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Stress as an adaptation II: Does experimental cortisol supplementation affect predation risk assessment in foraging gerbils?

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ABSTRACT

Background: Animals are well known for trading off food and safety, and we have previously shown for Allenby's gerbil (*Gerbillus andersoni allenbyi*) that the intensity of this trade-off changes with energetic state. Furthermore, we have shown that concentrations of corticosteroid metabolites in desert rodents' faeces change in response to changing levels of food availability, competitor density, and moonlight. This suggests that stress hormones play an important role in mediating the trade-off of food and safety and in managing foraging.

Hypotheses: Higher concentrations of the exogenous stress hormone cortisol will increase gerbils' marginal valuation of energy (MVE) and their vigilance. In general, cortisol will mediate responses to slowly changing factors associated with food and safety, but not to rapidly changing ones.

Methods: In order to test these hypotheses, we manipulated cortisol concentrations in a set of gerbils by injecting each subcutaneously with 21-day slow-release 0.01 mg cortisol pellets and compared their foraging behaviour with that of a control group. The experiment was conducted in a large outdoor vivarium where we could simulate features of the gerbils' desert environment, manipulate the presence of a predatory owl (i.e. a rapidly changing factor), and quantify patch use over the course of a lunar cycle from new moon to full moon (i.e. a slowly changing factor). Foraging behaviour was quantified by giving-up densities (GUDs; the amount of food left in a resource patch after foraging), time allocated to foraging, and harvest rate curves in artificial foraging patches (seed trays).

Results: Giving-up densities were affected by the interaction of cortisol treatment and moon phase, but not the interaction of cortisol treatment and owl presence. Gerbils implanted with cortisol foraged longer, but harvested food more slowly (suggesting greater vigilance and apprehension), than placebo-treated gerbils. This reaffirms that glucocorticoids affect energy

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acquisition, and provides a physiological context to explain how foragers manage risk and the trade-off between food and safety.

Keywords: cortisol, foraging behaviour, *Gerbillus andersoni allenbyi*, giving-up densities, glucocorticoids, microhabitat, moon phase, predation risk, quitting harvest rates, stress.

INTRODUCTION

Animals must survive in a world that poses threats to their lives and food resources. These can occur either directly from predation, or indirectly from slowly changing environmental factors such as moon phase that increase predation risk, and competition from high densities of conspecifics or interspecific competitors. Because foragers must often leave a refuge to seek resources, they deplete food in safe places before they deplete food in risky places, and predators tend to aggregate where prey seek their resources, so foragers typically must manage risk of predation and trade off food and safety (Lima and Dill, 1990). The tools for such management include *time allocation* (i.e. where, when, and how much time is devoted to foraging), *apprehension* (i.e. the redirection of attention from foraging tasks to predator detection while continuing to harvest food), and *vigilance* (i.e. an extreme form of apprehension in which all attention is directed towards predator detection and foraging ceases) (Brown, 1999; Kotler *et al.*, 2002, 2004, 2010; Embar *et al.*, 2011). Such risk management can be altered by the state of the forager (Kotler *et al.*, 2004).

Stress hormones are closely tied to such fitness-related behaviours and trade-offs and, as postulated by Wingfield *et al.* (1998), animals may use the modulation of stress hormone production to shape behaviour adaptively to maximize fitness (e.g. Sheriff *et al.*, 2009; Dantzer *et al.*, 2013; Jaatinen *et al.*, 2013). This includes foraging decisions.

