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

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4 **Running head:** phenotypic plasticity in rockhopper penguin egg-laying behaviour

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20

21 **Abstract**

22 Global climate change requires species to adapt to increasing environmental variability, rising  
23 air- and ocean temperatures and many other effects, including temperature-associated  
24 phenological shifts. Species may adapt to such rapid changes by micro-evolutionary  
25 processes and/or phenotypic plasticity. The speed of micro-evolutionary adaptation may  
26 critically be enhanced by between-individual differences in phenotypic plasticity. However,  
27 such between-individual differences have rarely been shown, especially for long-lived and  
28 migratory species that appear particularly vulnerable to phenological shifts. Southern  
29 rockhopper penguins (*Eudyptes chrysocome chrysocome*) are migratory, long-lived seabirds  
30 with a “vulnerable” conservation status. We studied clutch initiation date (CID) and  
31 investment into egg mass in individually marked females in response to broad-scale and local  
32 climate variables across 7 years. We thereby distinguished within-individual and between-  
33 individual variation and tested the existence of between-individual differences in the  
34 expression of phenotypic plasticity.

35         Due to both within-individual and between-individual variation, CID was  
36 significantly advanced under high Southern Annular Mode (SAM), reflecting colder  
37 environmental conditions and higher food availability. Total clutch mass increased under low  
38 local sea surface temperatures (significant within-individual effect), but was mostly  
39 accounted for by female identity. Intra-clutch egg-mass dimorphism was not affected by  
40 environmental variables at all. We found no indication for between-individual differences in  
41 phenotypic plasticity and overall, the expression of phenotypic plasticity appeared to be  
42 limited. This raises the question whether between-individual differences in phenotypic  
43 plasticity exist in other long-lived species and whether rockhopper penguins show sufficient  
44 phenotypic plasticity to adapt to predicted climate changes.

45 **Key words:** between-individual effects, breeding biology, *Eudyptes chrysocome*, phenology,  
46 within-individual effects

## 47 **Introduction**

48 Among other anthropogenic effects on the environment, global climate change is currently  
49 seen as the most wide-ranging and dangerous threat for plants and animals in the 21st century  
50 and beyond (e.g. Thomas et al. 2004). Across the globe, climate change scenarios predict  
51 increasing air and sea surface temperatures (SST), shifts in atmospheric wind systems and a  
52 general increase in climate variability, i.e. more extreme weather conditions (Collins et al.  
53 2013 and literature therein). These changes, and the speed at which they take place, may lead  
54 to reproductive failure and mortality for both plants and animals with effects on long-term  
55 population trajectories and species' survival (e.g. Menges 1992, Erikstad et al. 1998,  
56 Jenouvrier et al. 2003, Morris et al. 2008).

57         Temperature is an important trigger for phenology, i.e. the timing of seasonal  
58 activities, for example sprouting of plants, start of reproduction in animals or plants,  
59 migration of birds and hatching of insects (Schwartz 2013). Across the globe, in marine as  
60 well as in terrestrial species, there is a general trend to earlier timing of reproduction ascribed  
61 to global warming (Parmesan & Yohe 2003, Parmesan 2007, Poloczanska et al. 2013). A  
62 sufficient adaptation to climate change and variability appears particularly important in polar-  
63 and subpolar regions, where the time window during which climatic conditions are suitable  
64 for reproduction is very short and strongly linked to the seasonal peak in temperature and  
65 light (Wiegolaski & Inouye 2013). Yet, species appear to react to the warming trend at  
66 different speeds, and within interacting species (e.g. predator-prey relationships) one can find  
67 more and more mismatches in timing, especially in high latitudes (Wiegolaski & Inouye  
68 2013). Generally, lower trophic level prey species can advance their reproduction more than  
69 their predators can. This leads to mismatches, for example in the timing of seabirds'  
70 reproduction and the peak of prey availability (e.g. Hipfner 2008, Shultz et al. 2009).

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

79 Besides the timing of reproduction, these environmental variables may further –  
80 although often to a slightly lesser extent (Christians 2002) – affect the females’ investment  
81 into reproduction. As females need to trade off their investment into breeding with their own  
82 survival, and consequently life-time reproductive success, they may invest less energy into  
83 reproduction or entirely pause during a poor year (sensu the prudent parent hypothesis; Drent  
84 & Daan 1980). Under favourable breeding and foraging conditions, females may instead  
85 increase egg masses and/or clutch sizes and consequently expected reproductive output (e.g.  
86 Järvinen 1996, Ardia et al. 2006, Potti 2008). Within populations, variation in reproductive  
87 investment (e.g. egg and/or clutch size) as well as timing of reproduction may naturally also  
88 be linked to consistent differences between females. Consequently, egg size and to a lesser  
89 extent egg laying date may be repeatable within the same females across several years, and  
90 even heritable (reviewed in Christians 2002). This raises the question whether certain  
91 individuals are able to adapt to environmental variability and phenological shifts in prey  
92 availability better than others.

93 Due to their low reproductive rates and long generation times, rapid adaptation to  
94 environmental variability and phenological shifts in long-lived species depend largely on the  
95 level of phenotypic plasticity (Canale & Henry 2010, Vedder et al. 2013). Phenotypic

96 plasticity is the ability of a single genotype to modify its phenotype in response to  
97 environmental conditions (Houston & McNamara 1992). Phenotypic plasticity is thus  
98 expressed as within-individual variation in (e.g. behavioural or morphological) traits (e.g.  
99 Przybylo et al. 2000). In addition to phenotypic plasticity *per se*, the importance of  
100 differences in phenotypic plasticity between individuals for microevolutionary adaptations  
101 has recently been noted (Davis et al. 2005, Nussey et al. 2007, Gienapp et al. 2008). Such  
102 between-individual differences in phenotypic plasticity could increase the lifetime  
103 reproductive success of the better adapted individuals and increase the speed of  
104 microevolutionary adaptation to a warming world (Dingemanse & Wolf 2013). However,  
105 between-individual differences have so far been described only in few cases in short-lived  
106 songbird species (Brommer et al. 2005, Nussey et al. 2005b, Husby et al. 2010) and a long-  
107 lived mammal species (Nussey et al. 2005a) but not in long-lived seabirds (Reed et al. 2006,  
108 Hinke et al. 2012).

