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Individual variation in spatial memory performance in wild mountain chickadees from different elevations

R. Croston [a], [*], D. Y. Kozlovsky [a], C. L. Branch [a], T. L. Parchman [a], E. S. Bridge [b], V. V. Pravosudov [a]

[a] Department of Biology – Ecology, Evolution, and Conservation Biology, University of Nevada – Reno, Reno, NV, U.S.A.
[b] Oklahoma Biological Survey, University of Oklahoma, Norman, OK, U.S.A.

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For food-caching animals inhabiting environments with strong seasonal variation, harsh winter conditions may limit access to naturally available food and favour the evolution of enhanced spatial memory. Spatial memory enables animals to remember the locations of food caches for overwinter survival, therefore animals in harsher conditions may benefit more from more accurate spatial memory than conspecifics living under relatively mild conditions. Despite numerous laboratory studies lending indirect support to the hypothesis that a harsh environment favours the evolution of spatial memory, there is no direct evidence showing fitness consequences of variation in spatial memory. As a step towards evaluating this hypothesis in natural populations, we established spatial arrays of programmable bird feeders equipped with radio frequency identification technology (RFID) to test for individual variation in spatial memory in food-caching mountain chickadees, *Poecile gambeli*, at two elevations differing in winter climate severity. Individuals could only access food at a single rewarding feeder within an array of eight, and each individual had to learn the location of their unique rewarding feeder. Birds at higher elevations visited the arrays significantly more frequently than birds at lower elevations, suggesting more intense food caching. They also performed better at locating their rewarding feeder than birds from lower elevations. Individuals showing better performance participated in more overall trials, suggesting a link between food-caching propensity and memory performance, but higher overall levels of activity within each array yielded less accurate memory performance. Finally, rotating the arrays showed that birds relied specifically on spatial memory in order to locate their rewarding feeder. To our knowledge, this is the first explicit test of spatial memory performance in food-caching birds under natural conditions. Our results corroborate earlier laboratory-based work showing large individual variation in spatial memory performance and lay the groundwork for future investigation into the fitness consequences of individual variation and the evolution of spatial memory.

Variation in environmental conditions has long been hypothesized to impact the evolution of animal cognition (Dukas, 1998; Shettleworth, 1998), and, in particular, to drive the evolution of specific modular cognitive abilities in food-caching species (e.g. spatial memory; Krebs, 1990; Sherry, 2006). Animals living under seasonally variable conditions are often subject to variation in availability and abundance of food. In general, colder seasons are associated with harsher conditions, including decreased temperatures and increased snow cover, which may limit access to naturally available food sources. Storing food is one strategy that animals may use to cope with this uncertainty (i.e. food caching; Vander Wall, 1990). Scatter-hoarding species store large amounts of food across many different locations during periods of relative abundance (e.g. autumn), which they may then retrieve as needed in times of relative scarcity (e.g. winter). As food-caching animals rely on their caches for overwinter survival (Krebs, Sherry, Healy, Perry, & Vaccarino, 1989; Pravosudov & Roth, 2013; Sherry, Vaccarino, Buckenham, & Herz, 1989; Vander Wall, 1990), spatial memory may be critical for survival in these seasonally fluctuating environments.

Cache retrieval involves the use of spatial memory (Krebs et al., 1989; Sherry, 2005; Sherry et al., 1989). Therefore, it can be hypothesized that food caching as an adaptation to unpredictable

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[*] Correspondence: R. Croston, Department of Biology – Ecology, Evolution, and Conservation Biology, University of Nevada Reno, 1664 N. Virginia Street, Reno, NV 89554, U.S.A.
E-mail address: RebeccaLCroston@gmail.com (R. Croston).

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foraging conditions makes specific demands on spatial memory and its neural mechanisms (Krebs et al., 1989; Pravosudov & Roth, 2013; Sherry et al., 1989; Shettleworth, 1998, 2009). Spatial memory is an important component of cognition, defined here as the collection, retention and use of information about the environment (Dukas, 2004; Shettleworth, 1998), which specifically involves the use of geographical information and even basic geometry (Kamil & Jones, 1997) in evaluating the relationship between given locations. Evolutionary theory predicts that under conditions of particular climatic harshness (e.g. low ambient temperatures and lengthy seasonal snow cover), the spatial memory ability of year-round resident species may be under strong selection (Krebs et al., 1989; Pravosudov & Clayton, 2002; Pravosudov & Roth, 2013; Sherry et al., 1989). As a result, it has been predicted that even within species, animals living under harsher climate conditions should have better accuracy and retention of spatial memory than animals living under less harsh conditions (i.e. resulting in adaptive specialization; Pravosudov & Clayton, 2002; Pravosudov & Roth, 2013). This pattern may be predicted across gradients of latitude and longitude (Roth & Pravosudov, 2009), as well as across elevational gradients in the mountains, where dramatic changes in climatic conditions can take place across a relatively small geographical scale (e.g. Freas, LaDage, Roth, & Pravosudov, 2012).

