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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.

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

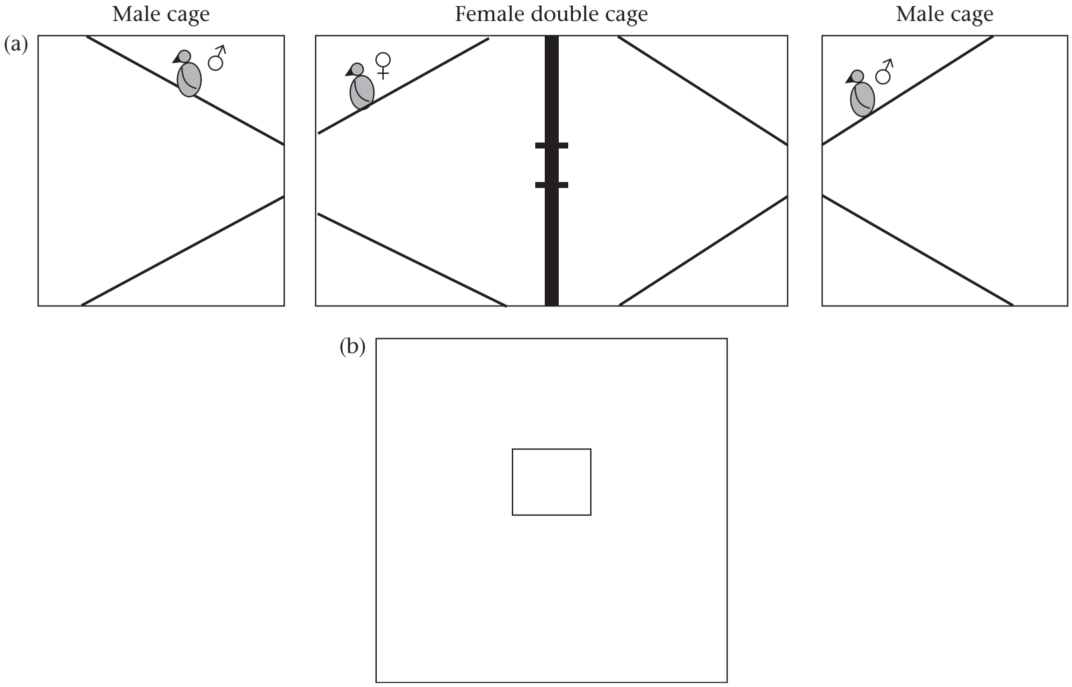

Figure 1. (a) Schematic of preference-testing cage set-up. Thin lines represent perches; the thick line represents the cardboard separator; the two lines on the thick line demarcate the 7.62 × 7.62 cm square opening in the centre of the cardboard separator. (b) Side view of cardboard separator showing placement of the square opening.

that each female spent next to the male from the same versus different elevation regardless of cage side.

Statistical Analysis

We analysed the data using a repeated measures general linear model (GLM) (STATISTICA 12) where the mean total time spent adjacent to males from the same versus different elevation across six trials was the repeated measure and elevation was the between-subject variable. Preference times were analysed separately for pre-photostimulation and post-photostimulation. Planned comparisons were used to assess pairwise statistical differences for high- and low-elevation females' preference for males from the same or different elevation.

We also calculated individual preference scores for each female by dividing the total amount of time each female spent with the same male over the total amount of time in the testing cage (maximum of 3600 s). Preference scores ranged from 0 to 1, spending no time on the side of the cage with the same male and spending all time on the side of the cage with the same male, respectively. We used paired t tests to compare preference scores to chance preference of 0.5 for high- and low-elevation females, separately for pre- and post-photostimulation. We also used a general linear model to compare high- and low-elevation female preference scores, separately for pre- and post-photostimulation.

Ethical Note

No birds were injured by mist netting or while collecting blood samples in the present study. We observed no infections or other detectable effects of mist netting or bleeding. Birds were handled for about 2–5 min after capture before being placed in transport cages covered with white translucent cloth to minimize disturbance. Birds always ate and drank water in these transport cages during the transport. All birds were released at the end of the experiment at our study site. Some of these birds were later resighted successfully breeding.

RESULTS

Pre-photostimulation

Prior to photostimulation, there were no significant differences between the mean amount of time that females from both elevations spent adjacent to males from the same versus different elevation (GLM: $F_{1,10} = 0.19$, $P = 0.67$). There was a significant difference in the mean amount of time that high- and low-elevation birds spent in both sides of the testing cage that counted towards preference time ($F_{1,10} = 10.62$, $P = 0.009$). The interaction between elevation and time spent adjacent to males from the same versus different elevation, however, was not significant ($F_{1,10} = 0.74$, $P = 0.410$; Fig. 2a). Planned comparisons showed no significant differences in the amount of time that high- and low-elevation females spent on the side of the cage with the male from the same versus different elevation (all $P > 0.05$).

