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Long-term moderate elevation of corticosterone facilitates avian food-caching behaviour and enhances spatial memory

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It is widely assumed that chronic stress and corresponding chronic elevations of glucocorticoid levels have deleterious effects on animals' brain functions such as learning and memory. Some animals, however, appear to maintain moderately elevated levels of glucocorticoids over long periods of time under natural energetically demanding conditions, and it is not clear whether such chronic but moderate elevations may be adaptive. I implanted wild-caught food-caching mountain chickadees (*Poecile gambeli*), which rely at least in part on spatial memory to find their caches, with 90-day continuous time-release corticosterone pellets designed to approximately double the baseline corticosterone levels. Corticosterone-implanted birds cached and consumed significantly more food and showed more efficient cache recovery and superior spatial memory performance compared with placebo-implanted birds. Thus, contrary to prevailing assumptions, long-term moderate elevations of corticosterone appear to enhance spatial memory in food-caching mountain chickadees. These results suggest that moderate chronic elevation of corticosterone may serve as an adaptation to unpredictable environments by facilitating feeding and food-caching behaviour and by improving cache-retrieval efficiency in food-caching birds.

Keywords: corticosterone; chronic stress; food caching; cache-retrieval efficiency; spatial memory; mountain chickadee

1. INTRODUCTION

It is widely believed that long-term chronic stress and associated long-term elevation of glucocorticoid hormone levels have negative effects on the cognitive abilities of animals by causing neuronal cell death and reducing neurogenesis (Sapolsky 1992, 1996; McEwen & Sapolsky 1995; McEwen 2000). Most animals respond to unpredictable and/or sudden changes in social and physical environment by rapidly elevating circulating glucocorticoid levels above baseline (Wingfield *et al.* 1997, 1998; Silverin 1998). By suppressing many physiological functions, which are not important at that moment, and enhancing functions critical for immediate survival, elevated glucocorticoid hormone levels significantly increase an animal's probability of survival (Wingfield *et al.* 1997, 1998; Silverin 1998). Whereas short-term effects of such elevations have consistently been regarded as beneficial for learning and memory, prolonged elevations of glucocorticoid levels are believed to be extremely damaging (McEwen & Sapolsky 1995; Wingfield *et al.* 1997, 1998).

Little is known about chronic elevations of glucocorticoid levels that only moderately exceed baseline (twofold or threefold versus more than tenfold increases under acute stress). For example, baseline levels of corticosterone in willow tits (*Parus montanus*), a small food-caching bird, appear to be twice as high during the most stringent winter months when foraging conditions are most demanding compared with the baseline levels during summer and early autumn (Silverin 1998). It is well known that short-term food deprivation elicits elevated levels of corticosterone (Harvey *et al.* 1984; Wingfield *et al.* 1997, 1998). Wingfield *et al.* (1998) referred to short-

term increases in corticosterone and associated changes in behaviour as 'emergency life-history stages', when a response to a sudden change in the environment interrupts the normal life-history cycle and re-directs behaviour and physiology towards survival. In particular, increased levels of corticosterone might facilitate foraging behaviour and trigger opportunistic migration and the mobilization of stored energy reserves to fuel increased locomotory activities (Astheimer *et al.* 1992; Wingfield *et al.* 1997, 1998; Lynn *et al.* 2003). During winter, however, extremely demanding environmental conditions may last for months, and resident birds, most notably food-caching parids (chickadees and tits), often devote almost all of their winter days to foraging (Pravosudov 1985). Food-caching parids depend on their caches to survive the winter and rely, at least in part, on spatial memory to retrieve previously made caches (Sherry 1992; Shettleworth 1995; Krebs *et al.* 1996). Thus, memory is an important fitness component for these birds as successful cache retrieval could be crucial for survival. Although food may be limited and unpredictable for long periods of time during the winter, many food-caching parids do not leave their home ranges for more favourable habitats (Pravosudov 1985, 1987). Furthermore, even experimentally increased levels of corticosterone failed to trigger migration in these birds during the winter (Silverin 1997). Pravosudov *et al.* (2001) experimentally demonstrated that long-term limited and unpredictable food supply results in moderately elevated corticosterone levels (lower than standardized stress response) in food-caching mountain chickadees (*Poecile gambeli*). Such small but chronic elevations in corticosterone levels triggered by unpredictable food supply were also correlated with enhanced cache-retrieval

