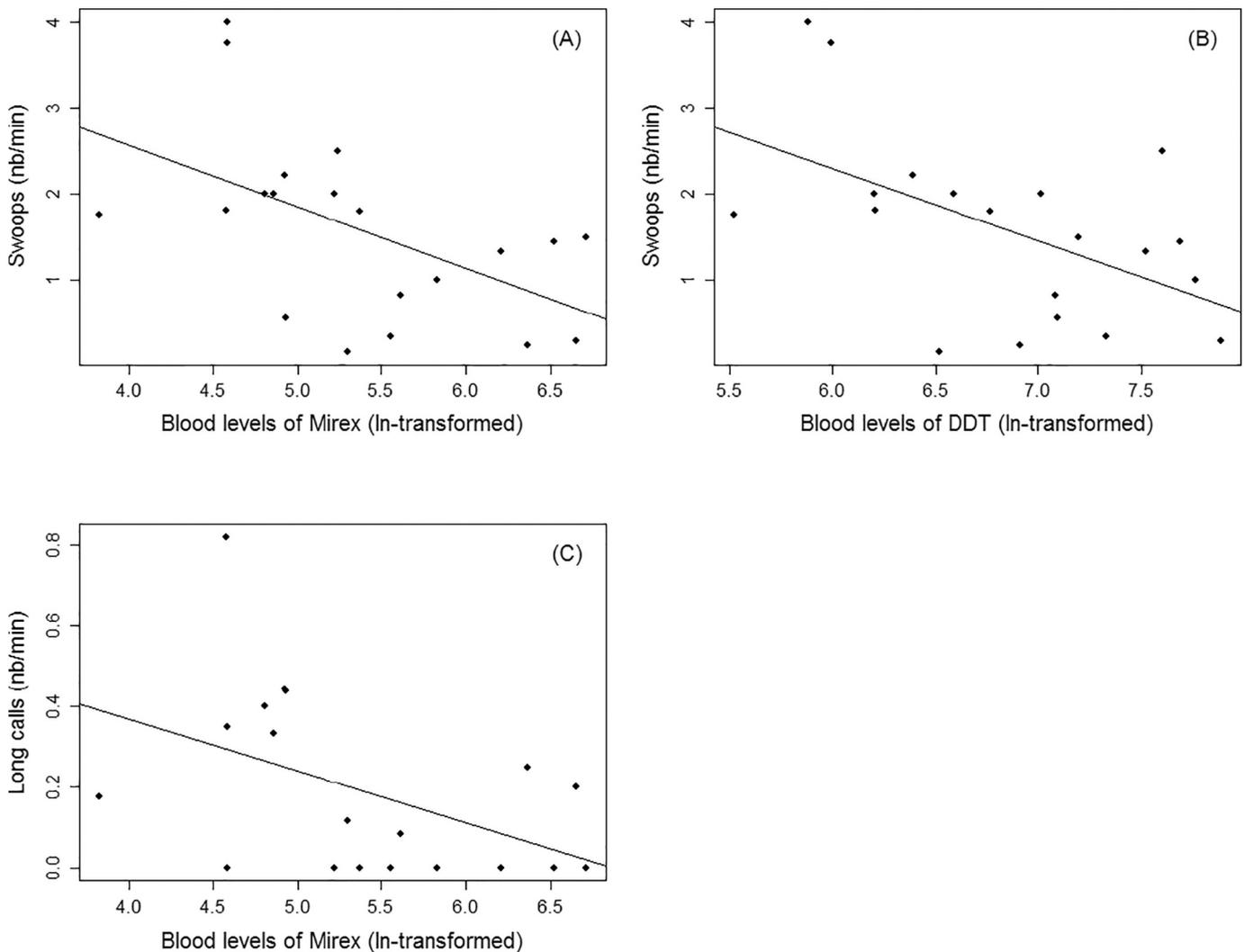
**Fig. 2.** Effects of blood standardized levels of mirex in 2005 on the long-term probability of raising successfully at least one chick in South polar skuas. The solid line is the mean probability; the dotted lines represent the 95% confidence intervals estimated using the delta method (Seber, 1982).

to BC or sampling date (Tables SM5 in Supplementary Material). No correlation was found between ln-transformed levels of PRL and POP families (Tables SM6C in Supplementary Material).

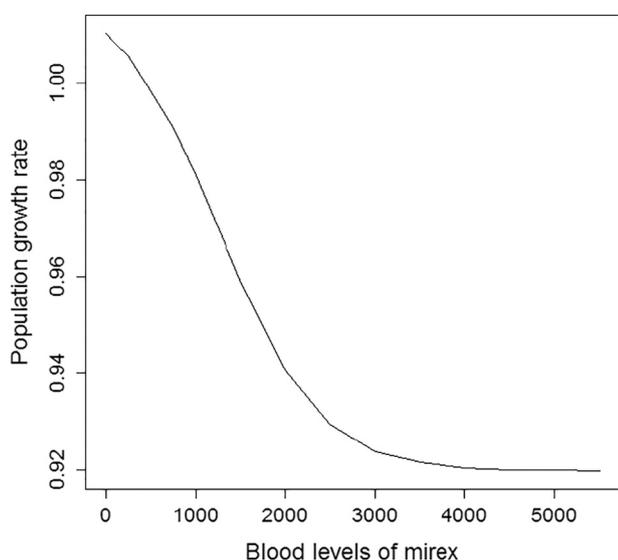
Nest defense behaviors in 2005 did not differ between females and males, were unrelated to BC and sampling date and tended to be higher in skuas rearing one chick compared to skuas rearing two chicks (Tables SM7A and B in Supplementary Material). The highest rank model was a decrease of number of long calls per minute with increasing ln-transformed levels of mirex (Fig. 3, Table SM8A in Supplementary Material). Similarly, number of swoops per minute decreased with increasing blood levels of Mirex and  $\Sigma$ DDT (Fig. 3, Table SM8B in Supplementary Material).