There were no significant differences in preference scores of females from high and low elevations ($F_{1,10} = 0.82$, $P = 0.39$). The individual preference scores for high- and low-elevation females also did not differ significantly from chance prior to photostimulation (paired t test: high elevation: $t_5 = 1.06$, $P = 0.34$; low elevation: $t_5 = 0.28$, $P = 0.79$, respectively; Fig. 3a).

Post-photostimulation

Following photostimulation to mimic breeding conditions, there were no significant differences in the mean amount of time that females from both elevations spent adjacent to males from the same versus different elevation (GLM: $F_{1,10} = 0.99$, $P = 0.34$). There was a significant difference in the mean amount of time that high- and low-elevation birds spent in the testing cage that counted

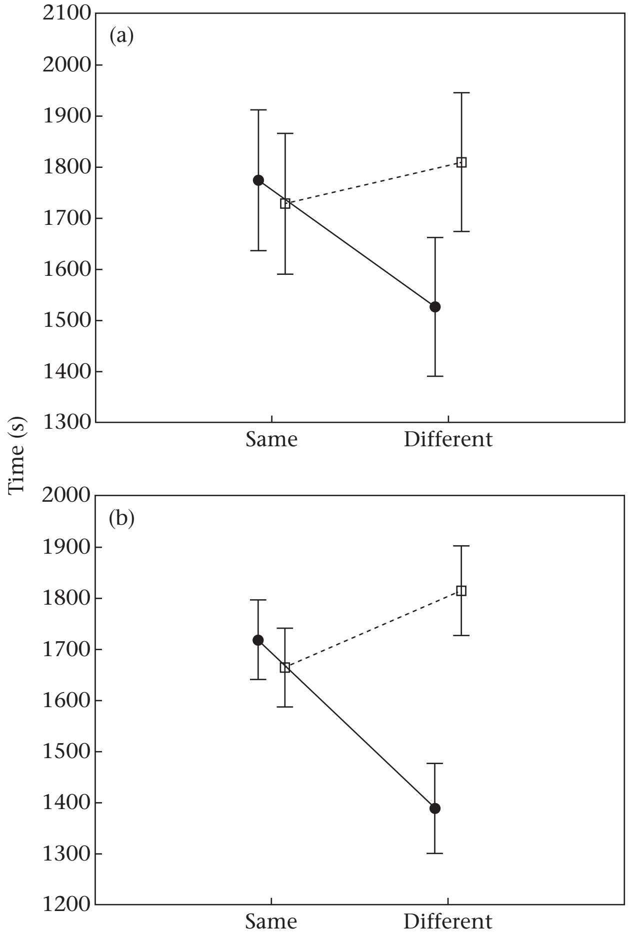

Figure 2. Total mean time (a) before and (b) after photostimulation that female mountain chickadees from high-elevation (solid circles) and low-elevation (open squares) sites spent on the side of the cage adjacent to the male from the same versus different elevation. Error bars represent SE.

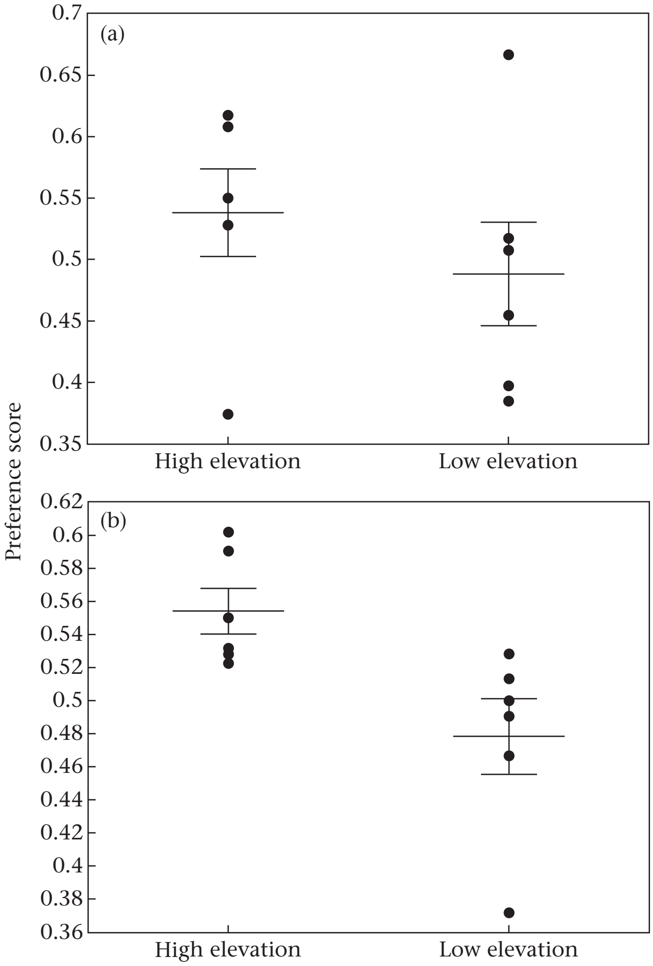

Figure 3. Individual (closed circles) and group-level (long horizontal lines: means; whiskers: SE) preference scores, calculated by dividing the total amount of time spent with the same male over the total amount of preference time, for female mountain chickadees from high- and low-elevation sites (a) before and (b) after photostimulation.