Proc. R. Soc. Lond. B (2003) **270**, 2599–2604
DOI 10.1098/rspb.2003.2551

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efficiency and spatial memory performance (Pravosudov & Clayton 2001). These results suggest that moderate elevations in corticosterone might be adaptive responses to environmental variability, enhancing cache-retrieval efficiency and spatial memory even on a long-term basis. Supporting the view that moderate elevations might enhance memory, hippocampal neuron firing rate was found to be positively correlated with corticosterone levels within an intermediate range, but negatively correlated with corticosterone levels within a high range in laboratory rats (Diamond *et al.* 1992). Thus, it is possible that only chronic elevations above some threshold would produce deleterious effects on learning and memory whereas chronic moderate elevations below the threshold might actually enhance spatial memory.

It was also shown that unpredictable food supply triggers more food caching in birds (Hurly 1992; Pravosudov & Grubb 1997), thus it is possible that corticosterone elevated in response to variable food supply (Pravosudov *et al.* 2001) also facilitates food-caching behaviour. As more caching and more efficient cache retrieval would significantly improve a wintering animal's probability of survival (Pravosudov & Lucas 2001), long-term elevation of corticosterone could be a highly adaptive response to energetically challenging environmental conditions in food-caching animals.

In this study, I tested whether chronic but moderate elevation of corticosterone levels in food-caching mountain chickadees has a direct effect on food-caching behaviour, cache-retrieval efficiency and spatial memory. More specifically, my predictions were that elevated corticosterone levels:

(i) facilitate more foraging;
(ii) facilitate food-caching behaviour; and
(iii) enhance cache-retrieval efficiency and spatial memory.

2. MATERIAL AND METHODS

Twenty-eight mountain chickadees were caught around Sage Hen, Tahoe National Forest, CA, USA between 13 and 16 October 2002 using mist nets near baited feeders. All birds were transported to the laboratory at the University of California in Davis, placed individually in wire-mesh cages (60 cm × 42 cm × 60 cm) and maintained on a 9 L : 15 D cycle at a constant 20 °C for the duration of the experiment. Birds were fed with a mixture of pine nuts, shelled and unshelled sunflower seeds, crushed peanuts and mealworms, and given water with vitamins *ad libitum*. Approximately two weeks after capture, I randomly chose four birds to calibrate the corticosterone implants. On 30 October 2002, I collected blood from each of the four chosen chickadees for radioimmunoassay analyses of baseline plasma corticosterone. On 1 November 2002, I gave these birds corticosterone implants of different sizes (0.01, 0.025, 0.05 and 0.1 mg of corticosterone) and two weeks later I collected blood from each bird again to determine the effect of the implants. I used biodegradable 90 days continuous time-release corticosterone implants (1.5 mm in diameter, Innovative Research of America) placed subcutaneously on the flank. These implants are designed to release a constant amount of corticosterone per unit time during the entire 90 day period. The implants caused an
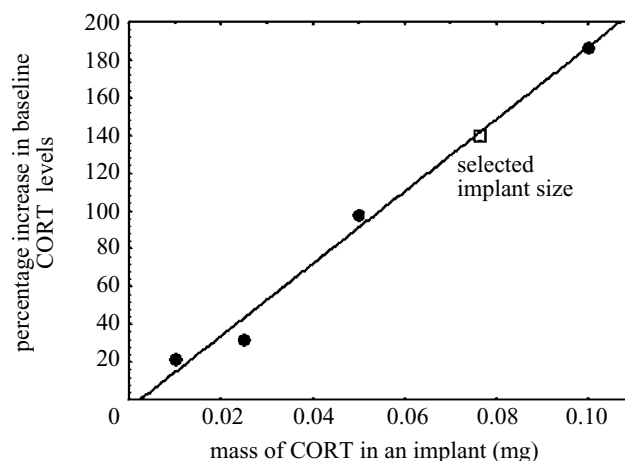
Figure 1. The relative increase in baseline corticosterone (CORT) levels in relation to the selected size of the CORT implant in mountain chickadees.

