

Limited individual phenotypic plasticity in the timing of and investment into egg laying in southern rockhopper penguins under climate change

Nina Dehnhard^{1,2,3,*}, Marcel Eens¹, Laurent Demongin^{1,2,3}, Petra Quillfeldt^{2,3,4},
Dan Suri⁵, Maud Poisbleau^{1,2,3}

¹Laboratory of Ethology, Department of Biology, University of Antwerp, Campus Drie Eiken, Universiteitsplein 1, 2610 Antwerp (Wilrijk), Belgium

²Department of Migration and Immuno-Ecology, Max Planck Institute for Ornithology, Am Obstberg 1, 78315 Radolfzell, Germany

³Department of Biology, University of Konstanz, 78457 Konstanz, Germany

⁴Department of Animal Ecology and Systematics, Justus-Liebig University Gießen, Heinrich-Buff-Ring 38, 35392 Gießen, Germany

⁵Met Office, FitzRoy Road, Exeter EX1 3PB, UK

ABSTRACT: Global climate change requires species to adapt to increasing environmental variability, rising air and ocean temperatures and many other effects, including temperature-associated phenological shifts. Species may adapt to such rapid changes by microevolutionary processes and/or phenotypic plasticity. The speed of microevolutionary adaptation may critically be enhanced by between-individual differences in phenotypic plasticity. However, such between-individual differences have rarely been shown, especially for long-lived and migratory species that appear particularly vulnerable to phenological shifts. Southern rockhopper penguins *Eudyptes chrysocome chrysocome* are migratory, long-lived seabirds with a 'vulnerable' conservation status. We studied clutch initiation date (CID) and investment into egg mass in individually marked females in response to broad-scale and local climate variables across 7 yr. We thereby distinguished within-individual and between-individual variation and tested the existence of between-individual differences in the expression of phenotypic plasticity. Because of both within-individual and between-individual variation, CID was significantly advanced under high Southern Annular Mode (SAM), reflecting colder environmental conditions and higher food availability. Total clutch mass increased under low local sea surface temperatures (significant within-individual effect) but was mostly accounted for by female identity. Intra-clutch egg-mass dimorphism was not affected by environmental variables at all. We found no indication of between-individual differences in phenotypic plasticity and overall, the expression of phenotypic plasticity appeared to be limited. This raises the question whether between-individual differences in phenotypic plasticity exist in other long-lived species and whether rockhopper penguins show sufficient phenotypic plasticity to adapt to predicted climate changes.

KEY WORDS: Between-individual effects · Breeding biology · *Eudyptes chrysocome* · Phenology · Within-individual effects

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INTRODUCTION

Among other anthropogenic effects on the environment, global climate change is currently seen as the most wide-ranging and dangerous threat for plants and animals in the 21st century and beyond (e.g.

Thomas et al. 2004). Across the globe, climate change scenarios predict increasing air temperatures and sea surface temperatures (SST), shifts in atmospheric wind systems and a general increase in climate variability, i.e. more extreme weather conditions (Collins et al. 2013 and literature therein). These changes, and

the speed at which they take place, may lead to reproductive failure and mortality for both plants and animals, with effects on long-term population trajectories and species' survival (e.g. Menges 1992, Erikstad et al. 1998, Jenouvrier et al. 2003, Morris et al. 2008).

Temperature is an important trigger for phenology, i.e. the timing of seasonal activities such as sprouting of plants, start of reproduction in animals or plants, migration of birds and hatching of insects (Schwartz 2013). Across the globe, in marine as well as terrestrial species, there is a general trend to earlier timing of reproduction ascribed to global warming (Parmesan & Yohe 2003, Parmesan 2007, Poloczanska et al. 2013). A sufficient adaptation to climate change and variability appears particularly important in polar and subpolar regions, where the time window during which climatic conditions are suitable for reproduction is very short and strongly linked to the seasonal peak in temperature and light (Wiegolaski & Inouye 2013). Yet, species appear to react to the warming trend at different speeds, and within interacting species (e.g. predator–prey relationships), one can find more and more mismatches in timing, especially in high latitudes (Wiegolaski & Inouye 2013). Generally, lower trophic level prey species can advance their reproduction more than their predators can. This leads to mismatches, for example in the timing of seabird reproduction and the peak of prey availability (e.g. Hipfner 2008, Shultz et al. 2009).

For migratory species, the detection of environmental cues that may indicate food availability or snowmelt at breeding sites adds another level of difficulty to finding the right timing of breeding. While resident species, relying on local climate conditions (e.g. air temperature), may be able to track phenological shifts relatively easily (Lynch et al. 2012), migratory species may rely on broad-scale climatic conditions, as reflected in indices like the North Atlantic Oscillation (NAO), the Southern Annular Mode (SAM) or the Southern Oscillation Index (SOI), as indicators of conditions at breeding sites and thus the right timing to reproduce (Frederiksen et al. 2004, Emmerson et al. 2011, Hindell et al. 2012).

Besides the timing of reproduction, these environmental variables may further, although often to a slightly lesser extent (Christians 2002), affect the females' investment into reproduction. As females need to trade off their investment into breeding with their own survival, and consequently lifetime reproductive success, they may invest less energy into reproduction or entirely pause during a poor year (*sensu* the prudent parent hypothesis; Drent & Daan 1980). Under favourable breeding and foraging con-

ditions, females may instead increase egg masses and/or clutch sizes and, consequently, expected reproductive output (e.g. Järvinen 1996, Ardia et al. 2006, Potti 2008). Within populations, variation in reproductive investment (e.g. egg and/or clutch size) as well as timing of reproduction may naturally also be linked to consistent differences between females. Consequently, egg size, and to a lesser extent egg-laying date, may be repeatable within the same females across several years and may even be heritable (reviewed in Christians 2002). This raises the question whether certain individuals are able to adapt to environmental variability and phenological shifts in prey availability better than others.