109         We tested for the existence of between-individual differences in phenotypic plasticity  
110 in southern rockhopper penguins (*Eudyptes chrysocome chrysocome*). We followed a set of  
111 individually marked females across seven years to investigate the effects of variable  
112 environmental conditions on the timing of egg laying and investment into egg masses.  
113 Southern rockhopper penguins are migratory, long-lived seabirds with a subantarctic  
114 distribution in the South Atlantic Ocean. They exhibit a consistently timed breeding cycle:  
115 egg laying dates, timing of incubation trips, chick hatching and fledging dates within colonies  
116 and between years are very synchronous (Warham 1963, Strange 1982, Hull et al. 2004).  
117 However, the extent of variability in these phenological traits within individuals (across  
118 years) and between individuals (within and across years) is not known, while perhaps being  
119 the key for this species to adapt to climate change. We therefore investigated both the within-  
120 and between-individual variability in response to four candidate environmental variables: the

121 two broad-scale climatic indices Southern Annular Mode (SAM) and Southern Oscillation  
122 Index (SOI) as well as local sea surface temperature anomaly (SSTA) and local air  
123 temperatures (AirT). SAM is the dominant mode of atmospheric variability in the Southern  
124 hemisphere (Marshall 2003). A positive SAM phase in the Southern Ocean is associated with  
125 lower SST (reflected in the negative correlation between SAM and SSTA; see Methods),  
126 stronger westerly winds and a higher primary productivity (Lovenduski & Gruber 2005,  
127 Hauck et al. 2013). SOI (also referred to as El Niño Southern Oscillation or ENSO) is defined  
128 as the air-pressure difference between the mid-Pacific (Tahiti) and west-Pacific (Darwin).  
129 Similarly to SAM, positive SOI indices are coupled to colder surface temperatures (Kwok &  
130 Comiso 2002, Meredith et al. 2008). Local SSTA and AirT represent a different spatial scale  
131 and thus reflect conditions close to the colony. All four environmental variables have  
132 previously shown to affect breeding biology or population dynamics of seabird species,  
133 including penguins (Frederiksen et al. 2007, Emmerson et al. 2011, Baylis et al. 2012,  
134 Hindell et al. 2012, Lynch et al. 2012). In southern rockhopper penguins, SAM-associated  
135 climatic conditions (low SST and increased westerly winds) have been linked to higher  
136 foraging success (Dehnhard et al. 2013a), and lower SST have also been related to higher  
137 trophic level prey (Dehnhard et al. 2011). Moreover, adult survival in this species has been  
138 shown to be sensitive to local SST, with highest survival under cold to average SST  
139 (Dehnhard et al. 2013b).

140         The marine foraging habitat of the southern rockhopper penguin is influenced by the  
141 cold, nutrient-rich Falkland Current that originates north of the Antarctic Peninsula (Peterson  
142 & Whitworth 1989, Arkhipkin et al. 2010). This area has undergone one of the strongest  
143 warming trends worldwide (Meredith & King 2005, Clarke et al. 2007), which is reflected in  
144 earlier timing of breeding, demographic responses and distribution shifts in penguin species  
145 breeding on the Antarctic Peninsula and adjacent islands(e.g. Forcada et al. 2006, Forcada &

146 Trathan 2009, Hinke et al. 2012, Lynch et al. 2012). However, not all penguin and seabird  
147 populations in the southern hemisphere show this trend, but some are delaying breeding as a  
148 reaction to local changes in food availability or access to breeding sites (Barbraud &  
149 Weimerskirch 2006, Boersma & Rebstock 2009, Cullen et al. 2009, Surman et al. 2012,  
150 overview in Chambers et al. 2013). Thus, global warming may require different phenological  
151 responses for species in different regions, depending on the importance of food resources or  
152 access to breeding grounds, necessitating a close look at local populations.

153         Southern rockhopper penguins exhibit reversed hatching asynchrony with chicks from  
154 first-laid (A-) eggs hatching about one day after the chicks from second-laid (B-) eggs  
155 (Poisbleau et al. 2008). Furthermore, the maternal investment for B-eggs is higher, as these  
156 are on average 28% larger and heavier than A-eggs (Poisbleau et al. 2008, Demongin et al.  
157 2010). A-chicks often die in the first days after hatching, and parents rarely fledge more than  
158 one chick (Strange 1982, Poisbleau et al. 2008). Environmental conditions have been  
159 suggested to influence the relative maternal investment into egg masses and consequently  
160 chances of A-chick survival (Poisbleau et al. 2008, 2011b, 2013). However, no study has  
161 investigated this in detail.

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

166         We hypothesized that, due to their dispersive behaviour during winter, CID and egg  
167 mass variation in southern rockhopper penguins could be better explained by broad-scale  
168 climate indices (SAM and SOI) than local environmental conditions (SST and AirT). We did  
169 not have a clear expectation regarding the direction of the relationships between CID/egg

170 mass and environmental variables, as trends for seabirds in the southern hemisphere are  
171 partly contrasting (Chambers et al. 2013). However, we expected that the phenotypic  
172 plasticity would be higher for CID than for investment into egg masses, as has been reported  
173 for other bird species (Christians 2002).