### 3.4. POP levels and population growth rate

Mirex negatively impacted population growth rate under a scenario with stress levels similar to those in 2005 (Fig. 4), with a steep decline ( $\lambda = 0.93$ ) until mirex levels reach approximately  $2.5 \mu\text{g}\cdot\text{g}^{-1}$  lw, and then a stabilization ( $\lambda = 0.92$ ). Population growth rate will increase ( $\lambda = 1.01$ ) with zero concentrations of mirex. Under a scenario with stress levels similar to those in 2003, blood levels of mirex did not impact vital rates according to the MSMR analyses, so that population



**Fig. 3.** Nest defense behaviour in 2005 in South polar skuas: number of swoops per minute according to ln-transformed blood levels of (A) mirex ( $\text{ng}\cdot\text{g}^{-1}$  lw) and (B)  $\Sigma$ DDT (sum of 2,4'-DDE (dichlorodiphenyldichloroethylene), 2,4'-DDT (dichlorodiphenyltrichloroethane), 4,4'-DDD (dichlorodiphenyldichloroethane), 4,4'-DDT, 4,4'-DDE), and (C) number of long calls per minute according to ln-transformed blood levels of mirex ( $\text{ng}\cdot\text{g}^{-1}$  lw).



**Fig. 4.** Modeled population-level growth rate response to an increase in mean mirex blood levels ( $\text{ng}\cdot\text{g}^{-1}\text{ lw}$ ) in South polar skuas under a scenario with environmental conditions similar to those in 2005.

growth rate will remain stable ( $\lambda = 1.001$ ) with an increase of mirex levels in the range of observed values (0 to  $5000\text{ ng}\cdot\text{g}^{-1}\text{ lw}$ ).

## 4. Discussion

### 4.1. POP levels in South polar skuas and inter-annual differences

The distribution of POP families in South polar skuas sampled in 2003 and 2005 at the Pointe Géologie Archipelago, Adélie Land (AL) followed the pattern  $\Sigma\text{PCB} > \Sigma\text{DDT} > \text{HCB} > \text{Mirex} > \text{CHL}$ . These chemicals are ubiquitous in the Antarctic, despite its isolation from direct sources of chemical pollution (Corsolini, 2009). POP inputs derive mainly from long-distance atmospheric transport. POPs are highly persistent, especially in Polar Regions, because they can be entrapped in ice over long time-periods and low temperatures limit their biodegradation. After being deposited to surface waters, POPs are incorporated in trophic webs and reached high levels in top predators (Bargagli, 2008; Corsolini, 2009). Plasma levels of POPs were comparable to those previously described in the same species and sampled during 2001 and 2002 at Svarthamaren, Dronning Maud Land (DML), Antarctica (mean  $\pm$  SE in  $\mu\text{g}\cdot\text{g}^{-1}\text{ lw}$  for DML/AL, *trans*-nonachlor:  $0.1 \pm <0.1/0.14 \pm 0.02$ ; 4,4'-DDE:  $2.0 \pm 0.1/1.65 \pm 0.17$ ; Bustnes et al., 2006b). HCB and especially mirex levels were higher in DML than in AL (HCB:  $2.3 \pm 0.1/1.22 \pm 0.12$ ; mirex:  $6.5 \pm 0.4/0.59 \pm 0.64$ , respectively). The insecticide mirex belongs to the “dirty dozen” listed under the Stockholm Convention in 2001 and was commonly used in the southern hemisphere, against ants and termites until it was banned in the late 70's (Kaiser, 1978).

In our study, much lower POP levels were observed in 2005 compared to 2003. Since blood samples were collected approximately two weeks earlier in 2005 compared to 2003, one possible explanation is that blood POP levels greatly varied daily and weekly, thus explaining the annual difference. However this hypothesis is not supported by the lack of significant relationships or negative correlation between POP levels and sampling date, during the one-month sampling period. Large inter-annual variations in circulating concentrations of PCBs and organochlorine pesticides were also observed in other seabird species, such as Black legged kittiwakes (Bustnes et al., 2017). One possible explanation of such variations could be changes in migratory routes and foraging ecology. Skuas breeding in Adélie Land perform wide-ranging migration to the north Pacific and stay during winter east of Japan (Weimerskirch et al., 2015). They are therefore exposed to POPs on

their breeding territories and foraging ranges, migratory routes as well as wintering areas. Inter-annual differences in ice conditions around the breeding areas or in atmospheric emissions in migratory and wintering grounds could then result in different exposures to organic micropollutants.

