Behavioral Ecology and Sociobiology (2020) 74: 40
https://doi.org/10.1007/s00265-020-2817-2

ORIGINAL ARTICLE

Elevation-related differences in annual survival of adult food-caching mountain chickadees are consistent with natural selection on spatial cognition

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Received: 10 October 2019 / Revised: 18 February 2020 / Accepted: 27 February 2020 / Published online: 11 March 2020

Abstract

Animals inhabiting montane gradients experience varying winter climates that may result in differential selection on survival-related traits. Higher elevations in temperate climates are characterized by harsher winters with greater and longer-lasting snow cover compared to lower elevations, potentially leading to stronger selection for traits that improve fitness under these harsher conditions. For food-caching mountain chickadees, *Poecile gambeli*, inhabiting harsh high elevation environments, individual variation in spatial cognitive abilities related to cache retrieval is associated with significant differences in overwinter survival. Compared to lower elevations, stronger predicted selection on traits needed for overwinter survival at higher elevations can be expected to result in higher adult annual survival despite harsher environmental conditions, indicating that individuals that survive their first winter are better suited to survive similar subsequent selection events. Here, we used a Bayesian hierarchical Cormack-Jolly-Seber (CJS) model to estimate and compare survival of adult mountain chickadees at higher and lower elevations over 3 years. We showed that adult survival was consistently higher at higher elevations despite much harsher environmental conditions, supporting our hypothesis that selection on overwinter survival-related traits (such as spatial cognition) is stronger at our high elevation study area than at lower elevations.

Significance statement

Understanding how environmental conditions are associated with different selection strengths on survival-related traits is an important question in behavioral ecology. Directly estimating differences in strength of selection is daunting, but comparing survival between environments may provide an alternative method. We tested for differences in adult survival in a resident food-caching species at higher and lower elevations varying in winter climate severity. These birds rely on food caches for winter survival, and juvenile birds with better spatial cognition (needed for cache retrieval) have higher survival during their first year at higher harsher elevations. Here, we report higher adult survival at higher elevations compared to lower elevations, despite much harsher winter environment. Such findings support our hypothesis for stronger selection in harsher winter conditions because individuals that survive their first year under stronger selection are better suited to survive subsequent selection events.

Keywords Annual survival · Natural selection · Food caching · Spatial memory · Chickadee · Evolution

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Communicated by D. Rubenstein

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Introduction

The neural processes involved with the acquisition, retention, storage, and use of information, generally referred to as cognition (Dukas 2004), give rise to a wide range of observable behaviors such as foraging decisions, predator avoidance, and mate selection (Morand-Ferron et al. 2016). Variation in cognition within populations has been attributed to short-term evolutionary processes (i.e., selection; Morand-Ferron and Quinn 2015), but evidence in natural populations has been limited due to various difficulties inherent in measuring cognitive traits in large groups of animals in the wild (Morand-Ferron et al. 2016).

The evolution of phenotypes by natural selection may occur via differential reproductive success or differential mortality (Endler 1986). In designing a field study to explore how selection may give rise to variation in cognition, the choice of species, study population, and cognitive test must all be carefully considered to ensure that that the expected relationships are relevant and measurable given the selective agent (i.e., the environment) and the cognitive trait in question (Morand-Ferron et al. 2016). Food-caching species thus present a good system because individuals depend on previously cached stores of food as a primary food source during winter (Vander Wall 1990). Many species rely on cognition to locate previously made caches; more caching and better cache recovery via spatial cognition is expected to directly lead to better survival (Sherry et al. 1989; Pravosudov and Roth 2013). In addition, in most food-caching species, spatial cognition is expected to only be involved with overwinter survival, rather than reproduction (Branch et al. 2019a).

