

# The relationship between environment, corticosterone, food caching, spatial memory, and the hippocampus in chickadees

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## 3.1 Introduction

Many species in the family Paridae are well known for their food-caching behavior (Haftorn 1956; Pravosudov 1985; Brodin and Lundborg 2003; Lucas *et al.* 2004). All North American Parids have been reported to cache food whereas in Eurasia there are a few species that do not cache (Brodin and Lundborg 2003a; Lucas *et al.* 2004). Natural food caching in free-ranging Parids has been studied most intensively in Eurasian species—willow, coal, crested, marsh, and Siberian tits (Haftorn 1956; Pravosudov 1985; Brodin 1994)—whereas data on natural food caching in North American Parids are extremely scant (Odum 1942; Brodin 2005). Some well-studied Eurasian Parids (willow and Siberian tits) have been reported to make more than a 100 000 individual food caches each autumn (Haftorn 1956; Pravosudov 1985; Brodin 1994) to be used throughout the winter. Food caching thus appears to be an important adaptation, promoting the birds' survival during the winter (e.g. Pravosudov and Lucas 2001), and it is important to understand how these birds retrieve their caches. It is known that food-caching birds rely, at least in part, on spatial memory to find their caches (review in Shettleworth 1995; Chapter 2) and research on spatial memory and the hippocampus, a part of the brain involved in spatial memory processing (Sherry and Vaccarino 1989; Hampton and Shettleworth 1996a, b), has focused on both Eurasian and North American Parids (Shettleworth

1995; Chapter 2). Glucocorticoid hormones are also known to affect spatial memory (Sapolsky 1996; McEwen and Sapolsky 1995; McEwen 2000) and thus the local environment might influence spatial memory via changes in glucocorticoid hormones levels (Pravosudov 2003). Here, I review studies dealing with the relationship between environment, food caching, spatial memory, corticosterone, and the hippocampus in North American chickadees while providing comparisons with similar studies done using Eurasian Parids.

## 3.2 Inter- and intraspecific differences in caching, spatial memory, and the hippocampus

### 3.2.1 Interspecific differences

Almost all food-caching birds live in environments with pronounced differences between seasons in accessibility of food. As a result, the benefits of strong spatial memory and food caching might typically be higher during the winter when environmental conditions are most energetically demanding. Also, some species experience more severe environmental conditions than others. Consequently, the advantages of food caching should be much higher for species living in more energetically demanding environments, resulting in higher selection pressure for more caching and more efficient cache recovery (Krebs *et al.* 1989,

1996). It has been hypothesized that the increased demands for the spatial memory needed to recover thousands of previously made food caches has resulted in enhanced spatial memory and enlarged hippocampus in food-caching birds—coined the adaptive specialization hypothesis (Krebs *et al.* 1989, 1996; Sherry *et al.* 1989; Chapter 2). This hypothesis has been mainly tested using species from two avian families—the Paridae and Corvidae—as both of these families contain food-caching and non-caching species (Sherry *et al.* 1989; Krebs *et al.* 1989, 1996; Chapter 2). Here I will briefly review the comparisons using Parids.

Healy and Krebs (1996) reported that food-caching Eurasian Parids have relatively larger hippocampal volume compared to non-caching species. Brodin and Lundborg (2003a) analyzed a large multispecies data set, including both Eurasian and North American Parids (the latter of whom all cache) as well as many other caching and non-caching species, and found little evidence that the degree of caching specialization is related to hippocampal volume. Lucas *et al.* (2004) reanalyzed Brodin and Lundborg's (2003a) data set, introducing a new variable—the continent on which the birds occurred—and their analysis supported the adaptive specialization hypothesis. The different conclusions reflected an apparent difference in hippocampal and brain volumes between Eurasian and North American Parids; once these differences were statistically controlled, the relative hippocampal volume appeared to be larger in food-caching Parids (Lucas *et al.* 2004, see also Chapter 2). Lucas *et al.* (2004) suggested that compared to North American species, relative hippocampus and overall brain size is larger in Eurasian birds, possibly due to different environmental conditions (Garamszegi and Lucas 2005; Chapter 2) but it remains possible, however, that these continental differences could be due to differences between laboratories in processing and analyzing the brains (Pravosudov and de Kort 2006).

While differences in hippocampal volume may indicate differences in the potential for spatial memory performance, behavioral tests to confirm that these differences occur have focused on only a handful of species. In Europe, most comparisons concerned food-caching marsh and coal tits and non-caching blue tits (Shettleworth 1995) while in

North America all comparative studies focused on food-caching black-capped chickadees and non-caching dark-eyed juncos (*Junco hyemalis*; Shettleworth 1995). The results of these comparisons were not consistent; in the majority of tests, food-caching birds outperformed non-caching species (Biegler *et al.* 2001; Shettleworth 1995), but some comparisons yielded non-significant results (see Shettleworth 1995 for review) and in one study non-caching dark-eyed juncos outperformed food-caching black-capped chickadees on one spatial memory task (Hampton and Shettleworth 1996b).

Hampton *et al.* (1995) compared three North American Parids—black-capped chickadees, Mexican chickadees, and bridled titmice—which appear to differ in their food-caching behavior. Of these three species, black-capped chickadees have a more northerly distribution and are well known food-cachers (Brodin 2005). Mexican chickadees and bridled titmice, on the other hand, occupy a more southerly range and have not been observed to cache food in natural conditions (Hampton *et al.* 1995). In captivity, however, both Mexican chickadees and bridled titmice cached food, indicating that caching behavior is present in these two species (Hampton and Sherry 1992; Hampton *et al.* 1995). Hampton *et al.* (1995) hypothesized that the more southerly Mexican chickadees and bridled titmice do not have a strong dependence on cached food for their survival because of their relatively mild, southern environmental conditions and, as a result, they should cache less food and have smaller hippocampi than black-capped chickadees. Indeed, Hampton *et al.* (1995) found that black-capped chickadees have relatively larger hippocampi than both Mexican chickadees and bridled titmice but the data on food caching were ambiguous. In two captive experiments there were no significant differences in caching rates between black-capped and Mexican chickadees. In one of the two experiments, there were also no statistical differences between all three species in the amount of food caching (Hampton *et al.* 1995).

