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4-1-2017

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Recommended Citation

Crossin, Glenn T.; Phillips, Richard A.; Lattin, Christine R.; Romero, L. Michael; Bordeleau, Xavier; Harris, Christopher M.; Love, Oliver P.; and Williams, Tony D.. (2017). Costs of reproduction and carry-over effects in breeding albatrosses. *Antarctic Science*, 29 (2), 155-164.
<https://scholar.uwindsor.ca/ibiopub/56>

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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 (E₂) 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

Species	Model	AICc
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
	breeding status + fCort	28.80
	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
	null (~1)	25.30

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
	fCort	-0.955	-2.196	0.028
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

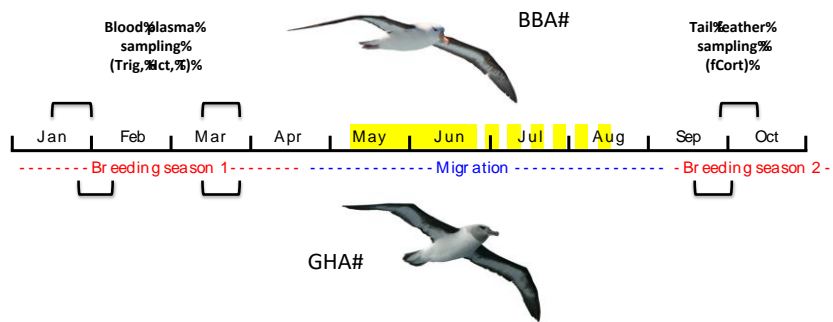


Fig. 1

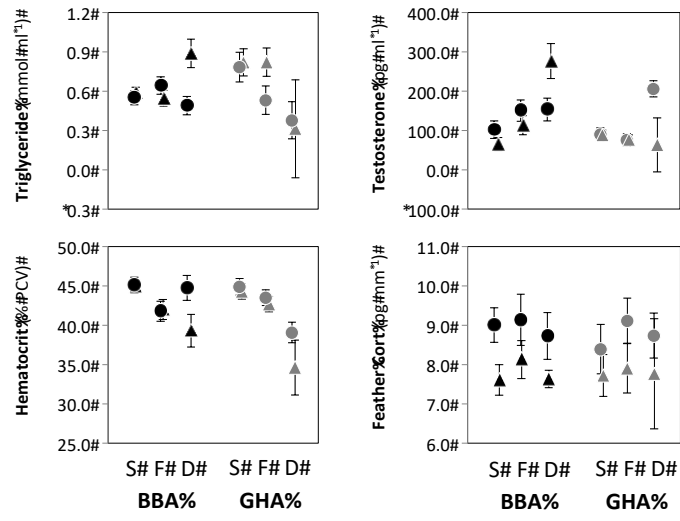


Fig. 2

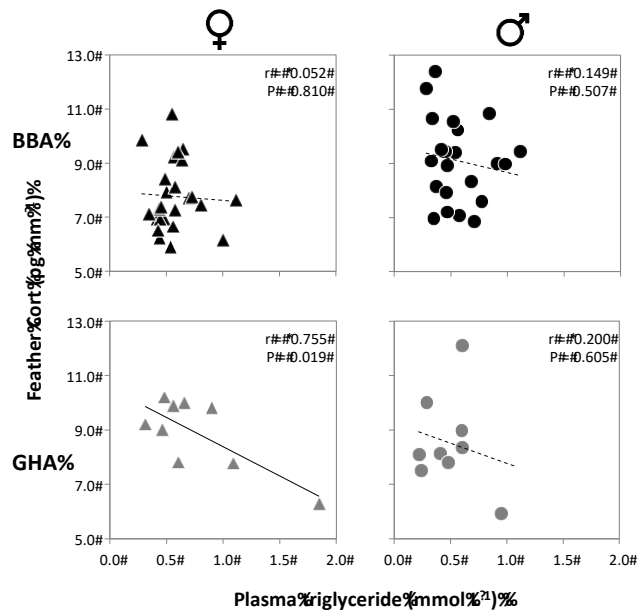


Fig. 3