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3

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25

26 **Abstract**

27 According to the cort-fitness hypothesis, glucocorticoid levels correlate negatively with  
28 fitness. However, field studies found mixed support for this hypothesis, potentially  
29 because the association between glucocorticoids and fitness might depend on prevailing  
30 environmental conditions. Based on the long-term monitoring of a natural rodent  
31 population, we tested whether individuals with elevated corticosterone levels were more  
32 likely to disappear, accounting for individual condition and among-year variation in food  
33 availability, population density and predation pressure. We used basal corticosterone  
34 levels measured at the onset of the pre-breeding season in 331 African striped mice from  
35 six generations. While basal corticosterone levels were highly repeatable within  
36 individuals, between-individual variation was large. Survival analysis revealed that  
37 disappearance risk over the pre-breeding season increased with elevated basal  
38 corticosterone levels for light but not for heavy individuals. High levels of corticosterone  
39 may be more deleterious to smaller individuals (i.e. through allostatic overload),  
40 eventually increasing their mortality risk, and disappearance would represent actual  
41 death. An alternative non-exclusive explanation could be that high levels of  
42 corticosterone selectively trigger dispersal in light individuals, and disappearance would  
43 rather reflect their departure from the population. Although environmental conditions  
44 varied considerably among generations, none of the interactions between corticosterone  
45 and environmental variables were significant. Disappearance probability was positively  
46 correlated with both predation pressure and food availability, a factor favoring dispersal.  
47 In sum, elevated basal corticosterone levels increased disappearance in light striped mice,  
48 either directly via reduced survival prospects and/or indirectly via dispersal.

49

50 **Keywords:** basal corticosterone level; body mass; cort-fitness hypothesis; disappearance;  
51 dispersal; environmental challenge; food availability; survival

52

## 53 **Introduction**

54 Adaptive physiological change in response to challenging periods of energy limitation is  
55 crucial to enhance survival probability. Organisms need to constantly adjust to both  
56 predictable and unpredictable changes in their environment (i.e. allostasis; McEwen and  
57 Wingfield, 2010; Romero et al., 2009; Wingfield, 2005). Among physiological processes,  
58 endocrine control mechanisms mediate the relationship of the organism to its  
59 environment (Ricklefs and Wikelski, 2002). They integrate both external cues and  
60 internal condition to release hormones that regulate many aspects of the phenotype (Zera  
61 et al., 2007). Hormones enable individuals to respond to changes in their environment  
62 through modifications of metabolism, osmoregulation, reproductive status and social  
63 behaviour (Wingfield, 2009). Such environmental changes include short-term stressors  
64 (e.g. inclement weather) or seasonal food shortage (McEwen and Wingfield, 2010). Thus,  
65 hormone secretion varies as an adaptive response to environmental stimuli, and endocrine  
66 response is expected to increase individual fitness (Hau et al., 2016; Wikelski and  
67 Ricklefs, 2001).

68         Glucocorticoids are important mediators of physiological adjustment as they  
69 regulate energy balance (Sapolsky et al., 2000), hence promoting allostasis, which is the  
70 physiological stability through change of specific mediators (McEwen and Wingfield,  
71 2003). Corticosterone, the main glucocorticoid hormone in most vertebrates, regulates  
72 metabolic processes to support energetically demanding activities (basal levels), as well  
73 as to overcome environmental challenges (stress-induced levels). Thus, the corticosterone  
74 regulatory network offers an efficient mechanism to deal with variation in energy  
75 requirements and periods of reduced resource availability (Reeder and Kramer, 2005;  
76 Romero et al., 2009). However, even though the adaptive value of the glucocorticoid  
77 stress response has been acknowledged (Boonstra, 2013; McEwen and Wingfield, 2003;  
78 Romero et al., 2009), elevated corticosterone levels have often been regarded as  
79 detrimental (Reeder and Kramer, 2005). According to the cort-fitness hypothesis, which  
80 predicts that baseline corticosterone correlates negatively with fitness (Bonier et al.,  
81 2010, 2009), elevated corticosterone levels would reflect individuals of poor condition  
82 with reduced survival prospects and/or reproductive success (Angelier et al., 2010;  
83 Bonier et al., 2009; Henderson et al., 2017).

