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Social dominance has limited effects on spatial cognition in a wild food-caching bird

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Social dominance has long been used as a model to investigate social stress. However, many studies using such comparisons have been performed in captive environments. These environments may produce unnaturally high antagonistic interactions, exaggerating the stress of social subordination and any associated adverse consequences. One such adverse effect concerns impaired cognitive ability, often thought to be associated with social subordination. Here, we tested whether social dominance rank is associated with differences in spatial learning and memory, and in reversal spatial learning (flexibility) abilities in wild food-caching mountain chickadees at different montane elevations. Higher dominance rank was associated with higher spatial cognitive flexibility in harsh environments at higher elevations, but not at lower, milder elevations. By contrast, there were no consistent differences in spatial learning and memory ability associated with dominance rank. Our results suggest that spatial learning and memory ability in specialized food-caching species is a stable trait resilient to social influences. Spatial cognitive flexibility, on the other hand, appears to be more sensitive to environmental influences, including social dominance. These findings contradict those from laboratory studies and suggest that it is critical to investigate the biological consequences of social dominance under natural conditions.

1. Introduction

Individual variation in cognition is widely assumed to be due, at least in part, to differences in individual experience and in individual environment [1,2]. The social environment has been implicated in affecting cognitive abilities—in particular, the stress associated with dominance interactions, especially the stress of a subordinate position, has been reported to negatively affect cognition [3–6]. Subordinate individuals can experience stress both from antagonistic interactions, and from restricted access to resources such as feeding sites or territory, which can be controlled by dominant individuals [7]. In fact, social dominance has been used as a model to investigate psychosocial stress and its negative effect on cognitive abilities, including impaired neurogenesis in socially subordinate animals [3–5,8,9].

However, most studies showing significant effects of dominance-related stress on cognition have been conducted in laboratory environments [10]. In such conditions, animals may have limited opportunities to avoid social conflicts, and hence the dominance-related stress and its effect on cognitive abilities may be greatly exaggerated. Additionally, it is common to investigate the effects of dominance on cognition by artificially pairing same-sex, similar-size individuals and examining these dyads in isolation, when naturalistic dominance hierarchies are usually more complex and involve multiple individuals in social groups [11]. Since social context can influence both the expression of dominance behaviours [11] and cognitive performance [1,12], the degree to which these results manifest in wild populations may vary.

Furthermore, natural environments also exhibit variation in other stressors, such as temperature, predation risk and food availability, and these differences can modulate the impact of social dominance. In mild environments, subordinate animals may have sufficient options for food and shelter even if dominants monopolize access to the best resources; but if resources are scarce, competition may be more intense, and the consequences of social subordination may be more severe [13,14]. To fully understand the associations between social dominance, dominance-related social stress, environmental stressors and cognition, it is critical to investigate animals in their natural environment.

Here, we tested for potential effects of social dominance status on spatial cognitive abilities using wild birds (mountain chickadees, *Poecile gambeli*) under natural conditions by measuring social dominance across a large number of individuals and conducting spatial memory tests [14–17]. Like all parids, mountain chickadees are highly social during the non-breeding season and live in social groups of around 6–18 birds with a linear social dominance hierarchy [18–22]. Mountain chickadees also rely on their spatial cognitive abilities to retrieve their food caches during the winter, making them an ideal subject to study the intersection of dominance and cognition.

Pravosudov *et al*. [6] and Pravosudov & Omanska [23] examined social dominance and cognition of mountain chickadees in laboratory conditions and reported significant effects of social dominance on spatial cognitive performance and a related underlying neural mechanism, hippocampal cell proliferation [6]. Using a dyadic interaction design, those studies showed that social subordination was associated with significant impairments in spatial learning and memory [6] and reduced cell proliferation rates in the hippocampus [23]. However, these were subject to many of the aforementioned confounds associated with captivity and experimentally imposed social environments. For example, to amplify social dominance effects, males of similar size were paired together, which can be expected to bring about the most intense antagonistic interactions. Considering that these matched pairs were maintained in relatively small enclosures, such a design likely induced the maximum possible social stress on subordinates as they had no way to escape or avoid the dominant partner. Hence, the design of these experiments casts some doubt on the ecological relevance of their results.

To address this uncertainty, we tested for a relationship between social dominance and spatial cognition in naturally occurring social groups of wild birds, across two montane elevations that differ in winter environmental harshness, and over two winter seasons. These birds were equipped with passive integrated transponder (PIT-) tags which allowed us to employ radio frequency identification (RFID) feeders to passively quantify displacement events as a means of assessing dominance relationships [24]. We also used a RFID-based design to measure spatial cognitive abilities following well-established methods [16–18,25]. Together, these measurements allowed us to compare social dominance status and spatial cognitive abilities in a large number of wild birds, without the potential confounds of a captive setting.

2. Methods

We used our long-term study system of mountain chickadees at United States Forest Service Sagehen Experimental Forest, north of Truckee, California, USA (Sagehen Creek Field Station, University of California, Berkeley). Our study area incorporated two elevation areas, high elevation (2400 m) and low elevation (1900 m), which differ in winter climate severity, with high elevation experiencing colder temperatures, and deeper and more persistent snow cover [15–17]. Since 2014, we have banded chickadees with unique combinations of PIT-tag leg bands (IB Technology, Leicestershire, UK) and colour bands. We trap and band birds annually using mist nets at established feeders across both elevations during autumn and winter and in nest-boxes during the summer breeding season.

