Although evidence for local over-citing is strong, our results do not reveal whether researchers in one region are more to blame than the other. This is because it is impossible to judge what an unbiased rate of citation for European or North American papers should be [5]. For example, if North Americans truly produced better science, the signature of over-citing in that part of the world would be justified, and the European bias would then be a sign of parochial practices (and vice versa). Notwithstanding such a possibility, however, the strength of geographical over-citing still raises concerns that both sides of the Atlantic could be engaging in parochial citation practices.

It is particularly alarming that differences do not diminish for older papers that should have had more time to become known by both Americans and Europeans regardless of who originally published the work. Of course, for empirical studies, differences could, to some extent, reflect acceptable patterns of local citing because they concern local natural history. Yet, theoretical papers (defined as no original data presented in the paper) published between 1984 and 2002 showed similar fates (Figure 1d; $n=59$ for *Ecology*, $n=42$ for *Journal of Animal Ecology*). However, in theoretical papers published in *Journal of Animal Ecology*, significant geographical over-citing is, intriguingly, replaced by papers of European origin being cited more by researchers on both sides of the Atlantic.

Our results, together with those reported in [5], suggest that the empirical and theoretical advancement of ecology in Europe differs significantly from that in North America. To a certain degree, this could reflect relatively neutral factors, such as differences in the topics that ecologists from different regions choose to specialize in. If, however, researchers are overlooking or ignoring the work of colleagues from elsewhere [1], fair recognition of the efforts of individual scientists is far from guaranteed, and the advancement of science itself is considerably hampered.

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It's a puzzle all right: the hippocampus and food hoarding

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In their recent *TREE* article, Healy *et al.* [1] paint, with a broad brush, critics of their view that variation in the size of the hippocampus results from natural selection for spatial learning. For instance, they claim that such criticism 'is essentially directed to all those scientists who have proposed species-specific or problem-specific differences in cognitive abilities and the putative brain regions underlying those abilities, from…to song learning and the song control nuclei of song birds'. Although I am more skeptical than are Healy *et al.* of the evidence presented to date for such adaptive species-specific cognition [2], I expect natural selection to influence cognition and behavior and, by extension, their neural substrates. An example of such an adaptive neural specialization is the high vocal center (HVC) song nucleus of songbirds, the size of which varies (across populations and species) with the size or complexity of the vocal repertoire. Given the obvious parallels, the HVC provides a useful yardstick against which to measure evidence that natural selection has caused an increase in hippocampal size in food-storing birds and mammals to enhance spatial memory.

As 'the HVC of spatial memory', the hippocampus is lacking in three important respects: (i) the degree of task specialization (song learning versus episodic memory); (ii) evidence that gross size differences in the relevant neural substrates are associated with specific behavioral and/or cognitive differences (the brain–behavior link); and (iii) assuming (ii), evidence that the neural difference causes the behavioral difference and not the reverse (the causal arrow). Owing to space limitations, I focus on (iii).

If hippocampal volume determines the ability to learn and remember spatial information, we would expect an increase in volume to precede spatial learning. Called 'experience-expectant' change by neurobiologists [3], the causal arrow points from brain to behavior. HVC volume increases in an experience-expectant way [4], whereas hippocampal volume does not. Instead, the only developmental studies conducted to date indicate that the hippocampus changes in an experience-dependent

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manner [5–7], as a muscle does in response to exercise. The causal arrow points from behavior to brain. Healy *et al.* acknowledge that these data demonstrate experience dependence, but suggest that experience dependence applies only to the 'normal development of the hippocampus' in young birds [1]. They argue for experience-expectant hippocampal changes in adult birds and, as evidence, they cite studies that failed to find an increase in hippocampal volume with increased food hoarding over short time periods [8,9]. However, at best these studies provide weak support for experience expectance, not enough to provide confidence that natural selection has shaped the hippocampal size differences in storing and non-storing birds and mammals.

Even if, as I have argued, the hippocampal changes are an effect, rather than a cause of observed differences in spatial learning, we need not abandon the search for naturally selected neural differences in storing and non-storing birds and mammals. We would, however, need to shift our gaze to other parts of the brain. The neural substrates for the motivation to store food would be a good place to start.

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Letters Response

Response to Francis: Puzzles are a challenge, not a frustration

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Francis argues that increases in hippocampal size should precede changes in spatial learning if variation in hippocampal size is the product of natural selection for spatial ability [1]. Studies of the development of the hippocampus in juvenile birds suggest that the hippocampus does not enlarge prior to experience of food storing, and Francis takes this as evidence that natural selection has not been involved in the enlargement of the hippocampus of food-storing species. However, we do not think that such 'experience-expectance' is necessary to demonstrate a role for natural selection in hippocampal enlargement.

Experiments in which young naive birds from storing and non-storing species had to search for hidden food shows that this experience triggered hippocampal growth only in birds from the storing species [2]. This finding suggests that the hippocampus of food-storers differs from that of non-storers in how it is predisposed to respond to spatial learning experience. If so, then 'experience-dependent' changes might be unique to the food-storing species, in which case we have evidence for selection having acted on hippocampal structure and function in food-storing birds.

In addition, experience dependence, as used in the muscle analogy by Francis, suggests a gradual increase in volume with an accumulation of experience: the more the muscle is used the bigger it gets. However, the increase in hippocampal volume in food-storing species requires only a minimal experience of food storing, after which the hippocampal volume does not increase any further. This pattern of growth suggests a species-specific predisposition to hippocampal enlargement, as opposed to the typical experience-dependent response of a gradual increase with use. We agree with Francis that we need not abandon the search for naturally selected neural differences in storing and non-storing birds and mammals. While we also agree that it would be interesting to investigate the neural substrates for the motivation to cache, we disagree that we need to shift our attention from the hippocampus to other parts of the brain.

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