

4-1-2017

## Costs of reproduction and carry-over effects in breeding albatrosses

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### Recommended Citation

Crossin, G., Phillips, R., Lattin, C., Romero, L., Bordeleau, X., Harris, C., Love, O., & Williams, T. (2017). Costs of reproduction and carry-over effects in breeding albatrosses. *Antarctic Science*, 29 (2), 155-164.  
<https://doi.org/10.1017/S0954102016000560>

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1 **Costs of reproduction and carryover effects in breeding albatrosses.**

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21 Running title: Costs of reproduction and carryover effects in albatrosses.

22 **Abstract**

23 We investigated the physiology of two closely related albatross species relative to their breeding  
24 strategy: black-browed albatrosses (*Thalassarche melanophris*) breed annually, while grey-headed  
25 albatrosses (*T. chrysostoma*) breed biennially. Via observations of breeding fate and blood samples  
26 collected at the end of breeding in one season, and feather corticosterone levels sampled at the  
27 beginning of the next breeding season, we found that in both species, some post-breeding  
28 physiological parameters differed according to breeding outcome (successful, failed, deferred).  
29 Correlations between post-breeding physiology and fCort, and links to future breeding decisions,  
30 were examined. In black-browed albatrosses, post-breeding physiology and fCort were not  
31 significantly correlated, but fCort independently predicted breeding decision the next year, which  
32 we interpret as a possible migratory carryover effect. In grey-headed albatrosses, post-breeding  
33 triglyceride levels were negatively correlated with fCort, but only in females, which we interpret  
34 as a potential cost of reproduction. However, this potential cost didn't carry-over to future breeding  
35 in the grey-headed albatrosses; none of the variables predicted future breeding decision. We  
36 suggest that biennial breeding in the grey-headed albatrosses may have evolved as a strategy to  
37 buffer against the apparent susceptibility of females to negative physiological costs of  
38 reproduction. Future studies are needed to confirm this.

39

40 **Keywords:** testosterone; hematocrit; feather corticosterone; glucocorticoids; triglycerides;  
41 migration

42

## 43 **Introduction**

44           There is considerable experimental evidence for costs of reproduction in birds, which  
45 include both short-term costs associated with specific stages of the breeding cycle (e.g. incubation  
46 or chick rearing; Monaghan *et al.* 1995, Monaghan *et al.* 1998), and longer-term costs that carry  
47 over to affect future reproductive investment (Daan *et al.* 1996). Carryover effects have been  
48 documented in several bird species, and influence traits such as the timing of breeding (Descamps  
49 *et al.* 2011, Harrison *et al.* 2011), breeding deferral (Ebbinge and Spaans 1995, Crossin *et al.* 2012,  
50 Crossin *et al.* 2013a) and breeding output (Ebbinge and Spaans 1995). The physiological  
51 mechanisms that underlie these costs however, and whether they involve limitations in food  
52 resource or energy, or some other non-resource based constraint arising from competing  
53 physiological systems, are uncertain (Williams 2012). Previous studies have, however, proposed a  
54 role for glucocorticoid hormones (Bortolotti *et al.* 2008, Crossin *et al.* 2013b), energy reserves  
55 (Harrison *et al.* 2011), and hematocrit or aerobic capacity (Williams 2012, Crossin *et al.* 2013a) as  
56 potential mediators of costs and carryover effects.

57           The role of the glucocorticoid hormones, specifically corticosterone and cortisol (called  
58 hereafter “Cort”), and whether they have a positive or negative relationship with particular life-  
59 history traits, depends on whether they are expressed at baseline or stress-induced levels (Bonier  
60 *et al.* 2009, Crossin *et al.* 2016). Given Cort’s fundamental role in energy acquisition and  
61 metabolism, Cort may be the key factor that explains individual variation in energy balance, body  
62 condition, and the condition-dependence of breeding activity (Descamps *et al.* 2011). In birds and  
63 mammals, an effective means of resolving such relationships involves the analysis of Cort in  
64 keratin-based structures, including feathers (Bortolotti *et al.* 2008, Lattin *et al.* 2011). Cort  
65 deposited into these structures from the general circulation is thought to provide an integrated  
66 measure of hypothalamo–pituitary–adrenal axis (HPA) activity over time-scales relevant to life-

67 history, e.g. transitions between non-breeding and breeding stages of the annual cycle. In birds,  
68 measurement of feather Cort levels (fCort) has revealed links between previous breeding activity,  
69 migration, and future reproductive investment, thus revealing carryover effects onto key traits,  
70 including breeding decisions (whether to lay or defer), laying date, and egg sizes (Bortolotti *et al.*  
71 2008, Crossin *et al.* 2013b, Kouwenberg *et al.* 2013).

72 Other studies have suggested that variation in energy reserves (or condition) might also  
73 mediate carryover effects (see review by Harrison *et al.* 2011; in this context, condition is  
74 presumably linked to Cort as a metabolic regulator, although as noted above the dynamics between  
75 Cort and condition in mediating carryover effects are poorly defined). Links between pre-breeding  
76 condition and breeding investment have been demonstrated in birds (Harrison *et al.* 2011,  
77 O'Connor *et al.* 2014), especially in capital breeders via modifications to laying date or breeding  
78 success, via trade-offs between current reproduction and survival (Prop *et al.* 2003), and via clutch  
79 size manipulations (Monaghan and Nager 1997). Harrison *et al.* (2011) note that low rates of pre-  
80 breeding energy intake can adversely affect reproductive traits in many birds and other species  
81 (Ebbinge and Spaans 1995, Prop *et al.* 2003). Plasma triglycerides provide one method for  
82 assessing individual condition, as these correlate with both energy intake and fattening rate in birds  
83 (Guglielmo and Williams 2003). As with body mass, variation in triglyceride levels in pre-breeding  
84 birds could signal a carryover effect with potential implications for subsequent investment  
85 decisions (Hennin *et al.* 2015).