increase in baseline corticosterone levels ranging from 21% (0.01 mg implant) to 186% (0.1 mg implant) and the relationship between the size of the implant and the relative increase in the baseline corticosterone level was highly significant (regression, $F_{1,2} = 188.20$, $p < 0.01$, $r^2 = 0.99$; figure 1). On average, the four birds prior to implantation had baseline corticosterone levels of 5.12 ± 0.95 ng ml^{-1} whereas after implantation these average levels increased to 8.73 ± 1.61 ng ml^{-1}. The baseline corticosterone values prior to implantation are similar to previously reported baseline corticosterone levels in mountain chickadees (Pravosudov *et al.* 2001, 2002, 2003). To simulate a moderate increase in baseline corticosterone levels, similar to those found in Pravosudov *et al.* (2001), I chose implants containing 0.075 mg of corticosterone, which should result in approximately a 140% increase in baseline corticosterone levels (figure 1). This is a modest increase, as mountain chickadees typically show greater than 800% increases above baseline during the standardized stress response (Pravosudov *et al.* 2001, 2002, 2003). On 5 December 2002, I implanted 12 mountain chickadees with the 0.075 mg corticosterone pellets (which are supposed to release *ca.* 833 ng of corticosterone per day continuously over 90 days) and 12 chickadees were implanted with matched placebo pellets (Innovative Research of America). All pellets were 1.5 mm in diameter and they were placed subcutaneously on the flanks of the birds.

To estimate the concentration of plasma corticosterone during the implant-calibration procedure prior to the experiment, I collected one capillary tube of blood from a brachial vein within 3 min of opening the cage between 12.00 and 14.00. In mountain chickadees, samples collected within 3 min represent baseline values of corticosterone (Pravosudov *et al.* 2001, 2002, 2003). Blood was emptied into 0.3 ml vials and kept on ice. All samples were centrifuged within 1 h of blood collection, and the collected plasma samples were frozen at −20 °C until assay.

Plasma corticosterone levels were estimated using an I^{125} radioimmunoassay kit from ICN Biomedicals (Costa Mesa, CA, USA), which has been previously used to analyse plasma samples from mountain chickadees (Pravosudov *et al.* 2003). Samples were assayed in duplicates and gave an intra-assay variance of 1.54%.

Seven days after implantation, I started testing the birds' caching behaviour and spatial memory performance individually in

a cache-recovery task and subsequently in two versions of a one-trial associative learning task (Pravosudov & Clayton 2001, 2002). Prior to behavioural tests, each bird was familiarized with the experimental room for 2 h in total during two separate 1 h sessions. During these sessions food was provided *ad libitum* and birds were allowed to eat and cache freely. I also placed seeds in cache sites so that birds learned to search for food in these sites.

(a) *Experimental room*

All birds were tested individually in the room (325 cm × 218 cm × 312 cm) and observed through a one-way Plexiglas window. The room contained 70 evenly spaced caching sites. There were two trees constructed with tree branches with 20 caching holes in each tree and 30 caching blocks, which were hung from wire-mesh screens attached to the two opposite walls of the room (15 blocks on each wall). Each caching block consisted of a wooden rectangle (8 cm × 14 cm × 3.5 cm). In the centre of the block there was a hole. Holes both in the trees and in wooden blocks were 0.5 cm in diameter and 0.5 cm deep. Each hole could be covered by a knot in the end of a short string attached above the hole to prevent the birds from seeing the contents of the hole (Pravosudov & Clayton 2001, 2002). A wooden perch was located below each hole. The birds readily cached food in all caching sites and inspected them for food.

I manipulated the lights and opened the flaps connecting the home cages with the room so that the birds could fly in and out of the experimental room. Thus, at the start of a trial, the lights were turned off in the home cage and turned on in the experimental room; at the end of the trial, the lights were reversed and the bird would fly into the home cage. By using this procedure, I avoided stress induced by handling the birds.