Because of their low reproductive rates and long generation times, rapid adaptation to environmental variability and phenological shifts in long-lived species depend largely on the level of phenotypic plasticity (Canale & Henry 2010, Vedder et al. 2013). Phenotypic plasticity is the ability of a single genotype to modify its phenotype in response to environmental conditions (Houston & McNamara 1992). Phenotypic plasticity is thus expressed as within-individual variation in (e.g. behavioural or morphological) traits (e.g. Przybylo et al. 2000). In addition to phenotypic plasticity per se, the importance of differences in phenotypic plasticity between individuals for microevolutionary adaptations has recently been noted (Davis et al. 2005, Nussey et al. 2007, Gienapp et al. 2008). Such between-individual differences in phenotypic plasticity could increase the lifetime reproductive success of the better-adapted individuals and increase the speed of microevolutionary adaptation to a warming world (Dingemanse & Wolf 2013). However, between-individual differences have so far been described only in a few cases in short-lived songbird species (Brommer et al. 2005, Nussey et al. 2005b, Husby et al. 2010) and a long-lived mammal species (Nussey et al. 2005a) but not in long-lived seabirds (Reed et al. 2006, Hinke et al. 2012).

We tested for the existence of between-individual differences in phenotypic plasticity in southern rockhopper penguins *Eudyptes chrysocome chrysocome*. We followed a set of individually marked females across 7 yr to investigate the effects of variable environmental conditions on the timing of egg laying and investment into egg masses. Southern rockhopper penguins are migratory, long-lived seabirds with a subantarctic distribution in the South Atlantic Ocean. They exhibit a consistently timed breeding cycle: egg-laying dates, timing of incubation trips, chick hatching and fledging dates within colonies and between years are very synchronous (Warham 1963,

Strange 1982, Hull et al. 2004). However, the extent of variability in these phenological traits within individuals (across years) and between individuals (within and across years) is not known, while perhaps being the key for this species to adapt to climate change. We therefore investigated both the within- and between-individual variability in response to 4 candidate environmental variables: the 2 broad-scale climatic indices SAM and SOI as well as local sea surface temperature anomaly (SSTA) and local air temperature (AirT). SAM is the dominant mode of atmospheric variability in the Southern Hemisphere (Marshall 2003). A positive SAM phase in the Southern Ocean is associated with lower SST (reflected in the negative correlation between SAM and SSTA; see 'Materials and methods: Statistics'), stronger westerly winds and higher primary productivity (Lovenduski & Gruber 2005, Hauck et al. 2013). SOI (also referred to as the El Niño Southern Oscillation or ENSO) is defined as the air pressure difference between the mid-Pacific (Tahiti) and western Pacific (Darwin). Similar to SAM, positive SOI indices are coupled to colder surface temperatures (Kwok & Comiso 2002, Meredith et al. 2008). Local SSTA and AirT represent a different spatial scale and thus reflect conditions close to the colony. All 4 environmental variables have previously been shown to affect breeding biology or population dynamics of seabird species, including penguins (Frederiksen et al. 2007, Emmerson et al. 2011, Baylis et al. 2012, Hindell et al. 2012, Lynch et al. 2012). In southern rockhopper penguins, SAM-associated climatic conditions (low SST and increased westerly winds) have been linked to higher foraging success (Dehnhard et al. 2013a), and lower SST has also been related to higher trophic level prey (Dehnhard et al. 2011). Moreover, adult survival in this species has been shown to be sensitive to local SST, with highest survival under cold to average SST (Dehnhard et al. 2013b).

The marine foraging habitat of the southern rockhopper penguin is influenced by the cold, nutrient-rich Falkland Current that originates north of the Antarctic Peninsula (Peterson & Whitworth 1989, Arkhipkin et al. 2010). This area has undergone one of the strongest warming trends worldwide (Meredith & King 2005, Clarke et al. 2007), which is reflected in earlier timing of breeding, demographic responses and distribution shifts in penguin species breeding on the Antarctic Peninsula and adjacent islands (e.g. Forcada et al. 2006, Forcada & Trathan 2009, Hinke et al. 2012, Lynch et al. 2012). However, not all penguin and seabird populations in the Southern Hemisphere show this trend, but some are delaying breed-

ing as a reaction to local changes in food availability or access to breeding sites (Barbraud & Weimerskirch 2006, Boersma & Rebstock 2009, Cullen et al. 2009, Surman et al. 2012, overview in Chambers et al. 2014). Thus, global warming may require different phenological responses for species in different regions, depending on the importance of food resources or access to breeding grounds, necessitating a close look at local populations.

Southern rockhopper penguins exhibit reversed hatching asynchrony with chicks from first-laid (A-) eggs hatching about 1 d after the chicks from second-laid (B-) eggs (Poisbleau et al. 2008). Furthermore, the maternal investment for B-eggs is higher, as these are on average 28% larger and heavier than A-eggs (Poisbleau et al. 2008, Demongin et al. 2010). A-chicks often die in the first days after hatching, and parents rarely fledge more than 1 chick (Strange 1982, Poisbleau et al. 2008). Environmental conditions have been suggested to influence the relative maternal investment into egg masses and, consequently, the chances of A-chick survival (Poisbleau et al. 2008, 2011b, 2013). However, no study has investigated this in detail.

Here, we aimed to identify (1) whether females adjusted clutch initiation date (CID) and investment into egg masses (total clutch mass and intra-clutch egg-mass dimorphism) to environmental variables and (2) whether individual females differed in their phenotypic plasticity in CID and egg mass in response to environmental variables.

We hypothesized that, due to the dispersive behaviour of southern rockhopper penguins during winter, CID and egg-mass variation could be better explained by broad-scale climate indices (SAM and SOI) than by local environmental conditions (SST and AirT). We did not have a clear expectation regarding the direction of the relationships between CID/egg mass and environmental variables, as trends for seabirds in the Southern Hemisphere are partly contrasting (Chambers et al. 2014). However, we expected that the phenotypic plasticity would be higher for CID than for investment into egg masses, as has been reported for other bird species (Christians 2002).

