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1 **Corticosterone mediated costs of reproduction link current to future breeding.**

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23 Running title: Feather corticosterone and trade-offs

24

25 **Abstract**

26 Life-history theory predicts that costs are associated with reproduction. One possible mediator of
27 costs involves the secretion of glucocorticoid hormones, which in birds can be measured in
28 feathers grown during the breeding period. Glucocorticoids mediate physiological responses to
29 unpredictable environmental or other stressors, but they can also function as metabolic regulators
30 during more predictable events such as reproduction. Here we show that corticosterone (“Cort”)
31 in feathers grown during the breeding season reflects reproductive effort in two Antarctic seabird
32 species (giant petrels, *Macronectes spp.*). In females of both species, but not males, feather Cort
33 (“fCort”) was nearly 1.5 fold higher in successful than failed breeders (those that lost their
34 eggs/chicks), suggesting a cost of successful reproduction, i.e. high fCort levels in females reflect
35 the elevated plasma Cort levels required to support high metabolic demands of chick-rearing.
36 Successful breeding also led to delayed moult prior to winter migration. The fCort levels and pre-
37 migration moult score that we measured at the end of current breeding were predictive of
38 subsequent reproductive effort in the following year. Birds with high fCort and a delayed
39 initiation of moult were much more likely to defer breeding in the following year. Cort levels and
40 the timing of moult thus provide a potential mechanism for the tradeoff between current and
41 future reproduction.

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44 **Key-words:** breeding-moult overlap, *Macronectes*, chick rearing, feather corticosterone,
45 foraging behaviour.

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47

48 **Introduction**

49 Life-history theory asserts that natural selection cannot simultaneously maximize both survival
50 and reproductive activity, and assumes that reproduction has costs [47]. The physiological basis
51 of these costs is not well understood, but glucocorticoid hormones (e.g. corticosterone) may be
52 involved in mediating such costs. Well known for their role in allostasis and the physiological
53 responses to unpredictable environmental stressors [3,36,42,51], glucocorticoids can trigger
54 breeding desertion and failure if threshold levels are exceeded, as individuals must re-direct
55 resources towards self-maintenance in order to cope with stressor at hand [9]. However,
56 glucocorticoids also function as metabolic regulators during more predictable events, like
57 migration and seasonal breeding, and can be positively correlated with measures of current
58 reproductive effort [13,23]. Studies detailing the role of corticosterone in the regulation of
59 parental care, via positive effects on foraging behaviour and provisioning effort, underscore its
60 ubiquitous role in organismal fitness [6,13,34].

61 Not surprisingly, the relationships between glucocorticoids and fitness measures are
62 complex and influenced by factors like age, breeding status, physiological condition, population,
63 species, and ecology. Two recent reviews illustrate how variation in plasma levels of
64 corticosterone (hereafter called “Cort”), at any single point in time, can be either positively,
65 negatively, or non-significantly related to fitness or surrogates thereof [4,9]. Understanding the
66 role of Cort in fitness, and predicting the direction of the relationship between the two, may
67 depend on whether baseline or stress-induced plasma levels are examined. However, in studies
68 where no relationship is observed (typically in studies examining seasonal phenomena), plasma
69 Cort offers only a “snapshot” view of an individual’s physiological condition (hours to day),
70 which maybe insufficient for resolving events operating over longer time-frames. A longer-term,
71 integrated measure of Cort secretion and hypothalamo-pituitary-adrenal axis (HPA) activity has

72 the potential to resolve Cort's role in broad temporal processes like seasonal migrations,
73 reproduction, or transitions between these life-history stages, especially in situations where
74 plasma Cort does not reveal any associations. Analysis of Cort in keratin-based tissues (feathers,
75 hair), which accumulate glucocorticoid hormones during growth (weeks to months), has been
76 used recently to provide a more useful means for interpreting variation in broad-scale life-history
77 events (birds [7,8]; mammals [19,35]). The analysis of Cort in feathers (hereafter called "fCort")
78 has the potential to increase our understanding of the mechanisms controlling avian life-histories
79 [7,8,33].

80 Experimental studies of captive birds have confirmed that fCort levels can reflect high, or
81 stress-induced, plasma Cort levels during the period when feathers are grown [7,33].
82 Furthermore, variation in fCort has been linked to reproductive effort in captive partridges
83 (*Alectoris rufa*) [7]. But only a small number of studies have linked natural variation in fCort to
84 fitness measures (e.g. reproductive success) in free-living birds. Fairhurst et al. [17] found that
85 variation in parental investment by a seabird species (Cory's shearwaters, *Calonectris diomedea*)
86 was reflected in fCort levels in the feathers of chicks. Specifically, they found that low foraging
87 efficiency by parents led to a suppression or down-regulation of Cort secretion by chicks, which
88 they interpreted as a buffer against nutritional stress and the deleterious effects of long-term HPA
89 activation, resulting in lower fCort levels. Although fCort levels were not measured in the parent
90 shearwaters, we might expect these to correlate positively with foraging effort [1,13], and with
91 chick growth [6,13]. More recently, Kouwenberg et al. [30] show positive correlations between
92 pre-breeding fCort levels and egg sizes in Atlantic puffins (*Fratercula arctica*), providing a link
93 between winter foraging effort and reproductive effort.

94 Collectively, the studies by Bortolotti et al. [7], Fairhurst et al. [17], and Kouwenberg et
95 al. [30] provide growing evidence for a positive link between variation in fCort and fitness

96 components in birds, but there is also an example of a negative fitness link. Koren et al. [29]
97 examined fCort levels in feathers grown during a post-breeding moult in sparrows (*Passer*
98 *domesticus*) and found that elevated levels were related to lower overwinter survival. This study
99 did not identify the underlying mechanism, but recent studies have shown that elevated Cort can
100 both slow the rate of moult and negatively affect feather quality [16,43,48], including reductions
101 in the insulating properties of feathers critical for survival at low winter temperatures.