In temperate climates, winter is typically the period of highest mortality for resident small-bodied endotherms and selection is expected to act on traits related to winter survival (Lack 1954; Jansson et al. 1981). Winter conditions such as snow depth and duration of snow cover typically increase in severity with increasing elevation, creating a montane gradient of environmental harshness with rapidly deteriorating conditions above a certain threshold (e.g., snowline) elevation (Barbour and Minnich 2000; Royce and Barbour 2001). This in turn likely leads to the differential survival of individuals carrying certain phenotypes and provides the opportunity to investigate different strengths of selection on survival-related traits within a small geographic area. Furthermore, first-year animals across many taxa are less likely to survive winter than adults, with some species experiencing up to 70% post-dispersal juvenile overwinter mortality (Munch et al. 2003). When there is strong selection on winter survival-related traits, juvenile individuals that survive their first winter and reach their first reproductive season (e.g., becoming adults) are expected to have higher probabilities of survival during subsequent winters (Reznick et al. 1996). This may lead to a difference in survival probability by age-class—higher mortality of juveniles, but higher survival of adults (Reznick et al. 1996).

In our long-term study of food-caching mountain chickadees (*Poecile gambeli*), we previously demonstrated directional natural selection on spatial cognition at higher elevations in the Sierra Nevada characterized by harsher winter conditions and longer lasting snow cover (Sonnenberg et al. 2019). At high elevations, juvenile chickadees that performed better on a spatial learning and memory task were more likely to survive their first winter, becoming adults, while those that performed worse on the spatial task died before maturity (Sonnenberg et al. 2019). Furthermore, we previously found significant cognitive, morphological, and behavioral differences between chickadees inhabiting different elevations that differ substantially in environmental harshness: chickadees at harsher, higher elevations were shown to have better spatial learning and memory abilities (in the lab: Freas et al. 2012; and in the wild: Croston et al. 2016, 2017; Tello-Ramos et al. 2018), larger hippocampi with higher total number of neurons (Freas et al. 2012, 2013), higher rates of caching (in the lab: Freas et al. 2012), and a greater mortality of first-year juveniles during their first winter (Branch et al. 2019b) compared to chickadees from milder, lower elevations. Winter conditions are always harsher at higher elevations than at lower elevations in any given year at our study area (Kozlovsky et al. 2018). If birds from both elevations were phenotypically the same, birds at harsher higher elevations would be expected to have lower survival due to harsher conditions. However, previous research showed that birds at high elevations cache more food and have better spatial cognition compared to birds at lower elevation (Freas et al. 2012, 2013) and we previously argued that such differences are a product of natural selection resulting in higher elevation birds being adapted to survival in harsher conditions. Based on these elevation-related differences, we hypothesize that natural selection on spatial cognition may be stronger at higher elevations than at lower ones, likely due to greater dependence on successful cache recovery needed to survive harsher winters.

In addition to previously demonstrating selection on cognition at higher elevations (Sonnenberg et al. 2019), we have also found indirect evidence for this hypothesis in that juvenile survival during their first winter is lower at high elevation (Branch et al. 2019b). Given these findings, if selection is stronger at high elevation, resulting in an adult population that has relatively better spatial cognition and so is well-adapted to survive harsh winter conditions, we would also expect these adults to show higher survival during subsequent years compared to adults from lower elevations with relaxed selection on cognitive traits. If selection is relaxed at lower elevations, adult survival would be more similar to that of juveniles at the same elevation, as it may be affected by a variety of factors including occasional and unpredictable winter events and predation.

Here, we present new data on annual survival rates of adult mountain chickadees to test our prediction that given stronger selection during the first winter of life, adults should have higher annual survival at higher elevations despite much harsher winter conditions. We use our long-term study area situated across an elevational gradient snowline in the Sierra Nevada, such that the difference in environmental harshness between our high and low elevation areas is substantial and ecologically relevant (Barbour and Minnich 2000; Royce and Barbour 2001; Croston et al. 2017; Branch and Pravosudov 2020). Our prediction was based on several previous findings: (1) birds at high elevation have better spatial cognition and a larger hippocampus (Freas et al. 2012, 2013) and (2) there is evidence of strong directional natural selection on spatial cognition at higher elevations where only birds with better cognition survive into adulthood (Sonnenberg et al. 2019).

The key detail is that this prediction only concerns survival of adults—once a juvenile survives the strong selection event (e.g., first winter season), the likelihood that the individual (now an adult) will survive subsequent years is higher than expected at low elevations where selection is relaxed. Considering that stronger selection should significantly reduce existing variation in cognitive abilities in juveniles resulting in adults with superior spatial cognition (e.g., Sonnenberg et al. 2019), these adults can be expected to successfully survive subsequent, albeit harsh, winters.