MATERIALS AND METHODS

Field methods

Fieldwork was done in the 'Settlement Colony' on New Island, Falkland Islands/Islands Malvinas (51° 43' S, 61° 17' W), between 2006/2007 and 2013/

2014. The colony held about 5700 breeding pairs in 2006/2007 and 8200 in 2013/2014. More specifically, we worked in one part of the Settlement Colony that includes almost one-quarter of the nests and is representative in vegetation and topography of the entire colony, hereafter referred to as 'study colony'. In this part, starting in 2006/2007, we gradually marked 461 adult females subcutaneously with passive integrated transponders (PITs; 23 mm long, glass-encapsulated; TIRIS, Texas Instruments; see Dehnhard et al. 2013a for more details). The sex of the birds was determined from a combination of morphological and behavioural observations, because males are larger than females, and penguins have a fixed pattern of nest attendance and incubation shifts (Poisbleau et al. 2010). The breeding cycle of southern rockhopper penguins has been described previously (Poisbleau et al. 2008). Briefly, males arrive in breeding colonies in the first week of October, followed by the females a few days later. Both males and females stay ashore and fast during the entire courtship and egg-laying period and the first incubation bout.

In the framework of an ongoing project on maternal investment (e.g. Poisbleau et al. 2009, 2011a, 2013), we collected data on egg-laying dates and egg masses within the study colony across multiple breeding seasons (2006/2007 to 2010/2011 and 2012/2013 to 2013/2014). We visited the colony daily from at least mid-October onwards to follow the egg laying of females with PITs. We recorded individual CIDs, which correspond to A-egg-laying dates. We weighed both A- and B-eggs to the closest 0.1 g using a digital balance (Kern CM 320-1N, Kern & Sohn) on the day when they were first observed. As incubation in rockhopper penguins typically does not start before clutch completion (Williams 1995), the A-eggs were not incubated at all, and the B-eggs were not incubated for longer than 24 h at weighing. We therefore assumed that embryo development and (potential) change in mass (see Poisbleau et al. 2011c) had not yet begun. We consequently calculated the total clutch mass (A-egg mass + B-egg mass) and the intra-clutch egg-mass dimorphism (A-egg mass/B-egg mass).

In the present study, we included only data from individual females for which we obtained all the data (CID, A-egg mass and B-egg mass) at least twice. This resulted in a database of 725 records (between 56 and 147 records per year) from 212 different females which were represented on average 3.4 ± 1.3 SD (min. 2, max. 7) times across 7 yr. All dates were based on the September equinox (= austral vernal equinox), with the date of the equinox = 0 (Sagarin 2001, Dickey et al. 2008).

Environmental variables

Similar to Lynch et al. (2012), we averaged the broad-scale climatic indices SAM and SOI as well as local SST from August through October. Local AirT was averaged for the month of October.

Monthly SAM data were downloaded from the British Antarctic Survey (www.nerc-bas.ac.uk/icd/gjma/sam.html), and monthly SOI data were obtained from the University Center for Atmospheric Research Climate Analysis Section Data Catalogue (www.cgd.ucar.edu/cas/catalog/climind/SOI.signal.ascii). For local SST, we selected a 2° grid in the west of New Island (50 to 52° S, 61 to 63° W). This area is known to be the major foraging location of southern rockhopper penguins from our study colony during the breeding season (Ludynia et al. 2012, 2013) and may also be used by the penguins shortly before arrival to the breeding sites in spring. Monthly SST data were downloaded as SSTA, calculated as the difference between monthly SST and long-term monthly average (data from 1971 to 2000). These data were obtained from NOAA (http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOiv2/.monthly/).

AirT data were obtained from automatic weather stations on New Island (Campbell Scientific; less than 1 km from the penguin colony, operated by the New Island Conservation Trust) and Weddell Island (about 30 km southeast; 51° 53' S, 60° 54' W, operated by the Met Office). Both weather stations recorded data hourly. Because of technical problems, none of the weather stations recorded data for the whole period of this study. The New Island weather station failed to record data from 11 October to 17 November 2009 and during the entire breeding season 2012–13. The Weddell Island weather station showed continuous minor gaps of up to 5 h for many days in all years. To obtain local AirT for the entire study period, we therefore first extrapolated the missing data for the Weddell Island dataset and subsequently inferred mean daily temperatures on New Island from those on Weddell Island.

Through the course of the day, AirT follows a polynomial function, with a peak in the early afternoon hours. Based on this, we fitted polynomial regression curves in the degree of 4 or 5 (using the one with the best fit) to Weddell Island data individually for the days with data gaps of a few hours. $R^2 \geq 0.73$ indicated a good to excellent fit for all curves. Using the obtained regression functions, we then calculated the values for the missing hours and subsequently calculated mean daily AirT values for Weddell Island.

Synchronously recorded daily mean temperature data (for days without any data gaps between October and mid-November, pooled for all years) between New Island and Weddell Island showed a significant correlation (Pearson's correlation coefficient = 0.897, $p < 0.001$, $n = 106$ d). We used this relationship and the regression coefficients (linear regression) to extrapolate the AirT on New Island from that on Weddell Island for the necessary time periods in the breeding seasons 2009–10 and 2012–13 to finally obtain average October AirT for all years.

Statistics

We tested the influence of environmental variables on CIDs and maternal investment into egg mass (total clutch mass and intra-clutch egg-mass dimorphism) by fitting linear mixed-effects models. To test for individual-level plasticity in CIDs and maternal investment into egg mass, we used within-individual-centred data to differentiate within-individual-level responses from between-individual-level responses, as previously described by van de Pol & Wright (2009). We calculated within-individual-centred SAM, SOI, SSTA and AirT as $(x_{ij} - \bar{x}_j)$. x_{ij} would, for example, reflect the average October AirT experienced by individual j in year i . \bar{x}_j would then be the average October AirT experienced by individual j across all years that individual j was included in the study (e.g. \bar{x}_j would be calculated as the average AirT of October 2006, 2007 and 2008 for an individual that was sampled in these 3 yr). In the models, $(x_{ij} - \bar{x}_j)$ would consequently reflect within-individual effects, and (\bar{x}_j) would reflect between-individual effects.

