

1 Feather Corticosterone of a Nestling Seabird Reveals Consequences of Sex-specific
2 Parental Investment

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16 Running headline: Parental investment and feather corticosterone

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24 SUMMARY

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26 Offspring of long-lived species should face costs of parental trade-offs that vary
27 with overall energetic demands encountered by parents during breeding. If sex
28 differences exist in how parents make the trade-off, sex-specific differences may exist in
29 the contribution of each parent to those costs. Adaptations of offspring facing such costs
30 are not well understood, but the hormone corticosterone likely plays a role. We
31 manipulated breeding effort in Cory's shearwaters (*Calonectris diomedea*) to increase
32 costs to offspring and used an integrated measure of corticosterone from chick feathers to
33 investigate how experimental variation in parental investment influences offspring
34 physiology. Average foraging trip duration and foraging efficiency of breeding pairs were
35 not related to chick corticosterone, but sex biases in foraging efficiency were. Adult male
36 investment was more strongly related to chick corticosterone than was female investment.
37 Importantly, we show for the first time suppression of adrenocortical activity in nestling
38 Procellariiform seabirds, and explain how our results indicate an adaptive mechanism
39 invoked by chicks facing increased costs of parental trade-offs.

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41 Keywords: Cory's shearwater, feather corticosterone, life history trade-offs, parental
42 investment, reactive scope, stress physiology

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47 INTRODUCTION

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49 The trade-off between current reproductive effort and future survival and
50 reproduction has been the subject of considerable research in life-history evolution
51 {Stearns, 1992 #549}. Adults of long-lived species, such as many seabirds, are expected
52 to favour their own condition over that of their young when faced with adverse
53 circumstances during the breeding season {Williams, 1966 #550; Stearns, 1992 #549;
54 Erikstad, 1998 #528}, and offspring may therefore face costs of this parental trade-off.
55 Although most studies on seabirds support this assertion {Mauck, 1995 #594;
56 Weimerskirch, 1995 #645; Weimerskirch, 1999 #593; Navarro, 2007 #512}, sex
57 differences may exist in the extent to which males and females make the trade-off. Such
58 differences are likely due to aspects of parental investment that differ between the sexes
59 {Velando, 2003 #646}. Male and female adult seabirds can differ in foraging strategies
60 {González-Solís, 2000 #604; González-Solís, 2000 #603; Lewis, 2002 #602} ability to
61 recover body condition {González-Solís, 2000 #604}, sensitivity to chick begging
62 {Quillfeldt, 2004 #590}, and contributions to nestling diet {Weimerskirch, 1997 #648;
63 González-Solís, 2000 #604; Gray, 2001 #595; Hamer, 2006 #607; Peck, 2006 #480;
64 Elliott, 2010 #600}. Thus, while costs experienced by chicks are expected to vary with
65 overall energetic demands encountered by parents, there may also be sex-specific
66 differences in the contribution of each parent to those costs. This may be especially true
67 when one sex is not willing or able to compensate for the other, such as during times of
68 poor food availability when parents prioritize their own condition.

69 Relatively little attention has been paid to the adaptations of offspring facing costs
70 of adverse parental decisions and how they may contribute to overall life-history
71 strategies. One important mechanism for coping with environmental perturbations in
72 general is activation of the vertebrate hypothalamic-pituitary-adrenal (HPA) axis in
73 response to unpredictable noxious stimuli (i.e., “stressors”; {Romero, 2004 #21}). The
74 HPA axis helps vertebrates regulate energy levels through secretion of glucocorticoid
75 (GC) hormones such as corticosterone (CORT), the primary avian GC. Nutritional
76 challenges are known stressors characteristic of intermittent feeding of seabird chicks
77 {Kitaysky, 1999; Wingfield et al. 1999; Kitaysky, 2001, Wingfield et al. 2001a}, and the
78 frequency of feeding, and quality and quantity of food delivered to chicks, can influence
79 the severity of the challenge {Kitaysky, 2005, Piatt 2005; Kitaysky, 2006, Piatt 2006}.

80 Interspecific variation exists in how nestling seabirds respond with CORT to
81 reductions in caloric intake and nutritional quality {Kitaysky, 2003 #54}. Some species
82 increase baseline or acute stress-induced CORT secretion to promote catabolism of fat
83 stores for increased energy availability, and to facilitate begging that encourages
84 increased parental provisioning {Kitaysky, 1999 #16; Kitaysky, 2001 #121; Kitaysky,
85 2003 #54; Harding, 2009 #545}. In doing so they risk reduced growth rate and immune
86 response, depletion of lipid reserves, protein catabolism, and impaired cognition as a
87 result of prolonged CORT secretion {Kitaysky, 1999 #15; Kitaysky, 2001 #121;
88 Kitaysky, 2003 #54; Saino, 2003, Martinelli 2003; Apanius, 1998 #513; Sapolsky, 2000
89 #24; Romero, 2004 #21}. In other species, nestlings respond to nutritional challenges by
90 modulating activity of the HPA axis to suppress one or more parameters of the CORT
91 response. This has been observed as a reduction in baseline or acute stress-induced levels

92 {Kitaysky, 2005 #109}, and also as a “muting” of the response, i.e., an increase or
93 stability in baseline with no change in stress-induced {Sears, 2008 #546}. It has been
94 proposed that this CORT suppression strategy leads to a disassociation of the nutritional
95 state of the chick and its HPA axis {Kitaysky, 2005 #109}. Thus, although this strategy
96 comes at a cost of a slowed growth rate, it avoids the deleterious effects of sustained
97 elevated CORT and allows chicks to maintain protein and fat stores {Kitaysky, 2005
98 #109}. Why variation in CORT responses to dietary restrictions exists is not well
99 understood {Kitaysky, 2003 #54}; however, it is apparent that CORT physiology plays a
100 crucial role and therefore may underlie an adaptive mechanism to cope with costs of
101 parental trade-offs {Ricklefs, 2002 #312}.

