



## Elevation-related differences in female mate preference in mountain chickadees: are smart chickadees choosier?



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Heterogeneous environments are often associated with differential selection pressures favouring the evolution of local adaptations, and assortative mating is one of the mechanisms that might enhance such local adaptations. Montane environments present an example in which environment changes rapidly and predictably along an elevation gradient, and such variation may be expected to lead to the evolution of local adaptations. In food-caching mountain chickadees, *Poecile gambeli*, reliance on food stores is likely to increase with elevation, and previous research has shown that individuals living at high elevations cache more food and have superior spatial memory, needed to recover food caches, while also being socially subordinate to low-elevation birds. Here, we asked whether such differences might be associated with assortative mating. Considering that superior spatial memory ability for recovering food caches may be more critical for survival at high elevations because of more severe winter conditions, it should benefit females from high elevations to mate assortatively with males from the same elevation. If spatial memory is costly but not critical at low elevations, females from low elevation should mate assortatively with males from low elevation, especially given their socially dominant status to high-elevation birds. We assessed female preference using a pairwise choice of high- and low-elevation males. We used the amount of time spent in proximity to males from the same versus different elevation to determine female preference. High-elevation females showed significant preference for high-elevation males, however, low-elevation females showed no elevation-related preference. These results suggest that high-elevation females are choosier than low-elevation females, and prefer males from their same elevation. © 2014 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Heterogeneous environments are often associated with differential selection pressures favouring the evolution of local adaptations, and assortative mating is one of the mechanisms that might enhance such local adaptations (Dieckmann & Doebeli, 1999; Gavrilets, 2003; Nosil, Egan, & Funk, 2008; Via, 2001). Montane environments present an example in which the environment changes rapidly and predictably along an elevation gradient, and such variation may be expected to lead to the evolution of local adaptations (e.g. Freas, LaDage, Roth, & Pravosudov, 2012; McCracken et al., 2009; Wilson, Peters, & McCracken, 2012). High elevations are characterized by predictably lower temperatures, more snowfall and longer period of winter conditions than low elevations (Cook, 2012; Graham, 1983; S. R. Hopkins & Powell, 2001; Shepson & Tinnesand, 2003). Individuals living in harsher

conditions at higher elevations may experience stronger selection on some ecologically relevant traits, including growth rate, age of maturity, haemoglobin, body size and spatial memory for recovering food caches than individuals living in more temperate conditions at lower elevations (Freas et al., 2012; McCracken et al., 2009; Miaud & Merila, 2001; Pravosudov & Roth, 2013; Wilson et al., 2012). These local adaptations might be enhanced by reduced movement between elevations and potentially maintained by assortative mating (Kondrashov & Shpak, 1998).

Here, we asked whether female mountain chickadees, *Poecile gambeli*, are contributing to potential separation between high- and low-elevation birds by mating assortatively with males from their respective elevation. Mountain chickadees are food-caching, resident montane birds that inhabit a range of elevations and use spatial memory, at least in part, to relocate their scattered caches (Pravosudov & Smulders, 2010). At our study site, high-elevation chickadees start breeding, on average, 2 weeks later than low-elevation birds, probably due to climatic differences in elevation (Kozlovsky, Branch, & Pravosudov, in press). Harsher winters associated with higher elevations have been hypothesized to

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generate higher dependence on food caches necessary to survive winter and hence successful cache recovery might have stronger fitness consequences at higher elevations than at lower elevations (Freas et al., 2012). Previous work has confirmed that compared to low-elevation chickadees, birds from high elevation have higher food-caching propensity and superior spatial memory associated with large morphological differences in the hippocampus, a brain region involved in spatial memory function (Freas et al., 2012). That these elevation-related differences were found in first-year juvenile birds residing in a uniform common garden laboratory environment prior to their first winter suggests that variation in memory and hippocampus morphology may be heritable (Freas, Bingman, LaDage, & Pravosudov, 2013; Freas et al., 2012; Pravosudov & Roth, 2013). In addition, high-elevation birds perform better on a novel problem-solving task than low-elevation birds (Kozlovsky, Branch, & Pravosudov, 2014) and overall high- and low-elevation chickadees seem to represent group-level behavioural types with high-elevation males additionally being slower explorers, less aggressive and socially subordinate to low-elevation males (Branch, Kozlovsky, & Pravosudov, 2014; Kozlovsky, Branch, Freas, & Pravosudov, 2014). Differences seen in social dominance status are particularly interesting given that chickadees form permanent flocks of unrelated individuals outside of the breeding season and individuals within flocks maintain a linear dominance hierarchy, with subordinate individuals usually experiencing lower fitness than dominant individuals (e.g. Ratcliffe, Mennill, & Schubert, 2007).