102 Plasma Cort is usually down-regulated at the onset of post-breeding moult. As a catabolic
103 steroid, this is presumably to avoid the breakdown of structural proteins at a time when anabolic
104 processes are needed (e.g. new feather synthesis), as well as the Cort-dependent inhibition of new
105 protein synthesis during feather growth [16]. For species that moult during chick-rearing, how is
106 the potential need to up-regulate baseline corticosterone in support of foraging and parental effort
107 reconciled against the need to down-regulate it to avoid negative effects on feather growth? More
108 importantly, what are the functional consequences of breeding activity and Cort secretion on the
109 rate of new feather growth, fCort levels, future survival, and future breeding?

110 In this study, we test the hypothesis that fCort in breeding adults can provide an integrated
111 measure of HPA activity in relation to current reproductive effort. We also hypothesize that fCort
112 would be correlated with future reproductive effort. To address this, we took advantage of the
113 unusual characteristic of giant petrels (*Macronectes spp.*), which unlike most birds (but see [10])
114 begin moulting during incubation or early chick-rearing, and continue growing new feathers until
115 the end of the breeding season [14,27]), i.e. they exhibit a breeding-moult overlap, coincident
116 with parental care. We measured both plasma Cort, and fCort in feathers grown by parents during
117 chick-rearing in year x (their current reproductive attempt), and compared levels in parent birds
118 whose chicks died earlier in the season. Comparisons between successful and failed breeders
119 should reveal the HPA activity and Cort secretion needed to support investment in chick rearing.

120 We therefore sampled successful and failed individuals from two species of giant petrels at the
121 end of a breeding season (northern *Macronectes halli* and southern *M. giganteus*). In addition to
122 Cort concentrations in feathers and plasma, we compared moult scores in successful and failed
123 breeders. We then followed and recorded the survival and breeding activity of the same
124 individuals over successive breeding seasons. By doing so, we could examine associations
125 between fCort, plasma Cort, and feather moult during the current reproductive effort (e.g. year x),
126 with future reproductive decisions (breeding vs. deferral) and survival (e.g. in year x+1).

127 We predicted three things. 1) That reproductive success in year x would be positively
128 related to fCort levels, based on an assumption that baseline Cort is up-regulated in successfully
129 breeding birds, relative to failed breeders, to support the higher metabolic demands of parental
130 care. Given its role in the stress response however, we expect the relationship between Cort and
131 parental care measures to fit an inverse U function, wherein low levels of parental care can result
132 from very low or very high levels (e.g. a stress response). But at the middle of this curve, high
133 levels should be positively linked to parental care. 2) We also predicted that the relationship
134 between Cort and reproductive effort would be more readily detectable in feathers than in plasma,
135 as feathers should integrate the hormonal signal over the extended period of feather growth
136 coincident with incubation and chick-rearing. Finally 3) we predicted that a relationship between
137 fCort levels and future breeding probability in year x+1 would indicate a long-term cost of
138 reproductive investment. Given that successfully breeding giant petrels in year x have a delayed
139 or slower rate of moult and feather growth than failed breeders [14,27], we predicted that high
140 fCort and delayed moult would provide a potential mechanism underlying the tradeoff between
141 current and future reproduction.

142

143 **Materials and Methods**

144 STUDY SITE AND SAMPLE COLLECTION

145 Data were collected from northern and southern giant petrels breeding on Bird Island, South
146 Georgia (54°00'S, 38°02'W) during chick-rearing in the the austral summer of 2008/09. Blood
147 samples and moult scores were collected in 2008/09 only, but survival and subsequent breeding
148 histories for all individuals were monitored closely during the 2009/10, 2010/11, and 2011/12
149 breeding seasons. Our principal aim was to link current breeding activity (2008/09 season) to
150 future reproduction (2009/10 season). Given the high breeding site fidelity of giant petrels, we
151 assumed that birds unobserved after the 2008/09 season had died at sea. Although we recognize
152 that there could be alternative reasons for birds being unobserved, a precedent for this assumption
153 was established by Foote et al.'s study of giant petrels [18].

154 Giant petrels lay only one egg, and parents share egg incubation and chick feeding duties
155 nearly equally [28]. Northern giant petrels laid from mid September to mid October, chicks
156 hatched from mid November to mid December and fledged from mid March to early April (Fig.
157 1). Southern giant petrels laid on average about 6 weeks later than northern giant petrels,
158 beginning in November, and chicks hatched in January and fledged in late April to May. Birds
159 with chicks were sampled on 5-13 March 2009, when chicks of southern giant petrels were ~ 2
160 months old, and those of northern giant petrels 6 weeks older and close to fledging. These dates
161 were at the end of the breeding season, shortly before out-migrations from the colony. On each of
162 these dates, failed breeders (those known to have lost their eggs/chicks) were also sampled. From
163 the colony database, it became apparent that nearly all failed birds had failed during the
164 incubation stage. Thus, at the season's end, we compared the physiological state and condition of
165 successfully breeding giant petrels with those who lost their eggs months earlier during
166 incubation. All birds were part of a long-term study population, were identifiable by alpha-

167 numeric Darvik leg bands, and were of known sex and breeding status. Also known were the
168 dates breeding failure occurred (loss of eggs or chicks).

169 Blood samples (2 ml) were collected from the tarsal vein using syringes with 25 gauge
170 needles, returned to the lab, and the plasma was separated by centrifugation and stored at -20° C.
171 In all cases, blood was collected in less than 3 min from first approach to the bird. Bill
172 measurements were made with calipers (to nearest mm). Body mass was measured to the nearest
173 10 g with a Pesola spring balance. Five newly grown breast feathers, which are easily
174 distinguished from older feathers by their darker colour and un-weathered condition (e.g. lack of
175 abrasions at the tips), were plucked and stored in labeled bags. Hunter [27] noted that in
176 *Macronectes spp.* body feathers grow continuously throughout the breeding season. Feathers
177 were stored in the dark, at 4° C until analysis. In addition to our breeding and failed-breeding
178 birds, we opportunistically sampled feathers from two non-breeding female giant petrels (a
179 Northern and a Southern) which did not lay but deferred reproduction altogether. This was to
180 provide a qualitative point of reference to the breeding birds, especially the failed breeders which
181 should be similar to non-breeders as they were not providing parental care in any form.