86 Although it seems intuitive that carryover effects could be generated by energy or nutrient  
87 limitation (Harrison *et al.* 2011), conceivably they could reflect deficiencies in other physiological  
88 currencies. In many migratory birds, hematocrit (red blood cell percentage) is up-regulated during  
89 migration to increase oxygen-transport capacity (Piersma *et al.* 1996), which is a key trait for  
90 sustaining high aerobic performance for long-distance flight. However, hematocrit can be impacted

91 negatively by reproductive processes, specifically by estradiol (E<sub>2</sub>) secretion during egg  
92 production, which can result in a debilitating reproductive anemia that can persist for up to a year  
93 (Kalmbach *et al.* 2004; Crossin *et al.* 2013a). Low hematocrit could therefore indicate a potential  
94 carryover effect in the form of reduced migratory performance and increased costs that ultimately  
95 constrain future reproductive investment. By extension, variation in testosterone levels could also  
96 be important as androgens are known to stimulate erythropoiesis, and affect breeding decisions in  
97 birds (Crossin *et al.* 2012). Previous work has shown that sex steroid expression (progesterone,  
98 testosterone) during the pre-breeding period can predict breeding decisions in albatrosses (Crossin  
99 *et al.* 2012, Crossin *et al.* 2013a). Sex steroids and Cort also affected breeding output in marine  
100 iguanas (*Amblyrhynchus cristatus*) and other reptiles (Vitousek *et al.* 2010).

101 Long-lived seabird species characterized by slow life-histories and single-egg clutches  
102 (Jouventin and Dobson 2002) provide ideal model species for exploring the physiological costs of  
103 reproduction and mechanisms involved in carryover effects. The congeneric black-browed  
104 albatross (*Thalassarche melanophris*) and grey-headed albatross (*T. chrysostoma*) breed  
105 sympatrically throughout much of their range in the sub-Antarctic, but display very different  
106 reproductive life-histories. As in the majority of bird species worldwide, black-browed albatrosses  
107 are annual breeders, although a small proportion breed in alternate years. In contrast, grey-headed  
108 albatrosses generally breed biennially if successful, as do all the great albatrosses (*Diomedea* spp.)  
109 and sooty albatrosses (*Phoebastria* spp.) (Tickell 2000). Sister species like the black-browed and  
110 grey-headed albatrosses, with markedly different breeding strategies, therefore provide a good  
111 contrast for exploring the potential physiological mechanisms underlying breeding frequency and  
112 links to costs of reproduction and carryover effects.

113 Biennial breeding is often associated with life-histories characterized by long periods of  
114 intensive bi-parental care. In wandering albatrosses and king penguins for example, birds usually

115 take a year or more to fledge their chicks, making it impossible, or at least impractical, for them to  
116 initiate another breeding attempt whilst still rearing young from the previous season (but see  
117 Weimerskirch *et al.* 2015). However, biennial grey-headed albatrosses rear their chicks in a single  
118 summer, on a schedule that starts one week earlier and ends 2-4 weeks later than that of the  
119 sympatric, annually-breeding black-browed albatrosses. Despite this, most grey-headed albatrosses  
120 will not attempt to breed in the successive year as annual breeders generally do (although some  
121 may if they fail breeding early in the previous year; Ryan *et al.* 2007), even though parental care is  
122 not as prolonged as in some other biennial species. This begs the question: why don't grey-headed  
123 albatrosses breed every year? It has been suggested that biennial breeding in grey-headed  
124 albatrosses is the result of a) the short time available to adults to recover body condition and replace  
125 flight feathers before the start of the following season (Ryan *et al.* 2007), which may either be  
126 related to, or resulting in, b) a physiological cost of reproduction that carries over to negatively  
127 affect future breeding effort (e.g. Crossin *et al.* 2013b).

128         In this study, we explore whether physiological costs link current to future reproduction,  
129 which would suggest a physiological carryover effect (Crossin *et al.* 2013b) We do so by  
130 comparing the annual and biennial breeding systems found within the genus *Thalassarche*. We  
131 determined the breeding fate (successful, failed, or deferred breeding) of black-browed albatrosses  
132 (annual) and grey-headed albatrosses (biennial) at the end of a breeding season, and sampled them  
133 for indicators of their energetic (triglycerides), aerobic (hematocrit), and hormonal (testosterone)  
134 condition. We then examined correlations between these indicators and Cort levels measured in  
135 tail feathers grown during the subsequent nonbreeding period. Assuming that variation in fCort  
136 levels indicate the “stress state” of non-breeding individuals after the breeding season, we then  
137 predict relationships between fCort and 1) previous breeding fate, and 2) post-breeding  
138 physiological condition of those individuals, as indicated by triglyceride, testosterone, and



139 hematocrit levels. For example, if low triglyceride and low hematocrit levels correlated with high  
140 fCort in the breeding birds (successful and failed) but not in the non-breeding deferring birds, then  
141 this would suggest a cost of reproduction that carries over into winter. Finally, we predict that 3)  
142 fCort would itself carry over to affect future reproductive investment, e.g. the decision to breed,  
143 with high fCort indicative of deferred breeding in the following season. We discuss our results  
144 relative to hypotheses regarding the physiological costs of reproduction, and speculate on the  
145 evolution of annual versus biennial breeding strategies.