(a) Data collection

All data in this study were collected using RFID-equipped feeders [16–18]. Each RFID feeder was fitted with a single perch with an embedded antenna, a motorized food access door and an Arduino control board [26]. Only one chickadee at a time could land on the perch and access the food (black oil sunflower seeds) inside the feeder. Feeders were active during all daylight hours and recorded the date, time and identity of all PIT-tagged birds landing on the perch with a 1 s resolution. Additionally, feeders could be set to one of three modes to control food access. In 'open' mode, the motorized feeder door was permanently open, and any bird could retrieve food. In 'all' mode, the feeder door was closed but would open for any bird with a PIT-tag landing on the perch. In 'target' mode, each feeder would record visits from all PIT-tagged birds but would only open the door to specific individuals programmed into that feeder's control board. Feeders were initially distributed individually throughout each elevation to measure displacement events, and later arranged in spatial arrays of eight feeders each to measure spatial cognition (electronic supplementary material, figure S1).

(b) Determining dominance ranks

To derive dominance ranks for individual birds, we recorded displacement events at individual RFID feeders distributed throughout the field sites at each elevation. We used nine feeders at low elevation spaced 339.8 ± 34.5 m apart, and six feeders at high elevation spaced 442.9 ± 198.1 m apart. All feeders were established as part of previous studies. Feeders were set to 'open' mode, with the feeder doors permanently open so that any bird could obtain food, and all visits by PIT-tagged birds were recorded and time-stamped. Food was available for at least 30 days during each season (table 1).

The feeders were designed to provide food only to one chickadee at a time, creating an environment where dominant birds may displace subordinates from the feeder [7]. To identify displacement events and determine dominance ranks we used methods developed by Evans *et al*. [24,27] for closely related black-capped chickadees (*Poecile atricapillus*) that have similar social structure and dominance hierarchy as mountain chickadees [19,20]. These methods were specifically developed for feeder visitation using RFID technology and validated using standard visual observations [24]. Dominance displacement events were identified by examining the differences in departure and arrival times of all individuals at each feeder. Repeated visits by the same individual within 5 s were merged into a single visit, as both our personal observations and others' [24,27] suggest that these visits are almost always due to an interruption in the PIT-tag's signal, rather than a bird departing and almost immediately returning. One bird was assumed to have displaced another if it arrived at the feeder within 1 s of the previous bird's departure, and if it then remained on the feeder for at least 5 s. We chose these

Table 1. Dates of each phase of data recording and cognitive testing. During the 2020–2021 season, the arrays were switched from 'open' to 'all' mode repeatedly due to mechanical issues with the motorized feeder doors. (Online version in colour.)

	2019–2020		2020–2021	
	high elevation	low elevation	high elevation	low elevation
single feeders	9 Sep 2019–16 Dec 2019	9 Sep 2019–16 Dec 2019	14 Oct 2020–20 Nov 2020	14 Oct 2020–20 Nov 2020
arrays ('open' mode)	16 Dec 2019–27 Dec 2019	16 Dec 2019–30 Dec 2019	20 Nov 2020–18 Dec 2020	20 Nov 2020–18 Dec 2020
			23 Dec 2020–28 Dec 2020	23 Dec 2020–28 Dec 2020
			30 Dec 2020–8 Jan 2021	30 Dec 2020–8 Jan 2021
arrays ('all' mode)	27 Dec 2019–20 Jan 2020	30 Dec 2019–20 Jan 2020	18 Dec 2020–23 Dec 2020	18 Dec 2020–23 Dec 2020
			28 Dec 2020–20 Dec 2020	28 Dec 2020–20 Dec 2020
			8 Jan 2021–13 Jan 2021	8 Jan 2021–13 Jan 2021
arrays (spatial learning and memory testing)	3 Feb 2020–7 Feb 2020	20 Jan 2020–24 Jan 2020	13 Jan 2021–17 Jan 2021	13 Jan 2021–17 Jan 2021
arrays (reversal spatial learning testing)	7 Feb 2020–10 Feb 2020	24 Jan 2020–28 Jan 2020	8 Jan 2021–13 Jan 2021	8 Jan 2021–13 Jan 2021

values based on Evans *et al.*'s [24] parameter selection and on our own observations of mountain chickadee activity at the feeders.

After identifying displacement events, we used them to determine dominance hierarchies. Since many birds visited multiple single feeders, but no birds visited all single feeders, calculating dominance hierarchies on a per-feeder basis would not accurately reflect the observed behaviour. Instead, we used social networks calculated from the single feeder data-streams to identify biologically relevant communities at each elevation, and we calculated dominance hierarchies within these communities. With the visitation data from single feeders, we constructed one network at each elevation using a 'gambit of the group' approach [28], which assumes that all individuals observed together were equally connected to each other and infers the strength of connections between dyads based on repeated co-occurrences across groups. We used a Gaussian mixture model (GMM; *gmmevents* function from the R package 'asnipe' [29]) and the 'double GMM' method [30] in R 4.0.15 [31] to define grouping events. We inferred association strengths among individuals from their co-occurrence in grouping events using a simple ratio index in asnipe (function *get_network*), defined as the number of times two individuals appeared in the same foraging event, divided by the number of foraging events containing at least one of the two individuals [32]. Individuals that appeared in fewer than five grouping events ($n = 1$) were excluded from network construction.

Once networks were constructed, we identified communities within each elevation using the *fastgreedy* modularity optimization algorithm in the 'igraph' R package [33]. If a community identified through this algorithm contained 30 members or more, which is substantially larger than can be expected for any chickadee flock size [19,20], we ran the algorithm a second time to identify subcommunities within this group.

Once we had identified community membership, we used only the displacement events occurring between members of a community to determine hierarchies (electronic supplementary material, table S1). These displacements were used to calculate David's scores [34], a standard method for ranking individuals' dominance based on their proportion of wins and losses relative to those of their opponents, for each individual within a community using the 'EloRating' R package [35]. Within-community dominance rank was scaled to between 0 and 1, with 1 being the most dominant individual, to control for variation in group sizes across communities [27].

