EVOLUTION

COLD weather cognition

Vladimir Pravosudov tells us about his career-long quest to understand the cognition of food caching chickadees, and how their respective environments affect their cognitive development.

IN THE LONG WINTERS NORTH OF THE POLAR Circle, where temperatures dip as low as -40˚C and when daylight lasts just a few hours, a small black and white bird survives even in such extreme conditions. With just a few hours of light for foraging, it seems barely possible that such a small, 12 gram bird get enough food to survive freezing nights that can last up to twenty hours. Yet chickadees and some tit species seem to be doing just fine as far north as the trees go, whether in northern Europe, Siberia or North America.

These birds store (or cache) food in the fall when it is plentiful and use these food caches throughout winter. Food caching might be at least one of the important adaptations allowing these non-migratory birds to spend their entire lives in the same seemingly inhospitable places. In previous research I have found that individuals of two tit species store up to half a million individual food caches during the year, each one in a unique spatial location. When food is available during the non-breeding season all they do is cache, stashing hundreds of thousands of seeds and invertebrates, each in its own individual location within the branches of trees. My interest in chickadees' food caching behaviour that started when I was a student has essentially shaped my entire research career.

One of the most puzzling things about food caching is how animals find their stores days, weeks and months after they made them. If the caches are important, birds should be able to find them when needed, hence, being able to remember location and orientation

EVOLUTION

© Vladimir Pravosudov

appears to be involved in the recovery of hidden food. Early research showed that food-caching species have better spatial memory and a larger hippocampus, a brain region involved in spatial memory, compared to species that don't cache food. It is generally thought that those animals that rely on food caches for survival have evolved better memories, as they rely on their spatial memory to locate their caches. Yet direct evidence showing that spatial memory in food caching species is advantageous, and therefore under selection, is still lacking.

In my laboratory we previously found that chickadees from more northern populations cache more food, perform better on spatial memory tests, and have a larger hippocampus and larger neurons in greater numbers. Moreover, we showed that these differences also persisted in a 'common garden' where we hand-reared birds from different environments in the same conditions. This suggests that these differences do not exist simply because of variation in the immediate environmental conditions, but are heritable – likely passed down through genes from one chickadee generation to another. These studies were done on a large spatial scale, but we wanted to see if the same patterns exist on a small spatial scale of large variation in winter severity present in the mountains where environment changes rapidly with elevation.

So we shifted our focus to pine-seed-caching mountain chickadees in Sierra Nevada. We indeed found that chickadees from higher elevations that experience colder, snowier and longer winters also cache more food, have better spatial memory and a larger hippocampus with more neurons compared to chickadees from lower, milder elevations. All of these differences were found in birds brought into captivity because studying cognition in the wild is extremely challenging. Yet, to understand whether selection may act on cognition, it is necessary to measure cognition in the wild and then see if any individual differences might be associated with how successfully an animal survives or reproduces.

So we needed to figure out how to test spatial memory in wild mountain chickadees at different elevations in Sierra Nevada. Developments in technology meant we were able to use Radio Frequency Identification technology (RFID) that allows automated detection of 'PIT-tags', small microchips that are imbedded into bands on the birds' leg. Each tag transmits a unique identification number to a reading device that uses radio frequency technology

EVOLUTION

© Vladimir Pravosudov

– an RFID. We trap and band all chickadees with unique PIT-tags during each fall. The RFID computer board connected to an antenna embedded into a perch at a feeder records the ID of any PIT-tagged birds landing on the perch as well as date and time. So equipping regular bird feeders with RFID technology allows monitoring all PIT-tagged birds that come to such feeders.

As we needed to test how well chickadees remember spatial locations we roughly emulated a standard radial maze paradigm in which animals first find food in one of the maze's arms and then use memory to return to this arm when placed in the maze again. Access to sunflower seeds was granted through a door, which was controlled via the RFID. We could specifiy that the RFID keep the door open constantly, or that it only allowed the door to open in certain circumstances – either when any PIT-tagged bird landed on the perch, or only when a specific PIT-tagged bird landed on the perch. As well as controlling the door, the bird's ID and time of visit were automatically recorded.