174

175

## 176 **Materials and methods**

### 177 *Field Methods*

178 Fieldwork was done in the “Settlement Colony” on New Island, Falkland Islands / Islas  
179 Malvinas (51°43’S, 61°17’W) between 2006/07 and 2013/14. The colony held about 5,700  
180 breeding pairs in 2006/07, and 8,200 in 2013/14. More specifically, we worked in one part of  
181 the Settlement Colony that includes almost one quarter of the nests and is representative in  
182 vegetation and topography of the entire colony, hereafter referred to as “study colony”. In this  
183 part, starting in 2006/07, we gradually marked 461 adult females subcutaneously with passive  
184 integrated transponders (PITs; 23 mm long, glass-encapsuled, TIRIS, Texas Instruments,  
185 USA; see Dehnhard et al. 2013a for more details). The sex of the birds was determined from  
186 a combination of morphological and behavioural observations, because males are larger than  
187 females and penguins have a fixed pattern of nest attendance and incubation shifts (Poisbleau  
188 et al. 2010). The breeding cycle of southern rockhopper penguins has been described  
189 previously (Poisbleau et al. 2008). Briefly, males arrive in breeding colonies in the first week  
190 of October, followed by the females a few days later. Both males and females stay ashore and  
191 fast during the entire courtship and egg laying period and the first incubation bout.

192 In the framework of an on-going project on maternal investment (e.g. Poisbleau et al.  
193 2009, 2011a, 2013), we collected data on egg laying dates and egg masses within the study  
194 colony across multiple breeding seasons (2006/07–2010/11 and 2012/13–2013/14). We  
195 visited the colony daily from at least mid-October onwards to follow the egg laying of  
196 females with a transponder. We recorded individual clutch initiation dates (CIDs), which  
197 correspond to the A-egg laying dates. We weighed both A- and B-eggs to the closest 0.1 g  
198 using a digital balance (Kern CM 320-1N; Kern & Sohn, Germany) on the day when they  
199 were first observed. As incubation in rockhopper penguins typically does not start before  
200 clutch completion (Williams 1995), the A-eggs were not incubated at all and the B-eggs were  
201 not incubated for longer than 24 h at weighing. We therefore assumed that embryo  
202 development and (potential) change in mass (see Poisbleau et al. 2011c) had not yet begun.  
203 We consequently calculated the total clutch mass (A-egg mass + B-egg mass) and the intra-  
204 clutch egg-mass dimorphism (A-egg mass / B-egg mass).

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

211

### 212 *Environmental Variables*

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

216 Monthly SAM data were downloaded from the British Antarctic Survey  
217 (<http://www.nerc-bas.ac.uk/icd/gjma/sam.html>), and monthly SOI data were obtained from  
218 the University Center for Atmospheric Research Climate Analysis Section Data Catalogue  
219 (<http://www.cgd.ucar.edu/cas/catalog/climind/SOI.signal.ascii>). For local SST, we selected a  
220 2° grid in the west of New Island (50–52°S, 61–63°W). This area is known to be the major  
221 foraging location of southern rockhopper penguins from our study colony during the breeding  
222 season (Ludynia et al. 2012, 2013) and may also be used by the penguins shortly before  
223 arrival to the breeding sites in spring. Monthly SST data were downloaded as SSTA anomaly  
224 (SSTA), calculated as the difference between monthly SST and long-term monthly average  
225 (data from 1971 to 2000). These data were obtained from the National Oceanic and  
226 Atmospheric Administration (NOAA)  
227 ([http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/  
228 .Reyn\\_SmithOIv2/.monthly/](http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOIv2/.monthly/)).

229 AirT data were obtained from automatic weather stations on New Island (Campbell  
230 Scientific, Logan, Utah, USA; less than 1 km away from the penguin colony; operated by the  
231 New Island Conservation Trust) and Weddell Island (about 30 km in the southeast; 51°53'S,  
232 60°54'W, operated by the Met Office). Both weather stations recorded data hourly. Due to  
233 technical problems, none of the weather stations recorded data for the whole period of this  
234 study. The New Island weather station failed to record data from 11 October to 17 November  
235 2009 and during the entire breeding season 2012/13. The Weddell Island weather station  
236 showed continuous minor gaps of up to 5 hours for many days in all years. In order to obtain  
237 local AirT for the entire study period, we therefore first extrapolated the missing data for the  
238 Weddell Island dataset and subsequently inferred mean daily temperatures on New Island  
239 from those on Weddell Island.

240 Through the course of the day, AirT follows a polynomial function with a peak in the  
241 early afternoon hours. Based on this, we fitted polynomial regression curves in the degree of  
242 4 or 5 (using the one with the best fit) to Weddell Island data individually for the days with  
243 data gaps of few hours.  $R^2 \geq 0.73$  indicated a good to excellent fit for all curves. Using the  
244 obtained regression functions, we then calculated the values for the missing hours and  
245 subsequently calculated mean daily AirT values for Weddell Island.

246 Synchronously between New and Weddell Island, recorded daily mean temperature  
247 data (for days without any data gaps between October and mid-November pooled for all  
248 years) showed a significant correlation (Pearson's correlation coefficient = 0.897,  $P < 0.001$ ,  
249  $N = 106$  days). We used this relationship and the regression coefficients (linear regression) to  
250 extrapolate the AirT on New Island from those on Weddell Island for the necessary time  
251 periods in the breeding seasons 2009/10 and 2012/2013 to finally obtain average October  
252 AirT for all years.

253

#### 254 *Statistics*

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

264 October 2006, 2007 and 2008 for an individual that was sampled in these three years). In the  
265 models,  $(x_{ij}-\bar{x}_j)$  would consequently reflect within-individual effects, and  $(\bar{x}_j)$  would reflect  
266 between-individual effects.