182 Giant petrels have 10 primary flight feathers and a minute 11th primary feather, which can
183 be difficult to check in a live bird and was thus ignored, as in previous studies [14,27]. Mass-
184 corrected primary feather moult in our birds was scored according to Dawson & Newton [15],
185 which involves scoring the growth of new primary feathers on a scale of 0 to 4: 0 = a dropped
186 feather but no new feather yet present; 1 = approximately one-quarter grown (i.e. from eruption
187 from the follicle to one-third fully grown); 2 = approximately half grown (i.e. one-third to two-
188 thirds fully grown); 3 = approximately three-quarters grown; and 4 = fully grown. The score (0–
189 4) for each primary position was divided by 4 (because a score of 1 = one-quarter total feather

190 length) and multiplied by the proportion that the final mass of that particular primary contributes
191 to total mass of all 10 primaries. Summing the scores of individual feathers thus produces a total
192 moult score (synonymous with new feather growth) ranging from 0.0 before moult to 1.0 in a
193 fully moulted bird. Data on individual primary feather mass were collected from fresh giant petrel
194 carcasses (from both species), which were found in the breeding colonies and which died of
195 natural causes.

196

197 HORMONE ASSAYS

198 Feather Cort was determined by a standard radioimmunoassay following Bortolotti et al. [7] and
199 modified by Lattin et al. [33]. Briefly, the calamus was removed from all five feathers and their
200 total length and weight were recorded. Feathers were then minced into pieces $<5 \text{ mm}^2$. Bortolotti
201 et al. [7,8] make a clear case for standardizing fCort by length, rather than mass, due to the way
202 feathers grow and elongate along their radial circumference. Although sample mass can affect
203 fCort concentrations [33], this effect only occurs with samples of low mass ($\leq 50 \text{ mg}$). All
204 samples used in this study were far above this threshold (range: 145-238 mg).

205 We added 7 ml methanol to each sample and incubated in a sonicating water bath for 30
206 min. Samples were then placed into a shaking water bath at 50° C overnight. The next day,
207 feather fragments were separated from samples using vacuum filtration, and the methanol
208 extracts dried using nitrogen gas at 50° C . Samples were reconstituted in phosphate-buffered
209 saline with glucose and run in duplicate through a standard radioimmunoassay as described in
210 Wingfield et al. [50] using an anti-corticosterone antibody suitable for feather extracts (Sigma-
211 Aldrich C8784, Saint Louis, MO, USA, lot 57K4791). We determined the intra-assay coefficient
212 of variation by measuring differences between duplicates, and the inter-assay variation by

213 measuring differences between standard samples (we used two standards: a known amount of
214 Cort, and pulverized, homogenized feathers). Intra-assay variation was 2.2%; inter-assay
215 variation was 5.2%. Assay parallelism was previously demonstrated by Bortolotti et al. [7].

216 Plasma Cort was determined by double antibody radioimmunoassay (^{125}I -RIA, MP
217 Biomedicals, 07-120103), according to Crossin et al. [14]. The assay detection limit was 3.13 pg
218 Cort per tube (i.e. the lowest Cort standard, 12.5 ng ml^{-1} , using a $50 \mu\text{l}$ assay volume). The low
219 Cort control and a consistent native plasma sample were analyzed in each assay to determine an
220 inter-assay variation (5.1%). Serially diluted native plasma samples were parallel to the
221 corticosterone standard curve. Coefficients of variation for final concentrations were 9.9% for
222 northern giant petrels ($N = 3$) and 7.5% for southern giant petrels ($N = 3$). These plasma Cort data
223 have been previously published [14], but are presented here for comparison with fCort levels.

224

225 STATISTICS

226 Analyses were run with the JMP 9.0 and R software packages. Data transformations were applied
227 when the distribution of residuals from models were non-normal, as determined by Shapiro-Wilk
228 tests. For the failed breeders, we used analysis of covariance (ANCOVA) to examine whether
229 there were species or sex differences in fCort and plasma Cort while controlling for variation in
230 fail date (e.g. date when breeding failure occurred, which ranged from 8.9 to 20.9 weeks before
231 our sampling dates and illustrates how failure by giant petrels usually occurs at the egg stage).
232 Then, because giant petrels are sexually size-dimorphic [28], we used linear regression to explore
233 the relationship between body mass and fCort in each species and sex independently. Because
234 these were related, variation in fCort and plasma Cort were therefore examined by three main
235 effects- species, sex, and breeding outcome (failed or successful), while also controlling for
236 allometric variation in body mass (ANCOVA). Interactions between all main effects were

237 included in the models, as was a sex*body mass term (due to sexual dimorphism). A similar
238 model was used to analyze variation in moult score. Finally, ANOVA was used to explore
239 differences in body mass between species and breeding outcome.

240 Nominal logistic regression was used to explore whether costs of reproduction (breeding
241 outcome, fCort, moult score) influenced the tradeoff between current and future reproduction.
242 Species, sex, breeding outcome (failed or successful in 2008/09), fCort, and moult score were
243 main effects (including all interactions) in the highest order model examining the probability of
244 deferred reproduction in the following year (year 2009/10).

245

246 **Results**

247 We sampled 80 giant petrels at or near their nests in 2008/09 (or year x; see Table 1 for numbers
248 sampled from each species and sex). No partner birds were sampled, meaning that the birds we
249 sampled represent 80 independent successful or failed breeding attempts. Of these 80 birds, 73
250 were re-sighted in subsequent years (91%; range 83-100% depending on species and sex; Table
251 1). From these re-sighting data, we determined overwinter survival rates and future breeding
252 activity.