We followed the same approach as Hinke et al. (2012) and first determined the best fixed-effect model structure and thereafter the best random-effect model structure. This was done separately for CID, total clutch mass and intra-clutch egg-mass dimorphism as dependent variables. For the fixed effects, we used a set of candidate models, each with 1 environmental variable. For each environmental variable, both $(x_{ij} - \bar{x}_j)$ and (\bar{x}_j) were included in the model. As several environmental variables were correlated with each other (e.g. SSTA and SAM: Pearson's $R = -0.24$, $p < 0.001$; SSTA and AirT: Pearson's $R = -0.16$, $p = 0.004$; AirT and SOI: Pearson's $R = 0.82$, $p < 0.001$), we decided against fitting several environmental variables into 1 model to avoid issues with collinearity. Consequently, a set of 4 candidate models was fitted (see Table 1, models F1 to F4, for the

model syntax for CID). The best model for the fixed effects was chosen based on Akaike's information criterion. We then followed the protocol in Zuur et al. (2009) by identifying the most parsimonious full model (fixed + random effects) structure. As previously done by Hinke et al. (2012), we included year as a random intercept in all models. In addition, we compared models with all possible combinations (4 candidate models) for the individual random effect to test whether CIDs and egg-mass investments differed among females (i.e. individual [= ID] intercept effect) and whether females differed in their response to environmental variations (i.e. ID slope effect) (see Table 1, models R1 to R4, for the model syntax for CID). After identifying the best random-effects structure, we validated the fixed-effects structure using likelihood ratio tests as described in Zuur et al. (2009) and tested for significance of the included environmental variables. The final model was re-fit using restricted maximum likelihood (REML).

In the final step, independent from the above-described modelling, we tested for the effect of CID (as explanatory variable) on egg-mass investment (total clutch mass and intra-clutch egg-mass dimorphism as dependent variables), including female ID and year as random-intercept variables. This procedure was necessary, as it was not possible (because of collinearity issues) to include CID as a covariate into models that contained environmental variables.

Models were fit with the lme4 package (Bates et al. 2011) in R (version 3.02; R Development Core Team 2014). R^2 values were obtained from model summaries for fixed-effects models. For random-effects models, we followed Nakagawa & Schielzeth (2013) to calculate marginal R^2 values (R^2_m , for the variance explained only by fixed effects) and conditional R^2 values (R^2_c , based on the variance explained by both fixed and random effects).

RESULTS

CID

Within the study period, average CID varied between years from 37.29 ± 2.12 d (mean \pm SD; in 2008) to 41.71 ± 2.27 d (in 2013) after the austral spring equinox, with CID thus being on average 4.42 d later in 2013 than in 2008 (Fig. 1).

SAM was the best predictor variable for CID and explained 20% of the variance in the model (F1, Table 1). Females initiated clutches earlier under high SAM (Figs. 1 & 2). Model fit was significantly

Table 1. Comparison of candidate models to explain clutch initiation date (CID). The model structure is presented as syntax in R. In the first modelling step, the best explanatory environmental variable was identified (upper part of the table; models F1 to F4). Subsequently, random-effects models were compared (lower part of the table; models R1 to R4) based on the best explanatory environmental variable, i.e. SAM, as the fixed effect in addition to the tested random effects. In a final step, the fixed-effects structure was once more validated (to remove fixed effects that had no explanatory power). Fixed-effects models (F1 to F4) were based on several environmental factors: SAM = Southern Annular Mode, SOI = Southern Oscillation Index, SSTA = local sea surface temperature anomaly and AirT = local air temperature. All environmental variables were expressed as within-individual-centred data, i.e. models contained both the within-individual-centred data point ($x_{ij} - \bar{x}_j$) as well as the average value for each individual across years (\bar{x}_j). Random-effects models (R1 to R4) all contained Year as a random intercept (1|Year). In addition, ID as random intercept (1|ID) and individual random slopes for individual-centred ($x_{ij} - \bar{x}_j$) SAM ($0 + \text{SAM}(x_{ij} - \bar{x}_j)|\text{ID}$) were included as random effects. R^2 values for linear models and R^2_c values for random effects models represent the variance explained

Model	Model structure	AIC	ΔAIC	AIC weight	R^2 or R^2_c
Linear					
F1	$\text{CID} \sim \text{SAM}(x_{ij} - \bar{x}_j) + \text{SAM}(\bar{x}_j)$	3327.8	0.0	1.00	0.196
F2	$\text{CID} \sim \text{SOI}(x_{ij} - \bar{x}_j) + \text{SOI}(\bar{x}_j)$	3413.2	85.4	<0.01	0.096
F3	$\text{CID} \sim \text{SSTA}(x_{ij} - \bar{x}_j) + \text{SSTA}(\bar{x}_j)$	3417.0	89.3	<0.01	0.091
F4	$\text{CID} \sim \text{AirT}(x_{ij} - \bar{x}_j) + \text{AirT}(\bar{x}_j)$	3463.1	135.3	<0.01	0.031
Random effects					
R1	$\text{CID} \sim \text{SAM}(x_{ij} - \bar{x}_j) + \text{SAM}(\bar{x}_j) + (1 \text{Year}) + (1 \text{ID})$	2956.3	0.0	0.73	0.723
R2	$\text{CID} \sim \text{SAM}(x_{ij} - \bar{x}_j) + \text{SAM}(\bar{x}_j) + (1 \text{Year}) + (1 \text{ID}) + (0 + \text{SAM}(x_{ij} - \bar{x}_j) \text{ID})$	2958.3	2.0	0.27	0.723
R3	$\text{CID} \sim \text{SAM}(x_{ij} - \bar{x}_j) + \text{SAM}(\bar{x}_j) + (1 \text{Year})$	3187.2	230.9	<0.01	0.391
R4	$\text{CID} \sim \text{SAM}(x_{ij} - \bar{x}_j) + \text{SAM}(\bar{x}_j) + (1 \text{Year}) + (0 + \text{SAM}(x_{ij} - \bar{x}_j) \text{ID})$	3189.2	232.9	<0.01	0.391