towards preference time ($F_{1,10} = 6.24$, $P = 0.032$), and the interaction between elevation and time spent adjacent to males from the same versus different elevation was also statistically significant ($F_{1,10} = 7.07$, $P = 0.024$; Fig. 2b). Planned comparisons revealed that high-elevation females spent significantly more time adjacent to high-elevation males ($P = 0.027$), while females from low elevation showed no significant preferences ($P > 0.05$).

High-elevation females had significantly higher preference scores than low-elevation females ($F_{1,10} = 7.96$, $P = 0.018$). At the same time, the preference scores for high-elevation females were also significantly higher than expected by chance (paired t test: $t_5 = 3.90$, $P = 0.011$), while low-elevation female preference scores were not significantly different from chance ($t_5 = 0.94$, $P = 0.39$; Fig. 3b).

DISCUSSION

Overall, we found that high-elevation females showed a significant preference for males from the same elevation while no significant preference was detected in low-elevation females, albeit the preference among high-elevation females was dependent on photoperiod. Prior to photostimulation, when high- and low-elevation females were still experiencing winter daylength, they spent similar amounts of time adjacent to both high- and low-elevation males, suggesting no particular preference. After being photostimulated to mimic breeding conditions, however, females from high elevation spent significantly more time adjacent to males from high elevation than they spent adjacent to males from low elevation. Low-elevation females, on the other hand, continued to spend similar amounts of time adjacent to males from both elevations. The fact that these patterns of preference were shown using multiple unique male pairs formed from unfamiliar birds (captured in different social flocks) suggests that such preferences are unlikely to be based on familiarity.

If the amount of time that a female spends on the same side of the cage with a male is indicative of her preference for that male in a breeding context (Amundsen et al., 1997; Collins et al., 1994; Leitao et al., 2014; Nolan & Hill, 2004; Woolley & Doupe, 2008), our results suggest that high-elevation female mountain chickadees are able to discriminate between high- and low-elevation males, and subsequently prefer males from their respective elevation. Our finding that high-elevation females prefer high elevation males only after photostimulation, and despite their socially subordinate status compared to low-elevation males (Kozlovsky, Branch, Freas, et al., 2014), socially subordinate birds experience reduced fitness compared with dominant individuals (e.g. Ratcliffe et al., 2007), suggests that their mate preference might be driven by the males' local adaptation to the females' local environment (e.g. superior spatial memory among other potential adaptations). If spatial memory is in part heritable (W. D. Hopkins et al., 2014), high-elevation females might be expected to be choosier than low-elevation females because of the strong reliance on spatial memory to successfully retrieve food caches necessary to survive winters at high elevations. Conversely, because low-elevation birds might have less selective pressure on their spatial learning abilities, they might show less elevation-based mate preference, again assuming the discrimination made by high-elevation females is somehow linked to this particular local adaptation.

Interestingly, our original hypothesis, that low-elevation females would prefer low-elevation males over high-elevation males because of their socially dominant status (Kozlovsky, Branch, Freas, et al., 2014), was not supported: low-elevation females spent similar amounts of time near high- and low-elevation males. It remains unclear whether no significant preference among low-elevation females was due to their inability to discriminate between males from different elevations or due to a lack or preference. Our results only suggest that, at the population level, there was no discrimination or significant preference among low-elevation females using a high- and low-elevation male dichotomy. This lack of preference suggests that low-elevation females may not prefer males based on any particular known elevation-related characteristic including spatial memory/hippocampus morphology, social dominance, novel exploration, aggression or problem solving (Branch et al., 2014; Freas, Bingman, et al., 2013; Freas et al., 2012; Freas, Roth, LaDage, & Pravosudov, 2013; Kozlovsky, Branch, Freas, et al., 2014; Kozlovsky, Branch, & Pravosudov, 2014).