253 Before comparing fCort and plasma Cort in successful versus failed breeders, we first
254 examined whether date of nest failure influenced these variables in the failed breeders, but there
255 was no significant effect (fCort, $F_{3,20} = 0.232$, $P = 0.873$; Cort, $F_{3,21} = 0.600$, $P = 0.622$). Of the
256 birds breeding in the 2008/09 season (year x), there were no significant differences in body mass
257 between species or between successful and failed breeders (females, $F_{2,37} = 0.444$, $P = 0.645$;
258 males, $F_{2,37} = 0.069$, $P = 0.934$), but linear regression revealed significant negative relationships
259 between body mass and fCort in both sexes, independently of species and breeding outcome

260 (both $P < 0.029$). Body mass was therefore used as a covariate when exploring differences in
261 fCort between species, sexes, and breeding groups.

262 An ANCOVA with species, sex, and current breeding outcome as main effects, and body
263 mass as a covariate, revealed that fCort was significantly related to all of these effects and to the
264 body mass covariate (full model: $F_{8,65} = 8.136$, $P < 0.001$) (see Table 2 for detailed statistical
265 output and effects sizes). Interactions terms were included in the model; only the sex*breeding
266 outcome was significant (Table 2). This interaction suggests that mean (least squares) fCort was
267 higher in successfully breeding females of both species than in failed breeders, but this was not
268 the case in males, which partially supports our first prediction (Table 2, Fig. 2). In contrast,
269 plasma Cort levels did not differ by species, sex, or breeding outcome, and did not vary with
270 body mass (full model: $F_{8,67} = 0.593$, $P = 0.780$), which supports our second prediction (Table 2,
271 Fig. 2). By way of contrast, fCort levels in the two non-breeding (deferring) female giant petrels
272 that we opportunistically sampled were similar to the mean value measured in all failed giant
273 petrels (1.78 and 1.91 versus a mean of 2.13 pg mm^{-1}).

274 Patterns of primary moult varied according to species, sex, and breeding outcome (Fig. 3).
275 By the end of the breeding, failed birds had progressed further in primary moult than successful
276 birds, and generally, moult was more advanced in males than in females. Successfully breeding
277 southern giant petrel females had initiated only about 5% of moult by the end of the 2008/09
278 season, which was significantly lower than all other successfully breeding birds (ANCOVA, full
279 model- $F_{8,71} = 22.17$, $P < 0.001$). This means that successful southern females must defer moult
280 to a greater extent than other species/sexes, and must therefore grow the majority of their
281 primaries at sea during the winter non-breeding period (see [27]).

282 A full nominal logistic regression model ($\chi^2 = 55.17$, $P < 0.001$, $N = 74$) examining the
283 probability of future breeding deferral revealed no significant effect of species ($P = 0.223$), but
284 significant effects of sex ($P < 0.001$), breeding outcome ($P = 0.017$), and their interaction
285 (sex*breeding outcome, $P < 0.001$). There was also a significant species*breeding outcome
286 interaction ($P = 0.008$). Due to this latter interaction, we ran subsequent species-by-sex models to
287 reveal that the main effects of fCort and moult score significantly predicted the probability of
288 future breeding deferral in female southern giant petrels only (see Table 3 for statistical output of
289 species-by-sex models). The effect of current breeding outcome did not predict future breeding
290 deferral. In other words, the combination of high fCort levels and low moult score at the end of
291 the breeding seasons increased the probability of deferred breeding the next year, independent of
292 breeding outcome in the current year. The only other significant effect was current breeding
293 outcome on future breeding deferral in male southern giant petrels, which suggests that
294 successful breeding increases the tendency for future deferral irrespective of fCort or moult
295 scores (Table 3). Using a similar logistic regression modeling approach, the probability of future
296 survival (to year $x+1$) was unrelated to species, sex, breeding outcome, fCort levels, or moult
297 scores (full model, $\chi^2 = 14.05$, $P = 0.446$, $N = 64$), which is not surprising given the high survival
298 and return rates of giant petrels noted here (Table 1) and elsewhere [11].

299
300 **Discussion**
301 Despite years of study, our understanding of the physiological mechanisms controlling life-
302 history events and individual fitness is rudimentary. In this study, we describe how natural
303 variation in feather Cort (or fCort) is linked to two important life-history events in free-living
304 birds. Both current reproductive success and future reproductive effort (breeding vs. deferral)

305 were significantly linked to fCort, such that high fCort levels were indicative of successful
306 breeding in female giant petrels. Conversely, high fCort was predictive of deferred breeding in
307 the following year, but in a context dependent manner which we describe in greater detail below.
308 Based on our results we propose that circulating Cort, as indexed by fCort, mediates a trade-off
309 between current and future reproduction.

310 Although our study is correlative by design, and so we can only speculate about the role
311 of Cort as a mediator between current and future reproduction, they nevertheless 1) show the
312 utility of fCort for resolving long-term patterns of HPA activity and glucocorticoid secretion with
313 links to the fitness-related events of current reproductive success and future breeding investment,
314 2) highlight the potential of using fCort as an integrated signal of metabolic up-regulation in
315 support of successful current reproductive investment rather than solely as an indicator of
316 cumulative physiological “stress”, and 3) reveal a potential cost of reproduction via an interaction
317 between fCort and the timing of moult that affects future breeding activity. Collectively, these
318 results suggest that a Cort-mediated mechanism underlies the trade-off between current and
319 future reproduction, thus lending support to the corticosterone-adaptation hypothesis [4] which
320 predicts positive associations between Cort secretion and fitness measures. Interestingly, this link
321 was not discernable via plasma Cort levels, which seemed insufficient for resolving broad-scale
322 associations between current and future breeding activity in this study. It was only through
323 analysis of feather Cort levels that we could resolve these links [7,8]. Finally, we also show that
324 fCort was unrelated to long-term survival in giant petrels, which is perhaps not surprising given
325 the high annual survival observed in these long-lived species (see Table 1). Clearly, further work
326 is needed to more rigorously test the role of Cort (measured in an integrated manner using fCort)
327 as the causal agent responsible for variation in these life-history events. Additionally, fCort and
328 plasma Cort are only two elements in a complex HPA regulatory network. Relating variation in

329 Cort to fitness thus requires an assumption that all other aspects of the HPA axis were expressed
330 similarly among individuals. Although we did not measure the activity of other elements of this
331 axis, we nevertheless demonstrate differences between fCort between individuals that link to
332 breeding success and future investment.