267 We followed the same approach as Hinke et al. (2012) and first determined the best  
268 fixed-effect model structure and thereafter the best random-effect model structure. This was  
269 done separately for CID, total clutch mass and intra-clutch egg-mass dimorphism as  
270 dependent variables. For the fixed effects, we used a set of candidate models, each with one  
271 environmental variable. For each environmental variable, both  $(x_{ij}-\bar{x}_j)$  and  $(\bar{x}_j)$  were included  
272 in the model. As several environmental variables were correlated with each other (e.g. SSTA  
273 & SAM: Pearson's  $R = -0.24$ ,  $P < 0.001$ ; SSTA & AirT: Pearson's  $R = -0.16$ ,  $P = 0.004$ ; AirT  
274 & SOI: Pearson's  $R = 0.82$ ,  $P < 0.001$ ), we decided against fitting several environmental  
275 variables into one model in order to avoid issues with collinearity. Consequently, a set of four  
276 candidate models was fitted (see Table 1, models F1–F4 for the model syntax for CID). The  
277 best model for the fixed effects was chosen based on Akaike's information criterion (AIC).  
278 We then followed the protocol in Zuur et al. (2009) by identifying the most parsimonious full  
279 model (fixed + random effects) structure. As previously done by Hinke et al. (2012), we  
280 included year as a random intercept in all models. In addition, we compared models with all  
281 possible combinations (4 candidate models) for the individual random effect to test whether  
282 CIDs and egg mass investments differed among females (i.e. individual (= ID) intercept  
283 effect) and whether females differed in their response to environmental variations (i.e. ID  
284 slope effect) (see Table 1, models R1–R4 for the model syntax for CID). After identifying the  
285 best random effects structure, we validated the fixed effects structure using likelihood ratio  
286 tests as described in Zuur et al. (2009) and tested for the significance of the included  
287 environmental variables. The final model was re-fit using restricted maximum likelihood  
288 (REML).

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

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

301

302

## 303 **Results**

### 304 *Clutch Initiation Date CID*

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

308 SAM was the best predictor variable for CID and explained 20% of the variance in the  
309 model (Model F1, Table 1). Females initiated clutches earlier under high SAM (Fig. 1 & 2).  
310 Model fit was significantly increased by adding both year and female ID as random intercepts  
311 (Model R1, Table 1), and this best-supported model explained 72% of the variance. In this

312 final model (R1, Table 1) both the within-individual effects ( $x_{ij}-\bar{x}_j$ ) and the between-  
313 individual effects ( $\bar{x}_j$ ) of SAM on CID were significant. Thus, individual females advanced  
314 CID in years in which they experienced positive SAM compared to those years with negative  
315 SAM (within-individual effect; Fig. 2a), and females that were on average sampled under  
316 positive SAM laid clutches earlier than females that were on average sampled under negative  
317 SAM (between-individual effect; Fig. 2b). Fitting female ID random slopes did not improve  
318 the model fit (Model R1 versus Model R2, Table 1), suggesting a similar level of plasticity in  
319 all females in response to changes in SAM among years.

320

### 321 *Maternal investment into egg mass*

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

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

335 For both total clutch mass and intra-clutch egg-mass dimorphism, the best full model  
336 structure included female ID as random intercept (Models R1 each, Tables 2 & 3), which  
337 markedly increased the model fit compared to the fixed-effects structure. Best-fit random-  
338 effects models explained 81 and 56% of the variance, respectively (Tables 2 & 3). Fitting  
339 female ID random slopes did not improve the model fit, suggesting (for total clutch mass) a  
340 similar level of plasticity of all females in response to changes in SSTA among years (Table  
341 2).

342

343 CID had no significant effect on total clutch mass (Random effects model with CID as fixed  
344 effect, female ID and year as random intercepts:  $t = -1.10$ ,  $P = 0.266$ ,  $R^2_m = 0.001$ ,  $R^2_c =$   
345  $0.813$ ). In contrast, intra-clutch egg-mass dimorphism significantly decreased with later CID  
346 ( $t = 4.91$ ,  $P < 0.001$ ,  $R^2_m = 0.046$ ,  $R^2_c = 0.561$ ; Fig. 4).

347

348

## 349 **Discussion**

350 Whether or not a population can cope with and evolutionarily adapt to rapid environmental  
351 changes depends largely on the extent of phenotypic plasticity at the individual level (e.g.  
352 Dingemanse & Wolf 2013). More specifically, individuals with a higher phenotypic plasticity  
353 should be able to adapt better to increasing environmental variability and consequently  
354 reproduce more successfully under global warming scenarios than individuals that are less  
355 plastic in their behavioural responses.

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

358 individual variation and thus adapted their timing of breeding and – to a much lesser extent –  
359 allocation into egg masses to environmental conditions. However, indicated by a lack of  
360 support for individual random slopes, our results suggested that the extent of phenotypic  
361 plasticity was similar across all individuals. Importantly, female ID explained the largest part  
362 of the variance for both clutch initiation date (CID) and egg mass investment, suggesting that  
363 individual females were very consistent in their egg laying behaviour across years. In the  
364 following part, we will discuss the observed effects of environmental variables on CID and  
365 egg investment both on the within- and between-individual scales and the implications for  
366 this species' adaptation to climate change.

367

#### 368 *Clutch Initiation Date*

369 In agreement with our expectation, a broad scale environmental index (SAM) was the best  
370 environmental predictor for CID. SAM explained up to 20% of the variance in models for  
371 CID, which was substantially more than for egg investment parameters (see below). This  
372 meets our expectation that the behavioural plasticity would be higher for CID than for egg  
373 mass. The plasticity in CID is shown by the significant within-individual effect of SAM,  
374 meaning that individuals adjusted CID to the environmental conditions they experienced.  
375 Along with this, we also found a significant between-individual effect, i.e. females  
376 experiencing high average SAM also laid earlier than females experiencing low average  
377 SAM (as reflected in Fig. 2b). This is in contrast to Hinke et al. (2012) who found a  
378 significant within-individual effect but a non-significant between-individual effect of AirT on  
379 CID in Adélie (*Pygoscelis adeliae*) and gentoo penguins (*Pygoscelis papua*).