84 Many field studies have investigated fitness correlates of glucocorticoid levels,  
85 but several reviews report no general trend (Bonier et al., 2009; Crespi et al., 2013; Hau  
86 et al., 2016). Instead, variation in basal glucocorticoid levels was sometimes negatively  
87 (Bonier et al., 2007), positively (Cyr and Romero, 2007; Lancaster et al., 2008), or not at  
88 all correlated with reproductive success (Magee et al., 2006). For instance in a population  
89 of great tits (*Parus major*) in Germany, high glucocorticoid levels at the beginning of the  
90 breeding season were associated with a large number of fledglings while such levels were  
91 associated with a low number of fledglings later in the season (Ouyang et al., 2013).  
92 Similarly, survival rates were either negatively related to (stress-induced) corticosterone  
93 levels (Blas et al., 2007; Romero and Wikelski, 2001), or positively related to baseline  
94 levels (Cabezas et al., 2007; Patterson et al., 2014). Mixed results were also found when  
95 comparing different population of American redstarts (*Sethophaga ruticilla*; Angelier et  
96 al., 2009) or the same population of song sparrows (*Melospiza melodia*) over several  
97 years (Macdougall-shackleton et al., 2013). It has been argued that this inconsistency  
98 might relate to variation in individual condition (life history stage, age, sex) as well as in  
99 environmental conditions (Bonier et al., 2009) between studies, most of which were  
100 conducted for only one season.

101 It is now acknowledged that the relationship between glucocorticoid levels and  
102 fitness might be context-dependent (Henderson et al., 2017). In periods of low resource  
103 availability, elevated glucocorticoid levels may be detrimental and reduce fitness when  
104 energy demand exceeds available resources, causing allostatic overload (McEwen and  
105 Wingfield, 2003; Romero et al., 2009). By contrast, elevated levels might have no effect  
106 or even be beneficial, and potentially increase fitness, when resources are not limited (i.e.  
107 allostatic load can be negated by available resources). Thus, the effects of glucocorticoids  
108 on fitness may change according to environmental conditions, especially food  
109 availability, but also predation pressure and population density (Dingemanse et al., 2010;  
110 Henderson et al., 2017). Variation in these additional environmental factors should be  
111 accounted for when studying the fitness consequences of basal glucocorticoid levels.  
112 Long-term, individual based studies monitoring several generations of a given species  
113 under varying environmental conditions would contribute to our understanding of

114 whether elevated basal glucocorticoid levels are associated with reduced fitness, and how  
115 this relationship depends on intrinsic and extrinsic parameters.

116 In the African striped mouse (*Rhabdomys pumilio*), an annual rodent, a generation  
117 born in spring has to survive the forthcoming summer and autumn (i.e. the pre-breeding  
118 season) characterised by low food availability, before reproducing in the next  
119 winter/spring, and typically die before the subsequent pre-breeding season (Schradin et  
120 al., 2012). While food availability decreases annually from spring to summer, the  
121 harshness of the pre-breeding season (i.e. extent and duration of reduction in food  
122 availability) differs unpredictably from generation to generation (Table 1). In striped  
123 mice, corticosterone is a potential trigger for dispersal (Schoepf and Schradin, 2013), and  
124 dispersal occurs mainly when food availability is high (Schoepf and Schradin, 2012).

125 We investigated whether basal corticosterone levels were related to disappearance  
126 over the pre-breeding season in striped mice. According to the cort-fitness hypothesis,  
127 elevated corticosterone levels are associated with poor condition or health, which would  
128 translate into a negative relationship between basal corticosterone levels and survival.  
129 Nonetheless, the relationship between basal corticosterone levels and survival may vary  
130 according to environmental conditions, including food availability, population density  
131 and predation pressure. We had three independent, non-exclusive hypotheses. First, the  
132 negative effects of elevated basal corticosterone levels are expected to be stronger in pre-  
133 breeding seasons with relatively lower food availability, but weaker (or even absent) in  
134 pre-breeding seasons with relatively high food availability. Second, if corticosterone  
135 mediates dispersal, then elevated basal levels should be related to disappearance in  
136 smaller (but not large) striped mice, which are most likely to disperse (Solmsen et al.,  
137 2011). Third, elevated basal corticosterone levels may enhance survival probability under  
138 high predation pressure, since energy mobilised by corticosterone secretion would  
139 promote predator escape responses.

140

## 141 **Material and methods**

### 142 *Study period and study area*

143 The study was conducted at the Succulent Karoo Research Station in Goegap Nature  
144 Reserve in South Africa (S29°42.414' E18° 02.526'), which lies within the Succulent

145 Karoo semi-desert. Data were collected over 6 years (2009-2014) from free-ranging  
146 striped mice on a 10-ha field site at the beginning of the pre-breeding season (January-  
147 February). Data were collected from philopatric striped mice of 6 weeks old minimum  
148 (born in the previous breeding season between July and December), since we know  
149 striped mice can breed from that age (Schoepf and Schradin, 2013; Schradin and Pillay,  
150 2004). Striped mice had to survive the pre-breeding season from summer to onset of  
151 winter (January-June) to reproduce during the subsequent breeding season, usually  
152 starting in July. We did not include breeders because less than 1% of them survive their  
153 second dry season (Schradin, unpublished data), making it impossible to study the effects  
154 of corticosterone on dry season survival in breeders. Summers are hot and dry with low  
155 food availability, while rains in autumn/winter increases food availability. The onset of  
156 rain varies, such that the period of food shortage (less than 4 food plants/2sqm associated  
157 with physiological parameters of starvation: reduced blood glucose levels and increased  
158 blood ketone levels; Schradin, unpublished data) varies from year to year (Table 1).  
159 Animal ethics clearance for our study was provided by the University of the  
160 Witwatersrand (AESC 2007/10/01 and 2007/39/04).