146

## 147 **Methods**

### 148 *Study site*

149 Fieldwork was conducted during austral summers 2008/09 and 2009/10 at Bird Island,  
150 South Georgia (54°01'S, 38°02'W), a sub-Antarctic island group that is one of the most important  
151 breeding sites, globally, for grey-headed and black-browed albatrosses. Individually banded  
152 albatrosses of known age and breeding history in long-term monitoring colonies were sampled  
153 (grey-headed albatrosses in Colonies B and E, and black-browed albatrosses in Colony J). All birds  
154 had bred at least once previously. Research was approved by the Ethics Committee of the British  
155 Antarctic Survey and carried out under permits issued by the Government of South Georgia and  
156 South Sandwich Islands. Sampling protocols conformed to guidelines established by the Canadian  
157 Committee on Animal Care (Simon Fraser University Animal Care Permit 897B-8).

158

### 159 *Study species*

160 The breeding and foraging ecology of grey-headed and black-browed albatrosses at Bird  
161 Island is well studied (Prince 1985, Phillips *et al.* 2004, Crossin *et al.* 2012, Crossin *et al.* 2013a).  
162 Both species are monogamous and lay a single egg. After a long incubation period, the single chick

163 is reared by both parents over the next 4-5 months. Grey-headed albatrosses (GHA) arrive at the  
164 breeding colony in spring, usually around mid September, approximately a fortnight earlier, have  
165 a slightly longer incubation period (72 vs. 68 days), and a longer chick-rearing period (141 vs. 116  
166 days), which makes their breeding season ~45 days longer than black-browed albatrosses (BBA).  
167 There is a degree of niche divergence partially mediated by differences in flight performance  
168 (Phillips *et al.* 2004), and although the diets overlap, chicks of grey-headed albatrosses are fed  
169 more squid, and those of black-browed albatrosses are fed more krill and fish. The lower energy  
170 density of squid contributes to the slower growth rate and longer fledging period of grey-headed  
171 albatross chicks. At South Georgia, approximately 80% of the breeding population of black-  
172 browed albatrosses returns to breed the following year, the absence of the remainder due principally  
173 to either natural mortality or loss of partner (Croxall *et al.* 1998). In contrast, only ~1% of  
174 successfully breeding grey-headed albatrosses will breed again the following year, 25-80% two  
175 years later, and all but a small minority within three or four years, whereas those that fail in  
176 incubation or early chick-rearing in one year will generally breed the next year (Ryan *et al.* 2007).  
177 All of our analyses however examined the post-breeding physiology and fCort relative to breeding  
178 activity in the very next year, not two or more years later.

179

### 180 *Sampling design*

181 A timeline of our sampling protocol is presented in Fig. 1. From 24 January to 6 February  
182 2009, we sampled non-breeding (i.e. deferring) black-browed and grey-headed albatrosses at nests  
183 in their respective colonies. Daily monitoring records of the albatross colonies at Bird Island,  
184 maintained by the British Antarctic Survey, allowed us to know the breeding status of all  
185 individuals. Deferring albatrosses return to and spend time in the colony each year, despite not  
186 breeding, presumably to re-establish pair bonds (Tickell 2000). Deferring black-browed albatrosses

187 typically depart South Georgia for winter migration in early February (Phillips *et al.* 2005), so our  
188 sampling plan aimed to capture these birds and deferring grey-headed albatrosses before their  
189 departures (see Table 1 for numbers of birds sampled). From 30 March to 2 April, we sampled  
190 successful and failed breeders before their out-migration in mid-April. Blood samples (2 ml) were  
191 collected from the brachial vein using syringes with 25 gauge needles, and returned to the  
192 laboratory where the plasma was separated by centrifugation and stored at -20 °C. In all cases,  
193 blood was collected in less than 3 min from first approach to the bird. Ultimately, we sampled 125  
194 albatrosses at the end of the 2008/09 season (BBA=62, GHA=63), 68 of which were resampled  
195 when they subsequently returned to breed in the following season in 2009/10. Therefore, the  
196 analyses conducted in this study were restricted to the 68 birds sampled in both 2008/09 and  
197 2009/10 (BBA=50, GHA=18). Upon arrival at breeding colonies in 2009/10, a single rectrix was  
198 collected from each bird. Specifically, we collected only the outer-most rectrix from the right side  
199 of the bird, by cutting the feather with scissors at the base of the feather shaft (calamus). This was  
200 done to ensure that we sampled newly moulted feathers, as the sequence of rectrix moult is from  
201 outer to inner (Prince *et al.* 1993). These were stored in labeled bags and kept in the dark at 4 °C  
202 until analysis of feather Cort.

203

#### 204 *Physiological assays*

205 Plasma samples and known standards were assayed in duplicate for total triglyceride levels  
206 (Trig) using a commercial triglyceride kit (Glycerol Reagents A and B, Sigma), and measured  
207 using a Biotek 340i microplate reader. Additionally, multiple duplicates of a domestic hen (*Gallus*  
208 *domesticus*) plasma pool were also assayed to provide a mean intra-assay coefficient of variation  
209 was 7.1%. The inter-assay coefficient of variation was 6.7%.

