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Memory in wild mountain chickadees from different elevations: comparing first-year birds with older survivors

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Understanding both inter- and intraspecific variation in animals' cognitive abilities is one of the central goals of cognitive ecology. We developed a field system for testing spatial learning in wild chickadees using radio frequency identification (RFID)-enabled feeders that allowed us to track individuals across multiple years. Mountain chickadees, *Poecile gambeli*, inhabit a continuous montane gradient, and individuals inhabiting higher elevations experience harsher winters than those at lower elevations. Previous studies found that chickadees at higher elevations cached more food and demonstrated better spatial memory, but they performed worse during reversal learning than chickadees at lower elevations. Here, we employed spatial learning, reversal learning and memory retention tasks to compare elevation-related performance of first-year juvenile birds with that of adults that had survived at least 1 year. Chickadees from high elevation performed better in the initial learning task but worse in the reversal task than birds from low elevation. There were no differences between first-year birds and adults in the initial learning task, but adults performed significantly better in the reversal test. First-year birds also made more errors associated with the initial target, which suggests higher levels of proactive interference. There were no significant differences between elevations or between juvenile and adults in memory performance after a 16-day retention. After retention, chickadees did not discriminate between the feeders that provided food during the initial task or during the reversal task prior to retention. These results are also consistent with the effects of proactive interference, as birds should have only visited the most recently rewarding feeder. Our findings suggest that the ability to quickly learn changing information is critical for chickadees at both elevations as surviving adults did better in the reversal task than first-year birds. Our results also suggest that selection may favour better reversal learning abilities associated with lower levels of proactive interference.

Animal species, populations and individuals may vary in their abilities to perceive, learn, remember and use different types of information, resulting in overall differences in cognition (Dukas, 2004; Shettleworth, 2010). Adaptation to the environment through natural selection is likely to be the driving mechanism behind most observed inter- and intraspecific differences in cognition (Krebs, Sherry, Healy, Perry, & Vaccarino, 1989; Pravosudov & Roth, 2013; Sherry, Vaccarino, Buckenham, & Herz, 1989). For example, in harsh environments where conditions change regularly, natural selection is expected to favour the ability to quickly learn new information (e.g. Pravosudov & Roth, 2013). On the other hand, if the environment were entirely unpredictable, there would be no advantage in learning new information as all information would soon be unreliable, and learning abilities would therefore not be favoured (Dunlap & Stephens, 2009). Indeed, laboratory artificial selection experiments suggest that cognitive abilities can be selected for in a predictable but changing environment (e.g. with fruit flies: Dunlap & Stephens, 2009). Laboratory studies, however, cannot establish whether existing individual variation in cognitive abilities is under selection and whether different environments might favour different cognitive abilities via differential fitness consequences.

Measuring fitness consequences of individual variation in learning abilities in wild animals that are under selective pressures is a challenge for cognitive ecologists, but it is key to fully

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understanding the evolution of cognition. Following the survival and reproductive success of wild animals of known cognitive abilities requires tracking the same individuals across space and time. In addition, it is critical to understand which specific cognitive traits might be especially important in particular environments. For example, spatial memory has several constituent traits: memory acquisition, memory retention, memory recall and memory flexibility; and these traits may or may not be equally important. In food-caching birds, it remains unclear whether all components of memory are superior compared to the noncaching species because of intensive selection for food-caching and recovery abilities (Pravosudov & Roth, 2013; Rowe & Healy, 2014). Rowe and Healy (2014) argued that only memory retention is of importance, but numerous studies suggest that memory acquisition, rather than memory retention, is superior in some species and populations with higher dependence on food caches (e.g. Pravosudov & Roth, 2013). Most of the previous comparative studies of food-caching species and populations have been conducted in artificial laboratory conditions using wild animals habituated to captivity, but captivity itself likely introduces confounds associated with either short-term or chronic stress (Harris, D'Eath, & Healy, 2008; Johnson, Boonstra, & Wojtowicz, 2010) that could affect cognitive performance. Testing cognitive abilities in wild animals in their natural environment might provide the necessary missing information in our understanding of how selection affects the evolution of cognition (Pritchard, Hurly, Tello-Ramos, & Healy, 2016).