161

#### 162 *Trapping, behavioural observations and radio-tracking*

163 The study population has been continuously monitored since 2002 by a combination of  
164 trapping, behavioural observations and radio-tracking (Schradin, 2006; Schradin and  
165 Pillay, 2004). Striped mice live in groups consisting of one breeding male, 1-4 breeding  
166 females, and non-reproductive offspring of both sexes that remain in their natal group  
167 after reaching adulthood (Schradin and Pillay, 2004). We typically monitored 12 focal  
168 groups at one time, although groups went extinct and new groups were formed every  
169 year. Each group was trapped at least twice a month at its nesting site for 3 days  
170 (minimum of 6 days per month) and observed at least twice a month for two days  
171 (minimum of 4 days per month) to confirm group composition.

172 Trapping was done with locally produced metal traps of Sherman style, baited  
173 with a mixture of bran flakes, sunflower oil, and dried currants. Trapped striped mice  
174 were weighed ( $\pm 1$ g), sexed, and permanently marked with ear tags (National Band and  
175 Tag Co., USA). All individuals above 25g were marked with hair dye (Inecto Rapido,

176 Pinetown, South Africa) to facilitate individual recognition during behavioural  
177 observations. Each group had at least one adult breeder (which was not part of the study)  
178 carrying a collar-mounted radio-transmitter (models BD-2C and PD-2C, Holohil,  
179 Canada; hereafter referred as transmitter). Striped mice that were initially trapped at a  
180 nest as juveniles (body mass < 30g) and trapped there subsequently were regarded as  
181 being philopatric to that group (as opposed to immigrants).

182

### 183 *Food availability*

184 Striped mice do not cache food but feed on plant leaves (Schradin and Pillay, 2006).  
185 Plant surveys were conducted on the 15<sup>th</sup> of each month, using the Braun-Blanquet  
186 Method (Werger, 1974). The number of food plants species (palatability known from  
187 behavioural observations; Schradin and Pillay, 2006) was recorded in each of eight  
188 monitoring plots of 2 x 2 m on the field site, located within the home ranges of eight  
189 different groups), and values were averaged monthly over all the plots. Every year, the  
190 mean value covering the period from January to June was then used as an estimate of  
191 food availability over the pre-breeding season.

192

### 193 *Population density*

194 Population density was calculated every year as the number of striped mice per hectare,  
195 based on the total number of striped mice present at the onset of the pre-breeding season  
196 (January) and the size of the field site estimated using Google Earth.

197

### 198 *Predation pressure*

199 Predation pressure during the pre-breeding season was estimated as the percentage of  
200 striped mice carrying transmitters known to have been predated among the total number  
201 of striped mice with transmitters. On average,  $13.2 \pm 4.9$  mice were carrying transmitters  
202 during the dry season, typically one or two mice per group. As the number of groups  
203 varied less between years than group size, this led to a larger variation of the percentage  
204 of mice from the total population carrying transmitters ( $11.1 \pm 10.8\%$  of the population,  
205 ranging from 3.3% in the year with highest population density to 37.4% in the year with  
206 lowest density). A striped mouse's death was attributed to predation when its transmitter



207 was found lying in an open area (indicating the individual had been eaten by a mammal  
208 or a raptor at this spot), at a predator's den or nest, or inside a snake.

209

#### 210 *Disappearance probability*

211 To determine when individuals disappeared from the population, trapping was performed  
212 continuously throughout the year and continued after the present study ended. A striped  
213 mouse was regarded as having disappeared after it had not been trapped and not been  
214 observed for at least one year, more than the average life span of striped mice at our site.  
215 The last day an individual was trapped was therefore determined as its day of  
216 disappearance. Striped mice initiate long-distance dispersal (outside of our study area) at  
217 the onset of the breeding season, dispersal being male biased although females also  
218 disperse (Solmsen et al., 2011). The breeding season typically starts in July/August, and  
219 thus striped mice that were still present on the 1<sup>st</sup> of July were regarded as having  
220 survived the pre-breeding season.