210 Hematocrit (Hct) was measured in fresh whole blood by centrifugation in microhematocrit  
211 tubes (2 per individual) for 5 min at 10,000 g, and is reported as packed cell volume (%).

212 Testosterone (T) was measured by first extracting plasma samples in dichloromethane and  
213 then quantifying hormone levels using a commercially available enzyme-linked immunosorbent  
214 assay (Cayman Chemicals Kit 582701). For each species, an extracted plasma pool was found to  
215 be parallel to the standard curve, and samples were assayed in triplicate at a 1:10 dilution. Samples  
216 were assayed across 6 plates yielding inter and intra-assay coefficients of variation of 4.6% and  
217 6.3%, respectively. Extraction efficiency was assessed by spiking 4 randomly-chosen samples for  
218 each species with a known amount of testosterone standard immediately before extraction and  
219 comparing measured hormone levels to their corresponding normally-assayed (unspiked) levels.  
220 Average recovery was found to be 76.4% for black-browed albatrosses and 79.7% for grey-headed  
221 albatrosses. Statistical analyses were run on values corrected for these extraction efficiencies.

222 Corticosterone measured in the feathers of the same birds upon their return to Bird Island  
223 reflect plasma Cort levels in the weeks-months immediately after their departure from the breeding  
224 colony when tail feathers are moulted and regrown (Prince *et al.* 1993, Catry *et al.* 2013, Bugoni  
225 *et al.* 2015). To assay fCort, we used a standard radioimmunoassay as per Bortolotti *et al.* (2008),  
226 modified by Lattin *et al.* (2011), and following the protocol detailed in Crossin *et al.* (2013b). We  
227 determined the intra-assay coefficient of variation by measuring differences between duplicates,  
228 and the inter-assay variation by measuring differences between standard samples (using two  
229 standards: a known amount of Cort, and pulverized, homogenized feathers) (Romero and Fairhurst  
230 2016). Intra-assay variation was 4.0%; inter-assay variation was 7.4%.

231

232 *Statistical analyses*

233 All blood variables were examined for correlations with the time required to collect the  
234 blood sample and the date of collection. Due to known differences in life-history, behaviour, and  
235 physiology, we ran models for each species separately. To test our first prediction that fCort levels  
236 are related to previous breeding fate, we examined fCort, for each species separately (ANOVAs),  
237 by sex and breeding fate (successful, failed, deferred) as categorical factors, along with their  
238 interaction (sex\*fate). We then ran similar models to describe the species' post-breeding  
239 physiological state (Trig, T, Hct) at the end of the 2008/09 breeding season. To test our second  
240 prediction of a relationship between end-of-breeding season physiological indicators and fCort,  
241 Pearson's correlations by species and sex were examined. To test our third prediction that variation  
242 in fCort carries over to affect future breeding decision by each species, we used backwards stepwise  
243 generalized linear models with binomial response distributions to explore the variables most related  
244 to future breeding decision (breed or defer), in the subsequent breeding season only (2009/10  
245 season). Explanatory predictors included fCort, as well as bird sex, previous breeding status  
246 (breeder or non-breeder), T, Trig, and Hct. We restricted this comparison to the 2009/10 year only  
247 so that the physiological links from one season to breeding in the next could be compared between  
248 species simultaneously and on identical time scales.

249

## 250 **Results**

251 As albatrosses were sampled in two different seasons (end of 2008/09 season for blood, and  
252 beginning of 2009/10 season for feathers), we explored whether any of the physiological variables  
253 correlated with sampling time or date. In 2008/09, there were no correlations between sampling  
254 time (number of seconds to collect the blood sample) or date with any of the blood parameter levels  
255 (Pearson's correlations with Trig, T, and Hct, all  $P > 0.09$ ).

256           The end-of-season physiological results were determined for each species by ANOVA  
257 models examining differences by sex and breeding fate (Fig. 2). In the black-browed albatrosses  
258 (N=50), Trig and T levels of females, but not males, were significantly higher in deferring breeders  
259 than in successful or failed breeders (Trig sex\*fate interaction  $\beta=0.142$ ,  $P=0.004$ . T: sex\*fate  
260 interaction  $\beta=53.42$ ,  $P=0.008$ ). Hct levels did not differ by sex, but were generally lower in  
261 deferring than in successful or failed black-browed albatrosses (sex  $\beta=-0.886$ ,  $P=0.126$ ; fate  $\beta=-$   
262  $1.030$ ,  $P=0.010$ ; sex\*fate  $\beta=-0.418$ ,  $P=0.163$ ).

263           In the grey-headed albatrosses (N=18), Trig did not differ between sexes or among breeding  
264 fates (sex  $\beta=0.044$ ,  $P=0.567$ ; fate  $\beta=-0.097$ ,  $P=0.095$ ; sex\*fate  $\beta=0.013$ ,  $P=0.437$ ). However, T was  
265 significantly higher in deferring males than in successful and failed males, while females did not  
266 differ among fates (sex  $\beta=-24.78$ ,  $P=0.030$ ; fate  $\beta=5.30$ ,  $P=0.187$ ; sex\*fate  $\beta=-9.140$ ,  $P=0.043$ ).  
267 Hct did not differ by sex, but was generally higher in successful and failed breeders than in  
268 deferring breeders (sex  $\beta=-0.980$ ,  $P=0.171$ ; fate  $\beta=-1.540$ ,  $P=0.001$ ; sex\*fate  $\beta=-0.345$ ,  $P=0.625$ ).  
269 Finally, fCort did not differ among grey-headed sexes or fates (sex  $\beta=-0.476$ ,  $P=0.151$ ; fate  
270  $\beta=0.109$ ,  $P=0.748$ ; sex\*fate  $\beta=-0.071$ ,  $P=0.897$ ).