(c) Spatial cognitive testing

Following the closure of the single feeders, supplemental food was made available at only four locations, each consisting of a spatial array of eight feeders [16–18]. The feeders in each array were attached equidistantly to a square aluminium frame (122 × 122 cm) suspended approximately 4 m above the ground [16,17]. We used two arrays at low elevation and two at high elevation, with approximately 1.5 km distance between the arrays within each elevation. The arrays were initially set to 'open' mode, allowing birds to see and obtain food at any of the eight feeders; then they were set to 'all' mode to habituate the birds to the motorized feeder doors; and finally, set to 'target' mode for cognitive testing. The dates of each phase are available in table 1.

In each of the two seasons, we tested chickadees on two spatial cognitive tasks: first on a spatial learning and memory task for 5 days and then on a reversal spatial learning task for 5 days (table 1), following our established protocols [16–18,25].

During the spatial learning and memory task, birds were expected to learn and remember the spatial location of a single rewarding feeder in the array [16,17]. Feeders were set to 'target' mode, restricting food access to assigned individuals. Each bird attending the array was assigned to one of the eight feeders, with assignments spread across all eight feeders pseudorandomly so that no birds were assigned to their most visited feeder from the previous 'open' and 'all' periods. During testing, only the bird's assigned feeder door would open when the bird landed on the perch, allowing that bird to take food. All other feeders would record that bird's visits but not allow access to food. Spatial learning and memory performance was measured as the number of 'location errors' or non-rewarding feeders an individual visited prior to visiting the rewarding feeder during each trial. A trial began when an individual visited any feeder in the array and ended when the individual visited its assigned rewarding feeder. We used the mean number of location errors per trial across the first 20 trials and during the entire cognitive task to estimate spatial learning and memory ability following our previous studies [16–18,25]. Previous testing has demonstrated that chickadees use spatial memory, rather than local features of the array, to solve this task [15]. We also assessed learning by examining the mean number of location errors over the first 3, 5, 10 and 20 trials.

During the reversal spatial learning task, we reassigned each bird to a new rewarding feeder within the array, so that the

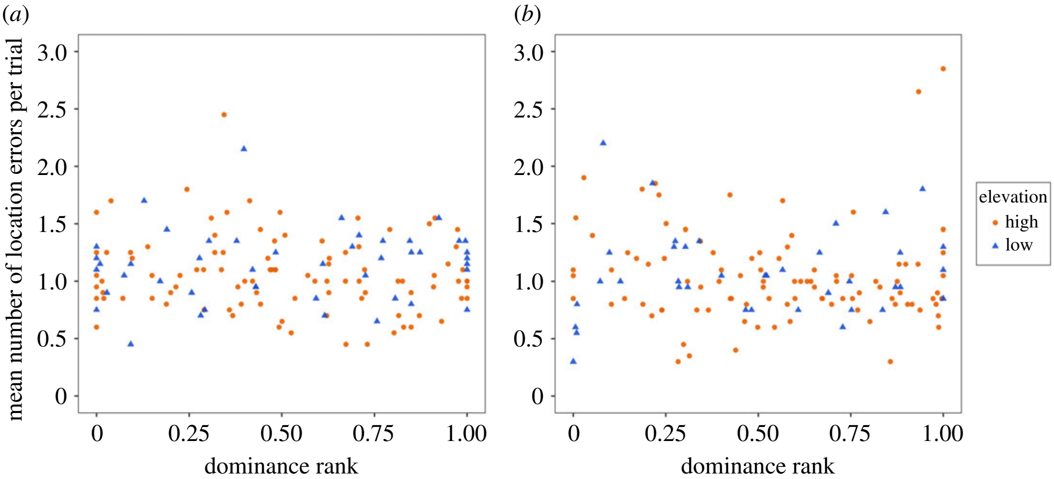

Figure 1. Spatial learning and memory scores over the first 20 trials and scaled dominance rank during the (*a*) 2019–2020 season and (*b*) 2020–2021 season. Rank ranges from 0 (least dominant) to 1 (most dominant). Spatial learning and memory scores are based on the number of location errors made with lower scores indicating better cognitive performance. There was no relationship between rank and cognitive performance in either year. (Online version in colour.)

previously assigned feeder no longer provided a food reward. Birds that had been assigned to the same feeder during the previous task were reassigned to different feeders from one another to reduce the possibility of social learning [16–18,25]. As in the previous task, we used the mean number of location errors per trial over the first 20 trials of the task as well as during the entire task to evaluate reversal spatial cognitive ability, as well as the mean number of location errors per trial over the first 3, 5, 10 and 20 trials.

(d) Statistical analyses

Data were analysed by multiple regression analyses with the mean number of location errors per trial (either over the first 20 trials or over the entire task) as the dependent variable, and rank, elevation, and their interaction as the independent variables. Only individuals that completed at least 20 trials in both the spatial learning and memory task and the reversal spatial learning task were included [18,25]. When analysing the performance over the entire cognitive task, we used the total number of completed trials as a covariate to control for individual differences in the number of trials [16].

We additionally analysed performance during the first 3, 5, 10 and 20 trials (e.g. learning curve) and grouped individuals into four quartiles based on their position in the dominance hierarchy from the most subordinate (first quartile) to the most dominant (last quartile) (electronic supplementary material, table S2). This quartile technique allows for comparisons between broader dominance categories, and aids in visualizing and comparing learning curves [16]. We used general linear mixed models with the mean number of location errors per trial as the dependent variable, the number of trials completed at each stage (3, 5, 10 or 20) as a categorical variable, elevation and dominance quartile as independent variables, and bird ID as a random effect. Analyses were performed using R v. 4.0.15 [31].