To test spatial memory, each bird was assigned just one of the 8 available feeders programmed to open the door when the assigned bird landed on the perch. Each bird within a flock would be assigned its own feeder so they could not learn from one another. Although when a bird landed on the wrong perch it did not get food, we still got a record of when it landed on that feeder. Initially, a bird would sample multiple feeders until it lands on the feeder it has been assigned, where it gets its food reward. If the bird remembers the rewarding feeder, it should come only to that feeder and avoid landing on the others. As the bird learns, we see a typical learning curve as the bird makes fewer and fewer 'erroneous' visits to the wrong feeders, before coming to the correct feeder. When we download the data from the feeders we are able to understand the exact path of feeder visits for each bird.

At first, we placed eight RFID-equipped feeders at the top of 10ft metal poles, which were inserted into the ground and arranged in a circle. Little were we to know that this setup severely underestimated the local black bears, which are common at our study site. We quickly learned how incredibly strong the bears are, easily bending our thick metal poles and even destroying poles that were doubled up - with a smaller pole inside a larger pole. The bears are very smart, persistent and can figure out how to get what they want – in this case, the seed meant for the birds. Electric fences and unwelcome mats did not even deter our 'mama bear', a large female that we got to know quite well.

In the end, the only way we were able to outsmart the bears was to attach the feeders to a square wooden frame and suspend the array of feeders 10-15 feet in the air by using a pulley system attached to 4 trees by metal wire cables. The bears could still smell the seeds but they were either unable to slide down from the tree to the feeders on the metal wires, or they could not figure out how to get to them. Claw marks on the trees told us that the bears, led by their noses, were climbing the trees up to the height of the feeders, but didn't seem to be going higher. They would need to get quite a bit higher to get to the metal cable attachment pulley. One clever bear reached a cable and shook the array, spilling the seeds, but once all feeders were firmly attached to the frame, seeds no longer spilled and the bear eventually gave up. So our working spatial array design was born – we would lower it to fill the feeders with seeds and download the feeder data and then lifted it up again into the sky. Nobody but the birds could get to the feeders, except of course when we received almost 10 feet of snow at our high elevation sites and lucky squirrels were able to jump onto the feeders. Thankfully, all testing was done by that time.

The tests were conducted in the depths of winter, with lots of snow which meant we travelled to our arrays by