Methods

Study site

We trapped and banded mountain chickadees from August 2014 to July 2018 at our long-term study system in Sagehen Experimental Forest, 10 km north of Truckee, CA, USA in the Sierra Nevada (Freas et al. 2012; Croston et al. 2016, 2017; Kozlovsky et al. 2018; Tello-Ramos et al. 2018). Birds were trapped from two elevations differing in environmental harshness (Kozlovsky et al. 2018): "low" elevation (ca. 1900 m) and "high" elevation (ca. 2400 m). Birds were trapped using mistnets set up around established feeders (nonbreeding season) or at one of ca. 350 nestboxes (breeding season) and fitted with a unique color band combination, including a plastic band containing a passive integrated transponder (PIT) tag (IB Technology, Leicestershire, UK). Birds were aged when initially processed according to at least one of four metrics: rectrix condition and shape (Meigs et al. 1983), molt of tail or wing feathers (Pyle 1997), breeding status (Branch et al. 2019a) during capture, and our previous records for birds with metal United States Geological Survey issued leg bands (which we previously banded as nestlings).

Sampling methods

Mountain chickadees are resident passerines with one short post-natal dispersal event and subsequent high site fidelity, and as such could be sampled year-round (Branch et al. 2016). Each 12-month sampling period started after post-natal dispersal (Aug) and ended after the subsequent breeding season (Jul) to ensure that each winter season (ca. Dec-Mar) would not be split between two sampling periods. We constructed a capture-recapture (CR) dataset consisting of one presence observation per individual per sampling period. It was not possible to record data blind because our study involved focal animals in the field. Birds were considered present if (1) captured or re-sighted using a nestbox during our annual breeding surveys (May–Jul; Kozlovsky et al. 2018; Branch et al. 2019a); (2) captured or recaptured during non-breeding season banding efforts using mistnets at established feeder sites (Aug-Feb); or (3) recorded automatically during the winter at one of four "smart" arrays, each consisting of eight feeders equipped with radio frequency identification (RFID) technology (Bridge and Bonter 2011) and attached to a square frame suspended from trees (Croston et al. 2016; Croston et al. 2017; Pitera et al. 2018). Presence was recorded once per 12-month sampling period regardless of season or number of recaptures, re-sightings, or automated recordings (hereafter all referred to as detections). For example, a bird detected during banding efforts in November 2017 and detected at a smart feeder in January 2018 would be recorded as present once during the 2017–2018 sampling period.

We only analyzed birds that were aged as adults at the first sampling period. Detection of juveniles during the non-breeding season at our low elevation site was insufficient during one winter of the study (2017–2018). This gap in detection was likely due to decreased motivation for chickadees to forage from supplemental feeders during mild autumn and winter conditions that might have led to more abundant natural food sources. Only our low elevation site experienced low detection during 2017–2018. Adult detection at both sites was buffered by additional opportunity for detection during breeding season. Thus, instead of potentially underestimating juvenile survival at our low elevation site, we only used adult data from both sites for this analysis.

Methods for estimating survival

To estimate annual apparent survival (ϕ) and the probability of detection (p), we fit a Bayesian hierarchical, single-state CJS model (Cormack 1964; Jolly 1965; Seber 1965) based on code developed by Kéry and Schaub (2012). In this study, apparent survival is the probability that an individual will be alive and present in the sampling period (t) given that it was alive and present during the previous sampling period (t-1). We expect that the apparent survival probability is close to the true survival probability in our system because dispersal distances of mountain chickadees are typically short, chickadees are known to be rather sedentary, and we do not appear to have substantial movement in or out of the study area (Ekman 1989; Branch et al. 2016).