3. Results

During the 2019–2020 season, we recorded 448 385 visits from 171 birds at high elevation and 206 779 visits from 98 birds at low elevation. From these data, we identified 67 264 displacement events at high elevation and 24 330 displacement events at low elevation. During the 2020–2021 season, we recorded 223 519 visits from 153 birds at high elevation and 36 788 visits from 80 birds at low elevation, and identified 23 282 displacement events at high elevation and 3273 displacement events at low elevation. We identified 10 communities at high elevation and seven communities at low elevation (electronic supplementary material, table S1a) during the 2019–2020 season (electronic supplementary material, figure S2), and 13 communities at high elevation and 11 communities at low elevation (electronic supplementary material, table S1b) during the 2020–2021 season (electronic supplementary material, figure S3).

Dominance was not significantly associated with the number of visits to the single feeders during the 2019–2020 season ($F_{1,139} = 0.65$, $p = 0.42$), and there was no effect of elevation ($F_{1,139} = 0.04$, $p = 0.846$) or dominance by elevation interaction on the number of feeder visits ($F_{1,139} = 0.49$, $p = 0.48$). However, during the 2020–2021 season, dominant birds made significantly more visits to the single feeders than subordinate birds ($\beta = 863.9$; $F_{1,131} = 5.95$, $p = 0.016$, adjusted $R^2 = 0.21$). There was no effect of elevation ($F_{1,131} = 2.51$, $p = 0.115$) and no interaction between elevation and dominance on the number of feeder visits ($F_{1,131} = 2.57$, $p = 0.111$).

(a) Dominance rank, spatial learning and memory performance

There was little to no evidence of a relationship between social dominance and spatial learning and memory performance for the 2019–2020 season. Our primary analysis, which compared social dominance and cognitive performance during the first 20 trials in 2019–2020, indicated no significant relationships (figure 1*a*; table 2), nor during the entire cognitive task (table 2).

However, when we analysed the effects of the dominance quartile on performance during the first 3, 5, 10 and 20 trials, there was a significant effect of dominance quartile during the 2019–2020 season (figure 2*a*; table 2). *Post hoc* Tukey HSD showed that the only significant differences was between quartile 1 (most subordinate) and quartile 4 (most dominant), and only during the first three trials, with the most dominant birds making fewer errors ($p = 0.012$). There were no significant differences among any of the dominance quartiles during the first 5, 10 or 20 trials.

In the 2020–2021 season, we also found no significant relationship between dominance score and spatial learning and memory performance over the first 20 trials (figure 1*b*; table 2*a*), nor over the entire task (table 2).

Table 2. Statistics for the relationship between social dominance score and spatial cognitive performance during the 2019–2020 and 2020–2021 seasons, for the first 20 trials of the cognitive task, the entire cognitive task, and the first 3, 5, 10 and 20 trials with birds grouped into quartiles by dominance score. Bold type indicates significance at $p < 0.05$.

		results	
test	**variable**	**2019–2020**	**2020–2021**
first 20 trials	dominance score	$F_{1,139} = 1.63$, $p = 0.20$	$F_{1,131} = 0.41$, $p = 0.52$
	elevation	$F_{1,139} = 0.20$, $p = 0.66$	$F_{1,131} = 0.18$, $p = 0.67$
	dominance × elevation	$F_{1,139} = 1.85$, $p = 0.18$	$F_{1,131} = 0.61$, $p = 0.44$
entire cognitive task	dominance score	$F_{1,138} = 0.01$, $p = 0.97$	$F_{1,130} = 1.50$, $p = 0.22$
	elevation	**$F_{1,138} = 4.65$, $p = 0.03$**	$F_{1,130} = 1.39$, $p = 0.24$
	dominance × elevation	$F_{1,138} = 0.38$, $p = 0.54$	$F_{1,130} = 1.94$, $p = 0.16$
	total trials completed	**$F_{1,138} = 108.5$, $p < 0.001$**	**$F_{1,130} = 39.7$, $p < 0.001$**
quartile analysis	dominance quartile	**$F_{3,268.37} = 4.32$, $p = 0.005$**	$F_{3,258.95} = 0.53$, $p = 0.66$
	elevation	$F_{1,268.37} = 0.16$, $p = 0.68$	$F_{1,258.95} = 0.11$, $p = 0.74$
	number of trials	**$F_{3,405.00} = 59.68$, $p < 0.001$**	**$F_{3,381.00} = 44.79$, $p < 0.001$**
	dominance × trials	$F_{9,405.00} = 1.71$, $p = 0.08$	$F_{9,381.00} = 0.46$, $p = 0.90$
	dominance × elevation	$F_{3,268.37} = 1.14$, $p = 0.33$	$F_{3,258.95} = 0.74$, $p = 0.53$
	elevation × trials	$F_{3,405.00} = 0.27$, $p = 0.85$	$F_{3,381.00} = 0.27$, $p = 0.85$
	dominance × elevation × trials	$F_{9,405.00} = 0.63$, $p = 0.77$	$F_{9,381.00} = 0.62$, $p = 0.78$

During this season, there was no significant effect of dominance quartile on cognitive performance during the first 3, 5, 10 and 20 trials (figure 2*b*; table 2).

(b) Reversal spatial learning

In the 2019–2020 season, there were no significant associations between social dominance score and performance during the first 20 trials (figure 3*a*; table 3) or during the entire reversal task (table 3).

There was, however, a significant association between social dominance performance during the first 3, 5, 10 and 20 trials when all individuals were split into four quartiles (figure 4*a*; table 3). Tukey HSD test showed that there were significant differences only at high elevation during the first three trials (quartile 4 versus quartiles 1, 2 and 3, $p < 0.01$) and during the first five trials (quartile 4 versus quartiles 1 and 2, $p < 0.03$) with the most dominant birds performing better.