### 4.2. POP burden and demographic traits

High POP burden did not jeopardize adult apparent rate of survival and long-term probability of reproduction in South polar skuas. To our knowledge, only two studies have detected an effect of POPs on mortality in seabirds: one on adult Glaucous gulls bearing high levels of oxychlordane, a metabolite of the chlordane mixture (Erikstad et al., 2013) and another on Black-legged kittiwakes with elevated levels of HCB and of the chlordane mixture (Goutte et al., 2015). The current study pointed out a decline in long-term breeding success with increasing levels of mirex.

Surprisingly, the effect of mirex on long-term breeding failure was detected in 2005 only, although skuas had lower circulating levels of POPs compared to 2003. This result suggests that the expression of a deleterious effect could be modulated by environmental conditions. In 2005, skuas exhibited higher baseline CORT levels compared to 2003, whereas breeding success and body condition were not significantly different between the two years. Since CORT is a good proxy of environmental stress, including food availability (e.g. Kitaysky et al., 2007) and foraging activities (e.g. Angelier et al., 2007), skuas were likely more energetically-challenged in 2005 than in 2003. Hence, the effect of mirex on long-term breeding outputs in 2005 may have been triggered by food scarcity and/or sustained energy expenditure. This result supports the assumption of synergistic interactions between pollution and stress. Accordingly, experimentally-improved feeding conditions removed adverse impacts of POPs on daily growth rate of chicks in Great skua *Stercorarius skua* (Bustnes et al., 2015). Similarly, the negative effect of food restriction on reproductive performance was enhanced in Ringed turtle *Streptopelia risoria* that were exposed to DDE (Keith and Mitchell, 1993). Finally, negative effects of maternal POP levels on chick growth rate were detected in Glaucous gulls undertaking long foraging trips, but not in those feeding near the colony (Bustnes et al., 2005).

### 4.3. Relationships between POP levels, hormones and territorial behavior

Potential endocrine and behavioral mechanisms were explored to better understand how POP levels may impair reproductive outputs. Modulations of CORT and PRL releases are known to mediate parental effort and reproductive success in seabirds (Angelier and Chastel, 2009; Angelier et al., 2016). CORT reached higher levels in 2005 than in 2003, while POP levels followed the opposite trend. Skuas were blood sampled approximately two weeks earlier in 2005 compared to 2003, which could also explain the inter-annual difference in CORT levels. At the individual level, circulating POP levels were not related to CORT or PRL levels, suggesting that POPs did not disrupt these endocrine axes in skuas at the reported concentrations. Stress-induced CORT and PRL levels were not measured. Several individual and environmental factors may influence these baseline hormone levels, making relationships between POPs and CORT or PRL appear complex in seabirds (Tartu et al., 2015a, 2015b; Verreault et al., 2008).

Moreover, the intensity of nest defense is considered to be a good proxy of parental investment (Montgomerie and Weatherhead, 1988). The blood levels of mirex and DDT family, but not other POP compounds, were negatively associated with the number of swoops and long calls in 2005, which was in line with the observed effect of mirex on long-term breeding failure. Weaker nest defense could be due to reproductive impairment, although no disruption of CORT or PRL release was detected in 2003 and no data for PRL levels was available in 2005. Parental disinvestment could also be linked to lower brood value,

since chicks' development may be impacted by high POP levels in female South polar skuas (Bustnes et al., 2007). Despite the negative effect of mirex on nest defense behavior, no direct consequences were detected on current breeding attempt. This could be due to the late blood sampling and behavioral monitoring, so that early reproductive failure, such as non-viable eggs and egg predation were not taken into consideration in the current study.

#### 4.4. POP burden and population growth rate

Predicting population vulnerability as a consequence of contamination is a challenging task in ecotoxicology. As previously projected for increasing Hg levels in the same skua population (Goutte et al., 2014a), we modeled a deceleration of population growth rate until 0.920 in response to an increase in mirex exposure, because of its effect on long-term breeding failure. Considering a mirex level of 858.7 ng·g<sup>-1</sup> lw (similar to the mean blood level measured in 2003), population size of skuas is expected to decline ( $\lambda = 0.986$ ). More favorable environmental conditions, such as those observed in 2003, would mask the population-level effect of pollutant burden at least in the range of observed POP levels in the current study.

## 5. Conclusion

The study shows for the first time an impact of the insecticide mirex on long-term reproductive success and population dynamics in a free-living vertebrate, through long-term mark-recapture survey. This effect may be due to behavioral impairment, since skuas with high mirex levels were less active in defending their chicks against intruders. Surprisingly the demographic effect of mirex was detected during 2005, the year of lower pollutants levels compared to 2003. One possible explanation is the synergistic interactions between pollutant burden and environmental stress on fitness-related traits, since baseline corticosterone levels were higher in 2003. The combination of proximate and ultimate approaches may thus offer new insight into population vulnerability of free-living vertebrates exposed to chemical and environmental stress.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2018.02.326>.

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