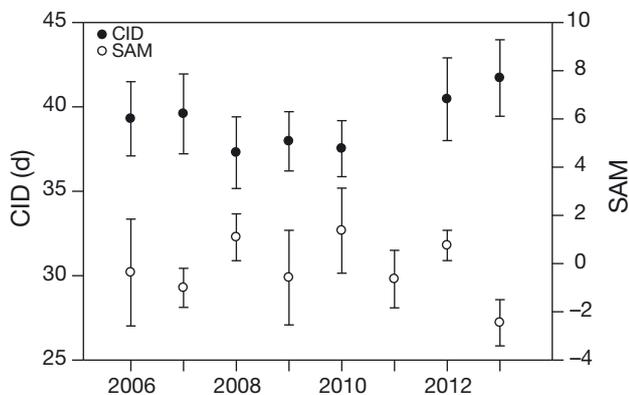


Fig. 1. Mean \pm SD clutch initiation date (CID, number of days after the austral spring equinox) and Southern Annular Mode (SAM) (3 mo period from August through October) across the study period from 2006 to 2013

increased by adding both year and female ID as random intercepts (model R1, Table 1), and this best-supported model explained 72% of the variance. In this final model (R1, Table 1), both the within-individual effects ($x_{ij} - \bar{x}_j$) and the between-individual effects (\bar{x}_j) of SAM on CID were significant. Thus, individual females advanced CID in years in which they experienced positive SAM compared to those years with negative SAM (within-individual effect; Fig. 2a), and females that were on average sampled under positive SAM laid clutches earlier than females that were on average sampled under negative SAM (between-individual effect; Fig. 2b).

Fitting female ID random slopes did not improve the model fit (R1 versus R2, Table 1), suggesting a similar level of plasticity in all females in response to changes in SAM among years.

Maternal investment into egg mass

Total clutch mass was best explained by SSTA (model F1, Table 2). Females laid heavier clutches under lower SSTA (significant within-individual effect; Fig. 3a), while the between-individual effect was not significant (Fig. 3b). Notably, the range of variation in average (\bar{x}_j) SSTA (i.e. the between-individual effect) experienced by the females was much smaller than the within-individual variation in SSTA ($x_{ij} - \bar{x}_j$). Also, we have to keep in mind that overall SSTA explained only 1.4% of the variance in the model; thus, environmental variability was not a good predictor for total clutch mass.

For intra-clutch egg-mass dimorphism, we at first identified AirT as the best explanatory environmental variable, explaining 2.8% of the variance (model F1, Table 3). Intra-clutch egg-mass dimorphism decreased with higher AirT. However, based on likelihood ratio tests performed on the full model, this effect was not significant (Fig. 3c,d). None of the selected environmental variables therefore appeared to account for variation in intra-clutch egg-mass dimorphism.

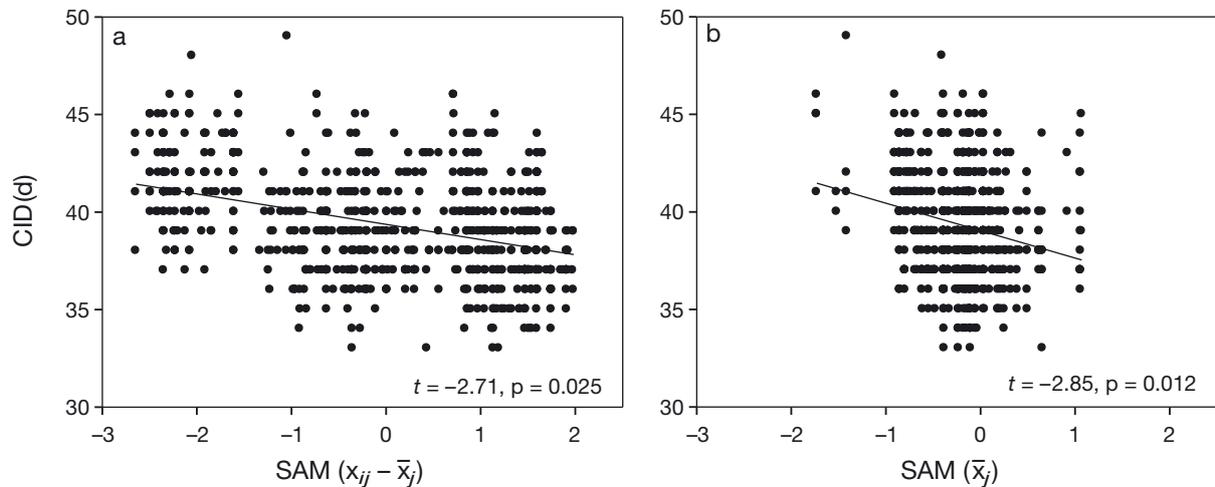


Fig. 2. Clutch initiation date (CID) in response to (a) within-individual-centred Southern Annular Mode (SAM) ($x_{ij} - \bar{x}_j$) and (b) average individual SAM (\bar{x}_j). Regression lines show the direction of the relationship when significant. t -values were obtained from the final (restricted maximum likelihood based) model, and p -values were obtained from likelihood ratio tests from the final model (Table 1)

Table 2. Comparison of candidate models to explain total clutch mass (TMASS). The model structure is presented as syntax in R. In the first step, the best explanatory environmental variable was identified (upper part of the table; models F1 to F4). Thereafter, based on the best fixed-effects model structure (model F1), the best random-effects structure was identified (lower part of the table; models R1 to R4). R^2 values for linear models and R^2_c values for random effects models represent the variance explained. For details, see explanations in Table 1

