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Abstract

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

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

Introduction

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

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

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

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

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

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

Material and methods

Study period and study area

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

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

Trapping, behavioural observations and radio-tracking

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

Trapping was done with locally produced metal traps of Sherman style, baited with a mixture of bran flakes, sunflower oil, and dried currants. Trapped striped mice were weighed (± 1g), sexed, and permanently marked with ear tags (National Band and Tag Co., USA). All individuals above 25g were marked with hair dye (Inecto Rapido, Pinetown, South Africa) to facilitate individual recognition during behavioural observations. Each group had at least one adult breeder (which was not part of the study) carrying a collar-mounted radio-transmitter (models BD-2C and PD-2C, Holohil, Canada; hereafter referred as transmitter). Striped mice that were initially trapped at a nest as juveniles (body mass < 30g) and trapped there subsequently were regarded as being philopatric to that group (as opposed to immigrants).

Food availability

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

Population density

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

Predation pressure

Predation pressure during the pre-breeding season was estimated as the percentage of striped mice carrying transmitters known to have been predated among the total number of striped mice with transmitters. On average, 13.2 ± 4.9 mice were carrying transmitters during the dry season, typically one or two mice per group. As the number of groups varied less between years than group size, this led to a larger variation of the percentage of mice from the total population carrying transmitters (11.1 ± 10.8% of the population, ranging from 3.3% in the year with highest population density to 37.4% in the year with lowest density). A striped mouse's death was attributed to predation when its transmitter was found lying in an open area (indicating the individual had been eaten by a mammal or a raptor at this spot), at a predator's den or nest, or inside a snake.

Disappearance probability

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

Immigration

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

Blood sampling and basal corticosterone levels

Striped mice were trapped early in the morning before they left their nest to forage. Basal corticosterone levels have a circadian rhythm and striped mice display higher corticosterone levels in the morning than in the afternoon (Schradin, unpublished data). To avoid any bias, all samples were collected within the first hour after the sun started to illuminate the field site and striped mice became active (Schradin et al., 2007). Traps were observed (average distance of 10m) so that as soon as a striped mouse entered a trap, it was removed. Striped mice were anaesthetized with diethyl ether and blood was sampled from a sub-lingual vein. The vein was pricked with a needle and blood was collected in a 2mL Eppendorf tube. The entire procedure (i.e. from the moment a striped mouse entered a trap until the end of blood sampling) lasted no longer than 3min (mean ± sd: 2.68 ± 0.38min, min-max: 1.40-3.00min), a period short enough to ensure the measurement of basal, rather than stress-induced, corticosterone levels (correlation between corticosterone levels and sampling time: Pearson $r = -0.02$, $n = 325$, $p = 0.737$; Romero and Reed, 2005). Striped mice were weighed after blood collection. Blood was left to clot at room temperature (approx. 25°C) for 45 min, centrifuged to allow the extraction of the serum, which was then stored at -20°C. Serum samples were analysed for total corticosterone using commercial ELISA kits (Immuno Biological Laboratories, Hamburg; previously validated for striped mouse serum; Schradin, 2008). For two different pools, intra-assay variability was 4.0% and 9.4%, inter-assay variability was 8.1% and 17.2%.