### 3.2.2 Intraspecific differences

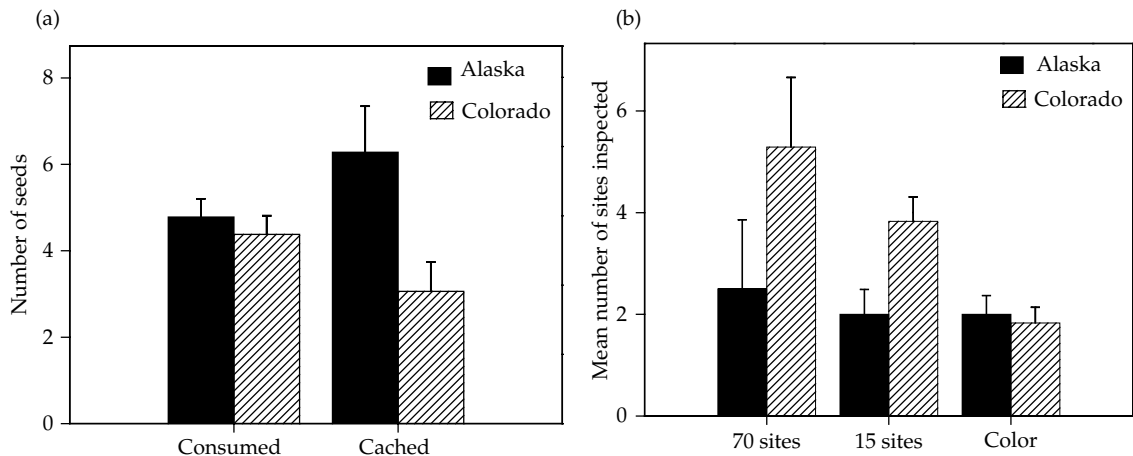
In all interspecific comparisons employed to test the adaptive specialization hypothesis, the main underlying assumption was that the biggest

difference between the species lies in their food-caching behavior (Krebs *et al.* 1989; Sherry *et al.* 1989; Brodin and Lundborg 2003a; Lucas *et al.* 2004; Chapter 2). However, it is possible that there are other differences between species, unrelated to caching behavior, that could have resulted in differential selection pressure on both spatial memory and the hippocampus. Comparing different populations within the same species might provide an opportunity to control for such differences.

Many food-caching Parids occupy extremely wide ranges, extending from south to north (Harrap and Quinn 1995) with greatly varying environmental conditions, especially during the winter. The range of black-capped chickadees, for example, extends from New Mexico in the south to Alaska in the north (Harrap and Quinn 1995). Compared to more southerly populations, Alaskan black-capped chickadees regularly experience longer winters with lower ambient temperatures, deeper and longer lasting snow cover, and, most importantly, much shorter day-length available for foraging during winter (Pravosudov and Clayton 2002). Obtaining enough food to build energy reserves sufficient to survive the night is crucial for survival in these small birds

(e.g. Pravosudov and Lucas 2001) and, in December, Alaskan chickadees have only about 5 hours of daylight to obtain enough energy reserves to survive about 19 hours of night. In Colorado, on the other hand, these birds have almost twice as much daylight hours to complete the same foraging task while probably requiring less energy due to generally warmer night-time temperatures (Pravosudov and Clayton 2002). In both environments, caches should provide a more predictable food source than naturally available food. Having sufficient food caches, and the capacity to successfully find them when needed should thus have much larger survival consequences for chickadees in energetically demanding Alaskan conditions. Such differences in the significance of cached food between southern and northern populations are likely to provide higher selection pressure in northern populations for more intense food caching, better spatial memory, and larger hippocampi.

When black-capped chickadees from Alaska and Colorado were acclimatized for 45 days and then tested in identical laboratory conditions, birds from Alaska cached significantly more food and performed significantly better on a spatial version of a one-trial associative learning task (Fig. 3.1;



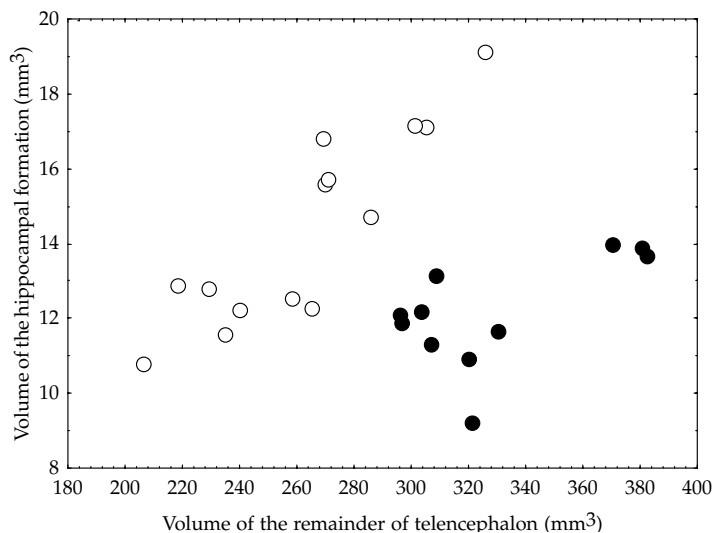
**Figure 3.1** Mean number of seeds consumed (fully or partially) and cached during 20-min food-caching trials (a) and memory performance in a one-trial associative learning task (b) by black-capped chickadees from Alaska (black bars) and Colorado (hatched bars) (redrawn from Pravosudov and Clayton 2002). Memory performance was measured as the number of sites inspected (= number of looks) in order to find the site previously containing food among either 70 or 15 available sites. Fewer looks indicate better memory performance. A color version of a one-trial associative learning task was used to investigate possible motivational differences between the groups. If one group were less motivated to search for food, it would show similar poor performance on both spatial and color versions of the task. If there were differences in spatial memory between the groups, there would be differences in performance on spatial but not on color version of a one-trial associative learning task.

Pravosudov and Clayton 2002). Interestingly, Alaskan chickadees were significantly smaller, with smaller brains, than chickadees from Colorado (Fig. 3.2; Pravosudov and Clayton 2002). Compared to Colorado chickadees, however, individuals from Alaska had significantly larger hippocampi with more neurons in both absolute terms and relative to telencephalon volume (Fig. 3.2; Pravosudov and Clayton 2002). These results support the adaptive specialization hypothesis; because Alaskan chickadees exist in a more energetically demanding environment, they cache more food, and have better spatial memory—which may be associated with their larger hippocampi containing more neurons—compared to conspecifics from Colorado (Pravosudov and Clayton 2002).