Optimal foraging theory (e.g. Charnov, 1976) is an excellent bridging tool that provides a framework to better understand the relationship between stress hormones and foraging behaviour (Clinchy *et al.*, 2013). In regard to patch use in a risky world, an optimal forager should exploit a food patch until the harvest rate from that patch (H) declines to equal its energetic (C), predation (P), and missed opportunity costs (MOC) for foraging (Brown, 1988, 1992), i.e. a forager should quit a patch when

$$H = C + P + MOC. \quad (1)$$

When the density of food in a patch is depleted to the point where equation (1) is satisfied, the forager should leave that patch for another one or change activities. This density is called the giving-up density (GUD). In regard to equation (1), the predation costs of foraging (P) and the missed opportunity costs (MOC) are complex costs that include the forager's marginal value of energy (MVE – added fitness from the next bit of food/energy obtained) (Brown, 1992; Iribarren and Kotler, 2012). As such, patch use and risk management can be expected to change with the energetic state of the forager, as has been shown in desert rodents such as gerbils, including the focus of this study, Allenby's gerbil, *Gerbillus andersoni allenbyi* (Kotler *et al.*, 2004).

Foraging and risk management change with animal state and environmental conditions in predictable and adaptive ways (Kotler, 1997), and these changes can be governed and entrained physiologically (Dantzer *et al.*, 2014). For example, stress hormone concentrations change with foraging costs and the marginal value of energy or vice versa depending upon species and ecological contexts (Wingfield *et al.*, 1998; Angelier *et al.*, 2009).

The glucocorticoids, or glucocorticosteroids (GCs), are a type of stress hormone, and their name is derived on the basis of their characteristics. They regulate glucose metabolism (Gluco-), are synthesized in adrenal cortex located on the kidneys (-cortic-), and are steroidal (-oid) in structure. These stress hormones help organisms fulfil energy requirements by increasing appetite (Dallman, 2010), increasing glucose metabolism (McGuiness *et al.*, 1993) or redistributing stored energy (Dallman *et al.*, 2004; Poggioli *et al.*, 2013). Examples include dexamethasone, cortisol (formally hydrocortisone), and corticosterone. In *G. a. allenbyi*, cortisol is the predominant hormone (Koren *et al.*, 2012), thus the focus of our study was to test the role of cortisol in the foraging ecology of this species.

Glucocorticoids are synthesized to help meet the energy demands (allostatic load) for long-term exigency effects, as opposed to immediate 'fight or flight' responses (Wingfield *et al.*, 1998; McEwen and Wingfield, 2003). Predators represent an emergency factor that may require split-second responses for survival, so mediation for such a response may be due to catecholamines from the adrenal medulla (Axelrod and Reisine, 1984). Although movements of predators such as the flight of an owl should not increase a forager's levels of glucocorticoids, the persistent presence of a predator (Sheriff *et al.*, 2009) or even predator odour could increase stress hormone concentrations (Thomas *et al.*, 2006). Slowly changing factors that are linked to predation risk can cause levels of glucocorticoids to shoot up (Dantzer *et al.*, 2014), including disruption of favoured microhabitats (Wingfield *et al.*, 1998), moon phases that render animals more visible to predators (St. Juliana, 2005; Gutman *et al.*, 2011), and high population densities resulting in severe competition and food deprivation (Bronson and Eleftheriou, 1964; Dantzer *et al.*, 2013). These factors either cause the animals to starve or result in a shortfall of food intake, and as a response levels of glucocorticoids will increase, which in turn stimulates the animal to search for food (Dallman *et al.*, 2004). Conversely, an abundance of food can override the effect of stress (Astheimer *et al.*, 1992; Angelier *et al.*, 2009). Thus, if levels of glucocorticoids rise in an animal in the presence of predators, it may not be because of the predators, but instead the lack of food intake resulting from the fear response to predation risk.

Based on these considerations, we hypothesize the following. Supplementing cortisol artificially in animals should:

- elevate their marginal value of energy (MVE);
- override the stress response induced by slowly changing factors such as moonlight (because of high MVE, GUD in cortisol-supplemented animals will be low both with a new and full moon);
- not mediate responses to quickly changing factors (e.g. presence of owls);
- cause increased vigilance and apprehension (Blanchard *et al.*, 1998).

To examine these possibilities, we manipulated stress hormones in foragers experimentally and quantified the foraging decisions of a small mammal under risk of predation.