221

#### 222 *Immigration*

223 Immigration was determined every month between 2005 and 2016 from the number of  
224 adult individuals that immigrated into the field site. This included males that immigrated  
225 into existing groups as the new breeding male, females that formed new groups (one or  
226 several adult females), and solitary breeding males (roamers) that did not originate from  
227 the field site.

228

#### 229 *Blood sampling and basal corticosterone levels*

230 Striped mice were trapped early in the morning before they left their nest to forage. Basal  
231 corticosterone levels have a circadian rhythm and striped mice display higher  
232 corticosterone levels in the morning than in the afternoon (Schradin, unpublished data).  
233 To avoid any bias, all samples were collected within the first hour after the sun started to  
234 illuminate the field site and striped mice became active (Schradin et al., 2007). Traps  
235 were observed (average distance of 10m) so that as soon as a striped mouse entered a  
236 trap, it was removed. Striped mice were anaesthetized with diethyl ether and blood was  
237 sampled from a sub-lingual vein. The vein was pricked with a needle and blood was

238 collected in a 2mL Eppendorf tube. The entire procedure (i.e. from the moment a striped  
239 mouse entered a trap until the end of blood sampling) lasted no longer than 3min (mean  $\pm$   
240 sd:  $2.68 \pm 0.38$ min, min-max: 1.40-3.00min), a period short enough to ensure the  
241 measurement of basal, rather than stress-induced, corticosterone levels (correlation  
242 between corticosterone levels and sampling time: Pearson  $r = -0.02$ ,  $n = 325$ ,  $p = 0.737$ ;  
243 Romero and Reed, 2005). Striped mice were weighed after blood collection. Blood was  
244 left to clot at room temperature (approx.  $25^{\circ}\text{C}$ ) for 45 min, centrifuged to allow the  
245 extraction of the serum, which was then stored at  $-20^{\circ}\text{C}$ . Serum samples were analysed  
246 for total corticosterone using commercial ELISA kits (Immuno Biological Laboratories,  
247 Hamburg; previously validated for striped mouse serum; Schradin, 2008). For two  
248 different pools, intra-assay variability was 4.0% and 9.4%, inter-assay variability was  
249 8.1% and 17.2%.

250

#### 251 *Statistical analyses*

252 Blood samples collected each year from mid-January to mid-February (onset of the pre-  
253 breeding season) were used for the survival analysis. At this time of the year, food  
254 availability was already low (Table 1) compared to the breeding season when the food  
255 plant index was above 5.0. For cases where the same individual had been sampled more  
256 than once over the period of interest, we considered the blood sample collected the  
257 closest to the 1<sup>st</sup> of February in the analysis. In total, data from 331 striped mice (159  
258 males and 172 females) were considered in the analysis.

259 Data were analysed with R 3.4.2 (R Development Core Team, 2008).  
260 Repeatability of basal corticosterone levels was examined using a second measurement  
261 from 65 (31 males and 34 females) out of the 331 individuals. Paired measurements were  
262 taken less than 7 weeks apart between January and March. The repeatability coefficient  
263 (R), its standard error (se) and the 95% confidence intervals (CI) were calculated from  
264 paired data using the 'rptR' package.

265 Survival over the pre-breeding season was analysed using a Cox Proportional  
266 Hazards model (function 'coxph' of the 'survival' package), with survival time since the  
267 1<sup>st</sup> of January being the dependent variable. The censoring date (i.e. time from which  
268 survival was no longer monitored) was set to the 1<sup>st</sup> of July to coincide with the onset of

269 both mating and male long-term dispersal, when immigration peaks (see results).  
270 Survival time was then calculated as the number of days from the 1<sup>st</sup> of January till last  
271 trapped or censoring date if still present and trapped later. In addition to basal  
272 corticosterone levels measured at the onset of the pre-breeding season, the initial model  
273 also included the following set of intrinsic and extrinsic factors: body mass at the onset of  
274 the pre-breeding season as an indicator of body condition; sex - behaviour is sex specific  
275 (e.g. male biased dispersal) and the reasons of disappearance may differ between sexes;  
276 mean food availability over the pre-breeding season as an indicator of the harshness of  
277 the pre-breeding season; predation pressure throughout the pre-breeding season as the  
278 percentage of striped mice that had transmitters being predated; and population density at  
279 the onset of the pre-breeding season as the number of adult striped mice/ha present in  
280 January. The interactions of basal corticosterone level with body mass, sex, duration of  
281 the pre-breeding season and each of the three environmental variables were also included  
282 in the initial model since: 1. leaner individuals could suffer from allostatic overload due  
283 to elevated corticosterone levels, while larger ones may be able to better cope allostatic  
284 overload thanks to their body reserves; 2. corticosterone may modulate sex-specific  
285 behaviours and strategies, resulting in one sex being more sensitive than the other to  
286 elevated corticosterone levels; 3. the effect of corticosterone levels on survival might  
287 depend on the harshness of the pre-breeding season, with elevated levels being  
288 detrimental to survival only when food availability is low; 4. the effect of corticosterone  
289 levels may differ according to predation pressure, with elevated levels being  
290 advantageous only when predation level was high and energy is required to escape  
291 predators; and 5. the effect of corticosterone levels might also be density-related, with  
292 elevated levels triggering dispersal in individuals of low competitive ability under low  
293 population density. The model also included a frailty term which allows for fitting a  
294 random effect for year, since data were collected over multiple years. We checked  
295 whether our initial model satisfied the proportional hazard assumption using scaled  
296 Schoenfeld residuals. Because there was evidence for non-proportional hazard for sex,  
297 we computed a second model where sex was including as a stratifying variable (allowing  
298 different baseline hazard functions for males and females). The Schoenfeld residuals of  
299 this final stratified model no longer indicated non-proportionality. Note that this