Based on the above data, however, it was not possible to unambiguously conclude whether the differences in caching, spatial memory, and hippocampal volume were genetic or experience based. Birds from both Alaska and Colorado were maintained and tested in identical laboratory environments, suggesting that the differences found between these groups were not related to the immediate environment. Alaskan chickadees cached more food and thus they had more food-caching

experience in the laboratory. A separate analysis of a control group of birds, which did not participate in the experiment while being maintained in the laboratory for the same duration of time, revealed no differences in the hippocampal volume or neuron numbers between the individuals that cached food and the ones that did not cache food (Pravosudov and Clayton 2002). At the same time, the differences between Alaska and Colorado remained even in individuals that did not cache food during the experiment, thus ruling out a possibility that larger hippocampus with more neurons in Alaskan chickadees resulted from more caching during the experiment. It remains possible, however, that differences between Alaska and Colorado chickadees in food caching and cache retrieval experience prior to capture produced long-term changes in memory and the hippocampus and thus further testing is necessary to differentiate between a genetic versus environmental basis of population differences.

Irrespective of the basis of these differences between Alaskan and Colorado black-capped chickadees, more food caching, better spatial memory, and an enlarged hippocampus with more neurons in Alaskan individuals appear to be highly adaptive to life in extremely energetically



**Figure 3.2** The relationship between the hippocampal volume and the volume of the rest of the telencephalon in black-capped chickadees from Alaska (open circles) and Colorado (filled circles) (redrawn from Pravosudov and Clayton 2002).

challenging environments. More research is needed to ascertain whether these differences have a genetic basis. Similar intraspecific studies may also be possible with tufted titmice, Carolina chickadees, Siberian and willow tits, or high-elevation populations of mountain chickadees, which would test the generality of environmental selection on caching behavior across species.

### **3.3 Unpredictable food, corticosterone, spatial memory, and the hippocampus**

#### **3.3.1 Seasonality in food caching and spatial memory**

Most food-caching Parids live in highly seasonal environments; food is abundant during summer and early autumn but during the winter it is often limited and unpredictable (Pravosudov and Grubb 1997a). Food-caching patterns mostly follow a seasonal cycle; birds cache most when food is plentiful outside the breeding season—late summer and early autumn and, sometimes, in spring when there is abundance of conifer seeds (Haftorn 1956; Pravosudov 1985; Brodin 1994). During these periods, birds can cache thousands of food items (Haftorn 1956; Pravosudov 1985; Brodin 1994). These food caches appear to be crucial for winter survival and thus the ability to retrieve them should be of paramount importance. Parids continue to cache throughout the winter although they cache a fairly small amount of food during that time (Pravosudov 1985). It is not clear whether winter caching involves storing newly found food or recaching previously hidden food stores (Pravosudov and Grubb 1997a), but winter short-term caching might be important for the birds' survival on a daily basis (Pravosudov and Lucas 2001).

In seasonal environments, demands for spatial memory do not appear to be equal throughout the year. If a bird does not remember where it stored food during summer and early autumn when natural food is abundant, it is unlikely to die of starvation. During the winter, however, failure to recover food caches is more likely to result in mortality and thus demands for spatial memory should be higher during the winter (Pravosudov and Clayton 2001). Thus there might be seasonal variation in the birds' spatial memory abilities and also in mechanisms

underlying spatial memory function. Because birds that cache more food appear to have larger hippocampi, it is possible to predict that if there is seasonal variation in spatial memory it may be accompanied by variation in hippocampal volume and/or neuron numbers.

Despite numerous suggestions that spatial memory might vary seasonally, there have been no studies documenting such variation. Whereas it may be difficult to measure seasonal variation in spatial memory, it is possible to test whether any of the parameters associated with seasonal changes in the environment, such as photoperiod or food supply, have an effect on spatial memory.

#### **3.3.2 Seasonal variation in hippocampus volume, neuron number, and neurogenesis rates**

Smulders *et al.* (1995, 2000) reported that hippocampal volume and neuron numbers change seasonally, with the largest hippocampal volume and most neurons occurring during October. Smulders *et al.* (1995, 2000) hypothesized that hippocampal volume should track seasonally changing demands for spatial memory and that the maximum hippocampal volume should be observed in the autumn when food caching is most intense (Haftorn 1956; Pravosudov 1985; Brodin 2005). Other food-caching Parids, however, do not rely on food caches during the period when caching rates are at maximum because natural food is relatively abundant during this period (Haftorn 1956; Pravosudov 1985). This appears to be also true for North American Parids (Brodin 2005). Successful retrieval of food caches may be more crucial later during the winter when failure to find caches might result in increased mortality (Pravosudov and Lucas 2001).

Smulders and Dhondt (1997) hypothesized that food-caching Parids might specifically need extra memory during food caching in order to memorize cache locations and to create optimal cache distribution that minimize cache pilferage. Based on these assumptions, they suggest hippocampal volume might be largest in October, when food caching was assumed to be most intense. Shiflett *et al.* (2003) argued that the hippocampus is involved specifically in memory encoding, which

occurs during food caching and that the hippocampus might not be involved in memory recall during cache retrieval. Clayton (2001), on the other hand, showed that young mountain chickadees that were allowed to cache, but not to retrieve, seeds had smaller relative hippocampal volume than chickadees that both cached and retrieved seeds. This result seems to suggest that retrieving caches might provide a stronger impact on hippocampal structure than food caching alone.

Another important detail is that, so far, there is little good data on seasonal variation in food-caching rates in North American Parids (Pravosudov 2006). A single study showed that black-capped chickadees cached most food at the end of September but no observations were available for August or early September (Brodin 2005). Much more extensive data on several Eurasian food-caching Parids show strong variation in food-caching rates; often these Parids cached most in September and cached as much food in August as in October (Pravosudov 2006). In addition, some Eurasian Parids might also cache food intensely during spring (Pravosudov 2006). Although North American Parids might have different seasonal food-caching patterns it remains difficult to interpret data on seasonal changes in hippocampal structure without knowing the precise patterns of food-caching activity.