MATERIALS AND METHODS

Our experiment was conducted in a large outdoor arena or vivarium ($34 \times 17 \times 4.5$ m) located at the Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, Israel during November–December 2013. The vivarium was divided into four equal-sized sectors by a one-metre tall rodent-proof fence and roofed

with chicken wire to contain owls. In each sector, we placed 18 bush-topped trellises to create two distinct microhabitats: bush and open. Six of these 18 stations, spaced at equal intervals, each received one artificial food patch (a seed tray, $28 \times 38 \times 8$ cm), for a total of 24 in the vivarium. These seed trays were each filled with 3 litres of sand into which we mixed 3 g of millet seeds that provided food for the gerbils. Three of the food patches in each sector were placed under trellises that mimic bushes and provide safety (i.e. the bush microhabitat); the other three were placed in the open just next to a trellis (i.e. the open microhabitat). The microhabitats of each tray were switched on alternating experimental nights by moving trays. Four of the 24 stations with seed trays were monitored using PIT (passive induction transponder) tag reader/loggers to record individual forager identity and the time and duration of each visit to the trays. Seed trays were opened at sunset at approximately 18.00 h (since the animals are nocturnal) and left open for gerbils to forage in until 03.00 h. Thus, the GUD and time spent in a patch reflected 9–10 hours of potential foraging

Our experimental animals were Allenby's gerbils (*G. a. allenbyi*; 24 in total, 14 females and 10 males), each marked with uniquely numbered PIT tags. Twelve (7 females, 5 males) of these gerbils were subcutaneously injected with 21-day slow-release 0.01 mg cortisol pellets (Innovative Research of America, Sarasota, FL) (the supplemented group) and the other 12 received placebo pellets (the placebo group). They were then released into different halves of the vivarium based upon the treatment to which they were allocated during a new moon and removed from the vivarium 22 days later following the full moon, so that experimental duration would coincide with the release period of cortisol from the pellets. Owls were introduced into the vivarium on alternating nights to provide a risk of predation. We collected data for 9 nights centred on the new moon and 7 nights centred on the full moon.

The following data were collected on experimental nights:

1. *Giving-up density*: Food trays that were foraged during the night by gerbils were sieved the following morning and any remaining millet seeds were collected and weighed to obtain the GUD for each tray.
2. *Reader data*: Data from electronic readers were downloaded onto a computer after each experimental session. Readers logged visits to trays, including the identity of the forager, the time of the visit, and its duration. From this we obtained cumulative duration of foraging time by all gerbils for each reader-equipped tray on each night. When foraging time is combined with quantity of food eaten from a tray and fit to a Holling's disc equation, we get harvest rate curves as a function of seed density (Kotler and Brown, 1990; Kotler *et al.*, 2010; Embar *et al.*, 2011) (see evolutionary-ecology.com/data/3060Appendix.pdf). The slopes of these curves reflect the foragers' level of vigilance and apprehensiveness, and the mean GUD on the curve reflects time allocated to foraging: shallower curves reflect more vigilant foraging, and points closer to the origin represent more time allocated to foraging (Brown, 1999).

The GUD and reader data (foraging time) were analysed by analysis of variance (ANOVA) using SYSTAT v.13. Tukey's HSD tests were used for *a posteriori* contrasts.

RESULTS

Patch use by gerbils as measured by GUDs was affected by hormone supplementation and risk factors. Supplemented gerbils had lower GUDs but this difference was not significant (MS = 1.564, $F_{1,343} = 1.657$, $P < 0.2114$; mean GUD in general for 3 g millet seed: supplemented = 1.144 ± 0.063 g, placebo = 1.275 ± 0.067 g; Fig. 1). Gerbils foraging during a full moon (MS = 29.860, $F_{1,343} = 61.945$, $P < 0.001$; mean GUD with new moon = 0.98 ± 0057 g, full moon = 1.504 ± 0.069 g; Fig. 2) and in the open microhabitat (MS = 60.320, $F_{1,343} = 125.135$, $P < 0.001$; mean GUD in open = 1.636 ± 0.066 g, bush = 0.783 ± 0.047 g; Fig. 2) had significantly higher GUDs, and gerbils had marginally higher GUDs in the presence of owls (MS = 1.821, $F_{1,343} = 3.777$, $P < 0.053$; mean GUDs with owls present = 1.257 ± 0.068, owls absent = 1.173 ± 0.062; Fig. 2).