300 procedure prevents from examining the effect of the stratifying covariate, but because  
301 neither sex nor any of its interaction with corticosterone were significant in the initial  
302 model, we considered the model with sex as a stratifying variable. Nonlinearity was  
303 checked through visual inspection of Martingale residuals, which exhibited no obvious  
304 trends. The significance level was set to  $p \leq 0.05$ .

305 Significant effects of covariates on hazard ratios and marginal effects of  
306 covariates in interactions were visualized by parametric simulations (package ‘simPH’;  
307 Gandrud, 2015). Ribbons indicate the areas containing the central 95% and 50% of 1000  
308 simulations, respectively, reflecting an empirical confidence interval. All variables were  
309 standardized (mean = 0 and sd = 1) so that estimates and simulations refer to effects with  
310 all other covariates set to their means, and effect sizes are in units of standard deviation.  
311 Increased hazard ratios therefore reflect increased disappearance rate relative to the  
312 average rate at mean covariate values and increased marginal effects reflect increased  
313 effect size at the respective value of the interacting covariate. Immigration and  
314 disappearance rates were compared using paired t-tests and effect sizes for these paired  
315 analyses are reported as Cohen’s  $d$  estimates.

316

## 317 **Results**

### 318 *Inter-individual variation and intra-individual repeatability for baseline corticosterone*

319 Inter-individual variation in basal corticosterone levels at the onset of the pre-breeding  
320 season was large, ranging from 134 to 2577 ng.mL<sup>-1</sup> (mean  $\pm$  sd = 978.54  $\pm$  451.2 ng.mL<sup>-1</sup>).  
321 Nonetheless, corticosterone levels measured at that same period of the year were  
322 repeatable among individuals ( $R = 0.51$ , se = 0.09, CI = 0.30-0.67,  $p < 0.001$ ; Fig. 1).  
323 Corticosterone levels did not significantly differed between sexes (991.5  $\pm$  491.6 versus  
324 966.5  $\pm$  411.3 ng.mL<sup>-1</sup> for males and females, respectively;  $t_{329} = 0.502$ ,  $p = 0.616$ ).

325

### 326 *Variation of environmental conditions among years*

327 Mean food availability over the pre-breeding season significantly varied between years  
328 (Kruskal-Wallis  $\chi^2 = 17.128$ , df = 5,  $p = 0.004$ ), indicating that the six generations of  
329 striped mice considered in this study experienced pre-breeding seasons of different

330 harshness. Population density and predation pressure also varied considerably among  
331 years (Table 1).

332

### 333 *Corticosterone and disappearance probability*

334 High basal corticosterone levels were associated with increased disappearance probability  
335 in light but not heavy individuals (significant interaction baseline corticosterone x body  
336 mass; Table 2; Fig. 2). None of the interactions between baseline corticosterone and food  
337 availability, population density and predation pressure were significant. Environmental  
338 conditions impacted disappearance probability, since disappearance was positively  
339 related to both food availability and predation pressure (Table 2; Fig. 3a,b).

340

### 341 *Immigration and disappearance throughout the year*

342 Immigration and disappearance occurred in all months, including the pre-breeding  
343 season, but both peaked at the onset of the breeding season (July-August; Fig. 4).  
344 Immigration rate (males:  $3.0 \pm 1.7\%$  of adult population, females  $1.3 \pm 0.2\%$  of adult  
345 population) was always lower than disappearance rates (males:  $7.90 \pm 6.4\%$  of adult  
346 population, paired  $t_{11} = 2.816$ ,  $p = 0.02$ , Cohen's  $d = 0.85$ ; females  $7.58 \pm 4.31\%$  of adult  
347 population, paired  $t_{11} = 5.230$ ,  $p < 0.001$ , Cohen's  $d = 1.57$ ). The Cohen's  $d$  estimates  
348 indicate that we can accept with great confidence that the disappearance rates are greater  
349 than immigration, suggesting that disappearance represented death in most cases (even if  
350 occurring during dispersal, see discussion). More males than females immigrated (paired  
351  $t_{11} = 4.117$ ,  $p = 0.002$ ; Cohen's  $d = 1.24$ ), while there was no sex difference in the  
352 probability of disappearance, neither for the entire year (paired  $t_{11} = 0.1896$ ,  $p = 0.85$ ;  
353 Cohen's  $d = 0.06$ ), nor for the pre-breeding season alone (paired  $t_5 = 0.129$ ,  $p = 0.90$   
354 Cohen's  $d = 0.06$ ). The extremely low Cohen's  $d$  estimates support the non-significant  
355 sex differences.