Studies on seasonal variation in hippocampal volume (Hoshooley and Sherry 2004) or total number of neurons (Barnea and Nottebohm 1994; Hoshooley and Sherry 2004), however, have also not found support for seasonal differences (see also Chapter 2). Barnea and Nottebohm (1994) did report seasonal variation in hippocampal neuron recruitment rates in black-capped chickadees; more new neurons were observed in the hippocampus of birds injected with a cell division marker during October than at any other time of year. Barnea and Nottebohm (1994) concluded that neurogenesis supports memory function because the highest neuron recruitment rates coincided with the predicted highest food-caching rates during October, but they did not present data on the actual variation in caching rates of birds during these time frames. Further, their results do contain some ambiguity, as they measured the number of neurons which survived at least 6 weeks

from October injections, rather than the number of neurons actually produced in October. Such a result can be achieved through increased neuron production, increased survival of new neurons, or both (Prickaerts *et al.* 2004; Chapter 2). Hoshooley and Sherry (2004) found no significant seasonal variation in neuron production rates in the hippocampus of black-capped chickadees, suggesting that Barnea and Nottebohm's (1994) results might be explained by higher survival rates of neurons that were born in October. Higher survival rates of new neurons coupled with stable total neuron numbers suggest that neuron turn over rates could potentially be lower during October. Neurons born in October may not be immediately functional, as it takes some time for the neurons to mature and to incorporate into the existing neuronal circuits in the hippocampus. Thus, these neurons may become functional only by the end of October–November and, because they appear to survive longer, these new neurons could remain functional in December and later. This might shift the significance of these neurons from October, one of the months when food caching is often assumed to be most intense, to November–December when food caching might be reduced (Haftorn 1956; Pravosudov 1985) and cache retrieval becomes crucial for survival. Neurons born in December were reported to have lower survival (Barnea and Nottebohm 1994), but these neurons would most likely become functional only in January–February.

Further research is necessary to understand whether hippocampal structure and neurogenesis consistently undergo seasonal changes specifically associated with changes in food-caching activity. In particular, it would be important to investigate whether hippocampal structure and neurogenesis vary in individual birds in relation to their specific food-caching behavior. More data are also necessary to document variation in seasonal changes in food-caching behavior.

### 3.3.3 Photoperiod

Seasonality is associated with predictable changes in photoperiod and thus it is possible that photoperiod could trigger seasonal changes, if any, in food caching, spatial memory, and the hippocampus (Chapter 4). Food caching is often most intensive

during autumn when day-length becomes shorter; however, intensive caching has also been reported during spring when day-length actually becomes longer (Haftorn 1956; Pravosudov 1985, 2006). Most laboratory manipulations of photoperiod have demonstrated that black-capped chickadees and marsh tits cache more food on short days (Krebs *et al.* 1995; Shettleworth *et al.* 1995; Clayton and Cristol 1996), suggesting that decreasing day-length may be responsible for the autumnal peak in food caching (but Karpouzou *et al.* (2005) reported no effect of photoperiod on food caching in black-capped chickadees). However, these results do not explain spring bursts of food caching and thus it remains possible that seasonal peaks in long-term caching are not necessarily under photoperiodic control (Pravosudov 2006).

It is also not clear whether spatial memory is affected by photoperiod. Clayton and Cristol (1996) reported that marsh tits switched from long to short days showed better spatial memory performance than their conspecifics maintained on long days. But when birds maintained on short, winter-like days were changed to long days and the birds maintained on long days were switched to short days, there were no differences between the groups in spatial memory performance, even though the birds on short days were caching more food. If photoperiod was involved in spatial memory regulation, birds on short days should have shown better memory performance, which did not happen during the latter test.

Experimental manipulation of photoperiod also failed to induce significant changes in the hippocampal volume in black-capped chickadees (Krebs *et al.* 1995; MacDougall-Shackleton *et al.* 2003) and baseline corticosterone levels were statistically indistinguishable between mountain chickadees maintained on short and long days (Pravosudov *et al.* 2002a). Thus whereas photoperiod appears to affect food-caching rates in captive birds, there appears to be insufficient evidence that it has an effect on spatial memory and the hippocampus.

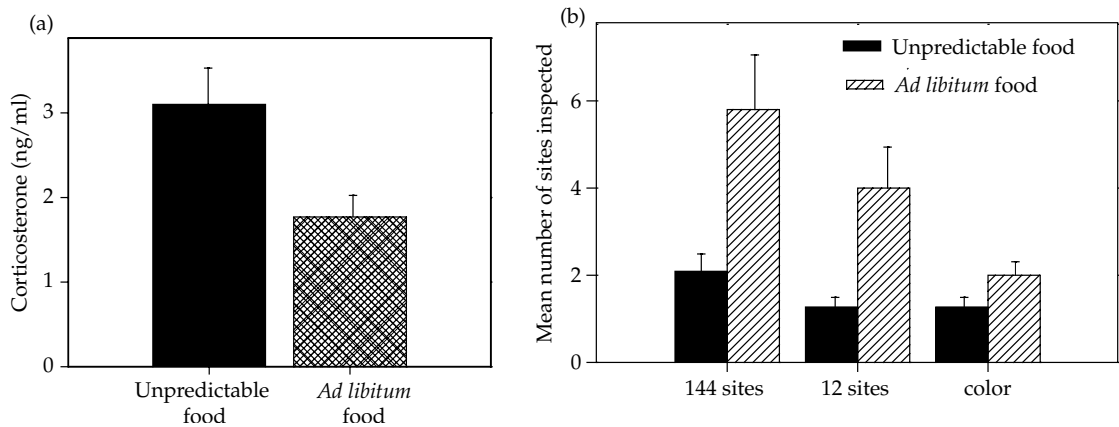
### 3.3.4 Unpredictable food supply

Most food-caching Parids live in the temperate zone and experience seasonal variation in food availability and predictability (Pravosudov and Grubb

1997a). Food is usually abundant in summer and autumn but becomes much less abundant during the winter. Winter is also the most energetically demanding season because of short days and low air temperature, and successful retrieval of food caches becomes critically important during the winter (Pravosudov and Lucas 2001). Thus food availability and predictability might directly affect food caching and cache retrieval (Pravosudov and Clayton 2001).