102 A previous study of Cory’s shearwaters (*Calonectris diomedea*) by Navarro and
103 González-Solís found that when one member of a breeding pair was experimentally
104 handicapped via increase of flying costs (i.e., breeding effort) it decreased its parental
105 investment and passed along the cost partly to its partner, but the cost was most strongly
106 experienced by the offspring {Navarro, 2007 #512}. Handicapped adults increased the
107 duration and distance of foraging trips resulting in longer incubation stints for their
108 partners and less food provisioned to chicks. In turn, chicks raised by handicapped pairs
109 were smaller, lighter, and had a lower cell-mediated immune response, and the authors
110 suggested that poor provisioning was responsible for these effects {Navarro, 2007 #512}.

111 Although foraging trip length did not differ significantly between the sexes, total mass
112 gained while foraging was greater in males than in females {Navarro, 2007 #512}.

113 Here, we suggest that nestling CORT responses to parental trade-offs can explain
114 the effects seen in chicks from the 2007 Navarro and González-Solís paper {Navarro,

115 2007 #512}, and we use an integrated measure of CORT physiology {Bortolotti, 2008
116 #393; Bortolotti, 2009 #517} from chick feathers collected during their experiment to
117 explore this possibility. Feather CORT values incorporate the amplitude and duration of
118 all CORT secretion, including response to stressors, during the period of feather growth
119 {Bortolotti, 2008 #393; Bortolotti, 2009 #517} and thus represent a biologically relevant
120 measure of CORT secretion {Romero, 2004 #21}. We hypothesize that variation in
121 parental investment was experienced by nestlings as variation in a nutritional stressor to
122 which the nestling HPA axis should be sensitive. Furthermore, sex differences in how
123 adults traded off provisioning their young in favour of their own condition should be
124 evident in the strength of relationships between offspring CORT and each of its parents'
125 investment.

126 We tested the following three predictions. First, nestling CORT should be related
127 to variation in duration of foraging trips and foraging efficiency of parents (i.e., rate of
128 mass gained at sea; see below) because these are measures of parental effort that vary
129 with increasing costs to parents {Navarro, 2007 #512; Navarro, 2009 #526}. In our
130 population, foraging costs increase with increasing trip length {Navarro, 2007 #512} and,
131 at least in other populations, longer trips result in less food being delivered per day to
132 shearwater chicks {Granadeiro, 1998 #649}. Individual differences in foraging efficiency
133 contribute to rules governing how parents allocate energy between themselves and their
134 offspring {Weimerskirch, 2003 #630} and thus influence the costs experienced by chicks.
135 Second, nestling CORT should be differentially sensitive to male and female foraging
136 efficiency, but not foraging trip duration, because the sexes differ in total mass gained at
137 sea but not in duration of foraging trips {Navarro, 2007 #512}. Third, nestling CORT

138 should be suppressed relative to controls when adult foraging costs are increased by
139 handicapping. Suppressed HPA activity is expected to occur in nestlings of species with
140 intermittent feeding, a prolonged nestling period to compensate for slow growth rate, and
141 parents that are relatively insensitive to offspring demands {Kitaysky, 2003 #54;
142 Kitaysky, 2005 #109}, and Cory's shearwaters exhibit all these characteristics {Zino,
143 1987 #544; Warham, 1990 #543; Navarro, 2007 #512}. Our study's methodological
144 perspective adds to a limited number of investigations into physiological adaptations of
145 nestlings to parental reductions in food provisioning.

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147 METHODS

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149 (a) *Study area and field methods*

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151 For more detailed information on field methods see {Navarro, 2007 #512}.

152 Briefly, the study was conducted on Gran Canaria (15°47'18''N; 27°50'41''E, Canary
153 Islands, Spain), from April to November 2004 at a breeding colony of about 150 pairs of
154 Cory's shearwaters. Breeding pairs were randomly assigned to the control (n=14) or
155 experimental group (n=28) and once the female had laid her egg, one adult from every
156 pair (50:50 male:female) in the experimental group was handicapped by clipping the tips
157 of every primary feather to increase flying costs by 5% {Navarro, 2007 #512;
158 Pennycuick, 1989 #819}. Thus, pairs from the experimental group included one
159 handicapped bird and its unmanipulated partner. Additionally, during incubation, 19
160 control and 19 handicapped adults were instrumented with a 10-g geolocator (GLS units,

161 British Antarctic Survey, Cambridge, United Kingdom) to measure foraging trip duration
162 and foraging locations. GLS units have a photoreceptor that measures light levels every
163 60 s, and they record the maximum reading within each 10-min interval with reference to
164 an internal clock-calendar. Sunset and sunrise times were estimated from thresholds in
165 light curves; latitude was derived from day duration and longitude from the time of local
166 midday with respect to Greenwich Mean Time and day of the year, providing 2 locations
167 day⁻¹ (one corresponding to midday and the other to midnight). The accuracy of the light-
168 level geolocation is relatively low (average error ~186 km). However, the aim of our
169 study was not a detailed description of the foraging trips, but a comparison of the
170 foraging behaviour between control and handicapped birds. Any position obtained in a
171 short period, as in the present study, is under the same accuracy error, and to avoid
172 potential selection biases of locations we applied a homogeneous filter based solely on a
173 velocity index (see {Navarro, 2007 #512} for more details). GLS units were 1/3 the mass
174 found to have an effect on shearwater flight performance {Passos, 2010 #608}, so
175 although we cannot rule out a possible influence in our study, we believe it to be
176 negligible and the effect balanced across treatment groups.