(b) *Cache-recovery task*

The cache-recovery task consisted of two phases separated by a retention interval of 5 h. Each bird was deprived of food for 2 h before night roost and 1 h following waking up in the morning prior to phase 1. During phase 1, an unlimited number of pine nuts were provided in a bowl. The birds were allowed to eat and to cache food individually for 20 min in the experimental room with 70 available caching sites. After phase 1, birds were returned to their home cages where they had *ad libitum* food (pine nuts, crushed peanuts and sunflower seeds). They were then deprived of food for 2 h prior to phase 2. Prior to phase 2, I also placed small pieces of pine nuts back in their original caching sites, which were different for each bird. During phase 2, birds were allowed in the experimental room for 10 minutes and the only food available to them was that which they had cached during phase 1. During phase 2, all 70 caching holes were covered with string knots so that the contents of caching sites were not visible. To retrieve a cache or to inspect the hole, a bird had to pull the string away from the hole (which all birds readily did). During the storage phase 1, I recorded the number of nuts cached and where they were located. During the recovery phase 2, I recorded the number of caches each bird recovered and the number of looks to find each nut. A bird was recorded as having made a look when it pulled at the string covering one of the potential cache sites. To calculate cache-retrieval efficiency, I used the number of looks made by a bird per number of successful cache retrievals.

Each bird performed two cache-recovery tests in which caching activity was unlimited (12–27 December 2002), starting on day 7 after the implantation of corticosterone, followed by a cache-recovery test in which each bird was limited to caching

only three nuts (28 December 2002 – 3 January 2003), ending on day 29 after implantation. The limited-caching test was performed to control for possible differences in the amount of cached food between the experimental groups. For statistical analyses, I averaged data from the two cache-recovery tests with unlimited caching.

(c) *One-trial associative learning task*

One problem with the cache-recovery task is that if birds differed in the number of caches they made, it would be more difficult to compare directly the birds' accuracies of cache recovery. In a one-trial associative learning task all birds have exactly the same experience because the experimenter effectively hides the caches and therefore controls for the number and location of items that need to be remembered. Thus, after the cache-recovery trials were completed, I also tested each bird individually in a one-trial associative learning task in which birds were trained to search for food in a site where they had found food previously.

In this task, birds were trained to search in phase 2 for food in a site in which they had found food previously during phase 1 of the trial (Pravosudov & Clayton 2001, 2002).

Each trial consisted of two phases separated by a retention interval of 60 min. In phase 1, each bird had to locate a visible piece of pine nut (which all birds did immediately without looking anywhere else). All birds were deprived of food for 2 h before night roost and 1 h in the morning following waking up prior to phase 1. Each bird was allowed to eat a small part of the nut for 30 s, after which the lights in the experimental room were turned off and the bird returned to its home cage. Birds received no food between phase 1 and phase 2. In phase 2, all food sites were covered with knots at the ends of the strings. The site containing the nut in phase 1 also contained a piece of pine nut covered by a string knot in phase 2 so the birds were rewarded for a successful search. If the bird remembered precisely where it had encountered the food, it should go directly to the site at which it had partially consumed the pine nut in phase 1 (Pravosudov & Clayton 2001, 2002). I recorded the number of sites inspected during phase 2 for each bird.

I used two versions of the one-trial associative learning task. In version 1 (4–11 January 2003, two trials), birds had 70 sites available to them and had to use spatial memory to remember the location of the baited site in phase 2. To control for the effect of motivation on performance, I also tested birds in a second version (13–15 January 2003) in which the baited site (one of 70 available) was marked with a unique colour pattern (using pieces of red and green tape) so that the birds did not have to rely on spatial memory to recall which site contained the hidden food. Motivation to search for food should affect performance in both versions of the task similarly, while, if there is a specific effect of treatment on spatial memory, it should not be evident in the easier colour-based task (Pravosudov & Clayton 2001, 2002). To avoid a treatment-order effect I performed another round of the spatial version of the task after performing the non-spatial (colour) version, and the last trial ended on day 48 after corticosterone implantation (16–22 January 2003, two trials). A different site was baited with food for each trial in both versions of the task.