Using radio frequency identification (RFID) technology, we developed and implemented a novel field system for testing spatial learning and memory in wild mountain chickadees, *Poecile gambeli*; this system allows continuous monitoring of spatial cognition in the same individuals over multiple years (Croston et al., 2016, 2017). Mountain chickadees are a resident food-caching species specializing on seeds of different coniferous tree species in the mountains (McCallum, Grundel, & Dahlsten, 1999) and are common across a large elevation gradient ranging from milder low elevations to harsher high elevations with significantly snowier, colder and longer winter seasons (Croston et al., 2016, 2017; Freas, LaDage, Roth, & Pravosudov, 2012; McCallum et al., 1999). Harsher winter conditions at high elevations are expected to be associated with more dependence on food caches for overwinter survival compared to low elevations (e.g. Pravosudov & Roth, 2013). Indeed, our previous laboratory and field work with chickadees from low and high elevations in the Sierra Nevada Mountains showed that, compared to low-elevation birds, chickadees at high elevations cache more food and show better spatial memory performance, both in acquisition (Croston et al., 2016; Freas et al., 2012; but see; Croston et al., 2017) and in retention (Freas et al., 2012), and have larger hippocampi, more hippocampal neurons and higher adult neurogenesis rates (Freas, Bingman, LaDage, & Pravosudov, 2013; Freas et al., 2012). The differences in environmental conditions and in cognitive abilities between high- and low-elevation birds indirectly suggest that birds from different elevations might be under different selection pressures for their spatial abilities.

In addition to the commonly measured and discussed memory components, such as acquisition and retention, our field study with wild chickadees suggested that memory flexibility, or the ability to learn new information that might conflict with older information, might also be associated with selection pressures related to food caching (Croston et al., 2017). High-elevation chickadees showed inferior performance in a reversal spatial learning task, which suggests that there might be a trade-off between acquiring and retaining initial memories with acquiring new, similar memories associated with proactive interference (Anderson & Neely, 1996; Epp, Mera, Kohler, Jesselyn, & Frankland, 2016; Gonzalez, Behrend, & Bitterman, 1967; Jacoby, Hay, & Debner, 2001). These data were consistent with some previous studies, which initially expected food-caching species to have less proactive interference, but, in fact, showed the opposite (Hampton, Shettleworth, & Westwood, 1998; Lewis, Kamil, & Webbink, 2013). Since our previous study (Croston et al., 2017) involved wild birds in their natural environment, it is possible that the differences we previously detected were due to specific environmental conditions of that year rather than due to differences in reversal learning ability; therefore, testing birds under different conditions during multiple years is necessary to resolve this issue.

In this study, we took advantage of our ability to test the same birds over 2 years using an identical experimental set-up and tested whether adult chickadees that had survived at least one full year (birds that were tested during the 2015–2016 winter season in Croston et al., 2017) differed in their learning and memory performance from first-year birds (first tested in the 2016–2017 winter season in the current study). In addition to testing birds in different environmental conditions (winter conditions differed drastically between winter seasons of 2015–2016 and 2016–2017), we aimed to test whether adults (birds that survived at least one full year) would perform better than first-year birds in some or all components of spatial memory. Mountain chickadees are nonmigratory resident birds that do not move after they settle following postnatal dispersal (e.g. McCallum et al., 1999), and since we had been banding extensively in our study area for 3 years prior to the 2016–2017 winter season, we considered any new, first-year birds to be juveniles. We added a memory retention task because (1) memory retention has never been tested in wild food-caching birds in the field and (2) using a memory retention task after a reversal learning task allows for an additional proactive interference test, as memory associated with learning the first rewarded location might interfere with long-term memory retention of the most recently rewarded location.

METHODS

Study Subjects and Site

We tested spatial memory performance in wild food-caching mountain chickadees that were fitted with unique passive integrated transponder (PIT) tag identifiers (IB Technology, Leicestershire, U.K.). Chickadees were trapped using mist nets at 11 independent tube-feeder sites and at nests at our long-term field site in Sagehen Experimental Forest, in the Sierra Nevada, northern California, U.S.A. Birds were trapped at low-elevation sites (ca. 1900 m) and at high-elevation sites (ca. 2400 m), following our previous work (Croston et al., 2016, 2017), and fitted with unique colour band combinations, including a band with an embedded PIT tag (2.3 mm inner diameter × 8 mm long; ca. 0.1 g representing <1% of total chickadee body mass).

During the 2016–2017 winter season, we tagged 247 new birds (100 birds at high elevation and 147 at low elevation), and tested a total of 182 birds (both first-year birds and adults), 87 at high-elevation arrays and 95 at the low-elevation arrays (Table 1). The number of birds varied between different tests as some birds either disappeared or did not complete different tests (Table 1).

'Smart' Feeders and Spatial Arrays

All spatial memory tasks (initial, reversal and retention tests) took place at four different spatial arrays, two per elevation at the exact same locations as during the 2015–2016 winter season (Croston et al., 2017). Within each elevation, the two arrays were separated by ca. 1.2 km.