271           Contrary to our first prediction, fCort did not differ between the sexes or among breeding  
272 fates in either species (BBA N=50: sex  $\beta=-0.584$ ,  $P=0.070$ ; fate  $\beta=0.034$ ,  $P=0.778$ ; sex\*fate  $\beta=-$   
273  $0.056$ ,  $P=0.925$ . GHA N=18: sex  $\beta=-0.476$ ,  $P=0.151$ ; fate  $\beta=0.109$ ,  $P=0.748$ ; sex\*fate  $\beta=-0.071$ ,  
274  $P=0.897$ ). However, we found partial support for our second prediction in that fCort showed a  
275 significant negative correlation with Trig levels in female grey-headed albatrosses ( $r=-0.703$ ,  $N=12$   
276  $P=0.011$ ), but not in male grey-headed albatrosses ( $r=-0.202$ ,  $N=15$ ,  $P=0.471$ ) or either black-  
277 browed albatross sex (females,  $r=-0.022$ ,  $N=23$   $P=0.921$ ; males,  $r=-0.314$ ,  $N=21$ ,  $P=0.116$ ) (Fig.  
278 3). The only other significant correlation in this set of analyses was a negative relationship between  
279 T and Hct in female black-browed albatrosses ( $r=-0.577$ ,  $N=30$ ,  $P<0.001$ ; data not shown).

280 Comparisons of generalized linear models examining future breeding decisions by black-  
281 browed albatrosses are presented in Table 2. The most parsimonious model identified via AICc  
282 selection identifies a significant effect of fCort on breeding decision, such that when fCort is high  
283 there is greater tendency to defer breeding ( $P=0.028$ ; Table 3), which supports our third prediction  
284 that variation in fCort indicates a carryover effect to future reproduction. For grey-headed  
285 albatrosses, no variables were significant predictors of breeding decision, with the null model  
286 receiving the best support (Tables 2 and 3).

287

## 288 **Discussion**

289 As the tail feathers of albatrosses are moulted and re-grown after their departure from  
290 breeding colonies (Prince *et al.* 1993, Catry *et al.* 2013), we predicted that variation in fCort levels  
291 would reflect the state or condition of individuals after breeding and suggest a cost of reproduction  
292 related to levels of breeding investment (e.g. successful, failed, deferred breeding). Working from  
293 the assumption that feather Cort levels are a key link between current and future reproduction, we  
294 found limited evidence with a link between post-breeding physiological state and fCort, and  
295 between fCort and future breeding decision. However, these results are very species specific, which  
296 we suggest may reflect the contrasting life-histories of black-browed and grey-headed albatrosses,  
297 e.g. annual versus biennial breeding. For example, in the black-browed albatrosses fCort did not  
298 correlate with any of the physiological parameters measured at the end of the breeding season, but  
299 fCort nevertheless predicted future breeding decision. Conversely, in the grey-headed albatrosses  
300 there was limited evidence for a link between post-breeding physiology and fCort, via a negative  
301 correlated with circulating triglyceride levels. But despite this correlation, fCort did not predict  
302 future breeding decision in the grey-headed albatrosses.

303           So what do our results suggest? For the black-browed albatrosses, the link between fCort  
304 and future breeding investment, in the absence of any clear link to previous breeding investment,  
305 might indicate that the more immediate experience of pelagic migration immediately after  
306 departure from breeding colonies influences Cort deposition more so than previous breeding  
307 activity does, and that it is winter experience itself that generates carryover effects onto future  
308 breeding decisions. Certainly, this and many other recent studies support a role of fCort in  
309 carryover effects and future breeding investment (Crossin *et al.* 2013, Kowenberg *et al.* 2013,  
310 Fairhurst *et al.* 2015, Harms *et al.* 2015). For the grey-headed albatrosses, we observed the opposite  
311 – post-breeding triglyceride levels showed a negative correlation with fCort (significant in females  
312 and trending in males), but neither variable had any discernable affect on future breeding decision.  
313 Why this might be for the grey-headed albatrosses we do not know, but it may that genetic  
314 programming for biennial breeding provides an buffer against physiological carryover effects.  
315 However, our sample of grey-headed albatrosses was low, which may limit our power to detect  
316 physiological links between breeding states, and so interpretation of our results should be made  
317 cautiously. Furthermore, concerning links to fCort, successful grey-headed albatrosses do not  
318 necessarily complete tail moult in a year’s time (Prince *et al.* 1993), which may have been the case  
319 for some of the seven successful breeders that we resampled the following year. So our power to  
320 detect a carryover effect might be low. However, we do not believe that this changes our general  
321 conclusions about future breeding decisions by the grey-headed albatrosses.