3. RESULTS

The entire experiment took 48 days from the day of implantation to the last day of the behavioural tests. Prior to the experiment, birds assigned to experimental and con-
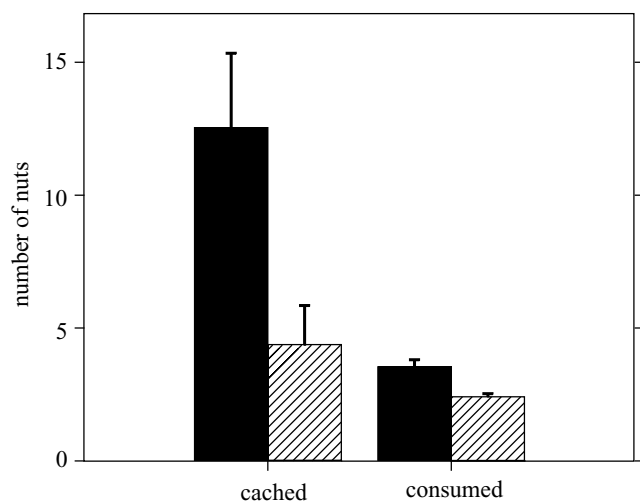
Figure 2. Mean number of pine nuts cached and mean number of nuts consumed (partly or fully) by corticosterone-implanted (filled bars) and placebo-implanted (hatched bars) mountain chickadees during unlimited cache-recovery trials.
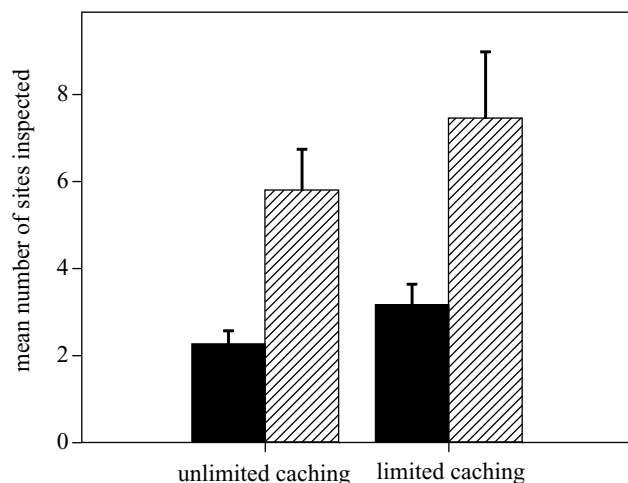

Figure 3. Mean numbers of sites inspected by corticosterone-implanted (filled bars) and placebo-implanted (hatched bars) mountain chickadees to find previously made caches during unlimited and limited cache-recovery trials.
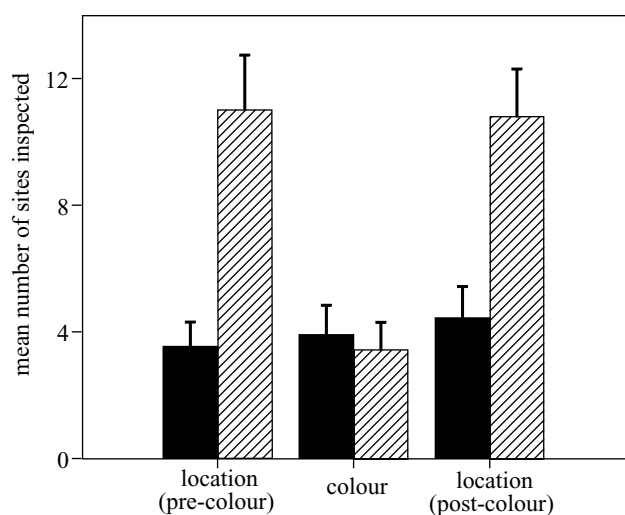

Figure 4. Mean numbers of sites inspected by corticosterone-implanted (filled bars) and placebo-implanted (hatched bars) mountain chickadees to locate previously found food during one-trial associative learning trials (location, spatial version; colour, non-spatial version).