Model	Model structure	AIC	Δ AIC	AIC weight	R^2 or R^2_c
Linear					
F1	TMASS ~ SSTA($x_{ij} - \bar{x}_j$) + SSTA(\bar{x}_j)	6151.9	0.0	0.86	0.014
F2	TMASS ~ SAM($x_{ij} - \bar{x}_j$) + SAM(\bar{x}_j)	6157.1	5.1	0.07	0.007
F3	TMASS ~ SOI($x_{ij} - \bar{x}_j$) + SOI(\bar{x}_j)	6157.5	5.5	0.05	0.007
F4	TMASS ~ AirT($x_{ij} - \bar{x}_j$) + AirT(\bar{x}_j)	6159.0	7.1	0.02	0.005
Random effects					
R1	TMASS ~ SSTA($x_{ij} - \bar{x}_j$) + SSTA(\bar{x}_j) + (1 Year) + (1 ID)	5503.6	0.0	0.64	0.813
R2	TMASS ~ SSTA($x_{ij} - \bar{x}_j$) + SSTA(\bar{x}_j) + (1 Year) + (1 ID) + (0 + SSTA($x_{ij} - \bar{x}_j$) ID)	5504.7	1.1	0.36	0.850
R3	TMASS ~ SSTA($x_{ij} - \bar{x}_j$) + SSTA(\bar{x}_j) + (1 Year) + (0 + SSTA($x_{ij} - \bar{x}_j$) ID)	6142.1	638.5	<0.01	0.018
R4	TMASS ~ SSTA($x_{ij} - \bar{x}_j$) + SSTA(\bar{x}_j) + (1 Year)	6144.1	640.5	<0.01	0.018

For both total clutch mass and intra-clutch egg-mass dimorphism, the best full model structure included female ID as a random intercept (model R1 each, Tables 2 & 3), which markedly increased the model fit compared to the fixed-effects structure. Best-fit random-effects models explained 81 and 56% of the variance, respectively (Tables 2 & 3). Fitting female ID random slopes did not improve the model fit, suggesting (for total clutch mass) a similar level of plasticity of all females in response to changes in SSTA among years (Table 2).

CID had no significant effect on total clutch mass (random-effects model with CID as fixed effect, female ID and year as random intercepts: $t = -1.10$,

$p = 0.266$, $R^2_m = 0.001$, $R^2_c = 0.813$). In contrast, intra-clutch egg-mass dimorphism significantly decreased with later CID ($t = 4.91$, $p < 0.001$, $R^2_m = 0.046$, $R^2_c = 0.561$; Fig. 4).

DISCUSSION

Whether or not a population can cope with and evolutionarily adapt to rapid environmental changes depends largely on the extent of phenotypic plasticity at the individual level (e.g. Dingemanse & Wolf 2013). More specifically, individuals with a higher phenotypic plasticity should be able to adapt better

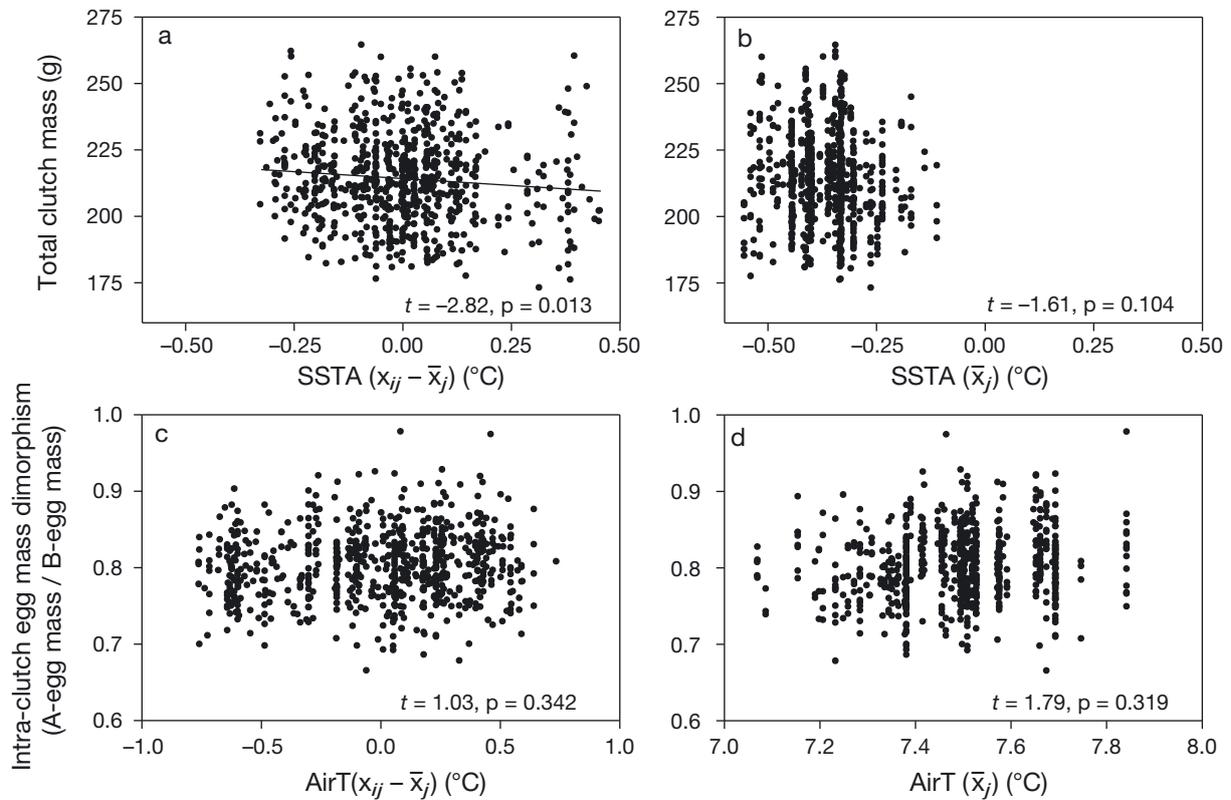


Fig. 3. Total clutch mass and intra-clutch egg-mass ratio in response to environmental variables (chosen according to the modelling procedures). Both the within-individual-centred values ($x_{ij} - \bar{x}_j$), reflecting within-individual effects, and the average values per individual (\bar{x}_j), reflecting between-individual effects, are presented. Regression lines show the direction of the relationship (for significant effects only). t -values were obtained from the final (restricted maximum likelihood based) random-effects model, and p -values were obtained from likelihood ratio tests based on this model