In the 2020–2021 season, there was a significant association between dominance score and reversal performance during the first 20 trials, with more dominant individuals performing better (figure 3*b*; table 3) (dominance score—$\beta = -0.18$, adjusted $R^2 = 0.02$), and during the entire reversal task (table 3). Considering the significant interaction between dominance score and elevation in the analyses of the reversal performance during the entire task, we tested the effect of dominance on reversal performance separately for high and low elevation in this season. At high elevation, more dominant individuals performed significantly better on the reversal learning task ($\beta = -0.10$, $F_{1,94} = 7.95$, $p = 0.005$, the total number of trials—$F_{1,94} = 27.54$, $p < 0.001$, adjusted $R^2 = 0.32$). By contrast, there was no significant association between dominance rank and reversal performance at low elevation ($F_{1,35} = 1.39$, $p = 0.24$, total number of trials—$F_{1,35} = 22.28$, $p < 0.001$).

There was also a significant association between social dominance quartile and reversal performance during the first 3, 5, 10 and 20 trials in the 2020–2021 season (figure 4*b*; table 3). Tukey HSD test showed that the most dominant birds performed significantly better than more subordinate individuals only at high elevation during the first three trials (quartile 1 versus quartiles 2, 3 and 4, $p < 0.03$) and during the first five trials (quartile 1 versus quartiles 3 and 4, $p < 0.04$), but no significant effect of quartile at low elevation.

Based on our data visualizations, as well as the linear nature of dominance hierarchies, we expected a graded change in performance (number of location errors) between the four quartiles ($1 > 2 > 3 > 4$). However, we found no such relationship for any number of trials (one-sided Jonckheere–Terpstra trend test; first 3 trials, $z = 1.36$, p-value $= 0.087$—first 5 trials, $z = 1.55$, p-value $= 0.061$—first 10 trials, $z = 0.86$ p-value $= 0.19$—first 20 trials, $z = -0.36$, p-value $= 0.63$).

4. Discussion

Our study detected no consistent association between social dominance rank and spatial learning and memory ability. We did observe that dominant individuals were consistently and significantly better at spatial reversal learning, but only at high elevation. The most dominant birds (those in the 4th quartile) showed better performance in the spatial learning and memory task compared to subordinates at high elevation during the 2019–2020 season, but only during the first three trials. It is not clear whether this result reflects true differences in performance, as there were no significant differences between any other comparisons: all dominance classes performed equivalently starting at the first five trials, and we found no similar significant differences during the 2020–2021 season.

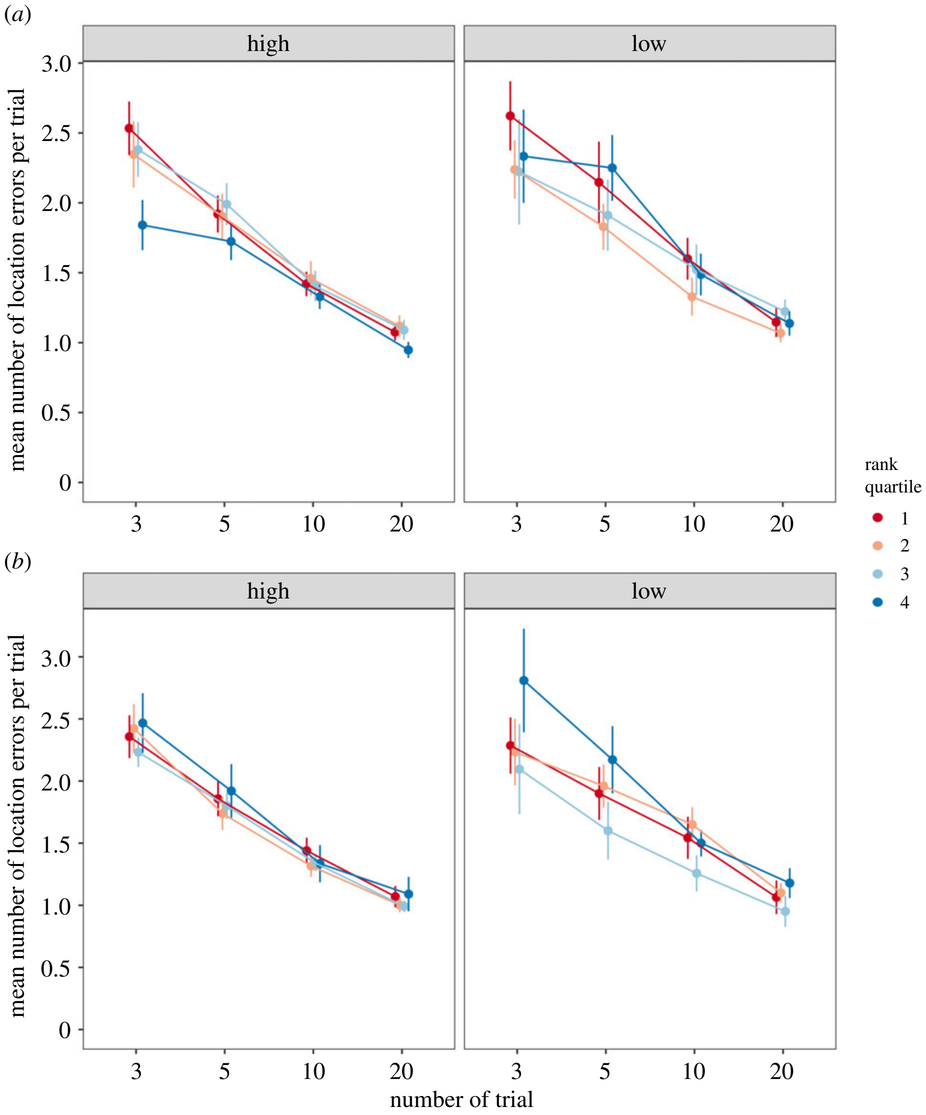

Figure 2. Relationship between dominance rank by quartile and performance during the first 3, 5, 10 and 20 trials during the spatial learning and memory task during the 2019–2020 season (*a*) and 2020–2021 season (*b*). Fewer location errors indicate better performance. Rank quartile 1 indicates the least dominant birds, while quartile 4 indicates the most dominant. Data from high elevation are shown on the left and data from low elevation are shown on the right. The most dominant birds showed significantly better learning and performance during the first three trials of the 2019–2020 season, but otherwise performance was not different between elevations or ranks. (Online version in colour.)