When food supply was made limited and unpredictable in a laboratory for 60 days, mountain chickadees demonstrated more efficient cache recovery (by searching significantly fewer available cache sites) and showed better spatial memory performance compared to individuals maintained on *ad libitum* food (Fig. 3.3; Pravosudov and Clayton 2001). Thus, it appears that chickadees might have better spatial memory, resulting in more efficient cache retrieval, during the winter when available food is rather scarce. To determine whether better performance on memory tests by food-deprived chickadees was associated with better spatial memory and not with higher levels of motivation to search for food, Pravosudov and Clayton (2001) used an associative learning task in which a site containing food was associated with a specific color (local) cues. If non-deprived chickadees were less motivated to search for food, they would show similar performance on both spatial and color-associative learning tasks. Pravosudov and Clayton (2001) found that differences in memory performance between deprived and non-deprived individuals were present only in the spatial test whereas in the non-spatial, color test the groups showed similar performance (Fig. 3.3). Such results suggested that the differences between food-deprived and non-deprived chickadees were most likely due to differences in spatial memory and not in motivation to search for food.

Hippocampal volume and the total number of neurons, however, were statistically indistinguishable between mountain chickadees maintained on limited and unpredictable food supply and those on *ad libitum* food supply (Pravosudov *et al.* 2002), which suggests that changes in spatial memory triggered by changes in food supply were not supported by structural changes in the hippocampus. Interestingly, baseline corticosterone levels were



**Figure 3.3** Baseline corticosterone levels (a) and memory performance in a one-trial associative learning task (b) in mountain chickadees maintained on limited and unpredictable food schedule (black bars) and on *ad libitum* food (hatched bars). ((a) is reprinted from *General and Comparative Endocrinology*, **123**, Pravosudov *et al.* Long-term unpredictable foraging conditions and physiological stress response in mountain chickadees (*Poecile gambeli*), pp. 324–331, Copyright (2001), with permission from Elsevier; b is redrawn from Pravosudov and Clayton 2001). Memory performance was measured as the number of sites inspected in order to find a single site previously containing food among either 144 or 12 available sites. Fewer sites inspected indicate better memory performance. A color version of a one-trial associative learning task was used to investigate possible motivational differences between the groups (see also legend Fig. 3.1).

significantly elevated in birds maintained on limited food (Fig. 3.3; Pravosudov *et al.* 2001). Thus relatively long-term (2 months) limited and unpredictable food supply resulted in moderately but significantly elevated baseline corticosterone and in enhanced spatial memory. Such results suggested that elevated corticosterone might have been directly responsible for spatial memory improvements observed in mountain chickadees in the absence of any changes in hippocampal volume or neuron numbers.

### 3.4 Corticosterone, food caching, spatial memory, and the hippocampus

It is well known that corticosterone has an effect on memory function (Sapolsky 1996; McEwen and Sapolsky 1995; McEwen 2000). It has generally been assumed that short-term (hours, days) elevations in corticosterone enhance spatial memory whereas prolonged, chronic (weeks) elevations might have extremely deleterious effects. Most of the research addressing the relationship between corticosterone elevation and memory has been focused on mammals (McEwen and Sapolsky 1995; McEwen 2000) but there are also studies suggesting that

corticosterone has an effect on memory in birds (Loscertales *et al.* 1997; Sandi *et al.* 1995; Sandi and Rose 1997). Saldanha *et al.* (2000) reported that short-term, strong corticosterone elevation resulted in improved spatial memory performance in mountain chickadees. Chickadees in the Saldanha *et al.* (2000) study received extremely high doses of corticosterone which likely resulted in unnaturally high corticosterone plasma levels (Pravosudov 2005); it thus remains unclear whether naturally occurring corticosterone elevations would provide similar effects on memory.

Unlike short-term (hours or maybe days), chronic (weeks or months) corticosterone elevations have been reported to result in memory impairments (Sapolsky 1996; McEwen and Sapolsky 1995; McEwen 2000). It appears, however, that baseline corticosterone levels may remain elevated in wintering Parids over several months (Silverin 1998—willow tits), which would fall under the long-term category for these rather short-lived birds. Experimental manipulations of food supply designed to decrease food predictability and/or availability also triggered a prolonged elevation of baseline corticosterone in mountain chickadees (Pravosudov *et al.* 2001) and in red

knots (*Calidris canutus*; Reneerkens *et al.* 2002). It is important to note that such elevations were only moderate and they exceeded the baseline levels only two or three times compared to stress-induced levels which might exceed baseline concentration by more than 10 times (Silverin 1998; Wingfield *et al.* 1997, 1998).

Thus it is not clear whether long-term but moderate corticosterone elevations are necessarily associated with the same negative effects on memory and the brain as long-term, stress-induced-like high elevations. It appears that prolonged, moderate corticosterone elevations might occur when birds face both the highest demands for feeding efficiency in order to survive and when memory for the location of food caches could also be most critical for survival (Pravosudov and Clayton 2001; Pravosudov 2005). Foraging conditions that caused long-term (2 months), moderate corticosterone elevation in mountain chickadees also resulted in enhanced spatial memory and more efficient cache retrieval (Pravosudov and Clayton 2001), a result potentially contradicting a conventional assumption that any chronic elevation in glucocorticoids might be deleterious for memory function (Sapolsky 1996; McEwen and Sapolsky 1995; McEwen 2000) and suggesting that elevated corticosterone might have actually caused the observed memory improvements.

When given corticosterone implants designed to maintain moderate corticosterone elevations (about 1.5 times higher than baseline; resembling those observed in natural conditions during winter (Silverin 1998) and in birds maintained on unpredictable food supply (Pravosudov *et al.* 2001)) for several weeks, mountain chickadees demonstrated better spatial memory performance compared to placebo-implanted individuals (Fig. 3.4b, Pravosudov 2003), supporting a link between elevated corticosterone and spatial memory. Furthermore, compared to placebo-implanted birds, corticosterone-implanted chickadees fed more intensively and cached significantly more food (Fig. 3.4a, Pravosudov 2003). Thus, long-term, moderately elevated corticosterone might facilitate more foraging and food caching while enhancing the spatial memory required for successful cache retrieval. This entire "suite" of behaviors is likely to