333 Key to the interpretation of our data was knowledge of species' ecology, which puts into
334 context the role of Cort in patterns of current reproductive effort. During the breeding season,
335 giant petrels exhibit marked sexual and spatial segregation of foraging behaviours [21,40]. That
336 we observed a significant link between variation in fCort levels in female petrels and not in males
337 we attribute to this segregation. Female giant petrels forage in pelagic waters, flying hundreds to
338 thousands of kilometers during trips to productive areas throughout the southern latitudes (e.g.
339 continental shelf breaks, Antarctic Convergence zone). These foraging trips are much longer in
340 duration and range than those made by males, particularly during incubation and early chick-
341 rearing when the latter feed to a much larger extent on local carrion [21,40]. Experimental up-
342 regulation of plasma Cort has recently been shown to increase foraging effort and provisioning
343 rates in seabirds, with positive effects on chick growth [1,5,13, but see also 2]. By demonstrating
344 that fCort levels were higher in successful than in unsuccessful females, our results suggest that
345 the higher metabolic demands of parental care in females requires HPA up-regulation to sustain
346 higher provisioning effort and meet the demands of growing chicks. In the failed females, nearly
347 all of whom failed at the incubation stage before the initiation of moult (female petrels begin
348 moulting at around the time of egg hatching; Hunter 1984), fCort levels were significantly lower
349 than in breeders. Presumably, these low fCort levels reflect the lack of parental commitment that
350 results from failed breeding; free from the demands of parenthood and a need to feed chicks,
351 females were free to forage with less urgency, on their own schedules. Indeed, failed females had
352 fCort values that were similar to those of two non-breeding (e.g. non-parenting) females that we

353 opportunistically sampled. In contrast, the lack of relationship between fCort and breeding
354 activity in the males was presumably due to the abundant carrion found on the beaches close to
355 breeding sites (which are usually dominated by males). With a food source so readily available,
356 the urgency to forage is perhaps less intense in breeding males than in breeding females, and
357 might not require HPA up-regulation in support of foraging effort. We should caution however
358 that the lack of relationship between fCort and current breeding effort in especially Northern
359 males was marginal ($P = 0.060$, Fig. 2), so we cannot say with certainty that fCort is not linked to
360 or correlated with their breeding fate. Nevertheless, given what we know about the positive role
361 of elevated baseline Cort on foraging behaviour and parental care in birds [4,5,6,13], we propose
362 that the observed differences in fCort reflect differences in parental effort. Direct telemetric
363 measurement of foraging behaviour and estimates of activity budgets, and sampling for fCort,
364 would be needed to explore causal relationships [1,2,13].

365 Another unusual feature of giant petrel ecology that may have bearing on our results is
366 their breeding-moult overlap [14]. Breeding and moult are both assumed to be energetically
367 expensive [39,45], and when moult is extensive and occurring simultaneously with reproductive
368 activity, a trade-off between adult somatic maintenance and parental care is predicted, which
369 could potentially reduce chick provisioning rates, chick fledging mass, or the number of chicks
370 fledged [38,49]. However, some studies have shown little to no effect of moult status on current
371 breeding effort [26,37,46]. Nevertheless, Hemborg [25] suggested that in breeding-moult overlap
372 species, where males initiate moult before females, females must increase reproductive effort to
373 compensate for the reduced parental care provided by their moulting partner. Coupled with the
374 routinely higher foraging effort required of female birds, we might anticipate longer-term costs of
375 breeding-moult overlap for females which would explain why, in this study, fCort was related to

376 breeding success in females but not males. However, we must caution again that the lack of
377 relationship in males was only marginally non-significant.

378 Cort secretion appeared to have some cost to giant petrels, given the negative correlation
379 between fCort and body mass in both males and females that we observed. Despite this apparent
380 cost, there were no significant differences in body mass between failed and successful
381 individuals, so the relationship between fCort and body mass might indicate a commitment to
382 current reproduction but without significant consequence for subsequent survival [20]. Indeed,
383 fCort was not related to overwinter survival in giant petrels in this study. This contrasts with
384 Koren et al. [29] who showed a link between fCort and winter survival in house sparrows, but
385 sparrow are of course much smaller and shorter-lived than seabirds. We did however document
386 significant association between fCort levels during current breeding with future reproductive
387 effort (breeding decision), such that high fCort in successfully breeding Southern giant petrel
388 females increased the probability for deferred breeding in the next year. This suggests that the
389 Cort up-regulation in support of current reproductive effort exacts a cost on future effort.

390 There is an intuitive appeal to the idea that stress, or the mechanisms underlying
391 responses to stress, can have negative effects on reproduction, and there is no shortage of studies
392 that document negative relationships between circulating Cort and the likelihood of breeding
393 successfully. The increased likelihood for deferred future breeding when fCort is high could be
394 interpreted as a potential “stress” effect. Certainly over-stimulation of the Cort-response due to
395 chronic stress can have long-term costs to reproduction [44]. In brooding king penguins
396 *Aptenodytes patagonicus* for example, plasma Cort was 2- to 4-fold higher in individuals that
397 abandoned eggs or chicks compared with those who were relieved by their partners [22].
398 However, barring chronic over-stimulation, an appropriate or adaptive physiological stress
399 response should allow an individual to cope with challenges over time without breaching a

400 threshold level beyond which deleterious effects occur [13,24,34]. Labeling Cort as a "stress
401 hormone" is thus overly simplistic, and obscures its essential role in regulating metabolism,
402 activity levels, and energy use [12,31]. We do not interpret the relationship between high fCort
403 levels and deferred future breeding to be a stress effect. We suggest that there is an interaction
404 between Cort levels, feather quality [32,41], and the timing of moult that underlies the deferred
405 breeding of Southern giant petrel females.