380

381 Our results indicated that CID was advanced under high SAM values, which reflect colder  
382 conditions but higher primary productivity (Lovenduski & Gruber 2005, Hauck et al. 2013).  
383 While it appears countercurrent to the observed trends to advanced phenological traits (e.g.  
384 earlier egg laying, earlier flowering) under warmer spring conditions (e.g. Visser & Both  
385 2005, Parmesan 2007), it is not uncommon among seabirds, particularly in the Southern  
386 Hemisphere, to breed earlier under colder conditions (Chambers et al. 2013). In accordance  
387 with our results, earlier CID with increasing SAM values have been described for Royal  
388 penguins (*Eudyptes schlegeli*) breeding on Macquarie Island in the Subantarctic Indian Ocean  
389 (Hindell et al. 2012) and Adélie penguins breeding in Eastern Antarctica (Emmerson et al.  
390 2011).

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

402

403 *Maternal investment into egg mass*

404 Of the selected environmental variables, local climate conditions had the largest relative  
405 explanatory power. However, environmental variability had only a very limited effect on total  
406 clutch mass, and there was no significant effect of environmental variation on intra-clutch  
407 egg-mass dimorphism at all. While we cannot rule out that we missed a relevant, better-  
408 explanatory environmental variable, the most likely explanation for this very low effect of  
409 environmental variability is the high consistency of individual females in their egg-mass  
410 allocation across years. In fact, female ID explained about 80% of variance in random effects  
411 models for total clutch mass, and based on the literature (Christians 2002), we had also  
412 expected to find a lower phenotypic plasticity in egg mass allocation compared to clutch  
413 initiation date.

414

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

421 The (albeit weak) within-individual effect of low SSTA on the increase of total clutch  
422 mass is most likely also driven by higher food availability as lower SSTA are linked to  
423 positive SAM (see above). This is consistent with previous studies that found a higher female  
424 investment in clutches (egg mass or number of eggs) with environmental conditions  
425 increasing food availability (e.g. Saino et al. 2004, Ardia et al. 2006, Potti 2008, Lehikoinen  
426 et al. 2011). Along with the significant within-individual effect, one could have expected a  
427 between-individual effect of SSTA as well. The lack thereof may partly be due to a smaller

428 range of variation in average SSTA ( $\bar{x}_j$ ) experienced by females compared to the within-  
429 individual SSTA ( $x_{ij}-\bar{x}_j$ ) (see Fig. 3).

430 Finally, we found that total clutch mass was independent of CID. This is in contrast  
431 with a range of studies which showed significant effects of CID on clutch size or mass (e.g.  
432 Birkhead & Nettleship 1982, Nilsson & Svensson 1993, Winkler & Allen 1996, D'Alba &  
433 Torres 2007). It appears that rockhopper penguins rather traded off total clutch mass with  
434 CID and initiated clutches as early as possible, but kept investment into total clutch mass  
435 consistent (also see Nilsson & Svensson 1993) – which may have also contributed to the low  
436 explanatory power of environmental variables on total clutch mass in general. Nevertheless,  
437 females traded off their relative investment into A- and B-egg mass according to CID, but  
438 again this effect was – albeit significant – comparatively weak. In addition, female identity  
439 explained a lower proportion (less than 50% of variance in models; see Table 3) for intra-  
440 clutch egg-mass dimorphism compared to total clutch mass. The drivers of variation in intra-  
441 clutch egg-mass dimorphism therefore remain open, and may partly be related to male quality  
442 (Poisbleau et al. 2013).

443

#### 444 *Implications for the species' adaptation to climate change*

445 Although rockhopper penguins adapted their CID to climatic conditions, the range of  
446 phenotypic plasticity appeared low compared to other seabird species (Frederiksen et al.  
447 2004, Brommer et al. 2008, Surman et al. 2012), including other penguin species (Emmerson  
448 et al. 2011, Lynch et al. 2012). Moreover, the lack of support for models with individual  
449 random slopes suggested a similar level of phenotypic plasticity in all individuals. On the  
450 other hand, our study was conducted during a relatively short study-period of 7 years that  
451 were apparently dominated by favourable conditions for rockhopper penguins: both our study

452 population and the population across the entire Falkland Island archipelago showed a steady  
453 population increase during this period (Baylis et al. 2013). As such, the outcomes of this  
454 study may be somewhat limited both in detecting environmental variables that drive  
455 phenology and reproductive investment and in detecting a stronger level of phenotypic  
456 plasticity within and between individuals. We can therefore not entirely rule out that  
457 rockhopper penguins are able to show a stronger level of phenotypic plasticity under adverse  
458 conditions. On the other hand, Hinke et al. (2012) did not detect individual phenotypic  
459 plasticity in Adélie penguins, even though the population was declining during the course of  
460 the study (across 19 years). Potentially, in colony-breeding species, synchronous-breeding  
461 may be more important (e.g. to avoid egg or chick predation) than adjusting CIDs  
462 individually (also see Reed et al. 2006, Hinke et al. 2012). Unfortunately, it was not possible  
463 in the framework of this study to monitor the breeding success and therefore if variation in  
464 CID and/or egg mass had effects on the actual reproductive output.

465         For the predicted future climate changes, including increased climatic variability  
466 (Collins et al. 2013), our results imply that the apparent lack of individual differences in  
467 phenotypic plasticity might hamper the species' microevolutionary adaptation (Davis et al.  
468 2005, Gienapp et al. 2008, Dingemanse & Wolf 2013). In addition, the low range of  
469 phenotypic plasticity on the population scale observed in this study and also previously  
470 (Dehnhard et al. 2013a, 2013b) should receive further attention (Canale & Henry 2010), the  
471 more because southern rockhopper penguins are already listed as "vulnerable" (Birdlife  
472 International 2012). Furthermore, our results in combination with previous similar findings  
473 for other seabird species (Reed et al. 2006, Hinke et al. 2012) raise the question whether other  
474 threatened and long-lived species, especially within the group of seabirds (Croxall et al.  
475 2012) exhibit individual differences in phenotypic plasticity.

476

477

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733

734 **Table 1.** Comparison of candidate models to explain clutch initiation date (CID). The model structure is presented as syntax in R. In the first  
 735 modelling step, the best explanatory environmental variable was identified (upper part of the table; models F1–F4). Subsequently, random-effects  
 736 models (R1–R4) were compared (lower part of the table), based on the best-explanatory environmental variable, i.e. SAM, as fixed effect in  
 737 addition to the tested random effects. In a final step, the fixed-effects structure was once more validated (with the aim to remove fixed effects that  
 738 did have explanatory power).