Statistical analyses

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

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

Survival over the pre-breeding season was analysed using a Cox Proportional Hazards model (function ‘coxph’ of the ‘survival’ package), with survival time since the 1st of January being the dependent variable. The censoring date (i.e. time from which survival was no longer monitored) was set to the 1st of July to coincide with the onset of both mating and male long-term dispersal, when immigration peaks (see results). Survival time was then calculated as the number of days from the 1st of January till last trapped or censoring date if still present and trapped later. In addition to basal corticosterone levels measured at the onset of the pre-breeding season, the initial model also included the following set of intrinsic and extrinsic factors: body mass at the onset of the pre-breeding season as an indicator of body condition; sex - behaviour is sex specific (e.g. male biased dispersal) and the reasons of disappearance may differ between sexes; mean food availability over the pre-breeding season as an indicator of the harshness of the pre-breeding season; predation pressure throughout the pre-breeding season as the percentage of striped mice that had transmitters being predated; and population density at the onset of the pre-breeding season as the number of adult striped mice/ha present in January. The interactions of basal corticosterone level with body mass, sex, duration of the pre-breeding season and each of the three environmental variables were also included in the initial model since: 1. leaner individuals could suffer from allostatic overload due to elevated corticosterone levels, while larger ones may be able to better cope allostatic overload thanks to their body reserves; 2. corticosterone may modulate sex-specific behaviours and strategies, resulting in one sex being more sensitive than the other to elevated corticosterone levels; 3. the effect of corticosterone levels on survival might depend on the harshness of the pre-breeding season, with elevated levels being detrimental to survival only when food availability is low; 4. the effect of corticosterone levels may differ according to predation pressure, with elevated levels being advantageous only when predation level was high and energy is required to escape predators; and 5. the effect of corticosterone levels might also be density-related, with elevated levels triggering dispersal in individuals of low competitive ability under low population density. The model also included a frailty term which allows for fitting a random effect for year, since data were collected over multiple years. We checked whether our initial model satisfied the proportional hazard assumption using scaled Schoenfeld residuals. Because there was evidence for non-proportional hazard for sex, we computed a second model where sex was including as a stratifying variable (allowing different baseline hazard functions for males and females). The Schoenfeld residuals of this final stratified model no longer indicated non-proportionality. Note that this procedure prevents from examining the effect of the stratifying covariate, but because neither sex nor any of its interaction with corticosterone were significant in the initial model, we considered the model with sex as a stratifying variable. Nonlinearity was checked through visual inspection of Martingale residuals, which exhibited no obvious trends. The significance level was set to $p \leq 0.05$.

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

Results

Inter-individual variation and intra-individual repeatability for baseline corticosterone

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

Variation of environmental conditions among years

Mean food availability over the pre-breeding season significantly varied between years (Kruskal-Wallis $Chi^2 = 17.128$, df = 5, $p = 0.004$), indicating that the six generations of striped mice considered in this study experienced pre-breeding seasons of different harshness. Population density and predation pressure also varied considerably among years (Table 1).

Corticosterone and disappearance probability

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

Immigration and disappearance throughout the year

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

Discussion

Our long-term analysis of the relationship between baseline corticosterone and disappearance in a natural population of striped mice indicates that elevated basal corticosterone levels were associated with higher risk of disappearance in light but not heavy individuals. This suggests either that high corticosterone levels are increasing mortality risk in striped mice of low body mass, or that they trigger dispersal in striped mice of low body mass. Although the fitness costs of glucocorticoids were expected to be stronger under harsh conditions, none of the interactions between basal corticosterone levels and any of the environmental variables considered here was significant. Disappearance risk nevertheless increased under high predation pressure, and more surprisingly also under high food availability, which might support the hypothesis of corticosterone mediating dispersal.

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

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

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

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

The success of light striped mice initiating long-distance dispersal to emigrate into another population remains unknown, however. Dispersing striped mice must travel up to several kilometres over unoccupied and unsuitable habitat until they find (or not) another population along another dry riverbed (see Fig. 1 in Solmsen et al., 2011), and such behaviour is expected to be risky and to induce high mortality. This hypothesis is supported by the comparison of long-term immigration data in our field site with disappearance from the population over the course of the study (Fig 4). Around five times more males, and eight times more females, disappeared than immigrated over the pre-breeding season. If most striped mice which disappear from a population disperse and successfully join other populations, the difference between disappearance and immigration rates should not be so marked, and immigration rate would likely be closer to disappearance rate. However, a lower immigration rate into our study population suggests that most striped mice that left their natal population did not reach another population, indicating that most striped mice that disappeared likely died, including those which dispersed. This supports the idea that dispersal is a risky strategy associated with high fitness costs. Overall, our results suggest that elevated corticosterone levels in striped mice of low (but not high) competitive ability (i.e. low body mass) could be regarded as an indicator of low fitness, either through direct deleterious physiological effects or through dispersal-induced mortality.

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

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

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Tables and figures captions

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

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

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

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

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

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

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

Table 1

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

Table 2

Variable	Coef	SE	Chisq	df	Hazard Ratio	95% CI	*p*
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	**0.019**
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	**0.016**
Corticosterone x Body mass	-0.246	0.087	8.06	1	0.782	0.660–0.927	**0.005**
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