There was more evidence for a relationship between dominance and cognitive flexibility as we detected a significant relationship between rank and performance in the spatial reversal learning during both seasons. However, the differences were small, present only at high elevation, and were especially pronounced during the 2020–2021 season. This inconsistency suggests that the effect of dominance on spatial reversal learning may be flexible and may depend on variable environmental conditions, such as temperature or snowfall, that could impact competition for resources. In our study system, the high elevation area is associated with a harsher and less predictable winter environment [16–18], and the 2020–2021 season also appeared to be harsher compared to the 2019–2020 season based on the colder temperatures and a larger number of birds attending the spatial arrays during cognitive testing. Increased feeder attendance suggests that less naturally occurring food was available in 2020–2021, driving birds to congregate at our supplementary food sources. In addition to increased feeder use, harsher environments are likely to be associated with higher levels of competition, more antagonistic interactions and more social stress.

Overall, our results do not support previous laboratory-based studies showing that socially subordinate individuals have impaired spatial cognitive abilities [6,9,36]. Our study suggests that these relationships between dominance status and cognitive abilities may be decreased or absent in wild conditions. Previous laboratory-based studies may have amplified social stress artificially by creating unnatural conditions in which dominance-based social conflicts cannot be resolved without direct and excessively frequent aggressive interactions. In wild species such as food-caching chickadees, individuals are not confined to restricted spaces and can potentially easily avoid direct confrontations. For example, a subordinate can simply wait until a dominant leaves a desired resource, such as a feeder, and avoid an altercation. Our study therefore suggests that naturally occurring social dominance relationships in wild animals may not cause such chronic psychosocial stress to negatively impact spatial cognition. As such, any conclusions from laboratory-based studies of social dominance should be considered with caution as they may not reflect the naturally occurring social dominance hierarchies.

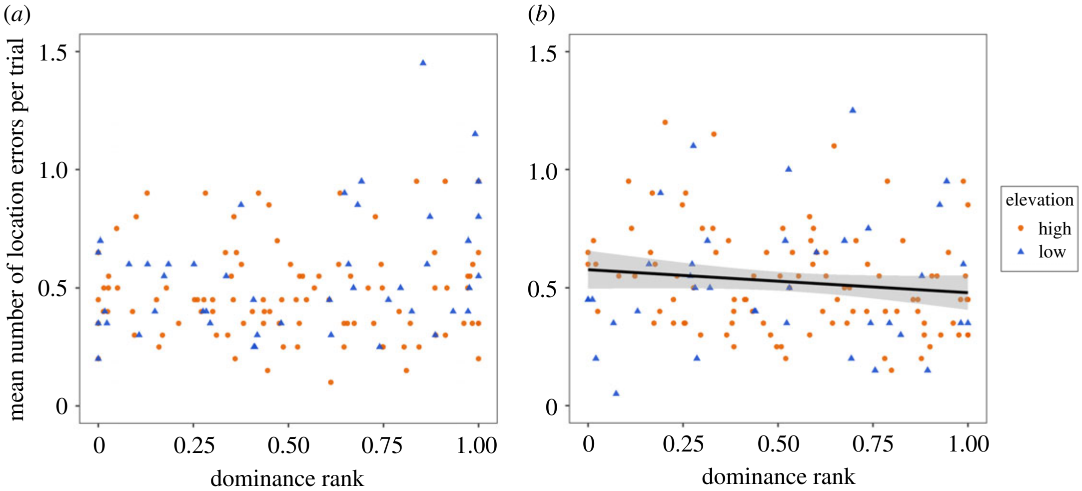

Figure 3. Reversal spatial learning scores over the first 20 trials and scaled dominance rank; (*a*) 2019–2020 season and (*b*) 2020–2021 season. The shaded area in (*b*) indicates 95% CI. Rank ranges from 0 (least dominant) to 1 (most dominant). Cognition scores are based on the number of errors made, so lower scores indicate better cognitive performance. During the 2020–2021 season, higher-ranked birds made fewer location errors in the reversal spatial cognition task. (Online version in colour.)

Table 3. Statistics for the relationship between social dominance score and reversal cognitive performance during the 2019–2020 and 2020–2021 seasons, for the first 20 trials of the cognitive task, the entire cognitive task and the first 3, 5, 10 and 20 trials with birds grouped into quartiles by dominance score. For non-significant effects of cognitive performance, and for all other effects, we present only ANOVA results; for significant effects of cognitive performance as a continuous variable, we have also reported regression results, including β and adjusted R^2. Bold type indicates significance at $p < 0.05$.