322           With this caution in mind, we suggest that fundamental differences in breeding life-history  
323 can explain the patterns that we observed. Both species undertake long-distance migrations during  
324 the non-breeding period, lasting 6-16 months (Croxall *et al.* 2004, Phillips *et al.* 2005). In both  
325 species, there is a degree of condition dependence to breeding investment and decision making,  
326 which might reflect altered hypothalamus-pituitary-gonadal axis signaling in response to



327 conditions experienced during migration (Crossin *et al.* 2012, Crossin *et al.* 2013a). In a species  
328 capable of breeding every year, like the black-browed albatross, the experiences and conditions  
329 encountered during the winter are likely to influence Cort dynamics, and thus carry over to affect  
330 pre-breeding condition in the spring. By then, previous breeding activity and its relative costs, if  
331 any, might be overshadowed. In contrast to the black-browed albatrosses, a significant negative  
332 correlation between end-of-season Trig levels and fCort was observed in the biennial grey-headed  
333 albatrosses, which might reflect a physiological or energetic cost of reproduction, although we  
334 acknowledge again that our samples size was small. However, it is not uncommon to observe  
335 negative correlations between measures of body condition (e.g. body mass, Trig levels) and Cort  
336 levels in birds (Love *et al.* 2004). The correlation between circulating Trig and fCort in our study  
337 suggests a cost of reproduction, wherein some individuals were in poorer energetic condition  
338 relative to others. But ultimately, neither Trig, fCort or any other post-breeding measure (T, Hct)  
339 predicted the decisions of either male or female grey-headed albatrosses to breed in the very next  
340 year. This raises intriguing questions about the physiological determinants of biennial breeding  
341 strategies, which we discuss below.

342         A previous attempt to explain the biennial breeding pattern in albatrosses took a  
343 comparative approach and examined how the duration of the breeding season and distance to  
344 foraging grounds predicted the breeding frequency in 12 species (Jouventin and Dobson 2002).  
345 The authors hypothesized that the length of the rearing period for some albatrosses is simply too  
346 long and energetically demanding for adults to recover sufficient body condition to breed again in  
347 a consecutive year. In support of this, the analysis showed that across all 12 species, those species  
348 with the longest rearing periods were generally biennial breeders. However, we would argue that  
349 it is perhaps less obvious how the comparatively small difference in breeding season duration  
350 would lead to energetic shortfalls that cannot be restored during the ~4 months of marine foraging

351 before the next breeding attempt, unless there is a significant effect on post-breeding moult  
352 dynamics (Rohwer *et al.* 2011) – a topic that should be explored in future studies.

353         The second hypothesis addressed by Jouventin and Dobson (2002) to explain the breeding  
354 patterns of albatrosses, predicts that travel to distant foraging areas during the breeding season  
355 should reduce reproductive rates, presumably due to increased effort, but also because longer chick  
356 feeding intervals could lengthen the breeding season. There was some support for this when  
357 comparing across 12 species. However, it is unclear how this might ultimately determine the  
358 breeding strategies of black-browed and grey-headed albatrosses, as although grey-headed  
359 albatrosses have longer foraging ranges in incubation, there is little difference during chick-rearing,  
360 which accounts for the last 5 months of the season (Phillips *et al.* 2004). Moreover, there is some  
361 sexual segregation during incubation, which was attributed to differences in wing loading and flight  
362 performance, as opposed to competitive exclusion (Phillips *et al.* 2004). Consequently, the slightly  
363 longer distances travelled during this stage by grey-headed albatrosses should not therefore be  
364 interpreted as marginalization to poorer foraging areas, with negative consequences for overall  
365 condition. Indeed, although we detected physiological differences in albatrosses at the end of the  
366 season that related to their breeding fate (successful, failed, deferred; Fig. 2), there were no  
367 significant differences between species or sexes (Fig. 2). Worthy of note was the significantly high  
368 T levels in deferring male grey-headed and deferring female black-browed albatrosses. Hector *et*  
369 *al.* (1986) observed significant increases in T levels in both species and sexes at the end of breeding,  
370 although the breeding status of those individuals was not known. The functional significance of  
371 these increases is not readily apparent. Although T had no bearing on future reproductive activity,  
372 high T in deferring individual could reflect intraspecific interactions (e.g. aggression) prior to out-  
373 migration, which might also have relevance for the onset and pattern of winter migrations as seen  
374 in some passerines (Silverin *et al.* 1989).

375 We did, however, observe a significant negative correlation between plasma Trig at the end  
376 of the breeding season and fCort levels in (female) grey-headed albatrosses, but not black-browed  
377 albatrosses. This could have functional consequences as grey-headed albatrosses usually migrate  
378 considerably longer distance during winter migrations than black-browed albatrosses (Croxall *et*  
379 *al.* 2005, Phillips *et al.* 2005). Together, low Trig and high fCort may signal relative need to recover  
380 lost body reserves after breeding, and thus indicate a cost (Love *et al.* 2004, Hennin *et al.* 2015).  
381 However, other studies are needed to more fully explore this possibility. Electronic tracking of  
382 individual winter migrations and foraging activity would lend insights to this possibility. However,  
383 as previously indicated, variation in fCort did not ultimately predict breeding decision in the next  
384 year, as it did in the black-browed albatrosses. We therefore suggest that biennial breeding may  
385 have evolved as a bet-hedging strategy in grey-headed albatrosses as a means for buffering the  
386 apparent susceptibility of females to negative physiological costs of reproduction (e.g. the negative  
387 Trig~fCort correlation, Fig. 3). There are a very few individual grey-headed albatrosses that  
388 attempt to breed in successive years (Ryan *et al.* 2007), and presumably only those in the best  
389 relative condition are able to do so (Crossin *et al.* 2013a).