The CJS model makes several assumptions, including that PIT tags are not lost, individuals are not misidentified, the marked and recaptured individuals represent a random sample of the study population, all individuals within groups have the same survival and recapture probabilities, individual survival and detection probabilities are independent, and captures are instantaneous, meaning that sampling periods are short and birds are released immediately to avoid variation in the intervals between sampling occasions that could introduce variation in survival probabilities. Our study design meets all but the last of these assumptions: due to our year-round sampling scheme, sampling periods were not instantaneous. However, we argue that the biases resulting from this assumption violation are minor compared to those that would result from only using one of the three detection methods we have available. The question driving this analysis is whether there is differential overwinter survival between adults at our two elevation sites that might suggest different strengths of selection as suggested in Branch et al. (2019b). To only use data from breeding season would bias our dataset towards adult birds that have already survived the major selection event (i.e., first winter), possibly resulting in overestimates of survival. To only use data from nonbreeding season banding efforts would bias our dataset towards unbanded adults because we have low rates of recapturing banded adults, possibly underestimating survival. To only use data from automated recordings during winter would limit our sample size to only birds that we have already tagged and that have already survived the initial stages of winter. Thus, we feel it is appropriate to use presence data from all three of these methods to increase the probability of detection (p) and obtain an overall less biased estimate for apparent survival.

Model likelihood

The model likelihood describes both a state process z, in which the individual chickadee i at sampling period t is either dead ($z_{i,\,t}$= 0) or alive ($z_{i,\,t}$= 1), and an observation process y, in which the individual is either detected ($y_{i,\,t}$= 0) or not detected ($y_{i,\,t}$= 1) during the sampling period. A chickadee's state (i.e., dead or alive) will depend on its state of the previous occasion $z_{i,\,t-1}$. A dead chickadee's state will not change to any other state than dead. An alive chickadee will change states depending on the probability of survival, $\phi_{i,\,t}$ [1]. The state of an individual chickadee at first capture z_{i,f_1} will always be 1 because we know the bird is alive when we initially band it [2]. As such, CJS models are conditioned on first capture, meaning that presence data from the first capture is not treated as survival data in the model because its value is constant for all individuals (Kéry and Schaub 2012). Hence, we use 4 years of data (2014–2018) but only report survival estimates for three sampling periods (2015–2018).

$$z_{i,t}|z_{i,t-1}\sim Bernoulli\left(z_{i,t-1}\phi_{i,t}\right) \qquad (1)$$

$$z_{i,f_1} = 1 \qquad (2)$$

Whether or not a chickadee is detected $y_{i,\,t}$ during a sampling period depends on the probability of detection $p_{i,\,t}$ and the state of the individual $z_{i,\,t}$, as a bird can only be detected by our methods if it was alive [3].

$$y_{i,t}|z_{i,t}\sim Bernoulli\left(z_{i,t}p_{i,t}\right) \qquad (3)$$

Model for survival

We fit the CR data with a fixed group effect of elevation and a fixed effect of time where β_g is the group effect ($\beta_L$or β_H for low and high elevation sites respectively) and γ is the time effect on the apparent survival ϕ of an individual chickadee i at sampling period t [4].

$$logit\left(\phi_{i,t}\right) = \beta_{g(i)} + \gamma_t \qquad (4)$$

To avoid an overparameterized model, we determined that γ_t represented the time effect on the first group and set the group effect of lower elevations to zero ($\beta_L = 0$; Kéry and Schaub 2012). We could then evaluate the posterior distribution of β_H as the difference in apparent survival between sites.

Statistical analysis

All CJS models were fitted in JAGS (version 4.3.0, Plummer 2003) using R (version 3.5.2; R Development Core Team 2011) and the R2jags wrapper package (version 0.5.7; Su and Yajima 2015). Goodness-of-fit (GOF) tests were conducted using the R2ucare package (version 1.0.0; Gimenez et al. 2017). The model was first tested for convergence with simulated data. Model fit with observed data was evaluated using the Gelman-Ruben diagnostic, prior posterior overlap (PPO), and by visual inspection of the posterior distributions of all parameters and data simulated from the joint posterior distribution. Confidence in the difference in probability of survival between elevations was determined by the degree of overlap with zero of the posterior distribution of β_H.

Results

From Aug 2014 to Jul 2018, we banded 1161 individual birds (552 at high, 609 at low) of which we detected 415 individuals again (219 at high, 196 at low). Of these, 336 birds were marked as adults when banded (152 at high, 184 at low), and of these, we detected 202 individuals again (106 at high, 96 at low). Across all four sampling periods, detections comprised 26.3% of the total observations and 37.5% of all adult observations.