739 Fixed effects models (F1–F4) were based on several environmental factors: SAM = Southern Annular Mode, SOI = Southern Oscillation Index,  
 740 SSTA = local Sea Surface Temperature Anomaly and AirT = local Air Temperature. All environmental variables were expressed as within-  
 741 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  
 742 across years ( $\bar{x}_j$ ).

743 Random effect models (R1–R4) all contained Year as random intercept (1|Year). In addition, ID as random intercept (1|ID) and individual random  
 744 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.

745

Model	Linear model structure	AIC	$\Delta\text{AIC}$	AIC-weight	$R^2$
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
Model	Random effects model structure	AIC	$\Delta\text{AIC}$	AIC-weight	$R^2_c$
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

746

747 **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,  
 748 the best explanatory environmental variable was identified (upper part of the table; models F1–F4). Thereafter, based on the best fixed-effects  
 749 model structure (Model F1), the best random-effects structure was identified (Models R1–R4). For details, see explanations in Table 1.

750

<b>Model</b>	<b>Linear model structure</b>	<b>AIC</b>	<b>ΔAIC</b>	<b>AIC-weight</b>	<b>R<sup>2</sup></b>
F1	TMASS ~ SSTA(x <sub>ij</sub> -x̄ <sub>j</sub> ) + SSTA(x̄ <sub>j</sub> )	6151.9	0.0	0.86	0.014
F2	TMASS ~ SAM(x <sub>ij</sub> -x̄ <sub>j</sub> ) + SAM(x̄ <sub>j</sub> )	6157.1	5.1	0.07	0.007
F3	TMASS ~ SOI(x <sub>ij</sub> -x̄ <sub>j</sub> ) + SOI(x̄ <sub>j</sub> )	6157.5	5.5	0.05	0.007
F4	TMASS ~ AirT(x <sub>ij</sub> -x̄ <sub>j</sub> ) + AirT(x̄ <sub>j</sub> )	6159.0	7.1	0.02	0.005
<b>Model</b>	<b>Random effects model structure</b>	<b>AIC</b>	<b>ΔAIC</b>	<b>AIC-weight</b>	<b>R<sup>2</sup><sub>c</sub></b>
R1	TMASS ~ SSTA(x <sub>ij</sub> -x̄ <sub>j</sub> ) + SSTA(x̄ <sub>j</sub> ) + (1 Year) + (1 ID)	5503.6	0.0	0.64	0.813
R2	TMASS ~ SSTA(x <sub>ij</sub> -x̄ <sub>j</sub> ) + SSTA(x̄ <sub>j</sub> ) + (1 Year) + (1 ID) + (0 + SSTA(x <sub>ij</sub> -x̄ <sub>j</sub> ) ID)	5504.7	1.1	0.36	0.850
R3	TMASS ~ SSTA(x <sub>ij</sub> -x̄ <sub>j</sub> ) + SSTA(x̄ <sub>j</sub> ) + (1 Year) + (0 + SSTA(x <sub>ij</sub> -x̄ <sub>j</sub> ) ID)	6142.1	638.5	<0.01	0.018
R4	TMASS ~ SSTA(x <sub>ij</sub> -x̄ <sub>j</sub> ) + SSTA(x̄ <sub>j</sub> ) + (1 Year)	6144.1	640.5	<0.01	0.018

751

752

753 **Table 3.** Comparison of candidate models to explain intra-clutch egg-mass dimorphism (RMASS). The model structure is presented as syntax in R.  
754 In the first step, the best explanatory environmental variable was identified (upper part of the table; models F1–F4). Thereafter, based on the best  
755 fixed-effects model structure (Model F1), the best random-effects structure was identified (Models R1–R4). For details, see explanations in Table 1.

<b>Model</b>	<b>Linear model structure</b>	<b>AIC</b>	<b><math>\Delta</math>AIC</b>	<b>AIC-weight</b>	<b>R<sup>2</sup></b>
F1	RMASS ~ AirT(x <sub>ij</sub> -x̄ <sub>j</sub> ) + AirT(x̄ <sub>j</sub> )	-2461.1	0.0	0.97	0.028
F2	RMASS ~ SOI(x <sub>ij</sub> -x̄ <sub>j</sub> ) + SOI(x̄ <sub>j</sub> )	-2454.3	6.8	0.03	0.019
F3	RMASS ~ SAM(x <sub>ij</sub> -x̄ <sub>j</sub> ) + SAM(x̄ <sub>j</sub> )	-2448.1	13.0	<0.01	0.011
F4	RMASS ~ SSTA(x <sub>ij</sub> -x̄ <sub>j</sub> ) + SSTA(x̄ <sub>j</sub> )	-2442.0	19.2	<0.01	0.002
<b>Model</b>	<b>Random effects model structure</b>	<b>AIC</b>	<b><math>\Delta</math>AIC</b>	<b>AIC-weight</b>	<b>R<sup>2</sup><sub>c</sub></b>
R1	RMASS ~ AirT(x <sub>ij</sub> -x̄ <sub>j</sub> ) + AirT(x̄ <sub>j</sub> ) + (1 Year) + (1 ID)	-2653.1	0.0	0.73	0.561
R2	RMASS ~ AirT(x <sub>ij</sub> -x̄ <sub>j</sub> ) + AirT(x̄ <sub>j</sub> ) + (1 Year) + (1 ID) + (0 + AirT(x <sub>ij</sub> -x̄ <sub>j</sub> ) ID)	-2651.1	2.0	0.27	0.561
R3	RMASS ~ AirT(x <sub>ij</sub> -x̄ <sub>j</sub> ) + AirT(x̄ <sub>j</sub> ) + (1 Year)	-2455.4	197.7	<0.01	0.087
R4	RMASS ~ AirT(x <sub>ij</sub> -x̄ <sub>j</sub> ) + AirT(x̄ <sub>j</sub> ) + (1 Year) + (0 + AirT(x <sub>ij</sub> -x̄ <sub>j</sub> ) ID)	-2453.4	199.7	<0.01	0.087