406 To summarize, our data support a role of Cort secretion in reproductive effort, and
407 support predictions from the corticosterone-adaptation hypothesis (*sensu* Bonier et al. [4]).
408 Successful breeding in female giant petrel was associated with high fCort levels, which we've
409 interpreted as a commitment to, and an increase in, current breeding effort compared to failed
410 females. This commitment had presumed costs in the form of delayed moult, which for the late
411 breeding southern species requires that they replace the majority of new feathers at sea during the
412 non-breeding, migration season, which contrasts with the earlier breeding northern species.
413 Coupled with a possible negative effect of elevated fCort on feather quality, this could lead to
414 increases in flying effort and to energetic shortfalls in southern females that result in future
415 breeding deferral [32,41]. High fCort, reduced body mass, and slower moult may thus influence
416 the decision to breed in the following year. Because many of these variables are correlated, our
417 models examining the relationships with future breeding should be interpreted with some caution,
418 especially as the relatively low samples sizes (Table 3) may limit our ability to determine whether
419 it is only one variable that exerts the most influence on future breeding effort (e.g. fCort), or
420 whether there is a synergistic effect of a suite of variables. Future work would benefit from
421 experimental manipulations of Cort, repeated fCort and plasma Cort measurements, and detailed
422 (e.g. telemetric) observation of current and future breeding effort.

423

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431

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555 Table 1: Breeding activity of giant petrels (*Macronectes spp.*) at Bird Island, South Georgia in the 2008/09
 556 and 2009/10 breeding seasons. The number of successful and of failed breeders sampled for blood plasma and
 557 feathers in 2008/09 are indicated in parentheses in the year x column. Breeding activity for the same
 558 individual was then monitored the next year in 2009/10, after winter migrations. Moults scores and feather
 559 samples were collected at the end of year x to provide measures of current reproductive effort, and links to
 560 subsequent, future reproduction are explored in this study. Northern giant petrels lay in mid September to mid
 561 October, on average 6 weeks earlier than southern giant petrels, which lay in November.

Species	Sex	year x:	year x+1:		No. breeding	No. deferring	Proportion breeding
		No. sampled	No. re-sighted †	Proportion surviving winter			
<i>M. halli</i>	F	17 (9,8)	16	0.94	16	0	1.00
	M	22 (17,5)	22	1.00	18	4	0.82
<i>M. giganteus</i>	F	23 (15,8)	20	0.87	13	10	0.65
	M	18 (14,4)	15	0.83	8	10	0.44

562

563 † Re-sighted birds were those sampled in year x and observed again at the colony in subsequent years, i.e. the
 564 2009/10 or 2010/11 breeding seasons. These re-sightings allowed us to calculate winter survival rates from
 565 year x to year x+1.

566 Table 2: Statistical output from analyses of covariance comparing feather corticosterone (fCort)
 567 and plasma corticosterone by species, sex, and breeding outcome. Bold *P*-values are significant
 568 with $\alpha=0.05$. See Fig. 2 for mean fCort and plasma Cort values.

Response	Model effects	<i>F</i>	<i>P</i>	effect size (η_p^2)
fCort	whole model (<i>N</i> = 74)	8.136	<0.001	
	species	6.813	0.011	0.091
	sex	20.704	<0.001	0.233
	breeding outcome	8.058	0.006	0.106
	mass	26.344	<0.001	0.279
	species*sex	2.399	0.126	0.034
	species*breeding outcome	2.934	0.092	0.041
	sex*breeding outcome	4.440	0.039	0.061
	sex*mass	2.939	0.083	0.046
	plasma Cort	whole model (<i>N</i> = 76)	0.593	0.780
species		0.989	0.324	0.016
sex		2.797	0.099	0.043
breeding outcome		1.170	0.283	0.018
mass		2.931	0.092	0.045
species*sex		0.155	0.695	0.002
species*breeding outcome		0.055	0.815	0.001
sex*breeding outcome		0.126	0.723	0.002
sex*mass		0.547	0.462	0.009

569

570 Table 3: Nominal logistic regression models examining relationships between metrics of current
 571 reproductive effort in 2008/09 (success or failure, feather corticosterone levels, and moult score),
 572 and the probability of breeding deferral in the subsequent year (2009/10). A highest order model
 573 that included species and sex as main effects was initially run, and both variables were significant
 574 (see Results). Based on this, and on known differences in life-history, physiology, and pattern of
 575 breeding activity in giant petrels, final models were run independently for each species by sex
 576 combination, and are presented here. Significant effects are indicated by bold text. Note that
 577 interaction terms were non-significant in all models and were thus removed from the final models
 578 to increase statistical power.

Species and sex	Effects	<i>n</i>	χ^2	LR χ^2	<i>P</i>
<i>M. halli</i> females	whole model	16			inestimable †
	current breeding outcome				
	feather corticosterone				
	moult score				
males	whole model	18	4.067		0.254
	current breeding outcome			<0.001	0.991
	feather corticosterone			1.443	0.230
	moult score			0.635	0.426
<i>M. giganteus</i> females	whole model	19	13.143		0.004
	current breeding outcome			1.694	0.193
	feather corticosterone			8.177	0.004
	moult score			4.035	0.045
males	whole model	16	9.543		0.023
	current breeding outcome			5.813	0.016
	feather corticosterone			0.535	0.465
	moult score			0.876	0.349

579 † All surviving female northern giant petrels sampled in 2008/09 breed again in 2009/10, i.e.
 580 none deferred and so there was no variation in breeding outcome.