The average annual apparent survival probability varied over time and between sites, with the lowest annual rate in 2016–2017 for both sites and consistently higher survival probabilities at the high elevation site (Figs. 1 and 2). Averaged across years, the survival rate for adults was ca. 10% higher at higher elevations ($\phi = 0.65$, 0.54–0.75) than at lower elevations ($\phi = 0.53$, 0.42–0.65). The 95% credible intervals for the posterior distribution of the difference in annual survival between sites did not overlap with zero (mean $\beta_H = 0.51$, 0.28–0.99), providing strong support for a nonzero difference in apparent survival between sites (Fig. 3). The PPO was 28.1%. Average detection probability was similar between sites but was slightly lower at higher elevations ($p = 0.77$, 0.65–0.87) than at lower elevations ($p = 0.91$, 0.79–0.98; Fig. 4).

Discussion

Our findings supported our prediction that adult chickadees at higher elevations had higher annual survival probabilities across all 3 years of the study compared to adults from lower elevations. Our previous work showed that the proportion of adult to first-year breeders was greater at higher elevations compared to lower elevations, suggesting greater juvenile mortality during the same 3 years of sampling at our high elevation site (Branch et al. 2019b). Combined, our current and previous findings suggest that there was a greater difference in survival probabilities by age-class at higher elevations than at lower elevations. These data lend further support for our hypothesis for stronger selection on traits related to winter survival at our harsher, higher elevation site compared to our lower elevation site. When selection on overwinter traits is strong, birds that carry those traits and survive their first winter are more likely to survive subsequent winters with similar conditions. When selection is relaxed, more birds without these traits survive their first winter. This may lead to winter-related mortality of birds lacking these traits later in life as adults, especially in environments with variable winter conditions. Thus, even though winter conditions are much harsher, adults at higher elevations actually have a higher probability of survival compared to adults at milder, lower elevations because more adults may carry traits that are advantageous to surviving harsh winters. We have previously found evidence for selection on spatial cognition, a trait essential to chickadee survival, at higher elevations (Sonnenberg et al. 2019). From our current findings that the strength of selection varies between higher and lower elevations, we infer that the strength of selection on spatial cognition may also vary between elevations.

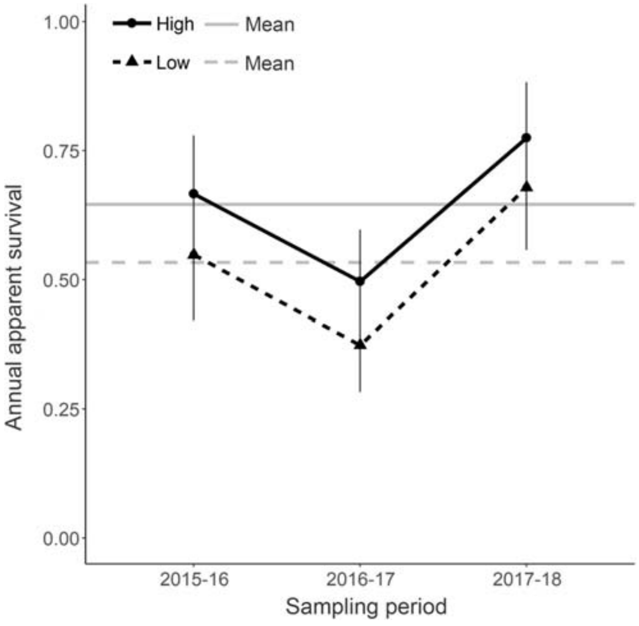

Fig. 1 Annual apparent survival probability of adult chickadees at our high and low elevation sites by year 2015–2018. Solid lines and circles indicate apparent survival at the high elevation site. Dashed lines and triangles indicate apparent survival at the low elevation site. Gray lines indicate the mean for each elevation. Black error bars indicate 95% credible intervals for the mean estimates for each elevation