177 During incubation we studied the changes in mass in all birds by weighing all
178 birds every 3 days until foraging trip departure, and then again upon subsequent return.
179 Birds were weighed between 1000 and 1200 hrs using a large bag and Pesola spring
180 balances. For those birds that we weighed 2 or 3 days before departure, we estimated the
181 mass at departure using the last mass recorded and the proportional daily loss of mass for
182 the appropriate sex (mean daily mass loss: males=15.38 g/day, females=14.25 g/day;
183 calculated from incubating birds that were weighed more than once).

184 We sampled 28 80-day-old chicks: 10 reared by control and 18 by experimentally
185 handicapped pairs. Chicks were ringed and weighed and their culmen, tarsus, and wing
186 were measured with digital callipers to the nearest ± 0.1 mm. A single back feather was
187 taken from each chick and stored in a paper envelope for subsequent quantification of
188 CORT (see below). Based on exact dates of hatching, all chicks were of a comparable
189 age when feathers were collected. All feathers were fully grown when collected, began
190 growing when chicks were ~ 50 days old, and completed growth around 70 days of age.
191 Aside from changes resulting from handicapping {Navarro, 2007 #512}, adult feeding
192 behavior was normal throughout the feather growth period. Adults and chicks were sexed
193 using molecular procedures {Navarro, 2007 #512}. Based on observations, all chicks
194 fledged successfully and at approximately the same time.

195

196 (b) *Feather CORT analysis*

197

198 Feather CORT assays followed {Bortolotti, 2008 #393}. Briefly, we extracted
199 CORT from feathers using a methanol-based technique. The length of the feather was
200 measured, the calamus was removed and discarded, and then the sample was cut into
201 pieces $< 5 \text{ mm}^2$ with scissors. We then added 10 mL of methanol (HPLC grade, Fisher
202 Scientific, Fairlawn, New Jersey, USA) and placed the samples in a sonicating water bath
203 at room temperature for 30 min, followed by incubation at 50°C overnight in a shaking
204 water bath. The methanol was then separated from feather material by vacuum filtration,
205 using a plug of synthetic polyester fibre in the filtration funnel. The methanol extract was
206 placed in a 50°C water bath and subsequently evaporated in a fume hood. Extract

207 residues were reconstituted in a small volume of phosphate buffered saline (0.05M, pH
208 7.6) and frozen at -20° C until analyzed by radioimmunoassay (RIA). We assessed the
209 efficiency of the methanol extraction by including feather samples spiked with a small
210 amount (approximately 5000 CPM) of ^3H -corticosterone in the extraction. Greater than
211 92% of the radioactivity was recoverable in the reconstituted samples. For more
212 information about validation, see Supplementary Appendix S1 in {Bortolotti, 2008
213 #393}.

214 Feather CORT levels were determined by RIA {Wayland, 2002 #520}.
215 Measurements were performed on reconstituted methanol extracts, and samples were
216 measured in duplicate. Samples were measured in a single assay with an intra-assay
217 coefficient of variation of 8.7%. The assay had a detectability limit (80% bound) of 14.20
218 pg/assay tube, but all samples were well above this value. Data values are expressed as
219 pg CORT per mm of feather, which gives a valid estimate of CORT per unit time of
220 feather growth {Bortolotti, 2008 #393; Bortolotti, 2009 #517} (and see {Bortolotti, 2010
221 #650} for validation). CORT assays were performed at the University of Saskatchewan,
222 Canada.

223

224 (c) *Variable definitions and statistical analyses*

225

226 Total foraging trip duration (TD) and foraging efficiency (FE) were defined
227 according to {Navarro, 2007 #512}. TD is the total number of days between departure
228 from the nest for foraging and subsequent return. FE is the rate of daily mass gain while
229 foraging, calculated as total mass gained during foraging trip / trip duration. TD and FE

230 were calculated separately for 17 males (TD_{male} , FE_{male}) and 15 females (TD_{female} ,
231 FE_{female}). In nine control breeding pairs we recorded both TD and FE for both partners.
232 For these cases, we assessed the relative parental effort of breeding pairs by computing
233 average TD and FE values for both partners [i.e., $(\text{male}+\text{female})/2$; TD_{pair} and FE_{pair}], and
234 assessed potential sex bias in TD and FE by computing the difference between the
235 partners [i.e., $(\text{male}-\text{female})$; TD_{bias} and FE_{bias}].

236 Because Navarro & González-Solís only collected feathers from a subset of
237 chicks in their 2007 paper {Navarro, 2007 #512}, we wanted to confirm that our subset
238 of TD and FE values were not affected by a subsampling bias. We therefore used separate
239 models with TD and FE as the response variable, adult sex and treatment as fixed factors,
240 and included a sex \times treatment interaction term. We also tested for a chick sex difference
241 in feather CORT, as well as a possible interaction between sex and treatment, using sex
242 and treatment as fixed factors and a sex \times treatment interaction term.

243 To determine the influence of within-pair variation in parental investment on
244 chick CORT, we modeled TD_{pair} , FE_{pair} , TD_{bias} , and FE_{bias} individually as fixed factors in
245 four separate models. To further confirm which sex's behaviour had the greater influence
246 on chick CORT, we used the same pairs but modeled TD_{male} and TD_{female} as separate
247 terms in the same model, rather than as within-pair averages or biases, and repeated this
248 approach for FE.