Taken together, these findings suggest that high-elevation birds may be somewhat restricted to high elevation because of their socially subordinate status, while low-elevation birds may be restricted to low elevation because of their inferior spatial memory, notwithstanding the short distance separating these birds. If birds have the highest fitness at their respective elevations, and their locally adapted traits are heritable (W. D. Hopkins, Russell, & Schaeffer, 2014), it would benefit females to mate with males from their respective elevation to ensure the highest fitness of their offspring.

We assessed female mountain chickadee preference for males from their respective elevation using a standard pairwise choice paradigm (Amundsen, Forsgen, & Hansen, 1997; Collins, Hubbard, & Houtman, 1994; Leitao, Monteiro, & Mota, 2014; Nolan & Hill, 2004; Woolley & Doupe, 2008). If high- and low-elevation birds are locally adapted to their environments, and females are able to discriminate between males from different environments, then given a pairwise choice of a high- or low-elevation male, we predicted that high-elevation females would spend more time adjacent to high-elevation males and that low-elevation females would spend more time adjacent to low-elevation males.

## METHODS

### *Study Subjects and Capture*

Twenty-four mountain chickadees were trapped using mist nets at established feeders on 30 November – 1 December 2013 from high-elevation (2400 m) and low-elevation (1800 m) sites at Sagehen Experimental Forest, Truckee, California, U.S.A. (sensu Freas et al., 2012; 'high' and 'low' elevation used here are the same elevations as 'high' and 'mid' in Freas et al., 2012; we use 'high' and 'low' here because they represent the largest differences in spatial memory and hippocampus morphology). Birds were captured from multiple flocks at multiple feeders to form pairwise choices using unfamiliar individuals. Approximately 100 µl of blood was taken from the brachial vein at the time of capture for genetic analysis of sex. All birds were transferred to the laboratory facilities at the

University of Nevada, Reno, U.S.A., and were held until 20 April 2014, when they were released back at Sagehen. Six males and six females each from both high and low-elevation sites were used in behavioural tests; sex was determined using genetic analyses following Fox, LaDage, Roth, and Pravosudov (2009). Birds were individually colour banded and housed singly in wire-mesh cages (42 × 60 and 60 cm high), visually but not acoustically isolated from each other. Cages were covered with a translucent white cloth to allow birds to habituate to individual cages with minimal outside disturbance for 3 weeks before testing (Pravosudov, Mendoza, & Clayton, 2003). Male and female birds were housed in separate rooms to reduce familiarization with vocalizations. Birds were initially maintained on a 10:14 h light:dark cycle to mimic winter conditions. On 8 February 2014, birds were photostimulated by shifting photoperiod to a 14:10 h light:dark cycle, mimicking spring breeding conditions. All birds showed signs of being affected by photostimulation (e.g. cloacal protuberances, increased singing).

### *Testing Apparatus*

During preference testing, a female was housed in a double cage with two joining compartments (84 × 60 and 60 cm high) and two males (one from high elevation and one from low elevation) placed in smaller cages (each 42 × 60 and 60 cm high) on either side of the female's cage. A cardboard divider with a small square opening (7.62 × 7.62 cm) in the centre separated the two adjoining compartments of the female testing cage (sensu Woolley & Doupe, 2008; see Fig. 1). Females were given a 2 h acclimation period, after which males were placed in both side cages and left for additional 1.5 h. All preference tests were videorecorded for a total of 2 h (last 30 min of female by herself and 1.5 h with males). The first 30 min with the males present was considered the females' assessment period. The final hour of recording was coded for female preference, blind to the position of males. The total amount of time spent on either side of the double cage was used to indicate preference (Amundsen et al., 1997; Collins et al., 1994; Leitao et al., 2014; Nolan & Hill, 2004; Woolley & Doupe, 2008); time spent on the centre cardboard divider was not included as preference time.

### *Testing*

Mate preference testing took place in two rounds, one prior to photostimulation (mimicking autumn/winter when chickadees form pairs within flocks; McCallum, Grundel, & Dahlsten, 1999) from 26 December 2013 to 7 February 2014 and the second, 12 days after photostimulation (to mimic actual breeding conditions) from 20 February 2014 to 30 March 2014. All 12 females were habituated to one of two identical testing rooms for 7 h prior to testing. Each of the 12 females was presented with the same six unique pairs of males across six trials prior to photostimulation. Then, after photostimulation, the male pairs were switched to form six new unique pairs, which were again presented to each of the 12 females. Therefore, during each of the six trials prior to and following photostimulation, each female experienced a unique pair of males. All high- and low-male pairings were size-matched using wing chord length. Two females were tested per day in separate, identical testing rooms, and females were tested sequentially such that 5 days passed between each testing. Female placement into the testing cage was counterbalanced for the left or right side of the cage across both testing rooms. Male placement in testing cages relative to the female (e.g. left or right) was also counterbalanced between trials to ensure that any preference a female might show was due to preference for a male rather than for a cage side. To assess female preference, we calculated the mean amount of time

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