The important point in our comparison is not elevation per se but differences in winter climate. This work follows extensive comparison of multiple populations of black-capped chickadees across a winter climate gradient on the continental scale and mountain chickadees at our current field area (Pravosudov and Roth 2013) showing a significant association between winter climate severity and spatial cognition. Following this highly consistent and repeatable association, we focused on mountain chickadees at high and low elevations as a model system to test specific evolutionary questions. Our high and low elevation study areas are situated strategically on opposite sides of the region's "snowline," a fairly narrow threshold elevation above which precipitation typically falls as snow during the intermediate seasons and below which falls as rain (Barbour and Minnich 2000; Kozlovsky et al. 2018; Branch and Pravosudov 2020). As such, winter conditions do not change continuously and gradually with the elevational gradient, but instead change rather abruptly around this "snowline" elevation; there is a stark difference in environmental harshness between habitats situated on either side of this boundary (Barbour and Minnich 2000). Therefore, we would not expect to see continuous variation in cognition or any other winter survival-related traits. Instead we would expect to see significant differences across the critical winter climate threshold around the snowline (Branch and

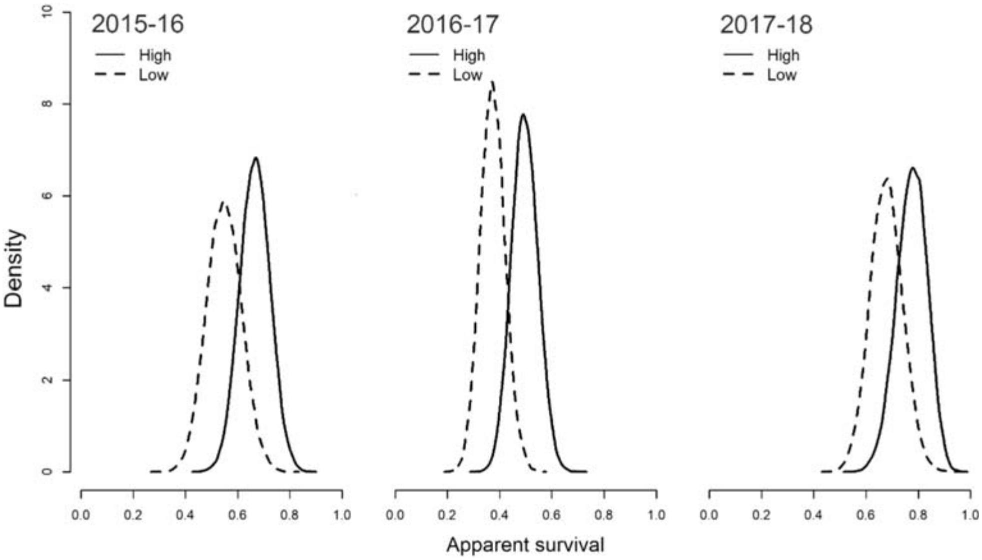

Fig. 2 Posterior distributions of apparent survival per sampling period and site (high, low)

Pravosudov 2020). Previous research from our lab has found significant differences between birds from each elevation for multiple traits (Freas et al. 2012, 2013; Kozlovsky et al. 2014, 2018; Croston et al. 2016). This wide suite of ecologically relevant differences between birds from these elevations, across multiple years, suggests that the chosen areas of study are appropriate to answer questions concerned with how differences in environment may give rise to different traits.

The obvious limitation is that our study is limited to a single mountain range because replicating the long-term study system across additional mountain ranges while maintaining the same level of detail would be unrealistic given the resources and effort required to collect data year-round from just one mountain range. Our long-term study system (established in 2011) includes individual data for over a thousand individual mountain chickadees collected from banding efforts, breeding surveys, and cognition tests. Although we do not sample discrete plots across different mountain ranges, we instead exhaustively sample a large area (over 200 ha) at high and low elevations year-round. A philosophical question remains: do studies that do not have clear replication on a larger scale still have value? We argue they do, because such studies may still capture a single event that provides key insights into evolutionary processes. Examples of such studies are widespread in the literature, but one notable example is the pivotal work by Boag and Grant (1981) showing selection on beak size in one species of finch on one island in the Galapagos. Despite lacking replication, this work documented the effects of an event on one population of finches and contributed hugely to the understanding of contemporary evolution.