trol groups did not differ significantly in their size (wing length: $t = 0.12$, d.f. $= 22$, $p = 0.91$) or body mass ($t = -0.49$, d.f. $= 22$, $p = 0.62$). At the end of the experiment, evening body mass (measured 2 h before night roost) was also not significantly different between the two groups ($t = -0.74$, d.f. $= 22$, $p = 0.46$) but corticosterone-implanted chickadees had more subcutaneous fat than placebo-implanted birds (fat score, one-tailed t-test: $t = 1.73$, d.f. $= 22$, $p = 0.04$). The one-tailed test was used here because an increase in fat levels as a result of elevated corticosterone levels was predicted prior to the experiment (Wingfield *et al.* 1997, 1998).

(a) Cache-recovery task

Corticosterone-implanted chickadees cached significantly more pine nuts during the unlimited trials than did placebo-implanted birds ($t = -2.51$, d.f. $= 21$, $p = 0.02$; figure 2), and they also consumed (fully or partly) significantly more nuts ($t = -3.64$, d.f. $= 21$, $p = 0.001$; figure 2). There was no significant difference in the numbers of retrieved caches between the two groups during the unlimited-caching trials ($t = -1.72$, d.f. $= 21$, $p = 0.10$), but corticosterone-implanted birds inspected significantly fewer sites to find previously made caches than did placebo-implanted birds ($t = 3.68$, d.f. $= 21$, $p = 0.001$; figure 3). As experimental birds also cached significantly more food than did the controls, it is possible that their superior performance could be explained by the fact that, even if searching randomly, they would need to inspect fewer sites to find their caches. When caching activity was limited to only three caches per bird for both groups, corticosterone-implanted chickadees maintained their superiority and inspected significantly fewer sites than control birds when recovering their caches ($t = 0.24$, d.f. $= 21$, $p = 0.01$; figure 3). There was no significant difference between the two groups either in the number of cached nuts ($t = -0.38$, d.f. $= 21$, $p = 0.80$) or in the number of retrieved caches ($t = 0.24$, d.f. $= 21$, $p = 0.81$) during the limited-caching trial.

(b) One-trial associative learning task

Corticosterone-implanted birds performed better than controls in the spatial version of the task (location), inspecting significantly fewer sites before finding the site containing food ($t = 4.05$, d.f. $= 21$, $p < 0.001$; figure 4). In the non-spatial (colour) version of the task, control birds performed as well as experimental birds ($t = -0.38$, d.f. $= 22$, $p = 0.71$; figure 4), indicating that both groups were equally motivated to search for food. When tested on the spatial version of the task (location) again after the non-spatial colour version, the differences re-appeared and corticosterone-implanted birds again showed superior performance, inspecting significantly fewer sites before finding food compared to placebo-implanted birds ($t = 3.24$, d.f. $= 19$, $p = 0.004$; figure 4). In both spatial versions of the task (preceding and following the non-spatial colour version), birds from both groups performed significantly better than would be expected from a random

search (corticosterone-implanted birds: $t < -30.5$, d.f. = 11, $p < 0.001$; placebo-implanted birds: $t < -16.00$, d.f. = 11, $p < 0.001$).

4. DISCUSSION

Supporting my predictions, this study demonstrated that chronically but moderately elevated corticosterone levels facilitate more feeding and food caching while enhancing cache-retrieval efficiency and spatial memory in mountain chickadees. This experiment also suggests that previously demonstrated effects of elevated corticosterone levels on body fat (Wingfield *et al.* 1997, 1998) persist on a long-term basis, as corticosterone-implanted birds maintained more subcutaneous fat even though their body mass was not significantly different from that of control birds.