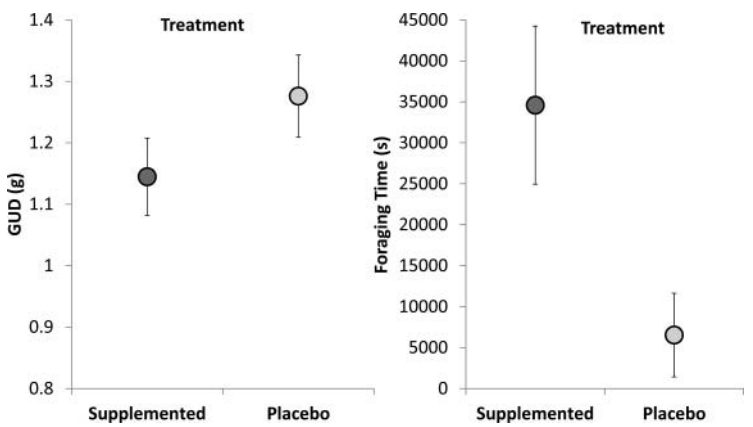

Fig. 1. Giving-up densities (GUDs; $n = 384$) and foraging durations ($n = 64$) for gerbils receiving hormone pellets (supplemented) and gerbils receiving a placebo. The effects of treatment on GUD and foraging time were not significant. Error bars indicate standard error of arithmetic mean.

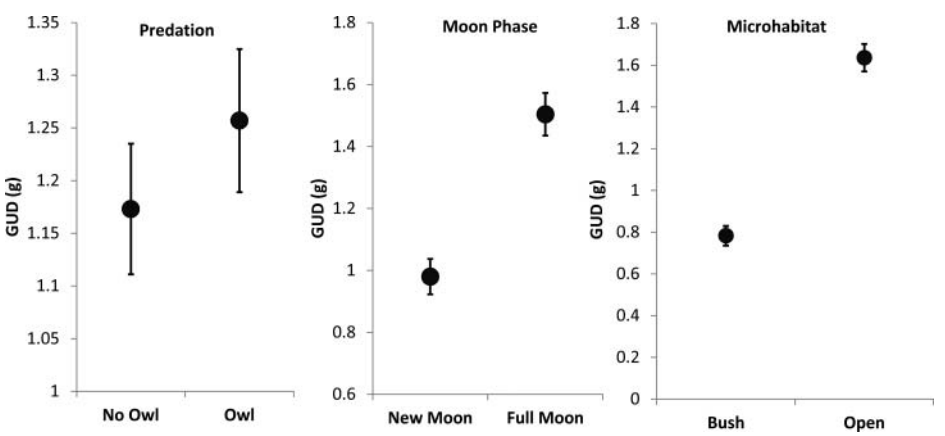

Fig. 2. Effects of predation, moon phase, and microhabitat on giving-up density (GUD) for both groups of gerbils ($n = 384$). The effect of predation was marginal; moon phase and microhabitat had significant effects. Error bars indicate standard error of arithmetic mean.

Interestingly, GUD was affected by an interaction between hormone treatment and moon phase (MS = 2.411, $F_{1,343} = 5.011$, $P = 0.026$; Fig. 3). During a new moon, the GUD of the hormone-supplemented group was significantly lower than that of the placebo group (Tukey's HSD test, $P = 0.012$; mean GUD with new moon: supplemented = 0.864 ± 0.075 g, placebo = 1.009 ± 0.085 g; Fig. 3), but not during a full moon (mean GUD with full moon: supplemented = 1.511 ± 0.094 g, placebo = 1.497 ± 0.102 g; Fig. 3). The effects of the treatment × owl and treatment × microhabitat interactions on GUD were not significant.