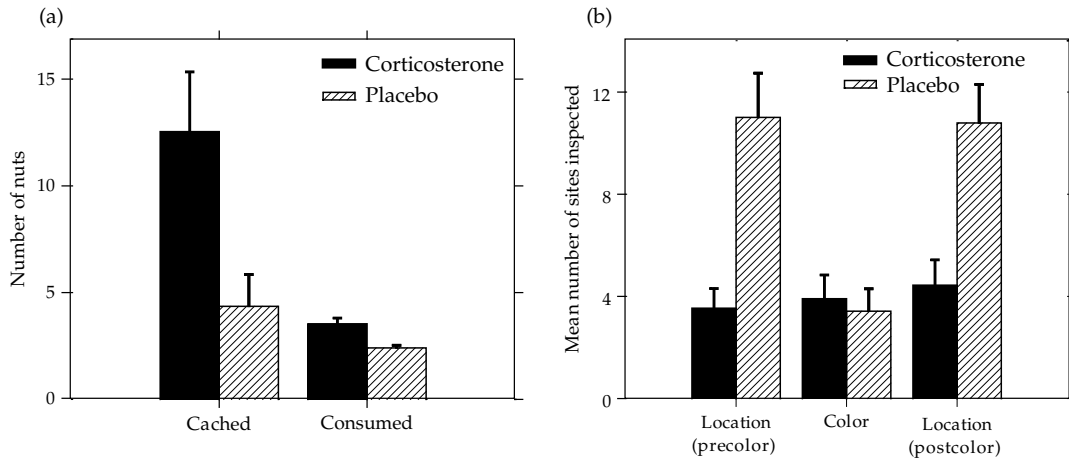
increase birds' probability of survival when environmental conditions are energetically demanding, such as during the winter. These results suggest that prolonged but moderately elevated corticosterone levels may be highly adaptive by enhancing memory rather than impairing it, as it has been widely suggested (Sapolsky 1996; McEwen and Sapolsky 1995; McEwen 2000).

Elevated corticosterone might have a positive effect on memory through several possible mechanisms including elevated glucose levels, enhanced protein synthesis in the brain, and increased hippocampal neuron firing rates (see review in Pravosudov 2005). Interestingly, hippocampal neuron firing rates seem to have an inverted-U relationship with corticosterone levels (Diamond *et al.* 1992), which is in agreement with our results suggesting that moderate corticosterone elevations might enhance spatial memory.

The fact that birds do not always maintain moderately elevated corticosterone levels despite its apparent benefits suggests that even moderate corticosterone elevations carry costs (e.g. weakening immune function, Wingfield *et al.* 1997, 1998). These costs, however, do not seem to concern memory function.

It has been suggested that chronically elevated corticosterone might impair memory through increased neuronal death but most experimental studies used high doses of corticosterone resulting in unnaturally high elevations (e.g.  $10 \times$  baseline) (Sapolsky 1996; McEwen and Sapolsky 1995; McEwen 2000). Such elevations might not necessarily occur under naturally stressful conditions and it is important to understand the consequences of naturally occurring corticosterone elevations.

Prolonged, moderately elevated corticosterone levels associated with unpredictable food had no detectable effects on hippocampal structure (Pravosudov *et al.* 2002b). Analogously, there were no significant differences between corticosterone- and placebo-implanted mountain chickadees in either hippocampal volume, total number of hippocampal neurons, or cell proliferation rates in the ventricular zone adjacent to the hippocampus and to the mesopallium (Pravosudov and Omanska 2005a). Thus relatively long-term (49 days with corticosterone implants and 94 days on limited and



**Figure 3.4** Mean number of consumed (fully or partially) and cached pine nuts during food-caching trials (a) and memory performance in a one-trial associative learning task (b) in mountain chickadees implanted with corticosterone (black bars) or placebo (hatched bars) (redrawn from Pravosudov 2003). Memory performance was measured as the number of sites inspected in order to find the site previously containing food. Fewer sites inspected indicate better memory performance. A color version of a one-trial associative learning task was used to investigate possible motivational differences between corticosterone- and placebo-implanted chickadees.

unpredictable food supply) moderate corticosterone elevation, similar to the elevation observed in chickadees maintained on unpredictable food schedule, had no detectable effect on hippocampal structure and cell proliferation rates. It has also been reported that prolonged stress and associated prolonged corticosterone elevation result in reduced neurogenesis rates (Gould and Tanapat 1999). Neurogenesis consists of cell proliferation and neuron survival (Prickaerts *et al.* 2004; Chapter 2) and thus it remains possible that even moderately elevated corticosterone levels might negatively impact neuron survival rates.

Experimental results with mountain chickadees thus suggest that relatively long-term, moderate corticosterone elevations in response to challenging environmental conditions might be adaptive, at least in wintering food-caching birds. When foraging conditions deteriorate, corticosterone levels might rise, facilitating more active foraging behavior and more food caching while enhancing spatial memory which is important for successful cache retrieval. When environmental conditions improve, corticosterone levels return to normal suggesting that corticosterone elevation has some costs, which might be outweighed by the benefits during energetically demanding periods.

### 3.4.1 Corticosterone in Alaskan and Colorado chickadees

Black-capped chickadees in Alaska regularly experience more energetically challenging environmental conditions than chickadees in Colorado (Pravosudov and Clayton 2002). Such conditions are likely to effect availability and predictability of food supply during the winter, and limited food supply is known to affect corticosterone levels in mountain chickadees (Pravosudov 2003). Moderately elevated corticosterone appears to provide benefits to wintering birds by mediating more intense foraging and food caching and by enhancing spatial memory, which plays an important role in cache retrieval (Pravosudov 2003). Whereas it appears that even moderately elevated corticosterone levels might carry some costs (Wingfield *et al.* 1997, 1998), for birds experiencing energetically demanding environments every year the benefits of elevated corticosterone might outweigh possible costs and thus selection may favor elevated corticosterone.

There were, however, no significant differences in either baseline or stress-induced corticosterone levels between Alaskan and Colorado chickadees, which indicates that differences in memory found

between these two populations were not related to changes in corticosterone levels (Pravosudov *et al.* 2004). The fact that Alaskan and Colorado chickadees did not differ in their corticosterone levels in identical laboratory conditions also suggests that different environmental conditions did not cause permanently elevated corticosterone levels in Alaskan birds. Instead, it appears that baseline corticosterone levels might only respond to immediate environmental conditions in both populations.

Compared to birds in Colorado, corticosterone levels in Alaskan environments may be elevated in black-capped chickadees as a result of differences in immediate conditions between Alaska and Colorado during the winter. Such elevation (if it exists) may aid spatial memory benefits already achieved through enlarged hippocampus (Pravosudov and Clayton 2002). Whereas the volume of the hippocampus and its number of neurons appear to be permanently larger in Alaskan chickadees, providing them with permanent advantages when it comes to spatial memory performance, temporary corticosterone elevations during the most difficult times may provide additional memory benefits (Pravosudov 2004).