EVOLUTION

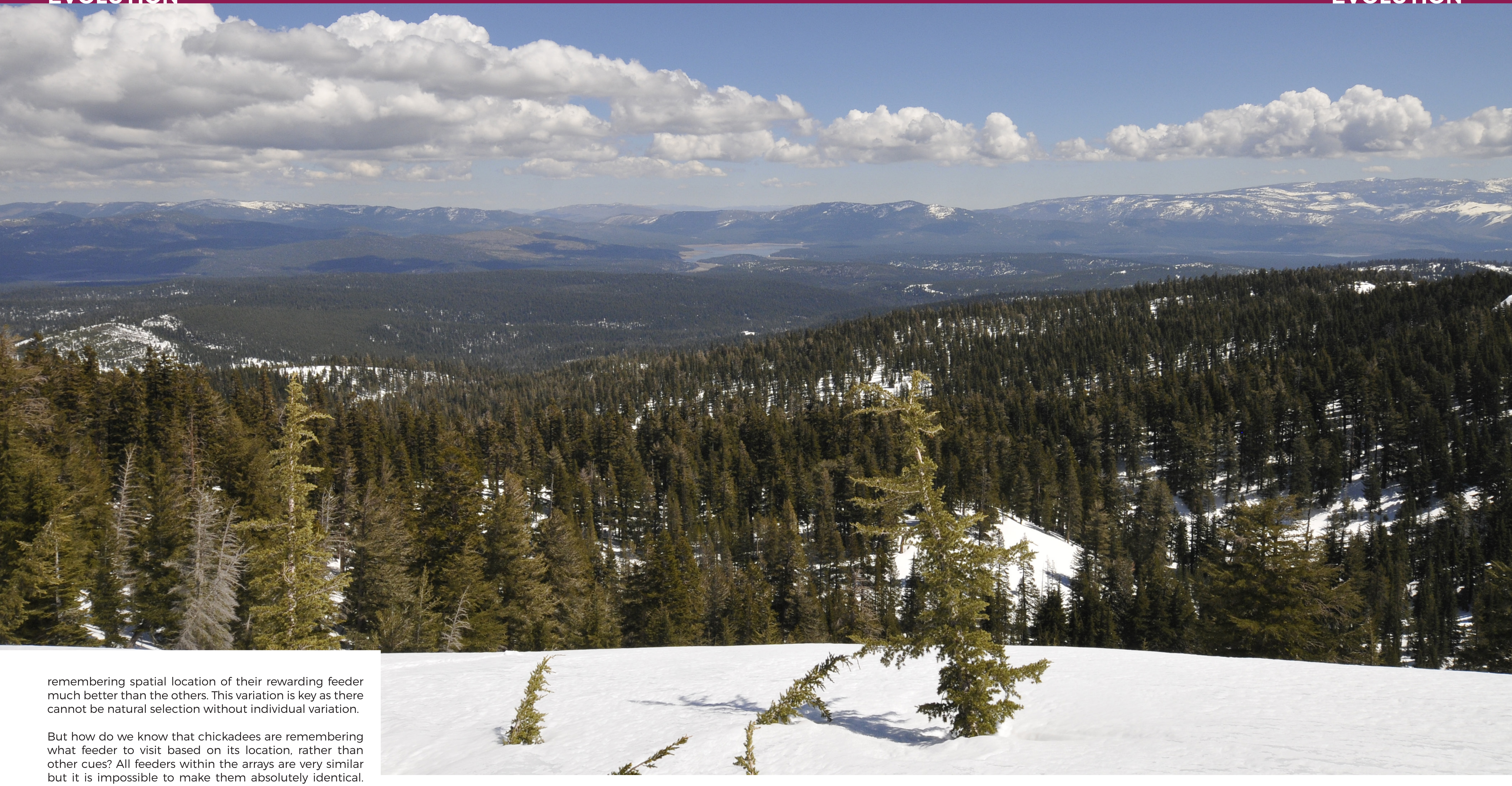
snowmobile, or snow-track equipped side-by-side All Terrain Vehicle three times a week. Some days, after a particularly massive snowstorm, the snowmobile couldn't even cope and we had to walk, snowshoes on feet, carrying all of our equipment on our backs. Finally at the arrays, we would download all data from memory cards, double check all feeder functions and go back home. Sounds simple, but this usually took three or four hours on a smooth day, and could eat up the whole day, seeing us work until dark if we came across electronic issues. Issues that did arise were fixed in the field, often at freezing temperatures with blustering wind and snow. Operating small metal tools with small computer boards inside relatively small feeders required the dexterity of ungloved hands, which, in such extreme weather, was painfully tricky.

Despite these challenges, our system works beautifully. Birds don't have to manipulate anything, just land on a perch and hope to be fed. First, we keep all feeders fully open so birds quickly learn that they can get food from the feeders. Then we keep the doors closed but program all feeders to open when any PIT-tagged bird lands on a perch. Doing so allows birds to adjust to the door opening and learn that the door will open only when they land on the perch even though they cannot see the seeds behind the closed door. Once all birds complete these two stages, we assign individual birds to different feeders by entering PIT-tags into the RFID so the door only opens to these birds while recording the identity and time of each visit for all birds. Birds start testing by making many errors but the number of errors is significantly reduced during the first 5 trials and within the first 20 trials birds visit on average just one non-rewarding feeder. We were able to test memory in more than 200 chickadees over the first two years. Chickadees learn our spatial task well, but there is a lot of individual variation with some birds learning and

Some days, after a particularly massive snowstorm, the snowmobile couldn't even cope and we had to walk, snowshoes on feet, carrying all of our equipment on our backs.