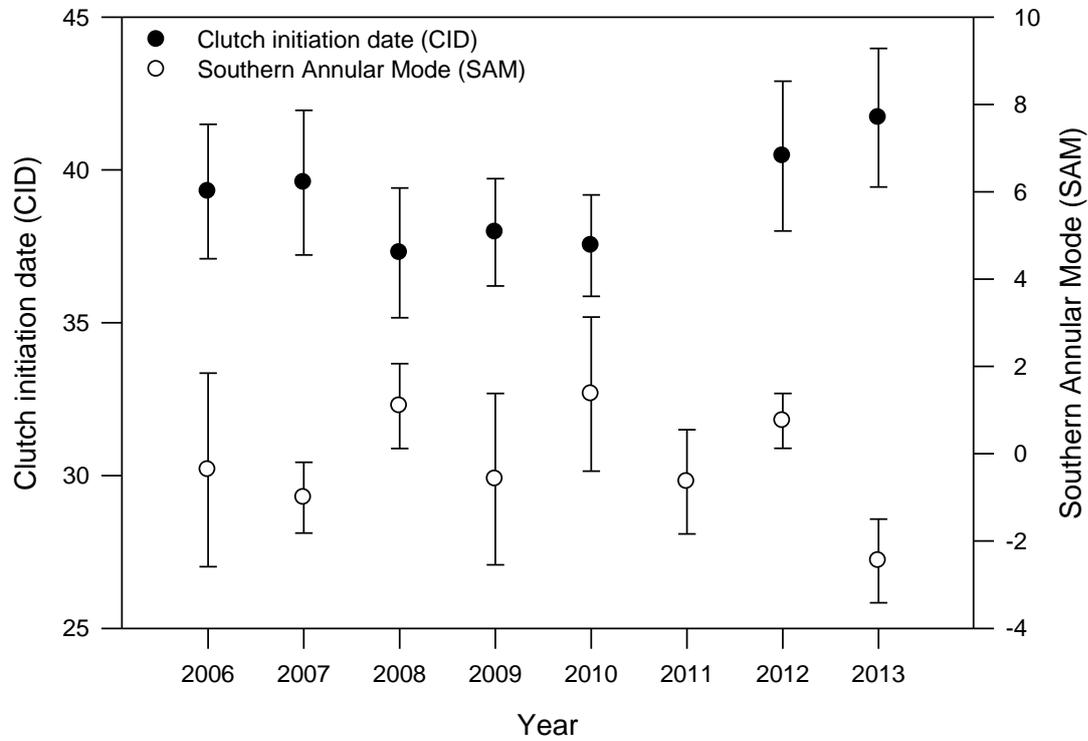
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759 **Figure 1.** Clutch initiation date (CID) and Southern Annular Mode (SAM; 3-month period  
760 from August through to October) as mean  $\pm$  SD across the study period from 2006 to 2013.