249 To address the relationships between parental handicapping, TD and FE, and
250 feather CORT, we expanded our sample size by considering all cases where we had TD
251 and FE for at least one member of a breeding pair and feather CORT data for the chick.
252 We used CORT as the response variable in two separate models and included treatment,

253 adult sex, behaviour (TD or FE), and a behaviour \times sex interaction term as fixed factors.
254 Non-significant interaction terms were removed from final models. All models used a
255 normal distribution of errors and an identity link function. Data were analyzed using
256 PROC GENMOD in SAS v. 9.1 (SAS Institute, Cary, NC).

257

258 RESULTS

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260 As in the 2007 paper by Navarro & González-Solís {Navarro, 2007 #512},
261 duration of adult foraging trips did not differ between the sexes for control breeding pairs
262 ($F_{1,16} = 2.64, P = 0.12$), but we detected a non-significant trend for trip durations of
263 experimentally handicapped females to be longer than those of males ($F_{1,13} = 4.17, P >$
264 0.06). We acknowledge this as a potential subsampling bias because the original study
265 did not find a difference between sexes in its larger sample of experimental adults
266 {Navarro, 2007 #512}, but combined the sexes for all subsequent analyses. A single
267 CORT value was three standard deviations greater than the mean, suggesting an
268 analytical error or an individual out of the norm for our population (e.g., an ill bird);
269 therefore this value was excluded from analyses. There was no significant interaction
270 between chick sex and treatment on CORT ($F_{1,23} = 3.13, P = 0.09$), and CORT did not
271 differ between chick sexes ($F_{1,23} = 1.89, P = 0.18$), so they were combined for subsequent
272 analyses.

273 We found no significant relationship between CORT and TD_{pair} (Fig. 1; $F_{1,7} =$
274 $1.34, P = 0.28$) or FE_{pair} ($F_{1,7} = 0.13, P = 0.73$). However, when we examined the
275 relationships between TD_{bias} and FE_{bias} and CORT, we found a non-significant effect of

276 TD_{bias} (Fig. 1; $F_{1,7} = 4.64$, $P = 0.07$) but a significant effect of FE_{bias} ($F_{1,7} = 8.12$, $P <$
277 0.03). This implies that within control breeding pairs as TD_{male} increased relative to
278 TD_{female} chicks expressed relatively higher CORT levels, albeit not significantly; and as
279 FE_{male} increased relative to FE_{female} , chicks expressed relatively lower CORT. This sex
280 effect was further evident in control pairs when we included FE_{male} and FE_{female} as
281 separate terms in the same model, because the former was significantly related to CORT
282 ($F_{1,6} = 10.65$, $P < 0.02$) whereas the latter was not ($F_{1,6} = 2.86$, $P = 0.14$). A similar
283 model for TD showed that neither TD_{male} nor TD_{female} was significantly related to CORT
284 (TD_{male} : $F_{1,6} = 4.01$, $P = 0.09$; TD_{female} : $F_{1,6} = 0.58$, $P = 0.48$), but the trends were in the
285 same direction as the FE models.

286 When we expanded our sample to include all cases where TD and FE were
287 measured for at least one pair member, overall experimental chicks had significantly
288 lower feather CORT than control chicks (Fig. 2; experimental = 4.45 ± 0.83 pg/mm,
289 control = 5.46 ± 1.61 pg/mm, $F_{1,23} = 7.08$, $P = 0.01$). Our model of TD and chick CORT
290 had a significant interaction between TD and adult sex ($F_{1,27} = 5.12$, $P = 0.03$), so we ran
291 separate models for each sex (Table 1). The final model for adult males revealed a
292 significant positive relationship between TD_{male} and CORT (Table 1) and experimental
293 chicks had significantly lower CORT than controls. The final model for adult females
294 revealed no significant relationship between TD_{female} and CORT (Table 1) and
295 experimental chicks did not differ significantly from controls.

296 We found a significant interaction between FE and adult sex ($F_{1,27} = 5.56$, $P <$
297 0.03), so we analyzed the sexes separately (Table 1). The interaction between FE_{male} and
298 treatment on CORT was significant, so we modeled each treatment separately for males

299 (Table 1). FE_{male} was negatively related to CORT in control chicks (Table 1, Fig. 3) but
300 was not related to CORT in experimental chicks. The interaction between FE_{female} and
301 treatment on CORT was not significant (Table 1), and the final model for adult females
302 revealed that FE_{female} was not significantly related to CORT (Table 1, Fig. 3) and did not
303 differ between control and experimental chicks.

304

305 DISCUSSION

306

307 Our study provides two conceptual advances in the understanding of life history
308 trade-offs: (1) we highlight the importance of sex-biased investment to offspring
309 physiology and show that adult male shearwaters play an important role in offspring
310 energy balance, and (2) we provide experimental evidence that free-living Procellariid
311 chicks can suppress CORT secretion as an adaptive response to cope with increased costs
312 of parental trade-offs. This result indicates flexibility in nestling physiology during
313 growth to better match nestling energetic need to parental provisioning.

314 Costs are expected to arise in chicks when parents favour self maintenance over
315 provisioning their offspring, and our study suggests that sex differences in how parents
316 resolve this trade-off differentially affects offspring CORT. In accordance with previous
317 studies {Navarro, 2007 #512; Kitaysky, 1999 #16; Kitaysky, 2005 #109; Kitaysky, 2001
318 #121; Sears, 2008 #546; Harding, 2009 #545}, it is likely that an overall caloric
319 restriction was the cost of adult trade-offs to which chick CORT was responding.