581 **FIGURE LEGENDS**

582 Fig. 1: Schematic of breeding activity of northern (*Macronectes halli*) and southern (*M.*
583 *giganteus*) giant petrels at Bird Island, South Georgia during the austral summer of 2008/09.

584 Broken bars indicate a particular event that continues once adult petrels have completed
585 reproduction. The black bars along the date axis indicates when individuals were sampled for
586 newly grown feathers and blood plasma, and when assessments of future survival and future
587 breeding decisions were made.

588
589 Fig. 2: Feather and baseline plasma corticosterone concentrations in male and female northern
590 and southern giant petrels sampled late in the breeding season, according to breeding outcome
591 (failed or successful). Columns represent least squares means which account for allometric
592 variation in body mass (ANCOVA). Error bars signify +SEM. Statistical significance was
593 assessed at $\alpha=0.05$.

594
595 Fig. 3: Proportion of total primary flight feather moult in northern (gray bars) and southern (white
596 bars) giant petrels completed by the end of the breeding season prior to winter migrations at sea.
597 Moult scores were collected late in the breeding season, and data are grouped by breeding
598 outcome and sex. Bars signify least squares means +SEM. Differing letters indicate statistically
599 significant contrasts ($\alpha=0.05$).

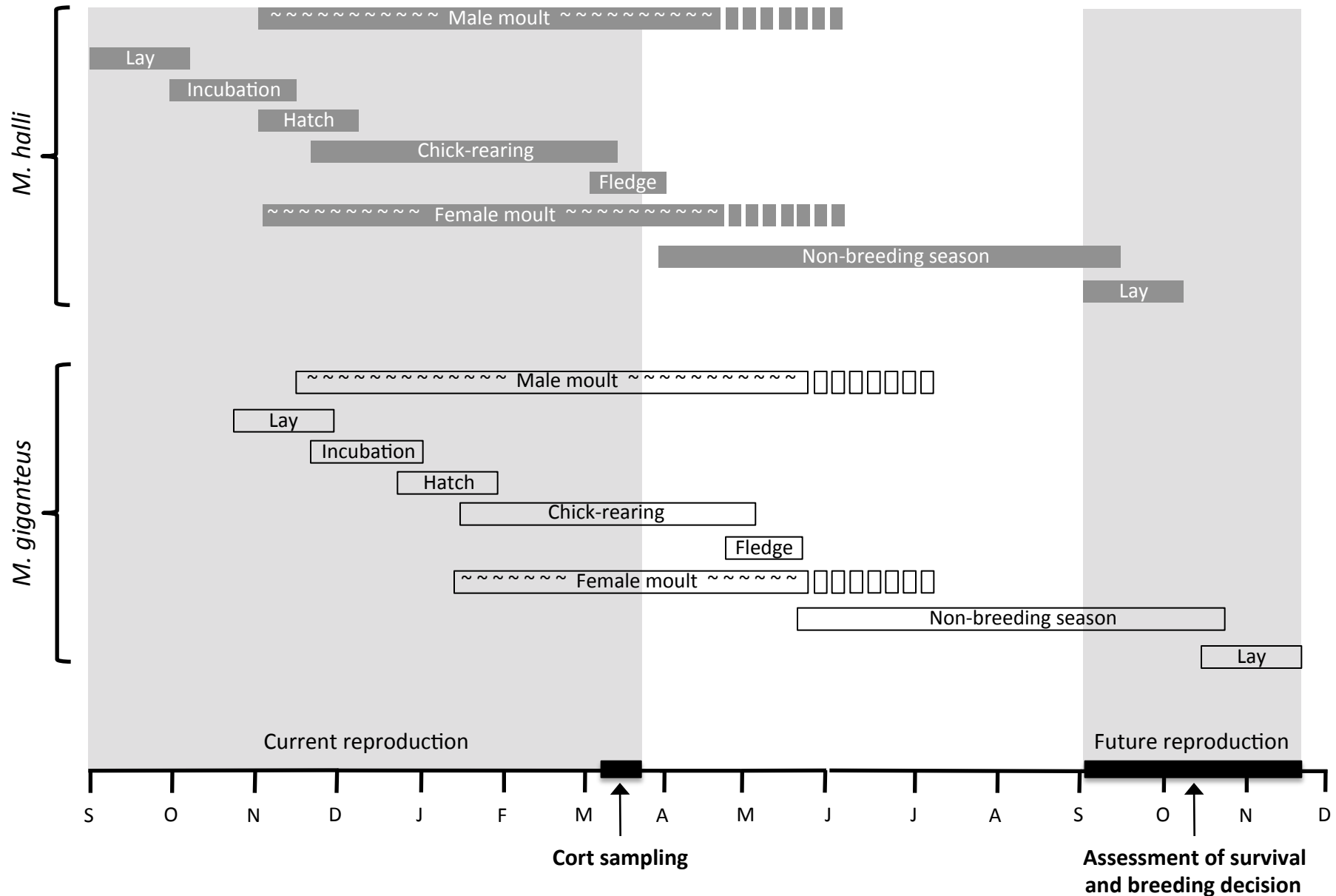


Fig. 1

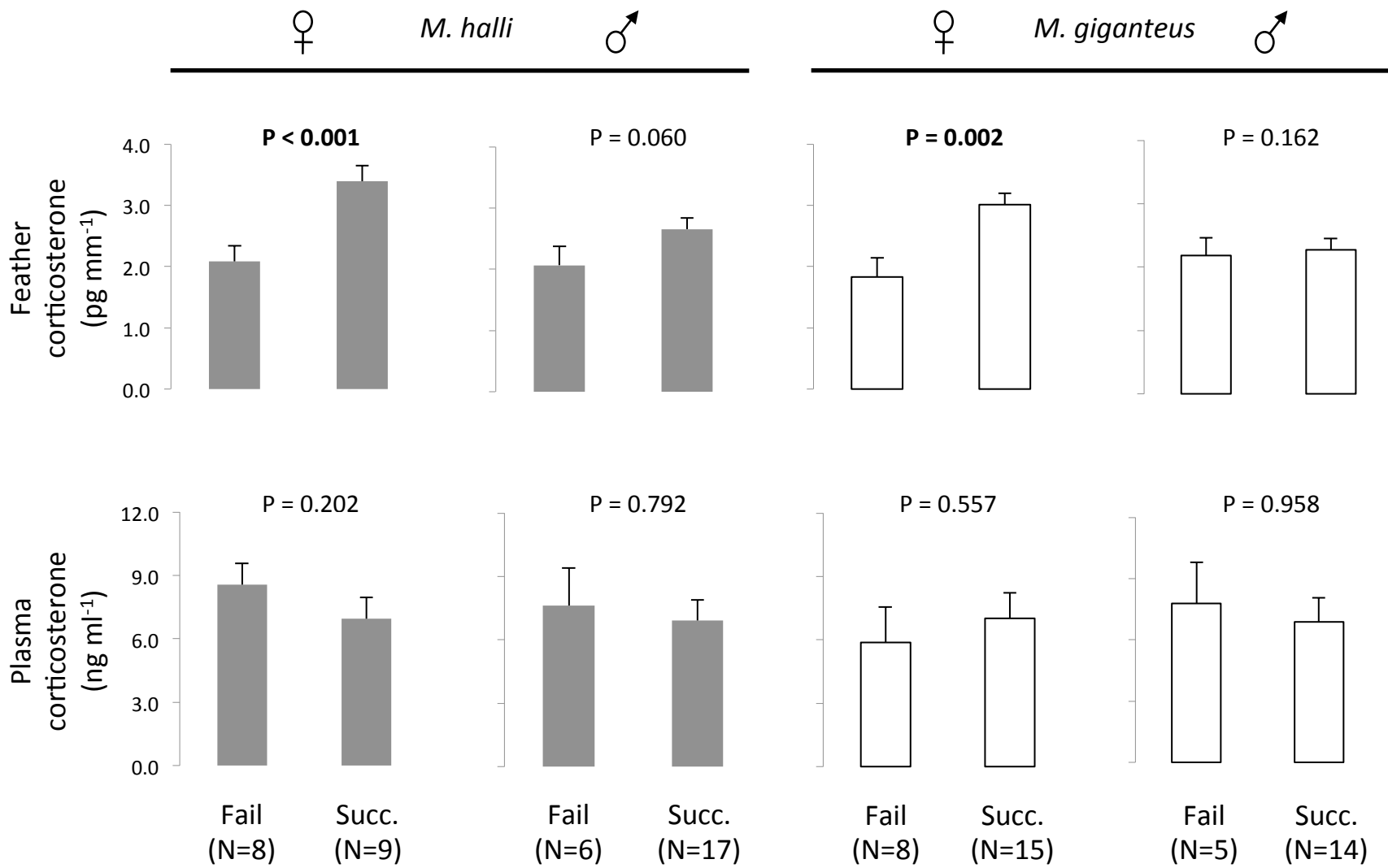


Fig. 2

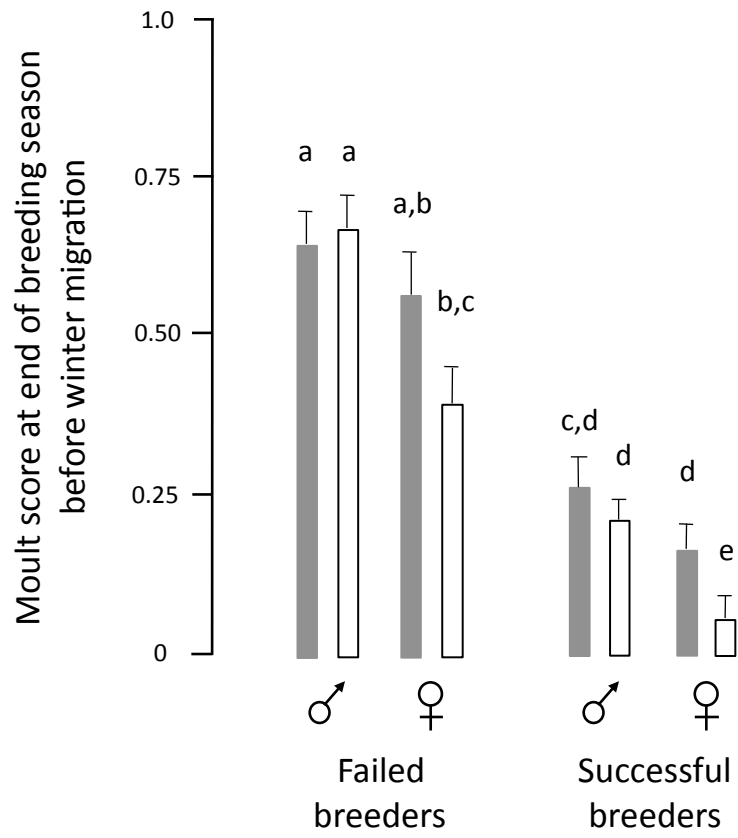


Fig. 3

HIGHLIGHTS

G.T. Crossin, R.A. Phillips, C.R. Lattin, L.M. Romero, T.D. Williams,

Corticosterone mediated costs of reproduction link current to future breeding.

For General & Comparative Endocrinology

- Cort in feathers grown while breeding reflect reproductive effort by giant petrels
- fCort was 1.5 times higher successful versus failed female breeders
- There were no differences in fCort between successful and failed male breeders
- We attribute these sex-differences to known differences in foraging ecology
- High fCort at breeding and slow moult predicted future breeding effort in females