Annual variation in seasonal harshness and food availability could impact annual survival rates. Among the 3 years of the study, 2016–2017 was characterized by the lowest survival estimates and the most severe winter snow conditions at both high and low elevations, as one of the snowiest years in ca. 100 years for the region (Kozlovsky et al. 2018). Survival estimates for the other 2 years (both characterized by average winter conditions; Kozlovsky et al. (2018) for 2015–2016 and

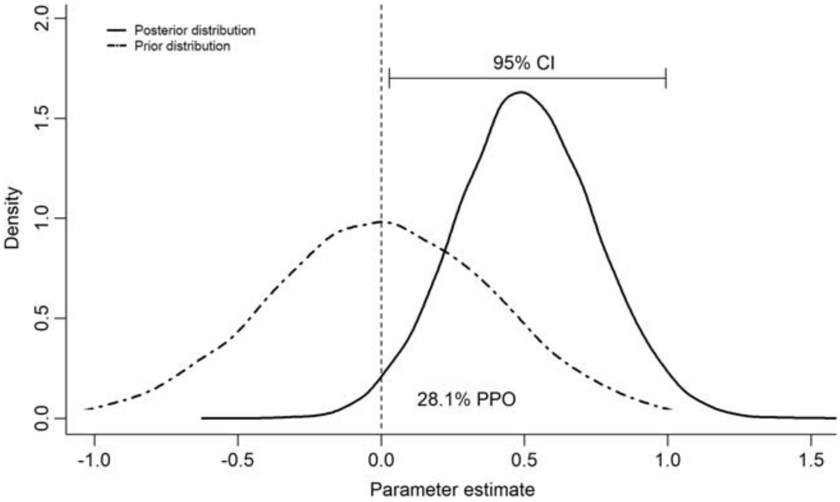

Fig. 3 Posterior and prior distributions of β_H and amount of prior posterior overlap (PPO). The 95% credible interval (horizontal line) does not overlap with zero (dotted line), providing strong evidence for a nonzero difference in the annual survival probability of adult chickadees between higher and lower elevations

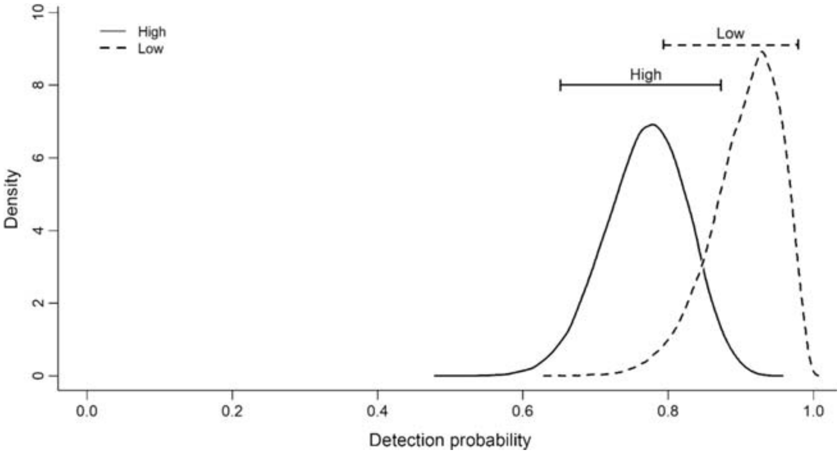

Fig. 4 Posterior distributions of detection probability per site (high, low). Horizontal lines indicate 95% credible intervals

unpublished data for 2017–2018) were similar, albeit different between elevations. Although our results do not appear to show that the differences among years were significant, this trend suggests that harsh winter conditions may be a primary cause of mortality in our system. Most importantly, survival rates at high elevation were consistently greater than at low elevation for all years, further supporting that even when environmental conditions become harsher, adult birds at high elevation still have a greater chance of surviving than birds at low elevation. At the same time, winter conditions are always harsher at high elevation in any given year (Kozlovsky et al. 2018). Chickadees are pine seed specialists and depend on food cached during autumn for overwinter survival. However, our rough estimates of various pine seed production in autumn do not appear to be associated with survival rates among the 3 years (VVP, unpublished data). More long-term data would be necessary to detect any potential associations among pine seed production, winter climate, and survival.