320 Responses were related to within-pair sex biases in how parents contributed to that cost.

321 Specifically, variation in male effort was more influential than variation in female effort.

322 Sex differences in parental investment in our study may have been due to
323 differences in the extent to which the sexes were willing to increase provisioning in
324 response to chick need {Ottosson, 1997 #644; Weimerskirch, 1997 #647}. Cory's
325 shearwaters exhibit fixed investment in reproduction and are predicted to not increase
326 their effort as chick demands increase {Navarro, 2007 #512}. However, some male
327 Procellariiform seabirds may be even less likely than females to increase effort. For
328 example, female Manx shearwaters (*Puffinus puffinus*) responded to chick begging by
329 adjusting meal size, whereas males did not {Quillfeldt, 2004 #590}. Additionally, during
330 poor food years female Wilson's storm petrels (*Oceanites oceanicus*) make longer
331 foraging trips than do males, and this may be due to greater responsiveness to chick need
332 by females than males {Gladbach, #747}. In cases where costs of the trade-off between
333 self maintenance and offspring provisioning is greater in males than in females, variation
334 in male investment could have a greater impact on chick physiology.

335 Importantly, we provide experimental evidence that shearwater chicks suppressed
336 CORT secretion when faced with extended nutritional challenges. Chick CORT was most
337 strongly related to male foraging efficiency (FE), which is a measure of parental effort
338 that incorporates duration of foraging trips, individual quality, and foraging decisions
339 {Weimerskirch 2003}. Not surprisingly, our results indicate that increased investment by
340 control males reduced costs in their chicks. However, when we considered
341 experimentally handicapped males, the CORT of their chicks showed no relationship
342 with FE. This suggests that increased costs of trade-offs from handicapped males resulted
343 in a relative insensitivity of the physiology of their chicks. Moreover, CORT was overall
344 significantly lower in chicks raised by experimental parents compared to controls. We

345 interpret these results as confirmation of our prediction that shearwater chicks suppress
346 CORT secretion when adult foraging costs are experimentally increased.

347 Is lower CORT in experimental chicks a result of an adaptive response, or simply
348 an expression of poor physiological functioning of birds with extended nutritional
349 deficits? It is possible that the nutritional condition of experimental chicks was such that
350 they were only able to mount a poor CORT response following nutritional challenges, or
351 they were developmentally delayed and incapable of mounting a better response.
352 However, it is unlikely that chicks expressing such comprised physiology would be able
353 to survive to fledging without indicators of lipid or protein reserves, or muscle damage
354 being affected {Smith, 2009 #522}. Yet, in their 2007 paper Navarro and González-Solís
355 found that levels of biochemical parameters related to lipid and protein reserves and
356 muscle damage were similar between control and experimental chicks {Navarro, 2007
357 #512}, and all chicks fledged at the same time (± 3 days). These evidences suggest that
358 the physiology of experimental chicks was operating within normal limits. Thus, we lack
359 the evidence to support a conclusion that experimental chicks were physiologically
360 impaired.

361 To the contrary, we reason that experimental chicks were within their
362 physiological ability to handle periods of nutritional deficit. CORT suppression was
363 therefore likely an adaptive response to cope with the increased costs of parental trade-
364 offs. We argue that cumulative costs of parental trade-offs in experimental chicks reached
365 a tipping point and CORT suppression allowed these birds to minimize the extent of
366 physiological damage caused by chronically elevated CORT {Kitaysky, 1999 #16;
367 Kitaysky, 1999 #15; Kitaysky, 2001 #392; Kitaysky, 2003 #54; Sapolsky, 2000 #24;

368 Romero, 2004 #21}. Experimental chicks paid for this because they were smaller, lighter,
369 and had reduced immune response {Navarro 2007}. Yet, these were not life-threatening
370 energy deficits because the prolonged period of shearwater nestling growth would allow
371 for compensatory growth {Kitaysky, 2003 #54; Kitaysky, 2005 #109; Zino, 1987 #544;
372 Warham, 1990 #543; Navarro, 2007 #512} and survival to fledging did not differ
373 between treatment groups {Navarro 2007}. CORT suppression need not entail a complete
374 alteration of the functioning of the HPA axis, as evidence from other species indicates
375 that even the most food-restricted individuals exhibiting CORT suppression are still able
376 to respond to stressors {Kitaysky, 2005 #109; Sears, 2008 #546}.

377 Understanding how and why individuals manage their exposure to CORT during
378 critical periods of post-natal development is important because CORT can affect nestling
379 phenotype {Butler, 2010 #651; Kitaysky, 2003 #54; Spencer, 2003 #340; Sockman, 2001
380 #533; Spencer, 2009 #535}; {Dufty, 2002 #138} and potentially fitness ({Blas, 2007
381 #350}; for reviews see {Breuner, 2008 #615; Bonier, 2009 #502}). Moreover, timing of
382 CORT exposure during development is important {Dufty, 2002 #138}. In our study,
383 handicapping of adults occurred at the onset of egg-laying and therefore increased costs
384 were experienced by nestlings throughout their post-natal development. Whether
385 shearwater nestlings would suppress CORT in response to less severe or shorter-term
386 increases in costs remains to be determined. Future investigations should focus on
387 identifying the ecological circumstances that promote a CORT suppression strategy and
388 must consider phylogeny, mode of nestling development (see {Adams, 2008 #487}), and
389 the type of nutritional challenge facing nestlings (i.e., feeding frequency, diet quality
390 and/or quantity).

391

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402 suggestions on the manuscript.

403

404 REFERENCES

405

406 TABLE AND FIGURE CAPTIONS

407

408 **Figure 1:** Relationships between measures of parental investment in Cory's Shearwater
409 breeding pairs and their nestling's feather corticosterone (CORT): (a) average duration of
410 foraging trips (TD_{pair}) and (b) average foraging efficiency (FE_{pair}). The within-pair
411 difference between males and females in (c) duration of foraging trips (TD_{bias}) and (d)
412 foraging efficiency (FE_{bias}); values greater than zero indicate male bias and values less

413 than zero indicate female bias. Data presented are for control pairs only. See text for
414 variable definitions.