The time that gerbils allocated to foraging resource patches was also affected by hormone supplementation and risk factors. Hormone supplementation caused gerbils to increase time allocated to foraging (supplemented = 34,590.73 ± 9658.582 seconds, placebo = 6523.176 ± 5109.247 seconds; Fig. 1), but this increase was not significant (MS = 3.526×10^9, $F_{1,30} = 3.788$, $P = 0.3859$). Moon phase also had an effect on time allocated to foraging (MS = 5.031×10^9, $F_{1,30} = 5.406$, $P = 0.027$), with foraging time being significantly shorter during a full moon (new moon = 34,143.500 ± 10,081.563 seconds, full moon = 10,042.579 ± 6299.441 seconds; Fig. 4). There was also a marginally significant effect of microhabitat (MS = 2.83×10^{10}, $F_{1,30} = 3.041$, $P = 0.091$), with a trend towards more time spent in the bush microhabitat (bush = 41,103 ± 10,889.2 seconds, open 5047 ± 4107.523 seconds; Fig. 4). In addition, time allocated to foraging showed a marginally significant interaction with microhabitat (MS = 3.813×10^9, $F_{1,30} = 4.097$, $P = 0.052$), with a trend towards the hormone-supplemented gerbils spending more time in the bush microhabitat (in bush habitat: supplemented = 57,171.86 ± 14,521 seconds, placebo = 12,982.500 ± 10,743.674 seconds; Fig. 5). Owls, hormone treatment, and the treatment × owl and treatment × moon interactions did not directly affect foraging time.

The harvest rate curves shown in Figs. 6 and 7 reveal how gerbils use time allocation and vigilance to manage risk in relation to hormone supplementation and the risk factors. Recall that these curves are derived through the use of GUDs and measures of time allocation to parameterize Holling disc equations (see 3060Appendix.pdf); they are not regression

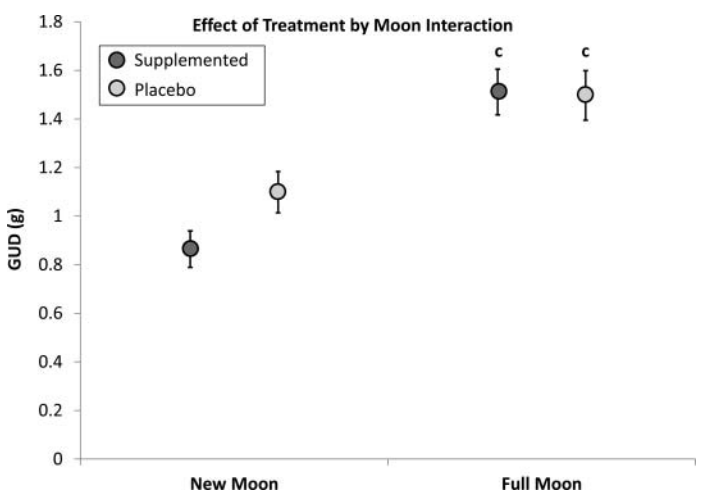

Fig. 3. Effect of the interaction between treatment and moon phase ($n = 384$). Treatment had a significant effect on giving-up density (GUD) during a new moon, as indicated by the experimental group foraging more food. Error bars indicate standard error of arithmetic mean.