Table 3. Comparison of candidate models to explain intra-clutch egg-mass dimorphism (RMASS). The model structure is presented as syntax in R. In the first step, the best explanatory environmental variable was identified (upper part of the table; models F1 to F4). Thereafter, based on the best fixed-effects model structure (model F1), the best random-effects structure was identified (lower part of the table; models R1 to R4). R^2 values for linear models and R^2_c values for random effects models represent the variance explained. For details, see explanations in Table 1

Model	Model structure	AIC	Δ AIC	AIC weight	R^2 or R^2_c
Linear					
F1	$\text{RMASS} \sim \text{AirT}(x_{ij} - \bar{x}_j) + \text{AirT}(\bar{x}_j)$	-2461.1	0.0	0.97	0.028
F2	$\text{RMASS} \sim \text{SOI}(x_{ij} - \bar{x}_j) + \text{SOI}(\bar{x}_j)$	-2454.3	6.8	0.03	0.019
F3	$\text{RMASS} \sim \text{SAM}(x_{ij} - \bar{x}_j) + \text{SAM}(\bar{x}_j)$	-2448.1	13.0	<0.01	0.011
F4	$\text{RMASS} \sim \text{SSTA}(x_{ij} - \bar{x}_j) + \text{SSTA}(\bar{x}_j)$	-2442.0	19.2	<0.01	0.002
Random effects					
R1	$\text{RMASS} \sim \text{AirT}(x_{ij} - \bar{x}_j) + \text{AirT}(\bar{x}_j) + (1 \text{Year}) + (1 \text{ID})$	-2653.1	0.0	0.73	0.561
R2	$\text{RMASS} \sim \text{AirT}(x_{ij} - \bar{x}_j) + \text{AirT}(\bar{x}_j) + (1 \text{Year}) + (1 \text{ID}) + (0 + \text{AirT}(x_{ij} - \bar{x}_j) \text{ID})$	-2651.1	2.0	0.27	0.561
R3	$\text{RMASS} \sim \text{AirT}(x_{ij} - \bar{x}_j) + \text{AirT}(\bar{x}_j) + (1 \text{Year})$	-2455.4	197.7	<0.01	0.087
R4	$\text{RMASS} \sim \text{AirT}(x_{ij} - \bar{x}_j) + \text{AirT}(\bar{x}_j) + (1 \text{Year}) + (0 + \text{AirT}(x_{ij} - \bar{x}_j) \text{ID})$	-2453.4	199.7	<0.01	0.087

to increasing environmental variability and consequently reproduce more successfully under global warming scenarios than individuals that are less plastic in their behavioural responses.

We were here able to show that, in southern rockhopper penguins—a species with an apparently highly synchronized and rather strict breeding pattern—females showed within-individual variation

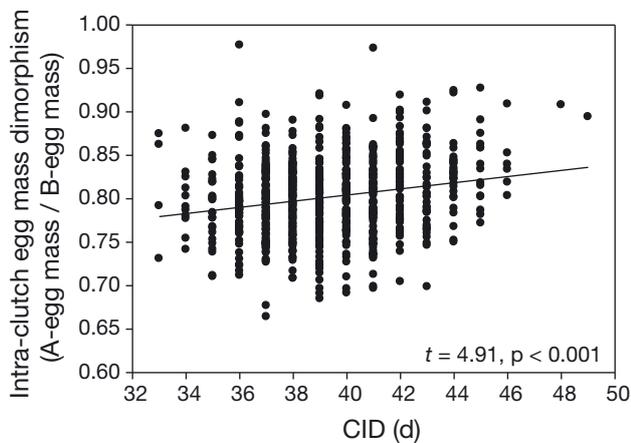


Fig. 4. Intra-clutch egg-mass dimorphism (calculated as A-egg mass/B-egg mass) in response to clutch initiation date (CID). The t -value was obtained from the restricted maximum likelihood based random-effects model, and the p -value was obtained from likelihood ratio tests based on this model

and thus adapted their timing of breeding and, to a much lesser extent, allocation into egg masses to environmental conditions. However, as indicated by a lack of support for individual random slopes, our results suggested that the extent of phenotypic plasticity was similar across all individuals. Importantly, female ID explained the largest part of the variance for both CID and egg-mass investment, suggesting that individual females were very consistent in their egg-laying behaviour across years. Here, we will discuss the observed effects of environmental variables on CID and egg investment on both within- and between-individual scales and the implications for this species' adaptation to climate change.

CID

In agreement with our expectation, a broad-scale environmental index (SAM) was the best environmental predictor for CID. SAM explained up to 20% of the variance in models for CID, which was substantially more than for egg investment parameters (see below). This meets our expectation that the behavioural plasticity would be higher for CID than for egg mass. The plasticity in CID is shown by the significant within-individual effect of SAM, meaning that individuals adjusted CID to the environmental conditions they experienced. Along with this, we also found a significant between-individual effect, i.e. females experiencing high average SAM also laid earlier than females experiencing low average SAM

(as reflected in Fig. 2b). This is in contrast to Hinke et al. (2012), who found a significant within-individual effect but a non-significant between-individual effect of AirT on CID in Adélie penguins *Pygoscelis adeliae* and gentoo penguins *Pygoscelis papua*.

Our results indicated that CID was advanced under high SAM values, which reflect colder conditions but higher primary productivity (Lovenduski & Gruber 2005, Hauck et al. 2013). While it appears counter-current to the observed trends to advanced phenological traits (e.g. earlier egg laying, earlier flowering) under warmer spring conditions (e.g. Visser & Both 2005, Parmesan 2007), it is not uncommon among seabirds, particularly in the Southern Hemisphere, to breed earlier under colder conditions (Chambers et al. 2014). In accordance with our results, earlier CID with increasing SAM values have been described for royal penguins *Eudyptes schlegeli* breeding on Macquarie Island in the subantarctic Indian Ocean (Hindell et al. 2012) and Adélie penguins breeding in eastern Antarctica (Emmerson et al. 2011).