We studied spatial learning and memory in mountain chickadees, *Poecile gambeli*, year-round residents that inhabit variably harsh conditions along an elevational gradient ranging from approximately 1900 m to 2400 m in the Sierra Nevada. Relative to birds living at ‘low’ (i.e. 1900 m) elevation conditions, birds living at ‘high’ (i.e. 2400 m) elevation within our study site are subject to lower ambient temperatures and increased snow cover, which remains longer across seasons, resulting in relatively limited access to natural food sources (e.g. insects and pine seeds) during the winter. Because of this, mountain chickadees inhabiting higher elevations may be selected for increased accuracy, capacity and/or longevity in spatial memory relative to conspecifics inhabiting lower elevations (Freas et al., 2012). Climate-based variation in spatial memory and neural morphology has been demonstrated in a laboratory setting both in black-capped chickadees, *Poecile atricapillus*, across latitudinal and longitudinal gradients (Pravosudov & Clayton, 2002; Roth, LaDage, Freas, & Pravosudov, 2011; Roth & Pravosudov, 2009), and in mountain chickadees collected at our specific study sites (Freas, Bingman, LaDage, & Pravosudov, 2013; Freas et al., 2012; Freas, Roth, LaDage, & Pravosudov, 2013). In particular, mountain chickadees from high elevations exhibit higher caching propensity, more accurate cache retrieval, increased retention of memory for cache location and larger hippocampi with more neurons and faster neurogenesis than do their conspecifics from low elevation under laboratory conditions (Freas et al., 2012).

While most laboratory studies support the hypothesis that harsh environments favour the evolution of better spatial memory and associated hippocampal morphology via natural selection (reviewed in: Croston, Branch, Kozlovsky, Roth, LaDage et al., 2015; Pravosudov & Roth, 2013), all of the existing support has been indirect. To establish that natural selection (as local adaptation) accounts for differences in memory and brain anatomy in different environments, it is necessary to demonstrate that heritable individual variation in spatial memory is associated with differential fitness in those environments (e.g. Croston et al., 2015). Understanding whether natural selection is involved in shaping differences in memory requires examination of cognitive phenotypes in the wild, in order to accurately connect variation in cognition with variation in fitness (Endler, 1986). To our knowledge, there have been no studies testing predictions associated with the adaptive specialization hypothesis (e.g. Krebs, 1990) for spatial memory ability in free-living food-caching animals.

In this study, we used radio frequency identification (RFID) technology to directly investigate variation in spatial learning and memory among mountain chickadees residing at two elevations (Freas et al., 2012). We designed and built spatial arrays each consisting of eight ‘smart’ RFID feeders, and implemented these in the field to test how readily resident mountain chickadees would learn the correct spatial location of an individually designated target reward feeder. We tested for individual variation in memory performance, based on the prediction that high-elevation birds would perform more accurately than their conspecifics at low elevation. We also tested for effects associated with the overall amount of bird activity at the array and experience on task performance, and attempted to disentangle the roles of spatial versus local cues in driving the observed performance.

METHODS

Study Subjects and Site

We trapped and banded mountain chickadees using mist nets at 17 established feeder sites throughout Sagehen Experimental Forest, near Truckee, CA, U.S.A. in the Sierra Nevada mountain range. Birds were trapped at two elevations: ‘low’ elevation (ca. 1900 m) and ‘high’ elevation (ca. 2400 m) following our previous work (e.g. Branch & Pravosudov, 2015; Freas, Bingman, et al., 2013; Freas et al., 2012; Freas, Roth, et al., 2013; Kozlovsky, Branch, Freas, & Pravosudov, 2014) and fitted with unique colour band combinations, including a plastic band containing a passive integrated transponder (PIT) tag (IB Technology, Leicestershire, U.K.; http://www.buyrfid.co.uk/store/index.php?route=product/category&path=42). For each bird, we recorded mass and wing chord length, and we sampled 100 μl of blood from the brachial vein as conditions allowed (we did not carry out blood sampling in especially cold conditions due to concerns for the welfare of the birds).

Sagehen Experimental Forest is a primarily mixed-conifer forest. With increasing elevation at this site, resident animals face lower ambient temperatures and increased snow coverage, resulting in harsher and less predictable conditions than at lower elevations. ‘Smart’ feeder spatial arrays were constructed at four previously established feeder locations within our study site, two each at high-elevation and low-elevation localities, used in our previous work (Branch, Kozlovsky, & Pravosudov, 2015; Branch & Pravosudov, 2015; Freas et al., 2012; Kozlovsky et al., 2014; Kozlovsky, Branch, & Pravosudov, 2015). The distance between two arrays within each elevation was approximately 1.2 km, and arrays drew entirely nonoverlapping sets of birds.

‘Smart’ Feeders and Spatial Arrays

We investigated spatial memory performance based on data from four spatial arrays, each consisting of eight RFID-programmable ‘smart’ feeders mounted on a square 122 × 122 cm wooden frame (Fig. 1). Within each array, feeders were arranged with two feeders on each side, spaced evenly throughout (ca. 28 cm between adjacent feeders) and with the openings facing outward (Fig. 1). Arrays were suspended from trees approximately 2.5 m above ground level to prevent access by rodents and black bears, *Ursus americanus*. Feeders were custom designed and manufactured for this study based on design specification by E.S.B. and V.V.P., using the RFID design described in Bridge and Bonter (2011).

The RFID circuitry as well as the data-logging and basic motor control were contained on a single printed circuit board similar to that described by Bridge and Bonter (2011). The main operational components of the reader were an RFID module (UB22270, Atmel