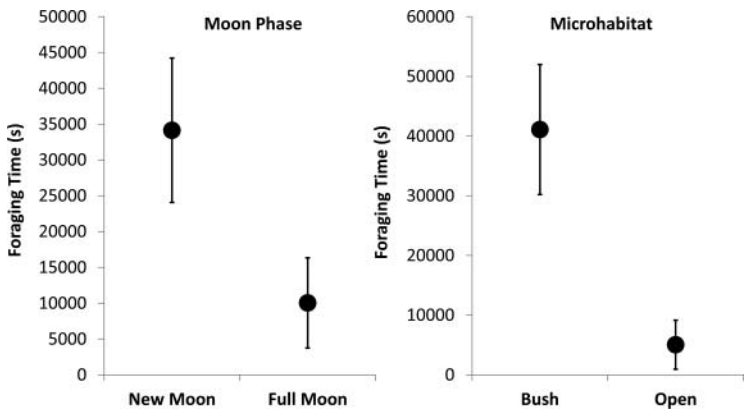

Fig. 4. Foraging time in response to moon phase and habitat ($n = 64$). The effect of moon phase was significant, but that of microhabitat was marginal. Error bars indicate standard error of arithmetic mean.

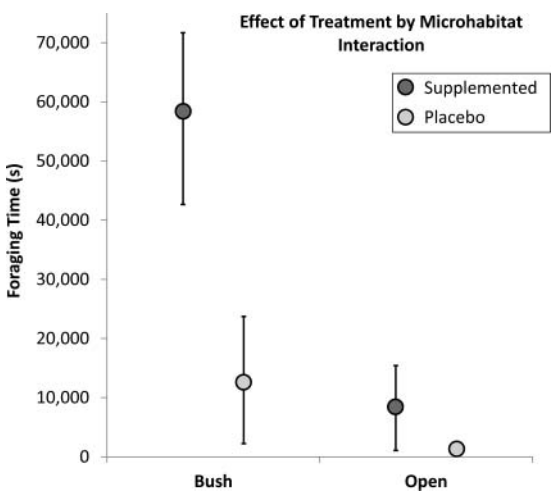

Fig. 5. There was a marginal effect of the treatment × microhabitat interaction on foraging time ($n = 64$). The experimental group spent relatively more time in bush microhabitat.

lines. Gerbils in the hormone treatment had shallower harvest rate curves, suggesting they displayed greater vigilance and apprehension than gerbils in the placebo group (Fig. 6a). When the environment was safer (as in the bush microhabitat, absence of owls, and new moon), the gerbils of both groups allocated more time to foraging, as indicated by mean GUDs closer to the origin. They were more vigilant in the bush microhabitat (Fig. 6b) and were only slightly more apprehensive during a new moon (Fig. 6d). The degree of apprehensiveness was the same regardless of whether owls were present or not (Fig. 6c). Regarding the interaction between treatment and other factors (Fig. 7), the hormone-supplemented group was more apprehensive than the placebo group, especially during a full moon (Fig. 7a) and in the open microhabitat (Fig. 7b).