Within the marine food web, southern rockhopper penguins are located at a relatively low trophic level position compared to other seabirds (Weiss et al. 2009) and are therefore likely to benefit rapidly from increased primary productivity. In agreement with previous findings (Dehnhard et al. 2013a,b), a positive SAM phase thus implies favourable foraging conditions for southern rockhopper penguins, and under these conditions, they lay earlier. Considering the high energy and nutrient requirements that egg laying means for female penguins (Meijer & Drent 1999), our results suggest that CID may be constrained by food availability. When resources are scarce, females may remain at sea longer to gain sufficient resources, resulting in later CID. This is consistent with a range of experiments showing that food supplementation leads to an advancement in CID (e.g. Magrath 1992, Nilsson & Svensson 1993, reviewed in Meijer & Drent 1999).

Maternal investment into egg mass

Of the selected environmental variables, local climate conditions had the largest relative explanatory power. However, environmental variability had only a very limited effect on total clutch mass, and there was no significant effect of environmental variation on intra-clutch egg-mass dimorphism at all. While we cannot rule out that we missed a relevant, better explanatory environmental variable, the most likely

explanation for this very low effect of environmental variability is the high consistency of individual females in their egg-mass allocation across years. In fact, female ID explained about 80% of variance in random-effects models for total clutch mass, and based on the literature (Christians 2002), we had also expected to find a lower phenotypic plasticity in egg-mass allocation compared to clutch initiation date.

The weak but significant within-individual effect of SSTA, and therefore of a local environmental variable, may reflect that maternal investment into eggs is regulated at a later time period than CID. In fact, egg formation of both A- and B-eggs starts while birds are still at sea, i.e. before arrival in the colonies, but is then completed in the colonies, while females are fasting (Crossin et al. 2012). This could explain the relatively stronger importance of local climatic conditions for egg masses.

The (albeit weak) within-individual effect of low SSTA on the increase of total clutch mass is most likely also driven by higher food availability, as lower SSTA is linked to positive SAM (see above). This is consistent with previous studies that found a higher female investment in clutches (egg mass or number of eggs), with environmental conditions increasing food availability (e.g. Saino et al. 2004, Ardia et al. 2006, Potti 2008, Lehikoinen et al. 2011). Along with the significant within-individual effect, one could have expected a between-individual effect of SSTA as well. The lack thereof may partly be due to a smaller range of variation in average SSTA (\bar{x}_j) experienced by females compared to the within-individual SSTA ($x_{ij} - \bar{x}_j$) (see Fig. 3).

Finally, we found that total clutch mass was independent of CID. This is in contrast to a range of studies which showed significant effects of CID on clutch size or mass (e.g. Birkhead & Nettleship 1982, Nilsson & Svensson 1993, Winkler & Allen 1996, D'Alba & Torres 2007). It appears that rockhopper penguins rather traded off total clutch mass with CID and initiated clutches as early as possible but kept investment into total clutch mass consistent (also see Nilsson & Svensson 1993), which may have also contributed to the low explanatory power of environmental variables on total clutch mass in general. Nevertheless, females traded off their relative investment into A- and B-egg masses according to CID, but again this effect (albeit significant) was comparatively weak. In addition, female identity explained a lower proportion (less than 50% of variance in models; see Table 3) for intra-clutch egg-mass dimorphism compared to total clutch mass. The drivers of variation in intra-clutch egg-mass dimorphism therefore remain open

and may partly be related to male quality (Poisbleau et al. 2013).

Implications for the species' adaptation to climate change

Although rockhopper penguins adapted their CID to climatic conditions, the range of phenotypic plasticity appeared low compared to other seabird species (Frederiksen et al. 2004, Brommer et al. 2008, Surman et al. 2012), including other penguin species (Emmerson et al. 2011, Lynch et al. 2012). Moreover, the lack of support for models with individual random slopes suggested a similar level of phenotypic plasticity in all individuals. However, our study was conducted during a relatively short study period of 7 yr that were apparently dominated by favourable conditions for rockhopper penguins; both our study population and the population across the entire Falkland Island archipelago showed a steady population increase during this period (Baylis et al. 2013). As such, the outcomes of this study may be somewhat limited both in detecting environmental variables that drive phenology and reproductive investment and in detecting a stronger level of phenotypic plasticity within and between individuals. We can therefore not entirely rule out that rockhopper penguins are able to show a stronger level of phenotypic plasticity under adverse conditions. However, Hinke et al. (2012) did not detect individual phenotypic plasticity in Adélie penguins, even though the population was declining during the course of the study (across 19 yr). Potentially, in colony-breeding species, synchronous breeding may be more important (e.g. to avoid egg or chick predation) than adjusting CIDs individually (also see Reed et al. 2006, Hinke et al. 2012). Unfortunately, it was not possible in the framework of this study to monitor the breeding success and therefore if variation in CID and/or egg mass had effects on the actual reproductive output.

For the predicted future climate changes, including increased climatic variability (Collins et al. 2013), our results imply that the apparent lack of individual differences in phenotypic plasticity might hamper the species' microevolutionary adaptation (Davis et al. 2005, Gienapp et al. 2008, Dingemanse & Wolf 2013). In addition, the low range of phenotypic plasticity on the population scale observed in this study and also previously (Dehnhard et al. 2013a,b) should receive further attention (Canale & Henry 2010), especially because southern rockhopper penguins are already listed as 'vulnerable' (Birdlife International 2012).

Furthermore, our results in combination with previous similar findings for other seabird species (Reed et al. 2006, Hinke et al. 2012) raise the question whether other threatened and long-lived species, especially within the group of seabirds (Croxall et al. 2012), exhibit individual differences in phenotypic plasticity.

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