High overwinter mortality in seasonal environments is likely due to starvation resulting from a paucity of food and can act to regulate populations (Lack 1954). In our system, daily foraging behaviors differed between elevations, suggesting that risk of starvation may be higher at our high elevation site: birds at higher elevations have foraging behavior that is consistent with higher risk of starvation and greater uncertainty of food availability while lower elevation birds seem to forage in a manner that is consistent with lower risk of starvation (Pitera et al. 2018). Fluctuating dispersal rates could also assist in regulating population size and were not directly addressed in this study; however, mountain chickadees show high site fidelity after fledging (Ekman 1989; McCallum et al. 1999) and detection probabilities of adults in the study were high for both sites. Birds in our system have short postnatal dispersal distances at both elevations (ca. 1 km), and despite having banded more than 2000 nestlings and more than 1000 birds during the fall and winter, we have not detected a single individual that permanently moved (i.e., detected breeding) between elevations (VVP, unpublished data 2014–2018). This suggests that the apparent survival we measured was likely close to the true survival of the population and not the result of dispersal or transience. Interestingly, even though we had more use of RFID feeders at our high elevation site, which could potentially lead to better detection of birds and hence to higher survival estimates, the detection probability was actually slightly higher at our low elevation site. This suggests that our sampling efforts were sufficient.

Predation rates were also not directly assessed in this study and could contribute to the difference in adult survival between sites. However, if the greater mortality we found at lower elevations was caused by higher predation rates, we would expect to also find greater mortality of juveniles, as juveniles are often less experienced and more vulnerable to predation (Kershner et al. 2004). We would also expect to detect differences between elevations in nest abandonment during breeding season, which could be indicative of predation (Williams and Wood 2002). However, the number of abandoned nests with eggs or nestlings did not differ between elevations (Branch et al. 2019a) arguing against potential significant differences between elevations in predation, at least during the breeding period. As this was not the case, we believe that predation likely played a negligible role in the detected differences between survival rates.

In summary, our results demonstrate that adult food-caching chickadees have higher annual survival at higher elevations compared to lower elevations despite more severe winter conditions. Coupled with our previous findings of significantly lower juvenile survival at higher elevation compared to low elevation across the same 3 years (Branch et al. 2019b), our results support the hypothesis for stronger selection on survival-related traits (i.e., spatial cognition) at higher elevations. Although we did not directly compare selection on spatial cognition between elevations and only demonstrated strong directional selection at higher elevations, such contrasts in annual survival rates between age classes (juveniles vs. adults) are what we would expect given differences in the strengths of selection pressures. Spatial cognition is essential for survival in mountain chickadees inhabiting harsh conditions (Sonnenberg et al. 2019) and our recent findings of lower juvenile survival but higher adult survival at harsh high elevations further support our previous findings that spatial cognition is under natural selection (Sonnenberg et al. 2019).

Acknowledgments We thank Rebecca Croston and Maria Tello-Ramos, who also participated in data collection. Thank you to Jeff Brown and staff of Sagehen Experimental Forest field station (University of California Berkeley) for the assistance at our field site. Thank you to Perry Williams (University of Nevada, Reno) and Noah Benedict for the advice in designing and implementing the Bayesian model. We thank Associate Editor (Dr. Dustin Rubenstein) and two anonymous reviewers for the constructive criticisms and suggestions resulting in a significantly improved manuscript.

Author contributions LMB, AMP, CLB, DYK, BRS, and VVP collected data during breeding and nonbreeding seasons across 4 years. ESB designed the RFID system and provided support throughout data collection. AMP coalesced data from multiple sources to construct presence dataset later used by LMB to construct the CR dataset. LMB conducted all analyses. LMB and VVP wrote the first draft of the manuscript. AMP, CLB, DYK, and BRS all contributed to the writing. VVP established the field system.

Funding information This research was supported by the National Science Foundation (NSF) grant IOS1351295 and IOS1856181 to VVP and Division of Biological Infrastructure grant 1556313 to ESB. CLB was supported by the NSF Doctoral Dissertation Improvement Grant 1600845.

Compliance with ethical standards

Ethics approval To the best of our knowledge, no birds were harmed by the collection of this data. All procedures were in accordance with the University of Nevada, Reno Institutional Animal Care and Use Committee (protocol no. 00046 and 00603) and California Department of Fish and Wildlife Permit SC-5210 (DocID: D-0019571790-9).

Data accessibility The data supporting this study are publicly available via GitHub at https://github.com/LMbenedict/Publications/.

Competing interests The authors declare that they have no competing interests.

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