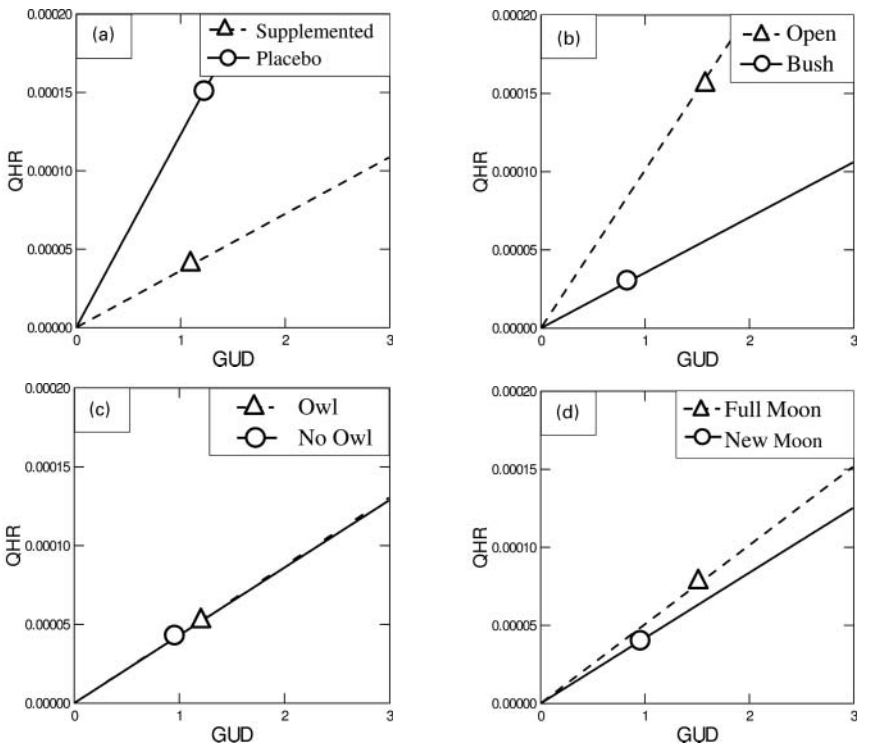

Fig. 6. Harvest rate curves show how the risk management tactics of the gerbils were affected by the experimental conditions (QHR = quitting harvest rate). The lines are not regression lines. We plot each line from a parameterized Holling disc equation. Then we highlight the single point on each that is the value of the equation at the mean giving-up density (GUD). Shallower curves indicate slower, more careful harvesting of seeds and therefore greater vigilance. Mean GUDs closer to the origin reflect more time allocated to foraging. (a) Cortisol as a supplement depressed the QHR line (slower harvesting with greater vigilance). (b) Foragers in the open showed high GUDs and quit at considerably higher harvest rates, but were not very vigilant (reflecting the comparative danger of the open). (c) QHRs did not depend on the presence or absence of owls. (d) Moon phase had a limited effect on the QHR lines themselves. But when foragers faced the relatively high risk of a full moon, they quit foraging at a higher QHR and higher GUD.

DISCUSSION

An effect of cortisol treatment on giving-up densities was only observed for the interaction between treatment and moon phase (Fig. 3): the hormone-supplemented group foraged to lower GUDs and harvested more seeds than the placebo group on nights with a new moon, but not nights with a full moon. In line with our first hypothesis, supplemented gerbils appear to increase their marginal valuation of energy (MVE). This may be a result of them eliciting higher metabolism and energy demands according to environmental conditions, as reflected in their lower GUDs (Richardson *et al.*, 1995; Wingfield *et al.*, 1998; Laiz-Carrión *et al.*, 2002). In contrast, on riskier occasions when there is a full moon, it may be that the elevated energy demand as a result of the cortisol supplementation was met in gerbils through other means such as burning stored energy rather than increasing food intake (Dallman *et al.*, 2004; Busch and

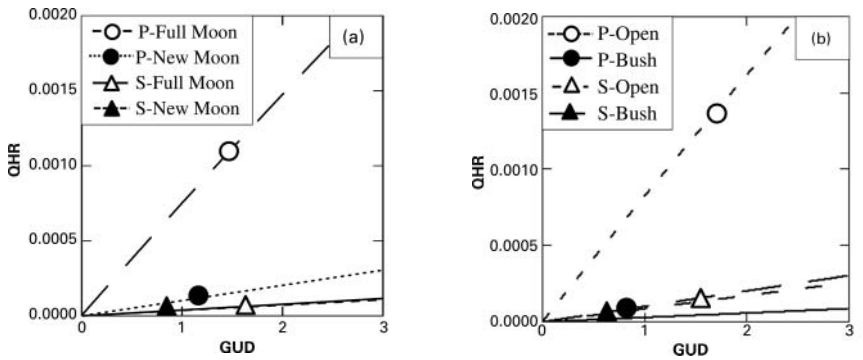

Fig. 7. Harvest rate curves for the interactions of hormone supplementation with (a) moon phase and (b) microhabitat. The plots are generated in the same manner as those in Fig. 6 and again are not regression lines. P = placebo and S = supplementation. The supplemented group was more apprehensive than the placebo group during nights with a full moon and in the open microhabitat. Also, there was no effect of moon phase on QHRs for supplemented gerbils, but placebo gerbils allocated more time to foraging. Supplemented gerbils were always highly apprehensive, while placebo gerbils differed across microhabitats in both time allocated to foraging and apprehension.