### 3.5 Dominance, corticosterone, spatial memory, and the hippocampus

Most Parids live in hierarchically structured social groups in which dominants enjoy priority of access to all available resources (Ekman 1989; Ekman and Lilliendahl 1993; Chapter 9). It has been suggested that subordinates experience less predictable conditions because of their low social status; even when they find food they can be supplanted by dominants at any time (Ekman and Lilliendahl 1993). Because social classes differ in the predictability of their environment they might invoke different tactics for managing their available energy resources. In particular, it has been suggested that birds in less predictable environments should accumulate and maintain more energy reserves as a buffer against the higher probability of starvation in case an adequate amount of food cannot be obtained at a critical time (Ekman and Lilliendahl 1993; Brodin *et al.* 2001; Chapter 17). Indeed, there is some experimental evidence that subordinate birds maintain

higher levels of fat reserves than dominants (Ekman and Lilliendahl 1993—willow tits; Chapter 9—black-capped chickadees), but other studies found either a reverse pattern (Koivula *et al.* 1995—willow tits; Verhulst and Hogstad 1996—willow tits; Pravosudov and Lucas 2000—Carolina chickadees) or no differences between dominants and subordinates (Pravosudov and Lucas 2000—Carolina chickadees).

In addition to storing energy reserves as body fat, food-caching birds can also accumulate and maintain energy reserves as food caches. Birds usually increase their caching rates when food becomes less predictable (Pravosudov and Grubb 1997), thus the idea that subordinates should maintain more energy reserves to buffer unpredictable conditions could be extended to food caching. Brodin *et al.* (2001) used a dynamic modeling approach to investigate the effect of social status on food-caching rates and their model confirmed this prediction and suggested that subordinates should cache more food than dominants. The model, however, relied heavily on the untested assumption that dominants can freely pilfer caches made by subordinates whereas subordinates could never pilfer dominant's caches, and it is not clear how the model's predictions would have changed if this assumption were changed. Empirical results were also not consistent; some studies of willow tits found that subordinates indeed cache more food than dominants (Lahti and Ryttonen 1996; Brodin and Lundborg 2003b), whereas other studies found either the reverse to be true or no differences between low and high social ranks (Pravosudov 1985—Siberian and willow tits; Hitchcock and Sherry 1995—black-capped chickadees; Lahti *et al.* 1998—willow tits; Pravosudov and Lucas 2000—Carolina chickadees; Lundborg and Brodin 2003—willow tits).

Most of the studies investigating the effect of dominance hierarchy on food-caching behavior used behavioral and ecological approaches while ignoring possible mechanisms of food-caching regulation. For example, unpredictable food triggers more intense food caching (Hurly 1992—marsh tits; Pravosudov and Grubb 1997b—tufted titmice) and at the same time it also triggers corticosterone elevation (Pravosudov *et al.* 2001—mountain chickadees). An implant study with

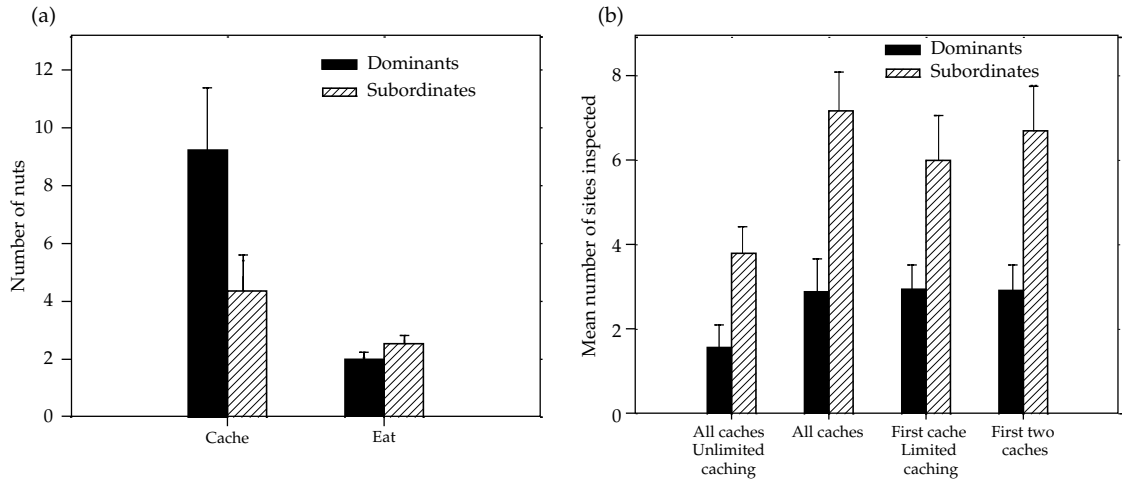
mountain chickadees (Pravosudov 2004) showed that elevated corticosterone facilitates more eating, more intense food caching, and enhanced spatial memory. Thus, corticosterone might be a mechanistic link between unpredictable foraging conditions and energy management tactics. If socially subordinate individuals experience an unpredictable environment their corticosterone levels might be elevated, which would support the idea that subordinates should cache more food and even have better memory for food caches. Available data on the relationship between dominance status and corticosterone levels from observational unmanipulated studies, however, do not show a consistent pattern (see Pravosudov *et al.* 2004 for review). In some studies corticosterone levels were higher in subordinate individuals whereas in other studies there were no differences in baseline corticosterone levels between dominants and subordinates.