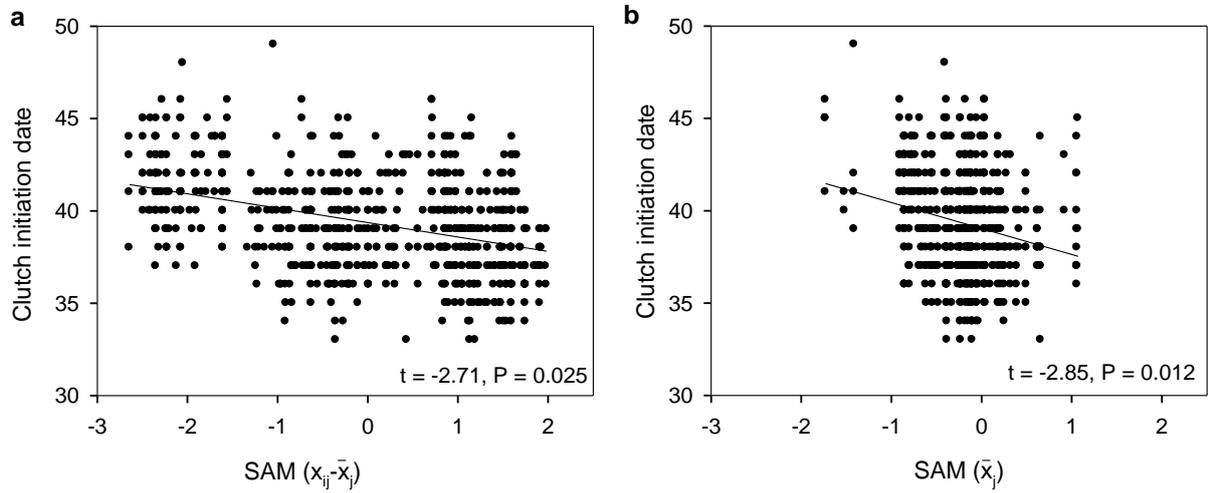
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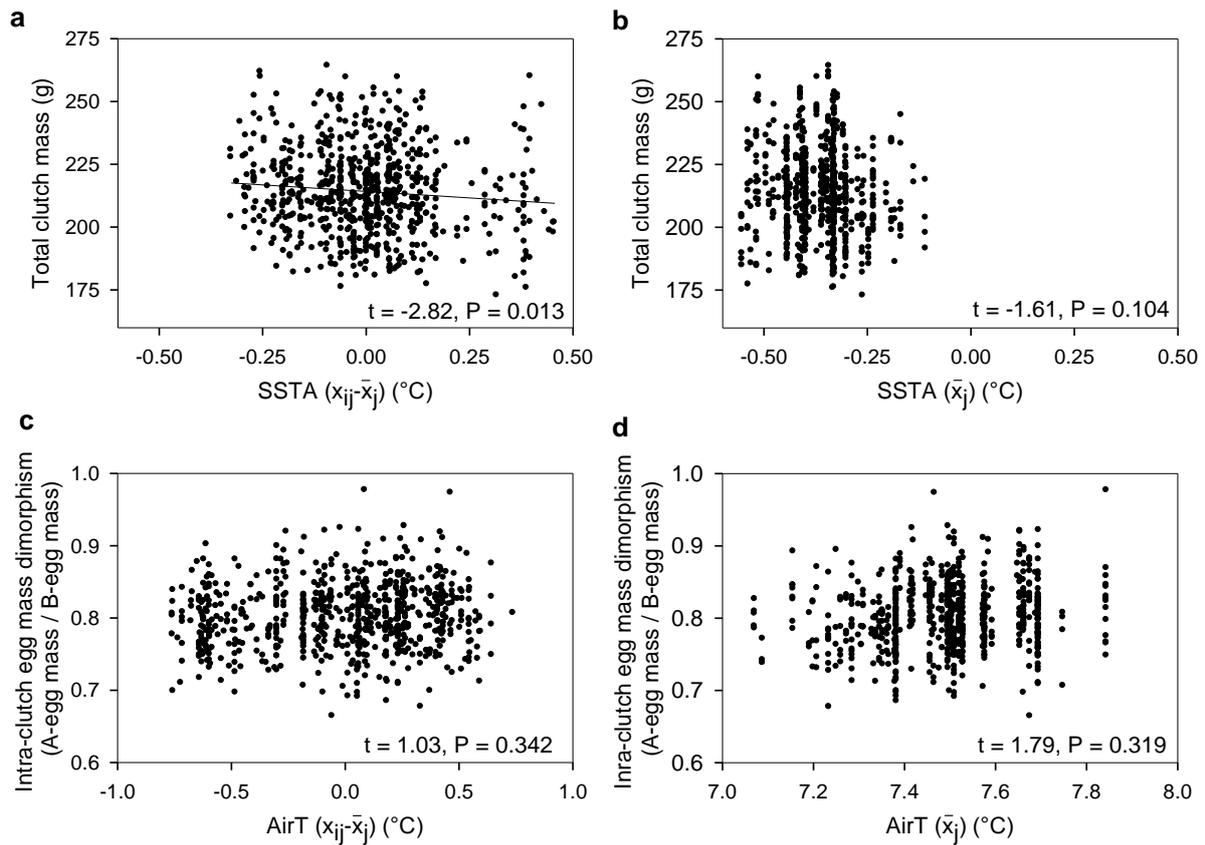
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764 **Figure 2.** Clutch initiation date in response to (a) within-individual centred Southern Annular  
765 Mode (SAM) ( $x_{ij} - \bar{x}_j$ ) and (b) average individual SAM ( $\bar{x}_j$ ). Regression lines show the  
766 direction of the relationship when significant. t-values were obtained from the final (REML-  
767 based) model and P-values from likelihood-ratio tests from the final model (Table 1).  
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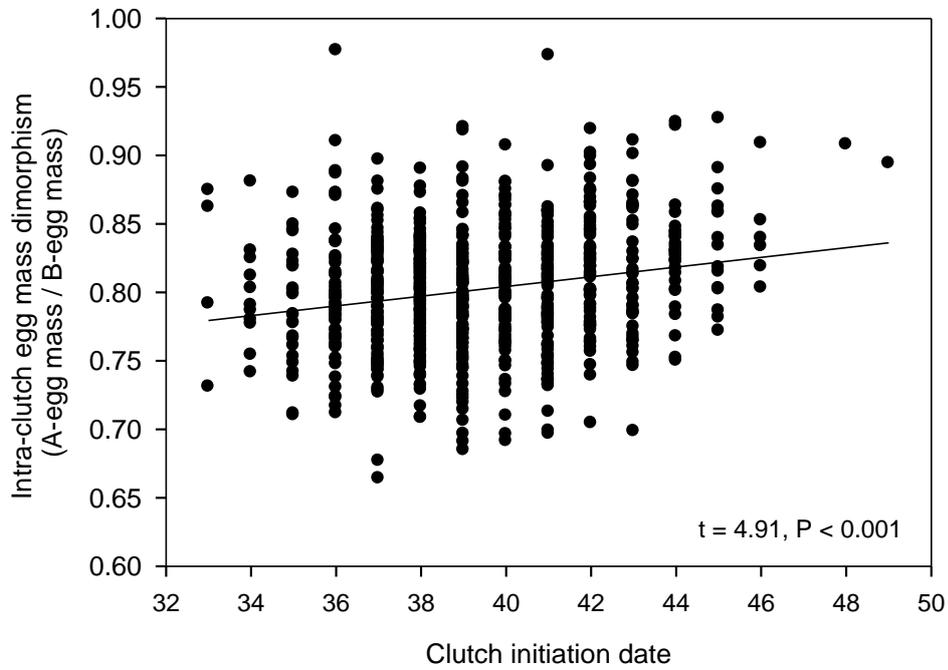
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772 **Figure 3.** Total clutch mass and intra-clutch egg-mass ratio in response to environmental  
 773 variables (chosen according to the modelling procedures). Both within-individual centred  
 774 values ( $x_{ij}-\bar{x}_j$ ), reflecting within-individual effects (left column) and average values per  
 775 individual ( $\bar{x}_j$ ), reflecting between-individual effects (right column) are presented. Regression  
 776 lines show the direction of the relationship (for significant effects only). t-values were  
 777 obtained from the final (REML-based) random-effects model and P-values from likelihood-  
 778 ratio tests based on these models.  
 779



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 781

782 **Figure 4.** Intra-clutch egg-mass dimorphism (calculated as A-egg mass / B-egg mass) in  
783 response to clutch initiation date (CID). The  $t$ -value was obtained from the REML-based  
784 random-effects model and the P-value from likelihood-ratio tests based thereupon.  
785



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