415

416 **Figure 2:** Mean (\pm SE) feather corticosterone (CORT) values of Cory's shearwater
417 chicks raised by experimentally handicapped adults (Experimental; n=17) and non-
418 handicapped control adults (Control; n=10).

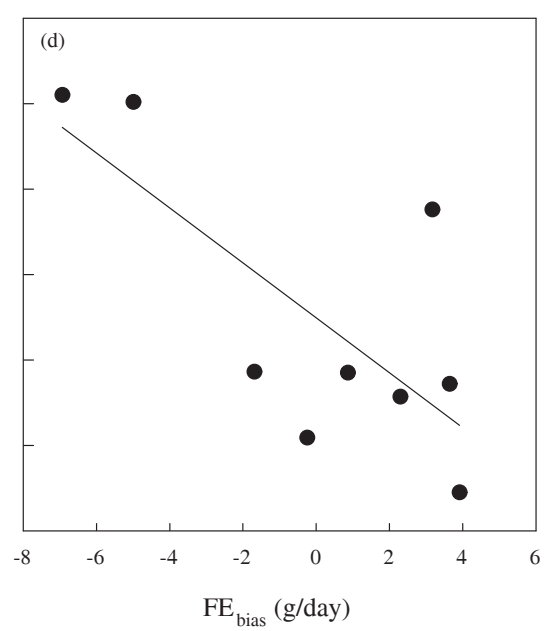
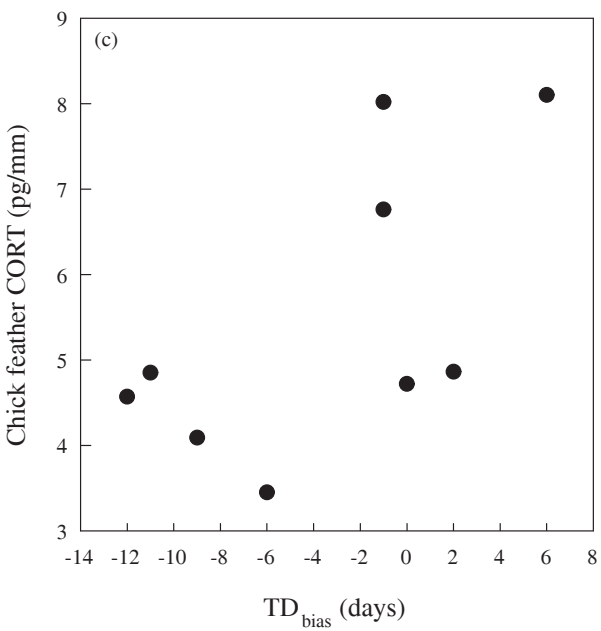
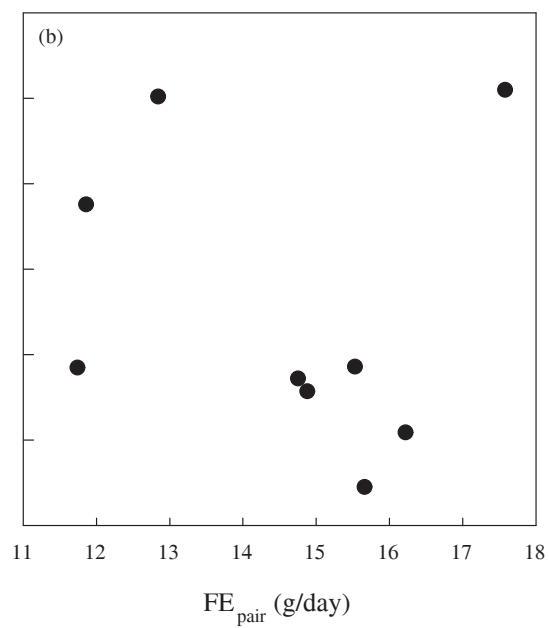
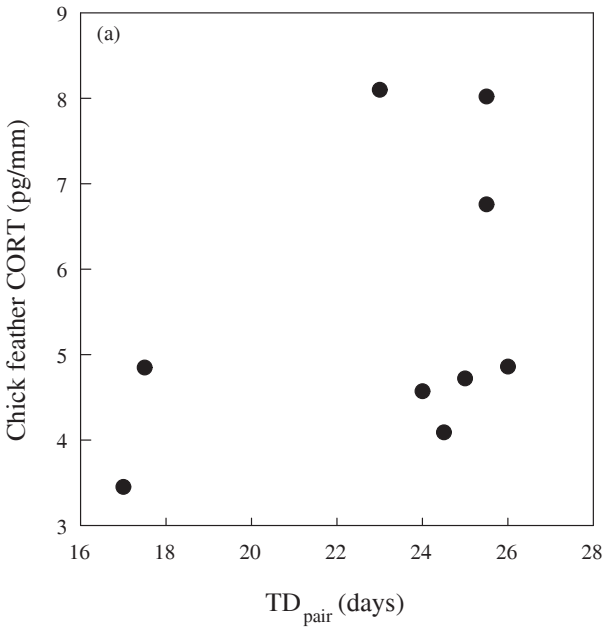