To test the hypothesis that dominance hierarchy has an effect on food caching and spatial memory, Pravosudov *et al.* (2004) compared experimentally created pairs of dominant and subordinate mountain chickadees. Previous laboratory studies investigating the effect of social dominance on food caching failed to find significant differences between dominants and subordinates (Pravosudov and Lucas 2000; Lundborg and Brodin 2003). However, in all of these studies, dominants and subordinates were tested together in a fairly small room in which subordinates could not escape the dominants' view. Thus it is likely that the immediate presence of dominants might have influenced the behavior of subordinates in these studies. In natural conditions, subordinates can easily move out of the dominant's sight, and, in fact, most birds avoid caching when in a presence of a group mate (Woodrey 1991; Lahti *et al.* 1998). Pravosudov *et al.* (2004) attempted to simulate a more natural environment by testing dominants and subordinates separately in an adjacent room. In this experimental design, subordinates were not affected by the presence of the dominants during the short duration of the food-caching trials. Results of this study were directly opposite to all predictions; subordinates cached significantly less food than dominants and they also performed significantly worse in a cache recovery task (Fig. 3.5). Baseline corticosterone

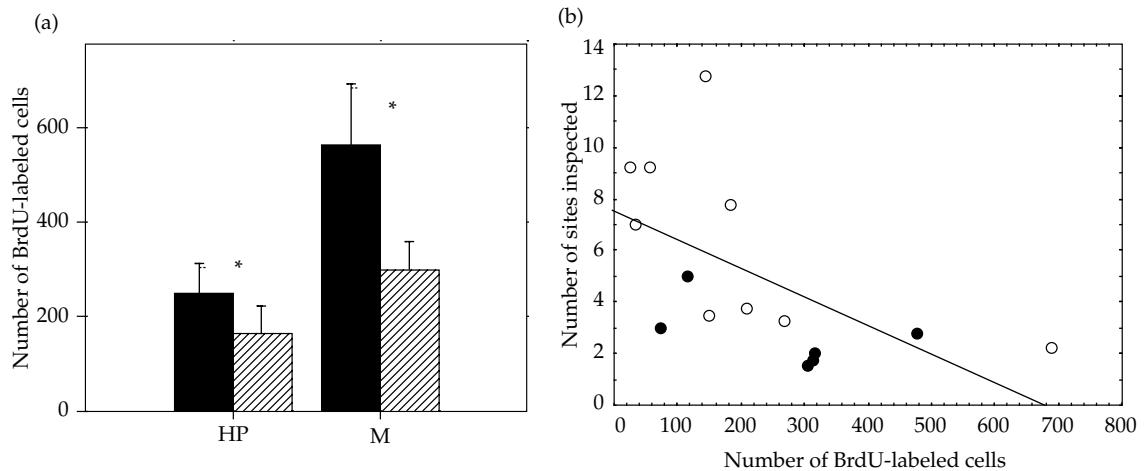
levels measured after almost 2 months following formation of dominance relationships were statistically indistinguishable between dominants and subordinates but maximum corticosterone levels achieved during a standardized stress response were actually higher in dominants (Pravosudov *et al.* 2004). These results suggest that whereas corticosterone might be involved in mediating food-caching behavior and spatial memory, changes in caching rates and memory can occur without changes in baseline corticosterone levels. The inferior spatial memory found in subordinate chickadees was not related to any changes in hippocampal volume or neuron numbers (Pravosudov and Omanska 2005b).

Barnea and Nottebohm (1994) suggested that spatial memory might be affected by changes in hippocampal neuron recruitment rates without changes in the total number of neurons. Interestingly, subordinate mountain chickadees which showed inferior spatial memory performance compared to their dominant group mates also had significantly lower cell proliferation rates in the ventricular zone adjacent to both the hippocampus and to the mesopallium (Fig. 3.6; Pravosudov and Omanska 2005b). Cell proliferation is a first step during the process of neurogenesis; after new cells are born, some of them will survive to become functional neurons and it is likely that the number of functional neurons is proportional to the number of new cells (Prickaerts *et al.* 2004). Pravosudov and Omanska (2005b) showed that differences in spatial memory performance were associated with differences in hippocampal cell proliferation rates, thus suggesting that cell proliferation and neurogenesis might be involved in spatial memory function (Fig. 3.6b). These data, however, are correlational and they do not establish a causal effect; it remains possible that social dominance simultaneously affected both memory and cell proliferation. In another study, hippocampal cell proliferation rates did not correlate with spatial memory performance (Pravosudov and Omanska 2005a), suggesting that elevated corticosterone might affect memory function without changes in hippocampal cell proliferation rates.

Irrespective of whether hippocampal cell proliferation is directly involved in spatial memory function, the results of the mountain chickadees



**Figure 3.5** Mean number of consumed (fully or partially) and cached pine nuts during food-caching trials (a) and memory performance (b) in a cache-recovery task in dominant (black bars) and subordinate (hatched bars) mountain chickadees. (Reprinted from *Hormones and Behavior*, 44, Pravosudov *et al.* The relationship between dominance, corticosterone, memory, and food caching in mountain chickadees (*Poecile gambeli*), pp. 93–102, Copyright (2003), with permission from Elsevier.)



**Figure 3.6** Mean number of BrdU-labeled cells in the ventricular zone adjacent to either hippocampus or mesopallium (a) and the relationship between the number of BrdU-labeled cells in the ventricular zone adjacent to the hippocampus rates and spatial memory performance (b) in dominant (black bars and circles) and subordinate (hatched bars and open circles) mountain chickadees (redrawn from Pravosudov and Omanska 2005b).

study suggest additional costs of subordination—subordinate chickadees might cache less food and might show inferior spatial memory performance as a result of their low social status. Stress of social subordination is also a likely factor suppressing hippocampal cell proliferation rates, although

dominants and subordinates did not differ significantly in the total number of hippocampal neurons (Pravosudov and Omanska 2005b). It is possible that neuron turnover rates are higher in dominants and that is why they do not have more neurons, despite the fact that more new cells are being born

in the ventricular zone. Lower caching rates and less efficient cache retrieval as a result of inferior spatial memory could potentially contribute to the higher mortality of subordinates commonly reported in literature.

### 3.6 Conclusions

Research on spatial memory in Parids has shown that environmental conditions might affect memory performance through several different ways:

1. Temporary, season-like changes in spatial memory associated with variation in food availability and predictability were related to changes in baseline corticosterone levels whereas hippocampal volume and neuron numbers appeared to remain stable.
2. In birds permanently living in higher latitudes with harsher conditions, on the other hand, enhanced memory was related to larger hippocampal volume and more neurons in the absence of any variation in corticosterone levels.
3. Changes in spatial memory associated with social dominance were unrelated to either corticosterone levels or to the hippocampal volume or neuron numbers, but they were associated with variance in hippocampal cell proliferation rates.

It is likely that all three of these patterns could be involved in the regulation of spatial memory, separately or jointly. Elevated corticosterone levels could provide yet another enhancement to spatial memory in chickadees occupying northern parts of their range, with less predictable conditions, in addition to enhancements achieved via an enlarged hippocampus with more neurons. Changes in hippocampal structure (volume and neuron numbers), however, are not necessary to induce changes in spatial memory in food-caching birds.

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