Hayward, 2009). With a full moon, gerbils produce cortisol naturally so that even the control (placebo) gerbils should have had higher cortisol concentrations on those nights (St. Juliana, 2005); thus the GUDs of the two groups did not differ significantly when there was a full moon. Therefore, our second hypothesis – that increasing cortisol concentrations (in the implanted group) would override the response to the full moon – can be rejected. In fact, we found the opposite: moon phase overrides the effect of hormone supplementation. It also provides support for Gutman *et al.* (2011), that higher glucocorticoid concentrations in riskier conditions may cause a reduction in foraging to avoid predation. Furthermore, the fact that gerbils in the supplemented group also markedly increased their GUDs during a full moon compared with the placebo group (Fig. 3) suggests that gerbils in the implanted group foraged more than those in the placebo group on safer nights and less on riskier nights. Based on our third hypothesis, we expected gerbils in the implanted group not to forage differently than those in the placebo group in the presence of owls, a rapidly changing factor. The lack of a predator × treatment interaction provides support for this hypothesis.

Foraging time was found to differ marginally based on the treatment × microhabitat interaction (Fig. 5). The supplemented group tended to spend more time in the bush microhabitat, perhaps because the anxiety brought on by glucocorticoids led the gerbils to be more vigilant to the risk of predation (Blumstein, 2010). The gerbils that were implanted with cortisol were more apprehensive than the control gerbils under all conditions; this finding supports our fourth hypothesis that higher cortisol concentrations increase vigilance. Slower harvest rates were observed in safer circumstances (new moon and in bush microhabitat), with gerbils tending towards being more apprehensive. The opposite was true for the riskier conditions in which gerbils in both groups spent little time exploiting trays and displaying little vigilance, instead using a 'grab-and-go' tactic (St. Juliana, 2005; Mukherjee, 2010). The level of apprehension in general was the same both in the presence and absence of owls. Thus, when owls were present, gerbils managed predation risk by reducing time allocated to foraging and increasing GUD. The harvest rate curves for the treatment × moon interaction suggest that cortisol implants swamp the gerbils' ability to alter their apprehensiveness

according to moon phase, thus partly supporting our second hypothesis that cortisol supplementation nullifies any effect of moon phase. The supplemented group showed the same level of apprehension regardless of whether there was a new or a full moon; however, they did spend less time foraging during a full moon. In contrast, placebo gerbils used a combination of vigilance and time allocated to foraging to manage risk across moon phases.

In conclusion, our hormone manipulation experiment sheds light on the physiological mechanisms that influence gerbil foraging decisions, based on environmental threats. Since higher stress hormone concentrations increase MVE (Wingfield *et al.*, 1998), gerbils that received 0.01 mg cortisol pellets harvested more food and foraged for longer. Nonetheless, this higher food intake was observed only with a new moon, not a full moon. This suggests that the foraging response in gerbils to a full moon may be hardwired (Gutman *et al.*, 2011) and is not influenced by exogenous steroid manipulation. Our results are consistent with the hypothesis that cortisol does not mediate responses to fast changing factors such as the presence of owls; however, we failed to find a significant treatment × owl interaction, and so this result is only tentative. Finally, experimental implantation of cortisol caused gerbils to be more apprehensive when foraging. Although the experimental animals were equally apprehensive across moon phases, the time they allocated to foraging differed across moon phases. Therefore, our second hypothesis that higher cortisol overrides the effect of moon phase holds true for harvest rates but not GUDs.

Experimental gerbils spent more time foraging, but did so more carefully. In this way, stress hormones may allow foragers to change adaptively the rate at which they trade off food and safety in response to their internal state and the state of the environment. This in turn affects foraging success of individuals, species interactions, and the co-existence of close competitors under the risk of predation.

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