That elevation-related differences in social dominance had no detectable effect on female preference might have several potential explanations. Even though high-elevation males are socially subordinate to low-elevation males (Kozlovsky, Branch, Freas, et al., 2014), they cache more food and have superior spatial memory needed to recover food caches and superior problem-solving ability (Freas et al., 2012; Kozlovsky, Branch, & Pravosudov, 2014). The question is whether higher dominance status can compensate for cognitive deficiencies. If that were the case, dominant individuals may be expected to cache less and to show inferior spatial memory even within the same social groups, as they might simply capitalize on taking food from subordinate individuals. Yet, the opposite has been reported, with dominant individuals caching more food and having superior spatial memory compared to subordinate individuals (Pravosudov et al., 2003; Pravosudov & Omanska, 2005). In other words, females at high elevation should value traits related to more successful food caching and cache retrieval over dominance status. However, it is also possible that within elevations, female may additionally prefer socially dominant males. In addition, it may be that females are unable to assess relative dominance status in the absence of any male—male interactions.

Several concerns with the present study should be noted. (1) Because males from high and low elevations were housed in the same room, there could be a potential issue of call convergence (Mammen & Nowicki, 1981), if females use calls to identify males from their respective elevation. Although we did not measure call convergence, the fact that high-elevation females were able to discriminate between the high- and low-elevation males suggests that either call convergence did not occur, or females might use multiple cues in discrimination. In addition, although there is evidence of within-flock call convergence in chickadees from the same population (black-capped chickadees, *Poecile atricapillus*: Mammen & Nowicki, 1981), it is not clear whether chickadees from different populations can even be expected to converge.

(2) We do not know whether time spent in proximity to a male directly translates into mate choice or breeding in our birds. Our assumption of this was based on results of other studies that have used this methodology and that have shown that it is indicative of mate preference (Amundsen et al., 1997; Collins et al., 1994; Leitao et al., 2014; Nolan & Hill, 2004; Woolley & Doupe, 2008). However, the fact that high-elevation females only showed a preference for high-elevation males once they were photostimulated to spring breeding conditions supports the notion that this discrimination or preference may be important for breeding. In addition, in resident parids such as mountain chickadees, pairs form prior to winter when birds join stable social groups after natal dispersal (e.g. Ekman, 1989). Essentially, we changed the birds' social settings and so preferences expressed in the new social settings are likely to reflect new pair formation.

(3) Prior to photostimulation, high-elevation females also tended to prefer males from the same elevation, but the preference for high-elevation females was only significant after photostimulation. That we saw a preference after, but not before, photostimulation using the exact same sample sizes suggests that it was not an issue of power, but rather that the preference actually became stronger or more biologically relevant once all birds were in spring breeding conditions (all birds showed cloacal protuberances and singing rates increased).

Note, however, that we did not test spatial memory in this particular set of birds, and thus, we are not suggesting that females' preference is based on memory ability per se, but rather that there may be a proxy by which females can discriminate males from high versus low elevations. Previous studies have established significant elevation-related differences in spatial memory and the hippocampus (Freas, Bingman, et al., 2013; Freas et al., 2012; Freas, Roth, et al., 2013), and other behavioural traits (see above; Branch et al., 2014; Kozlovsky, Branch, Freas, et al., 2014; Kozlovsky, Branch, & Pravosudov, 2014). Our results suggest that high-elevation females might constrain movement between high and low elevations by preferentially selecting high-elevation males, despite a small distance (ca. 10 km). Such preference indirectly suggests that adaptations to high elevations in these resident birds might be especially crucial for survival and hence for female fitness. Our first step was to address whether females aid in maintaining local adaptations at high and low elevations by assessing female discriminability or preference for males from their respective elevation. Future research will now aim to assess potential proxies used by females to discriminate between high- and low-elevation males. We are specifically interested in potential structural variation in male song, because of its importance in mate choice (Searcy, 1984), and differences in achromatic contrast in males (see Doucet, Mennill, Montgomerie, Boag, & Ratcliffe, 2004; Mennill, Doucet, Montgomerie, & Ratcliffe, 2003) from different elevations that may serve as potential mechanisms for group-level identification and female mate choice in mountain chickadees.

Species experiencing disparate environmental conditions leading to local adaptations are of particular importance in evolutionary biology because they can shed light on the process of adaptive divergence (Streicher et al., 2014). The mountain chickadee system of the Sierra Nevada is a particularly useful system for addressing this question because these are resident birds, locally adapted to their respective elevation, and this local adaptation occurs across a small spatial scale. It will be paramount to gain insight into the heritability of spatial memory used in food cache recovery as well as the level of gene flow between birds at high and low elevations. Given the high mobility of avian species and the lack of a geographical barrier between the groups of individuals, it seems unlikely that there is no gene flow between these populations. However, the results found here suggest that females from high elevations may be contributing to separation between populations by mating assortatively with males from their respective elevation. Although we currently have no data on genetic population structure, nonrandom mating may be important for maintaining local adaptations regardless of the presence of gene flow (Kondrashov & Shpak, 1998; McCracken et al., 2009; Wilson et al., 2012). In our study system, these new findings provide further support for elevation-related adaptations associated with differences in winter climate.

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