Elevated corticosterone levels resulted in more intense feeding and food caching in experimental birds. Whereas the effect of corticosterone on feeding has been suggested previously (Astheimer *et al.* 1992; Wingfield *et al.* 1997, 1998), not much is known about the relationship between corticosterone levels and food-caching behaviour. Saldanha *et al.* (2000) reported that short-term elevations in corticosterone levels did not significantly affect caching rates in mountain chickadees but the fact that the corticosterone doses given to the experimental birds could have resulted in plasma levels exceeding stress-induced levels makes it difficult to interpret the results. My study suggests that both feeding and food-caching behaviour are affected by moderately elevated corticosterone levels. As both more feeding and more food caching are common responses to energetically challenging and variable environments (Pravosudov & Grubb 1997; Pravosudov & Lucas 2001), corticosterone appears to regulate both behaviours simultaneously.

Whereas our previous results suggested a possible link between unpredictable food, elevated corticosterone levels and spatial memory (Pravosudov & Clayton 2001; Pravosudov *et al.* 2001), this study confirmed it. Moderately elevated corticosterone levels resulted in enhanced cache-retrieval efficiency and enhanced spatial-memory performance on one-trial associative learning tasks. Enhanced performance in spatial-memory tasks could arise if corticosterone-implanted birds paid more attention to the cache sites during caching and therefore encoded the information more accurately, or if they were more accurate at recalling the sites in which they cached food. These results do not distinguish between differences in attention during encoding and differences in memory recall. However, either could be used to explain the enhanced spatial memory of the treatment group.

Distinguishing between memory and motivation to perform in spatial-memory tasks is a key to the interpretation of this type of study. Corticosterone-implanted chickadees cached more food and they also attempted to eat more food than did the controls. However, when motivational levels were tested in the non-spatial colour version of the learning task, there was no difference between experimental and control birds, suggesting that birds from both groups were sufficiently and equally motivated to search for hidden food. When control birds were tested on the spatial version following the non-spatial version, their per-formance significantly deteriorated to the levels found in the first spatial task, indicating that such performance was not the result of motivation but rather of spatial memory. Both experimental and control chickadees also performed significantly better than would be expected from a random search, again suggesting that placebo-implanted birds were as motivated to search for hidden food as corticosterone-implanted birds as a result of food deprivation prior to testing. These findings suggest that the differences found between corticosterone-implanted and placebo-implanted chickadees are specific to differences in spatial memory and not to differences in motivation.

The fact that these birds maintain reduced corticosterone levels when conditions are favourable (Silverin 1998; Pravosudov *et al.* 2001) suggests that maintaining moderately elevated corticosterone levels has costs even though these costs appear to be different, at least in part, from previously assumed costs implying deficits in memory and learning. Suppressed immune response, for instance, could be one such cost (Wingfield *et al.* 1997, 1998). Thus, chronic moderate elevation of corticosterone levels might be considered a trade-off: more efficient foraging and cache retrieval could provide greater benefits when environmental conditions are energetically demanding even when such benefits are associated with some costs. When conditions are favourable, however, the costs might outweigh the benefits provided by elevated corticosterone levels and thus reduced corticosterone levels would result in higher fitness.

This experiment suggests that chronic but moderate elevation of corticosterone levels could be adaptive to a highly variable environment. As environmental conditions during the winter can be energetically demanding and variable (limited and unpredictable food supply, cold ambient temperature, etc.), food-caching birds living at high latitudes could respond to such conditions by maintaining moderately elevated corticosterone levels, which would facilitate more intense foraging, fat accumulation, food caching and more efficient cache retrieval through enhanced spatial memory. All of these would greatly increase food-caching birds' survival probability in winter (Pravosudov & Lucas 2001). The results of my experiment challenge the widespread belief that any chronic elevations of glucocorticoid levels must be deleterious. Here, long-term intermediate elevations positively affected food caching, cache-retrieval efficiency and spatial memory in a wild bird. Such positive effects of chronically, but moderately, elevated glucocorticoid levels may be prevalent, but as yet unexplored. This study suggests that chronic moderate elevations in corticosterone levels might be adaptive responses within the normal range of baseline corticosterone levels regularly and routinely experienced by animals during different stages of their life cycles.

801080-01 and a permit from Tahoe National Forest (00-MU-11051760-009). All experiments were performed in accordance with the University of California Davis animal care protocol 9788.

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