356

## 357 **Discussion**

358 Our long-term analysis of the relationship between baseline corticosterone and  
359 disappearance in a natural population of striped mice indicates that elevated basal  
360 corticosterone levels were associated with higher risk of disappearance in light but not

361 heavy individuals. This suggests either that high corticosterone levels are increasing  
362 mortality risk in striped mice of low body mass, or that they trigger dispersal in striped  
363 mice of low body mass. Although the fitness costs of glucocorticoids were expected to be  
364 stronger under harsh conditions, none of the interactions between basal corticosterone  
365 levels and any of the environmental variables considered here was significant.  
366 Disappearance risk nevertheless increased under high predation pressure, and more  
367 surprisingly also under high food availability, which might support the hypothesis of  
368 corticosterone mediating dispersal.

369         Previous short-term field studies found mixed support for the cort-fitness  
370 hypothesis, which postulates that glucocorticoids negatively relate to fitness (Bonier et  
371 al., 2009; Crespi et al., 2013; Hau et al., 2016). This hypothesis is based on the idea that  
372 elevated basal glucocorticoid levels could serve as physiological indicators of poor  
373 individual condition or health and thus of low fitness, especially under harsh  
374 environmental conditions (Bonier et al., 2010, 2009). The pre-breeding season in the  
375 natural habitat of our study population is characterised by low food and water availability  
376 combined with ambient temperatures regularly exceeding 40°C at ground level, where  
377 striped mice live. Striped mice must survive these harsh conditions to reach the next  
378 breeding season. It has been shown previously that the health status (evaluated through  
379 12 different blood parameters) at the onset of the pre-breeding season was related to  
380 survival probability in our study population, and that health progressively deteriorates  
381 over the pre-breeding season (Schoepf et al., 2016). More importantly, striped mice that  
382 disappeared had impaired health status compared to survivors, especially blood  
383 parameters indicative of nutritional state (albumin, glucose and total protein; Schoepf et  
384 al., 2016). In contrast, here we found no evidence for an overall negative effect of  
385 corticosterone, as we showed that elevated basal corticosterone levels were associated  
386 with increased disappearance risk in light but not heavy individuals. This suggests that  
387 high corticosterone levels in the pre-breeding season might only indicate poor condition  
388 in individuals of lower body mass.

389         Body mass might correlate with overall condition, in which case striped mice of  
390 low body mass would be more sensitive to the physiological costs of elevated  
391 corticosterone levels, resulting in increased mortality risk and thus disappearance.

392 Individuals exhibiting high basal glucocorticoid levels face the risk of increased energy  
393 expenditure, since glucocorticoids stimulate activity by mobilising energy stores (Reeder  
394 and Kramer, 2005; Sapolsky et al., 2000). This could be detrimental when energy  
395 availability is low, and particularly so for lean individuals with limited body reserves.  
396 These individuals could enter allostatic overload (i.e. negative energy balance) much  
397 more rapidly, with potential detrimental consequences for their physiology and health,  
398 and ultimately their fitness (McEwen and Wingfield, 2010, 2003; Romero et al., 2009). In  
399 contrast, heavier individuals with greater body reserves could be more capable of  
400 overcoming energy shortage, preventing them going into allostatic overload. Endogenous  
401 energy reserves (i.e. fat stores) might serve as a buffer against energetically constraining  
402 conditions. In Galapagos marine iguanas (*Amblyrhynchus cristatus*), the increase in  
403 corticosterone in response to an environmental challenge was disproportionately higher as  
404 body condition worsened (Romero and Wikelski, 2001), supporting the idea that  
405 glucocorticoids and body condition can covary in a nonlinear manner, with potentially  
406 different effects on fitness.