© Vladimir Pravosudov

EVOLUTION



© Vladimir Pravosudov

remembering spatial location of their rewarding feeder much better than the others. This variation is key as there cannot be natural selection without individual variation.

But how do we know that chickadees are remembering what feeder to visit based on its location, rather than other cues? All feeders within the arrays are very similar but it is impossible to make them absolutely identical. There is a chance that birds may memorise unique features of individual feeders rather then their spatial location. We tested this by rotating the arrays 180 degrees after chickadees learned the rewarding feeders. If birds use unique feeder features, they should follow the feeder in its new location rather then continue visiting a new feeder in the spatial location of the previously rewarding feeder. After the rotation, chickadees were coming to different feeders that were now occupying the same spatial locations of the previously rewarding feeders – clear evidence that birds use spatial memory in our testing paradigm.

In our first season, we also confirmed our previous lab results – chickadees from high elevation were better at learning and remembering spatial locations of feeders compared to birds from low elevation. We also found that there was large individual variation in the how often chickadees visited their rewarding feeder over the two-week testing period. While some birds did so hundreds of times, others visited them thousands! What is especially interesting is that birds that completed more trials showed better learning and memory performance already at the first few trials – individuals with better learning performance from the start did more trials, meaning that they came to the feeders much more. Chickadees cannot eat thousands of seeds in such a short time, but rather they cache these seeds. So our results suggest that birds with better spatial memory also cache more food and birds from high elevation competed more trials, which is in line with our previous lab studies showing that high elevation birds cache more than low elevation birds.

During the second season, we extended our study and asked whether chickadees are cognitively flexible and can quickly learn new locations once the old feeders stopped providing food – something called a reversal-learning task. While this seems simple, re-learning might be affected by something called proactive interference – where old memories might make learning new and similar information more difficult. High elevation chickadees appear to rely on food caches more compared to low elevation birds and they also cache more food and have better memory retention. Memory retention may be associated with more proactive interference and, as a result, high elevation birds might be less cognitively flexible. That was indeed what we found – high elevation birds did worse when challenged to learn a new feeder location after learning the initial location of a rewarding feeder. At the same time, they continued to visit the old, previously rewarding location more frequently compared to the low elevation birds. And, on an individual level,

EVOLUTION

birds that continued visiting the old location did worse at learning the new location. These results were consistent with our idea that strong older memories might interfere with forming new memories. Low elevation chickadees cached less food, did worse on spatial memory tasks and so appear to be less reliant on food caches compared to birds from higher elevations. However, they were more cognitively flexible, as shown on the reversal memory task.

So cognitive flexibility seems to be associated with memory trade-offs – better flexibility is associated with less memory retention, but better memory retention is associated with more proactive interference and hence with less flexibility. Which one is more valuable? Well, that depends. At high elevations with the harsher winters that go with it, longer-lasting memories of a greater number of food caches might be more important then being able to be flexible. At milder, lower elevations, cognitive flexibility might pay off more, as memory for food caches might be slightly less important, while quickly learning about a changing environment could be more advantageous.

The key question, however, is why we see these differences, and whether natural selection played a role in shaping them. We don't have the answers yet, but we continue to track the survival and reproductive success of the birds. If we find that the ability to learn, or that of reversal learning, is associated with higher overwinter survival or reproductive success, it would indicate that these traits, and environment-related variation in memory, might be being shaped by natural selection. Regardless of the complexity of the answers, the chickadees continue to thrive in their respective environments. The fascinating and intricate variations in their strategies for survival will keep me asking questions for years to come.

Croston, R., Branch, C. L., Pitera, A. M., Kozlovsky, D. Y., Bridge, E. S., Parchman, T. L., & Pravosudov, V. V. (2017). Predictably harsh environment is associated with reduced cognitive flexibility in wild food-caching mountain chickadees. Animal Behaviour, 123, 139-149.