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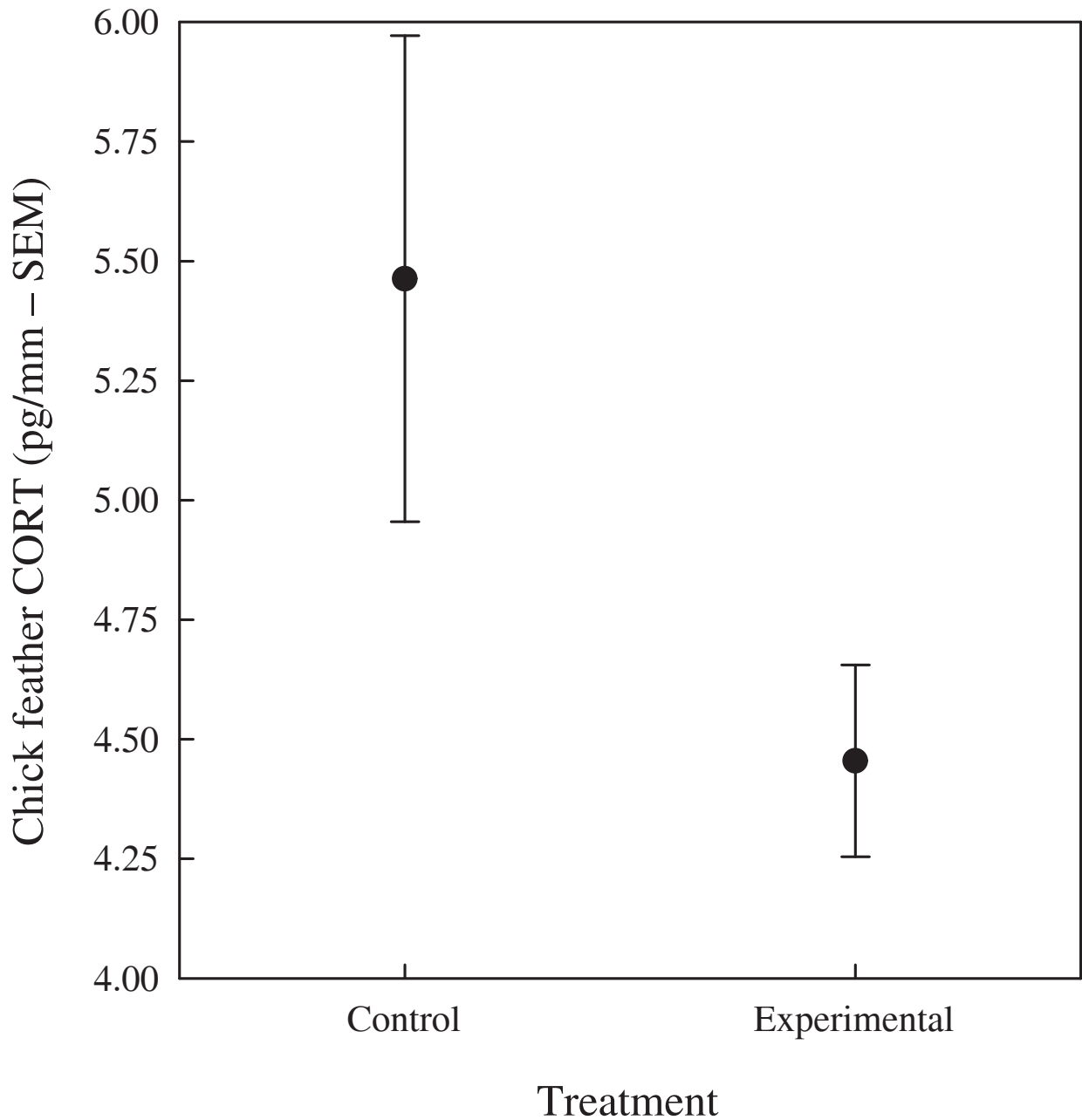
420 **Table 1:** Summary of results from GENMOD models testing for the influence of
421 experimental handicapping of parents, sex differences in parental foraging trip duration
422 (TD) and foraging efficiency (FE), and their interaction on feather corticosterone (CORT)
423 in Cory's shearwater chicks. Significant values are in bold.