		results	
test	**variable**	**2019–2020**	**2020–2021**
first 20 trials	dominance score	$F_{1,138} = 0.01, p = 0.92$	**$F_{1,131} = 5.21, p = 0.02$**
			$\beta = -0.18$, adjusted $R^2 = 0.02$
	elevation	**$F_{1,138} = 0.64, p = 0.045$**	$F_{1,131} = 2.86, p = 0.09$
	dominance × elevation	$F_{1,138} = 3.78, p = 0.054$	$F_{1,131} = 3.47, p = 0.064$
entire cognitive task	dominance score	$F_{1,138} = 0.11, p = 0.74$	**$F_{1,130} = 5.13, p = 0.025$**
			$\beta = -0.08$, adjusted $R^2 = 0.33$
	elevation	$F_{1,138} = 0.49, p = 0.48$	$F_{1,130} = 3.69, p = 0.06$
	dominance × elevation	$F_{1,138} = 2.84, p = 0.094$	**$F_{1,130} = 6.49, p = 0.012$**
	total trials completed	**$F_{1,138} = 35.14, p < 0.001$**	**$F_{1,130} = 50.06, p < 0.001$**
quartile analysis	dominance quartile	**$F_{3,131.41} = 3.38, p = 0.02$**	**$F_{3,255.83} = 6.71, p < 0.001$**
	elevation	$F_{1,131.41} = 2.23, p = 0.14$	$F_{1,255.83} = 2.08, p = 0.15$
	number of trials	**$F_{3,195.00} = 43.73, p < 0.001$**	**$F_{3,381.00} = 89.79, p < 0.001$**
	dominance × trials	$F_{9,195.00} = 1.18, p = 0.31$	$F_{9,381.00} = 1.82, p = 0.06$
	dominance × elevation	**$F_{3,131.41} = 3.68, p = 0.013$**	**$F_{3,255.83} = 4.06, p = 0.008$**
	elevation × trials	$F_{3,195.00} = 1.02, p = 0.38$	$F_{3,381.00} = 0.06, p = 0.98$
	dominance × elevation × trials	$F_{9,195.00} = 1.24, p = 0.27$	$F_{9,381.00} = 1.63, p = 0.10$

It is possible that our failure to find a clear association between social dominance status and spatial cognitive abilities is due to methodological and sample-size deficiencies. However, we argue that our study was robust against these shortcomings. First, our study had a very large sample size of over 400 individual birds across 2 years. Second, our measurements of social dominance status are based on methods developed for a closely related chickadee species with similar social structure [24]. Third, our measurements of spatial cognitive performance have enough resolution to detect differences between elevations [17] and between juveniles and adults [17,18], as well as individual variation associated with differences in overwinter survival [18] and in female reproductive investment [37]. In addition, the same spatial learning and memory tests yielded consistent scores within individuals in their first (juvenile) and second (adult) years of life [18]. By contrast with spatial learning and memory, dominance status typically changes as birds transition from their first to their second year, because adults are socially dominant over juveniles within the same sex [19,22], although rank is more stable after reaching adulthood [7]. If dominance status, but not cognitive performance,

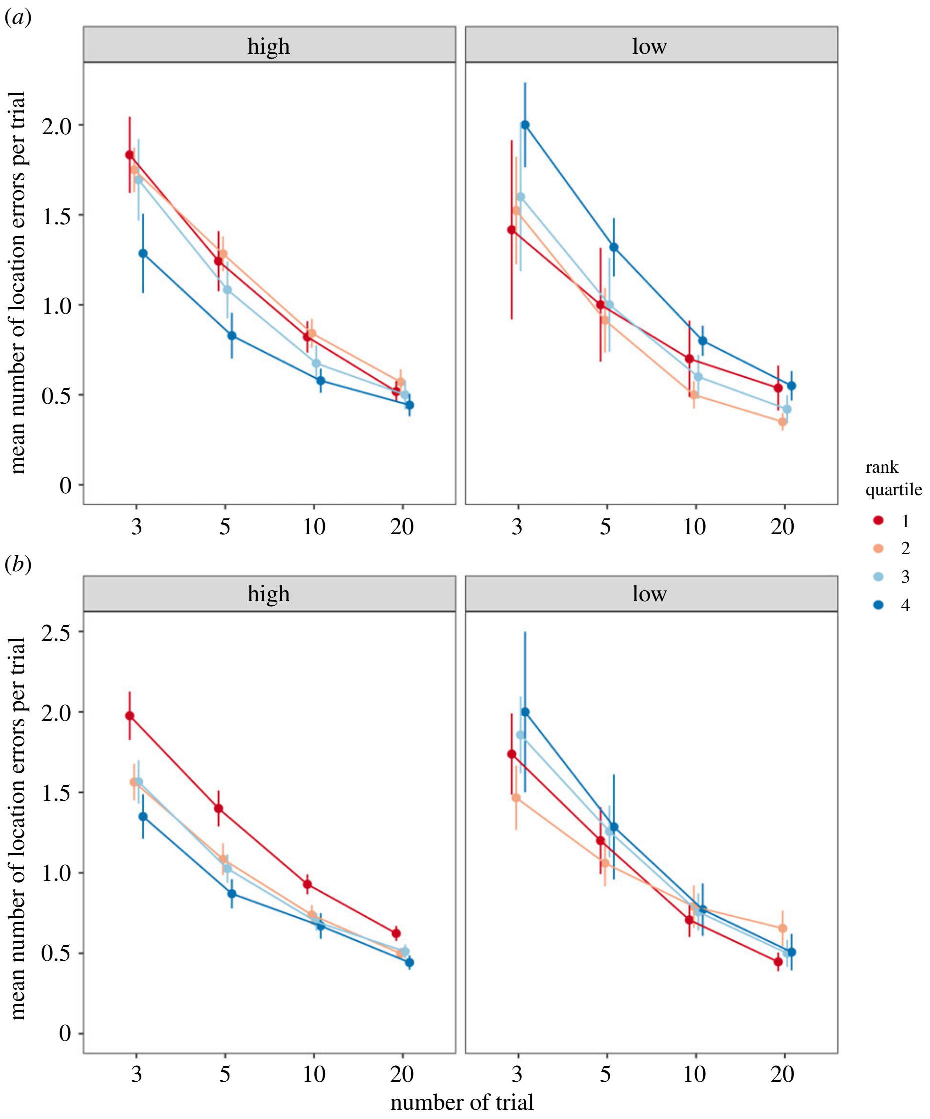

Figure 4. Relationship between dominance rank by quartile and performance during the first 3, 5, 10 and 20 trials during the reversal spatial cognition task during the (*a*) 2019–2020 season and (*b*) 2020–2021 season. Fewer location errors indicate better performance. Rank quartile 1 indicates the least dominant birds, while quartile 4 indicates the most dominant. Data from high elevation are shown on the left, and data from low elevation are shown on the right. The least dominant individuals performed significantly worse over the first three and five trials at high elevation during the 2020–2021 season.

changes with age, this observation is consistent with our findings that social dominance status may not be associated with significant differences in spatial cognition.