390 Previous work with other biennial species lends support to a fundamental role of Cort and  
391 body condition in mediating biennial versus annual breeding strategies (Vitousek *et al.* 2010). For  
392 example, in the biennially-breeding iguana (*Amblyrhynchus cristatus*) females in poor  
393 physiological condition at the onset of breeding are likely to produce smaller hatchlings with poor  
394 survival prospects, and risk their own survival. Iguanas that defer reproduction tend to have higher  
395 glucocorticoid levels and sensitivity, which might be a response to some exogenous factor like  
396 local resource availability, thus enhancing survival probability and subsequent fitness.

397 Although our study provides evidence for both costs of reproduction and carryover effects,  
398 and suggests plausible mechanisms, it is observational by nature. An alternative approach to

399 advance our understanding of physiological control of breeding frequency and glean insights into  
400 the evolution of biennial breeding strategies, would be controlled experimental manipulations of  
401 glucocorticoid levels at the onset of the non-breeding season, in tandem with electronic tracking  
402 (Crossin *et al.* 2014), especially of female albatrosses.

403

#### 404 **Acknowledgements**

405 We thank Derren Fox and Andy Wood at the British Antarctic Survey for field and data  
406 support. We also thank the suggestions of two anonymous reviewers. Financial support was  
407 provided by the Antarctic Science International Bursary, awarded to GTC. Additional support was  
408 provided by the British Antarctic Survey through a Natural Environment Research Council  
409 (NERC) Collaborative Gearing Scheme awarded to RAP and others, a Natural Sciences and  
410 Engineering Research Council of Canada (NSERC) Post-doctoral Fellowship to GTC, NSERC  
411 Discovery Grants to TDW, OPL and GTC, and a National Science Foundation (USA) grant IOS-  
412 1048529 to LMR. This study represents a contribution to the Ecosystems component of the British  
413 Antarctic Survey Polar Science for Planet Earth Programme, funded by NERC.

414

#### 415 **Author contributions**

416 GTC performed the field work, collected the data, performed the triglyceride and  
417 hematocrit assays, analyzed the data, and wrote the manuscript. RAP assisted with the coordination  
418 of the field plan, provided funding and logistical support through BAS, and contributed to the  
419 writing. XB assisted with statistical analysis. CRL and LMR ran the corticosterone assays. CH and  
420 OPL ran the testosterone assays. TDW provided logistical and intellectual guidance with respect  
421 to the field plan, the analyses, and the framing of the manuscript, as well as providing financial and  
422 other support. All authors reviewed and edited the final submitted manuscript.

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539 WILLIAMS, T.D. 2012. *Physiological adaptations for breeding in birds*. Princeton University  
540 Press, Princeton, New Jersey, USA.

541 Table 1 | The numbers and fates of black-browed (*Thalassarche melanophris*, BBA) and grey-  
 542 headed (*T. chrysostoma*, GHA) albatrosses sampled in two consecutive breeding seasons at Bird  
 543 Island, South Georgia (austral summer 2008/09 to 2009/10). To link current 2008/09 breeding to  
 544 future 2009/10 breeding, the dataset was restricted to albatrosses sampled for tail feathers in  
 545 2009/10 (future breeding).

546

Species	Sex	2008/09			2009/10	
		Successful	Failed	Deferred	Bred	Deferred
BBA (total N=50)	Female	15	9	4	22	6
	Male	11	5	6	19	3
GHA (total N=18)	Female	5	3	1	3	6
	Male	2	4	3	4	5

547

548 Table 2: Comparison of models exploring the effects of breeding status (successful breeder, failed breeder, or deferred breeder) and post-  
 549 breeding season physiological condition of black-browed and grey-headed albatrosses on reproductive decision a year later. Output were  
 550 generated from a backward stepwise generalized linear model with a binomial response and logit link function. Species were run  
 551 separately due to known differences in breeding strategy and physiology.

552

<b>Species</b>	<b>Model</b>	<b>AICc</b>
BBA (N=50)	sex + breeding status + hematocrit + triglyceride + testosterone + fCort	38.04
	breeding status + hematocrit + triglyceride + testosterone + fCort	35.21
	breeding status + triglyceride + testosterone + fCort	32.99
	breeding status + triglyceride + fCort	31.02
	<b>breeding status + fCort</b>	<b>28.80</b>
	null (~1)	37.99
GHA (N=18)	sex + breeding status + hematocrit + triglyceride + testosterone + fCort	40.49
	sex + breeding status + hematocrit + testosterone + fCort	33.14
	sex + breeding status + hematocrit + fCort	27.49
	<b>null (~1)</b>	<b>25.30</b>

553

554 Table 3 | Results of a generalized linear model comparing the binomial breeding decision (breed  
555 or defer) of black-browed (*Thalassarche melanophris*, BBA) and grey-headed (*T. chrysostoma*,  
556 GHA) albatrosses. Models are the most parsimonious as determined by AICc model comparisons  
557 (Table 2). Given differences in breeding strategy (BBA are annual breeders, and GHA are biennial  
558 breeders), separate models were run for the two species. Significant model effects are indicated by  
559 bold text.