424

425 **Figure 3:** Relationships between foraging efficiency (FE) of control (filled circles, solid
426 lines) and experimentally handicapped (open circles, dash lines) (a) male and (b) female
427 adult Cory's shearwaters and the feather corticosterone (CORT) of their chick.

428





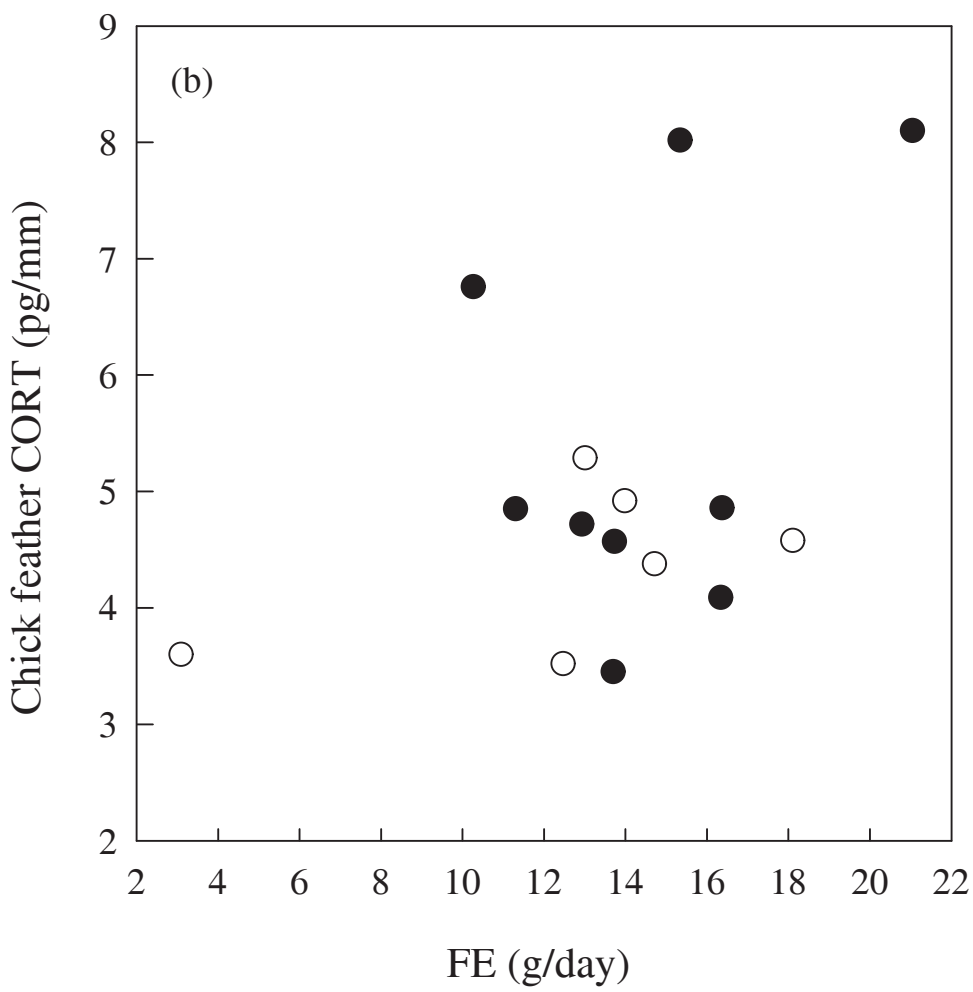
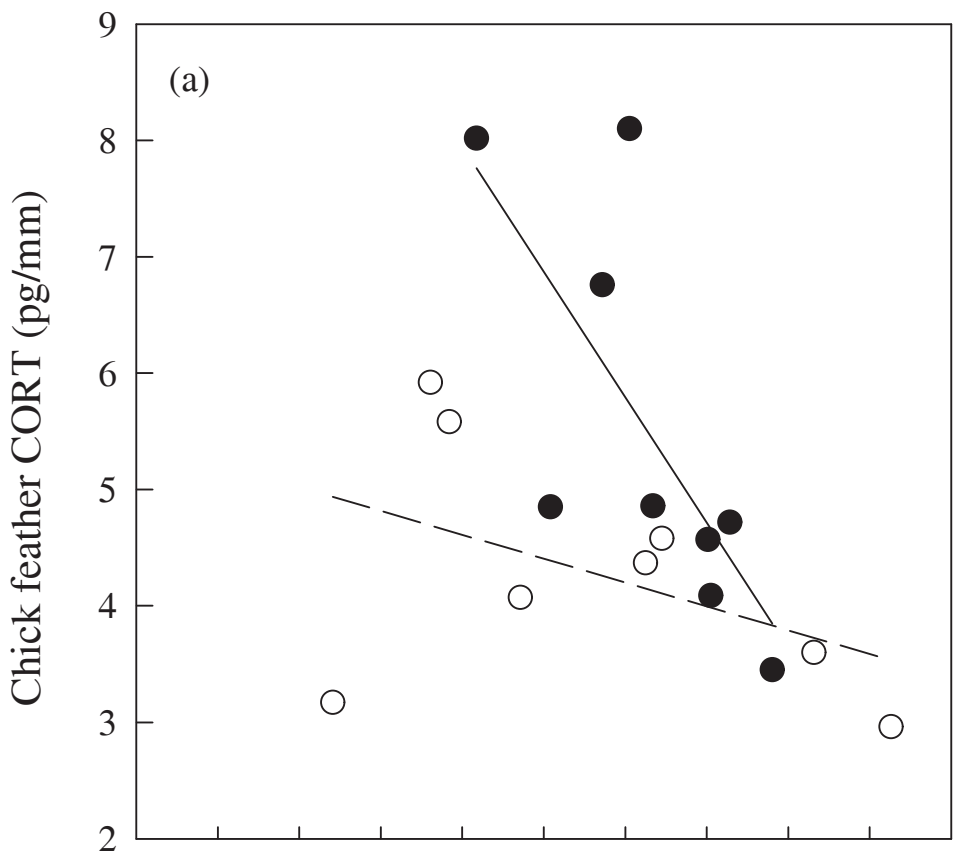


Table 1. Summary of results from GENMOD models testing for the influence of experimental handicapping of parents, sex differences in parental foraging trip duration (TD) and foraging efficiency (FE), and their interaction on feather corticosterone in Cory's shearwater chicks. Significant values are in bold.

	Model term	estimate	standard error	<i>F</i> -statistic (df)	<i>p</i> -value
Males	Treatment	1.6053	0.6070	6.99 (1,14)	0.019
	TD	0.1825	0.0680	7.21 (1,14)	0.018
	TD × Treatment			0.00 (1,13)	0.972
Females	Treatment	0.8274	0.7968	1.08 (1,12)	0.320
	TD	-0.0958	0.0982	0.95 (1,12)	0.349
	TD × Treatment			0.02 (1,11)	0.903
Males	Control	-0.5393	0.1895	8.10 (1,7)	0.025
	Experimental	-0.1025	0.0809	1.60 (1,6)	0.252
	FE × Treatment			4.91 (1,13)	0.045
Females	Treatment	0.8673	0.7479	1.34 (1,12)	0.269
	FE	0.1213	0.0949	1.64 (1,12)	0.225
	FE × Treatment			0.33 (1,11)	0.580