It is likely, however, that our study did not capture the full range of wild dominance interactions. We conducted our study during the winter, when aggressive interactions between groupmates largely consist of displacement events at food sources. The primary cost of these interactions appears to be a temporary delay in food access, as the displaced individual typically returns to the feeder shortly after the displacer leaves. Compared to aggressive interactions at other times of year, such as physical fights during the early breeding season [7], winter may be a time of relatively low socially induced stress for subordinates. In other environments where food takes more time to extract, dominant birds could monopolize profitable or sheltered feeding sites, leaving subordinates to forage in riskier environments [38], but this was not likely to be the case at our feeders. Additionally, the presence of feeders could have reduced the stress on subordinates by making foraging more predictable. We do not find this a likely explanation for our findings, however, because most field studies use feeders to measure dominance [27,39] and our feeders were not maintained with unlimited food during the entire winter, only during the testing periods. Furthermore, even when provisioned with supplemental food sources, mountain chickadees forage as though access to these resources is not predictable, especially at high elevation [40].

Considering that food-caching species have strong reliance on spatial cognition for survival [41], it is possible that they have evolved some degree of resistance to social stress with regard to its effects on cognition [42], at least in a natural setting. Laboratory-based studies have sought to induce artificially high levels of social stress by closely confining matched pairs of individuals. The question remains whether such artificial levels of social stress are relevant to natural systems. In pheasants, a non-caching species, there was some tendency for socially dominant birds to do better on a learning task [9,43]. However, cognitive performance was measured using a binary choice task without any control for potential motivational differences. Binary choice tasks are not ideal for detecting subtle differences in spatial cognitive abilities, as animals may also exploit non-spatial cues, such as an enclosure wall next to one of the two available choices.

Our study suggests that to fully understand the implications of social dominance, it is important to measure both social dominance and cognitive abilities using relevant tests under naturalistic conditions.

By contrast to spatial learning and memory abilities, spatial reversal learning appears to be more flexible and dependent on environmental conditions and previous experiences [44]. In our study, dominance-related differences in spatial reversal learning performance were detected in both years, but only at high elevation with harsher winter conditions. The effect of dominance rank on reversal performance was also strongest during the colder 2020–2021 season. These results suggest that spatial reversal learning abilities may be more sensitive to environmental influences, either directly (dominants and subordinates may experience different environmental predictability due to their differences in social rank) or indirectly (individuals in more dangerous or less predictable environments may conduct more frequent, intense, or stressful antagonistic dominance interactions). In a study of closely related great tits, dominant birds in colder environments with lower food availability exhibited more aggressive behaviour than dominant birds in milder conditions, and dominant birds exhibited better body condition than subordinate birds only in the harsh environment [14], further suggesting that environmental stressors can exacerbate the impact of social dominance on subordinates.

The dominance-related differences in spatial reversal were small: on average, the most dominant birds made only one or two fewer errors than the most subordinate birds over the first 20 trials. It is difficult to know whether such small differences in performance have significant fitness consequences, but our previous work has shown that similarly small variation in spatial learning and memory performance was associated with significant differences in overwinter survival [18]. Therefore, it is likely that even small differences in cognitive performance are ecologically relevant. These differences in reversal performance may also be related to behavioural patterns revealed in previous studies wherein birds with better reversal cognition foraged significantly more in the morning and less throughout the rest of the day [40]. This temporal pattern is consistent with foraging behaviour displayed in milder seasons, suggesting that birds with better reversal performance may perceive or actually experience greater environmental predictability and a lower risk of starvation [40]. Particularly under harsh conditions, individuals with better reversal cognition could be more likely to survive and rise in rank with age [39].

Overall, our study of naturally occurring social dominance hierarchy and spatial cognition in wild food-caching chickadees showed no consistent support that socially dominant individuals have better spatial cognitive abilities. Yet we did detect an effect of dominance on spatial reversal abilities, albeit only in harsher winter environments. Our results suggest that many negative consequences of social subordination shown in laboratory-based studies may have been exaggerated due to their experimental design and highlight the importance of studying social behaviour and its consequences under natural conditions.

Ethics. All research was approved by the University of Nevada Reno IACUC (protocol 00818) and followed local and federal guidelines (California Department of Fish and Wildlife Permit D-0011776516-4). The study was conducted in accordance with the University of Nevada Institutional Animal Care and Use Committee protocols 20-11-1103, 20-06-1014 and 20-08-1062, California Department of Fish and Wildlife Scientific Collecting Permit D-0011776516 and Federal Bird Banding Permit 22878.

Data accessibility. Data and code are available at https://doi.org/10.5061/dryad.kh189326b [45].

Authors' contributions. V.K.H.: Conceptualization, data curation, formal analysis, investigation, methodology, project administration, software, visualization, writing—original draft, writing—review and editing; L.M.B.: investigation, methodology, writing—review and editing; A.M.P.: formal analysis, methodology, visualization, writing—review and editing; B.R.S.: data curation, investigation, writing—review and editing; E.S.B.: resources, software, writing—review and editing; V.V.P.: conceptualization, formal analysis, investigation, methodology, project administration, validation, writing—original draft.

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