407 Elevated basal corticosterone levels could also trigger dispersal in individuals of  
408 lower competitive ability, thus accounting for the positive association between  
409 corticosterone and disappearance in striped mice of low body mass. Glucocorticoids are  
410 thought to influence dispersal behaviour in mammals (Wada, 2008), including the striped  
411 mouse (Schoepf and Schradin, 2013) in which small individuals of low competitive  
412 ability are more likely to disperse (Solmsen et al., 2011). The most competitive males  
413 only disperse into neighbouring territories, where they become breeders with high  
414 reproductive success (Schradin and Lindholm, 2011). Although dispersal is male-biased  
415 in striped mice, females also disperse (Solmsen et al., 2011). Hence, the significant  
416 interaction between corticosterone and body mass may reflect different dispersal  
417 strategies among individuals with high corticosterone levels, where small individuals  
418 leave while larger competitive individuals would remain in the study population.

419 The success of light striped mice initiating long-distance dispersal to emigrate  
420 into another population remains unknown, however. Dispersing striped mice must travel  
421 up to several kilometres over unoccupied and unsuitable habitat until they find (or not)  
422 another population along another dry riverbed (see Fig. 1 in Solmsen et al., 2011), and

423 such behaviour is expected to be risky and to induce high mortality. This hypothesis is  
424 supported by the comparison of long-term immigration data in our field site with  
425 disappearance from the population over the course of the study (Fig 4). Around five times  
426 more males, and eight times more females, disappeared than immigrated over the pre-  
427 breeding season. If most striped mice which disappear from a population disperse and  
428 successfully join other populations, the difference between disappearance and  
429 immigration rates should not be so marked, and immigration rate would likely be closer  
430 to disappearance rate. However, a lower immigration rate into our study population  
431 suggests that most striped mice that left their natal population did not reach another  
432 population, indicating that most striped mice that disappeared likely died, including those  
433 which dispersed. This supports the idea that dispersal is a risky strategy associated with  
434 high fitness costs. Overall, our results suggest that elevated corticosterone levels in  
435 striped mice of low (but not high) competitive ability (i.e. low body mass) could be  
436 regarded as an indicator of low fitness, either through direct deleterious physiological  
437 effects or through dispersal-induced mortality.

438 While increased disappearance probability under higher predation pressure was  
439 expected and supports our approach, the positive association between food availability  
440 and disappearance risk seemed counterintuitive at first. Instead, we predicted a negative  
441 association, as well as the effects of elevated corticosterone to be more pronounced when  
442 food availability (and thus energy availability) was low. Indeed, striped mice are more  
443 likely to disperse when food availability was high (Schoepf and Schradin, 2012),  
444 meaning that higher food abundance would promote dispersal. Furthermore, a  
445 demographic study conducted on the same population from a larger capture-mark  
446 recapture dataset (1609 females over 11 years) also documented that female striped mice  
447 disappearance was positively related to food availability and likely due to dispersal  
448 (Nater et al., 2016). Additionally, previous studies showed that philopatric male striped  
449 mice with high corticosterone levels are more likely to disperse than males with low  
450 corticosterone levels under low population density (Schoepf and Schradin, 2013, 2012).  
451 However, we found no evidence that population density or its interaction with  
452 corticosterone, influenced disappearance risk. Altogether, these results indicate that food  
453 availability might be an important ecological factor influencing dispersal, and that this



454 risky behaviour could be modulated by the interplay between basal corticosterone levels  
455 and individual condition.

456 The diverse results from studies that investigated the relationship between  
457 glucocorticoids and fitness (Bonier et al., 2009) implies that the fitness consequences of  
458 elevated glucocorticoid levels could be species and context specific (Hau et al., 2016).  
459 Importantly, the endocrine phenotype reflects a plastic response where hormone levels  
460 are adjusted according to specific environmental conditions and current individual  
461 condition, including social tactic, reproductive and nutritional states (Crespi et al., 2013;  
462 Hau et al., 2016). Thus, between individual variation in basal hormone levels might not  
463 be related to fitness if different levels represent individually optimised levels (Bonier and  
464 Martin, 2016). The strength and direction of the relationship between glucocorticoids and  
465 fitness might also depend on environmental conditions (Henderson et al., 2017). Apart  
466 from basal glucocorticoid levels, stress-induced levels would be interesting to measure in  
467 striped mice, together with the form of their stress response. Indeed, stress-induced  
468 glucocorticoid levels in barn swallows have been reported to predict their offspring  
469 survival (Vitousek et al., 2014), and the negative feedback of the stress response in  
470 marine iguanas to predict their survival during starvation (Romero, 2012). Although we  
471 considered the interaction between basal corticosterone levels and different  
472 environmental variables, we found no evidence that the relationship varied according to  
473 environmental harshness. For striped mice, surviving the long pre-breeding season is  
474 critical, but basal glucocorticoid levels were only related to survival in individuals of low  
475 body mass. This result partially supports the cort-fitness hypothesis, while also adding to  
476 the growing evidence that glucocorticoids might be important physiological mediators of  
477 dispersal.