560

Species (N)	Effects	estimate	z	P
BBA (50)	Previous breeding fate	-19.567	-0.005	0.996
	<b>fCort</b>	<b>-0.955</b>	<b>-2.196</b>	<b>0.028</b>
GHA (18)	Null (intercept)	0.357	0.724	0.469

561

562 **Figure legends**

563 Fig. 1 | Schematic representing annual cycle of black-browed (BBA, *Thalassarche melanophris*)  
564 and grey-headed (GHA, *T. chrysostoma*) albatrosses at Bird Island, South Georgia during the  
565 austral summer of 2008/09 (breeding season 1) and 2009/10 (breeding season 2). Brackets indicate  
566 times when physiological samples were collected. The yellow bars indicate the period when tail  
567 feathers are moulted and regrown; the dashed segment indicates that the duration of the period of  
568 tail feather growth is presently unknown. See Table 1 for samples sizes.

569  
570 Fig. 2 | Physiological variables in black-browed (BBA, *Thalassarche melanophris*) and grey-  
571 headed (GHA, *T. chrysostoma*) albatrosses measured at the end of the 2008/09 breeding season.  
572 Feather Cort levels reflect circulating Cort in the weeks/months after breeding, when tail feathers  
573 are moulted and then replaced. Data are classified according to species and breeding fate  
574 (S=successful breeders, F=failed breeders, D=deferred breeders). Females are indicated with  
575 triangles and males with circles, while GHA values are in grey and BBA values are in black. Values  
576 represent least squares means  $\pm$ SEM.

577  
578 Fig. 3 | Correlations between plasma triglyceride levels and residual feather corticosterone levels  
579 in black-browed (BBA, *Thalassarche melanophris*) and grey-headed (GHA, *T. chrysostoma*)  
580 albatrosses. Triglyceride levels were measured at the end of breeding in the 2008/09 season, while  
581 fCort levels reflect circulating Cort at the time of feather regrowth in the early to mid nonbreeding  
582 season. Females are indicated with triangles and males with circles, while GHA values are in grey  
583 and BBA values are in black. All feathers (whether from breeding or deferring albatrosses) were  
584 sampled at the beginning of the 2009/10 season.

585

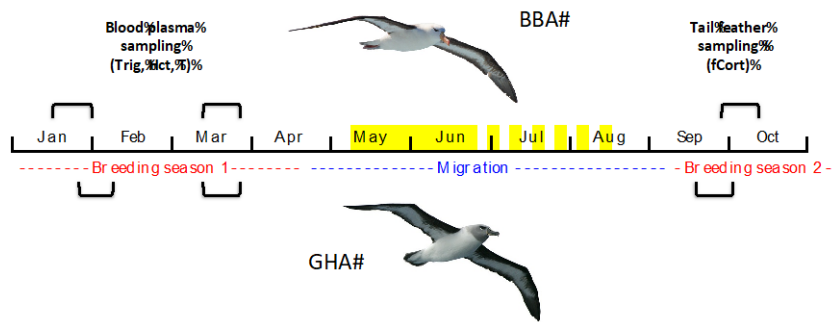


Fig. 1

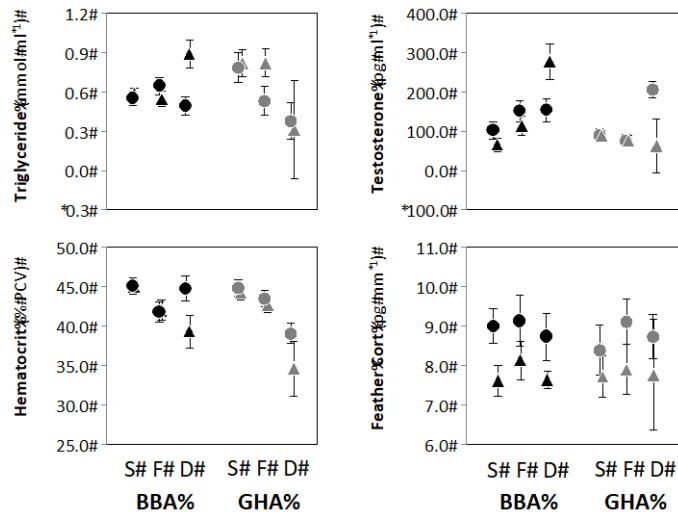


Fig. 2



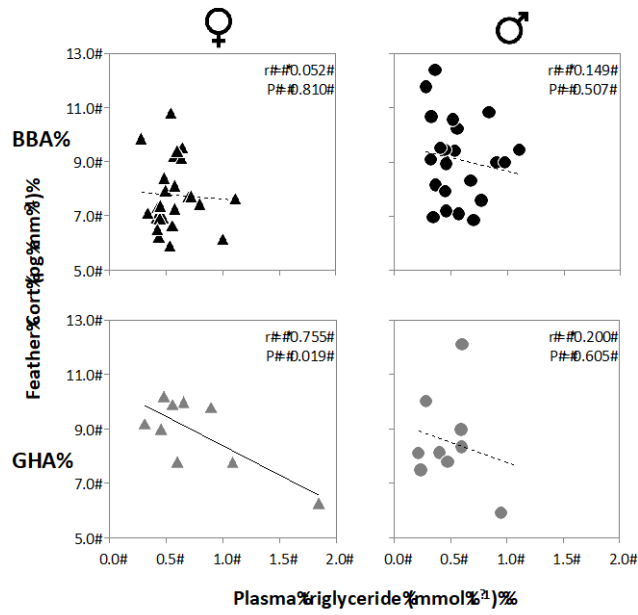


Fig. 3