478

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493

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626

627 **Tables and figures captions**

628

629 Table 1. Monthly food availability from January to June (mean number of food plant  
630 species averaged over 8 monitoring plots of 4sqm), food availability during the pre-  
631 breeding season (mean  $\pm$  sd over the 6-month period), population density (number of  
632 striped mice per hectare) and predation pressure (percentage of predated striped mice  
633 carrying transmitter, T) from 2009 to 2014.

634

635 Table 2. Cox proportional hazards model testing for the effects of baseline corticosterone,  
636 body mass, food availability, population density, predation pressure, and the two-way  
637 interactions of corticosterone with each of the other covariates, on striped mice  
638 disappearance over the pre-breeding season (n = 331). All variables were standardized  
639 (mean = 0 and sd = 1). Sex was included as a stratifying variable to correct for non-  
640 proportional hazard and year was included as a frailty term since data were collected over  
641 multiple years. Hazard ratios [exp(coef)] and their 95% confidence intervals (CI) are  
642 presented. Significant effects are marked in bold.

643

644 Figure 1. Repeatability of baseline corticosterone at the onset of the pre-breeding season  
645 in free-ranging striped mice (n = 66 paired measurements; black and grey circles indicate  
646 males and females, respectively). Values on the x-axis are those used for the survival  
647 analysis while values on the y-axis correspond to a second measurement for the same  
648 individuals within less than 7 weeks.

649

650 Figure 2. The risk of disappearance from the population increased with elevated basal  
651 corticosterone levels for light but not heavy individuals in free-ranging striped mice (Cox  
652 proportional hazard model, n = 331, significant interaction baseline corticosterone x body  
653 mass). The simulated marginal effects (line), 50% (dark blue shaded area) and 95% (light  
654 blue shaded area) confidence intervals are shown.

655

656 Figure 3. Relationship between disappearance risk and food availability (a) and predation  
657 pressure (b) during the pre-breeding season for free-ranging striped mice (Cox

658 proportional hazard model,  $n = 331$ ). The simulated hazard ratio (line), 50% (dark blue  
659 shaded area) and 95% (light blue shaded are) confidence intervals are shown.

660

661 Figure 4. Percentages of males (black boxes) and females (grey diamonds) that  
662 disappeared from the population (solid lines; averaged over 6 years) and that immigrated  
663 into the field site (dashed lines; averaged over 12 years) per month.

664



665 **Table 1**

Year	Monthly food availability						Food availability	Population density	Predation pressure
	(nb food plants averaged over 8 plots)						(mean $\pm$ sd)	(mice/ha)	(% disappeared mice with T)
	<i>Jan</i>	<i>Feb</i>	<i>Mar</i>	<i>Apr</i>	<i>May</i>	<i>Jun</i>	<i>Pre-breeding season</i>		
2009	3.00	3.25	3.5	3.88	4.00	5.00	3.77 $\pm$ 0.71	48.6	7.6
2010	2.25	2.13	3.13	2.75	2.88	3.63	2.79 $\pm$ 0.56	28.3	17.5
2011	2.25	2.00	2.38	1.88	2.50	3.63	2.44 $\pm$ 0.63	13.9	11.7
2012	2.00	1.75	1.63	1.00	1.38	2.13	1.65 $\pm$ 0.41	30.3	7.5
2013	2.75	2.50	2.00	1.38	6.13	5.75	3.42 $\pm$ 2.01	37.6	12.9
2014	2.25	2.25	1.75	1.63	3.00	3.00	2.31 $\pm$ 0.59	39.8	18.8

666

667

668 **Table 2**

<b>Variable</b>	<b>Coef</b>	<b>SE</b>	<b>Chisq</b>	<b>df</b>	<b>Hazard Ratio</b>	<b>95% CI</b>	<b><i>p</i></b>
Baseline corticosterone	0.048	0.085	0.31	1	1.049	0.888–1.239	0.580
Body mass	0.026	0.083	0.10	1	1.027	0.873–1.208	0.750
Food availability	0.227	0.097	5.54	1	1.255	1.039–1.516	<b>0.019</b>
Population density	-0.003	0.089	0.00	1	0.997	0.837–1.189	0.980
Predation pressure	0.214	0.088	5.85	1	1.238	1.041–1.473	<b>0.016</b>
Corticosterone x Body mass	-0.246	0.087	8.06	1	0.782	0.660–0.927	<b>0.005</b>
Corticosterone x Food availability	-0.048	0.100	0.24	1	0.953	0.784–1.158	0.630
Corticosterone x Population density	-0.051	0.084	0.36	1	0.951	0.807–1.121	0.550
Corticosterone x Predation pressure	0.047	0.085	0.31	1	1.049	0.888–1.238	0.580

669