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ORIGINAL PAPER

Social position indirectly influences the traits yellow-bellied marmots use to solve problems

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Abstract
Animals adapt to changing environments by behaving flexibly when solving problems. Traits, such as sex and age, and specifically behavioral traits like persistence–the amount of time spent attempting to solve a problem, are positively associated with successful problem-solving. However, individuals face social pressures, such as aggression, which may directly alter an individual's behavior or interact with sex or age, when they attempt to problem-solve. We examined the direct and indirect effects of social position and individual behavioral traits on solving a novel puzzle box in facultatively social yellow-bellied marmots (*Marmota flaviventer*), using both generalized linear mixed models and confirmatory path analysis. We found strong support that marmots who used a diversity of behaviors were more successful problem-solvers and weak support that those who received more aggression were less successful. Additionally, marmots who received more aggression were less behaviorally diverse, less behaviorally selective and less persistent while trying to open the puzzle box. Thus, we show that aggression indirectly decreases problem-solving success by acting on the behavioral traits that an individual uses. We conclude that specific social relationships, including the type of interaction and whether they are recipients or initiators, influences the ways in which an individual interacts with cognitive tests and should be considered in analysis of individual problem-solving.

Keywords Social networks · Structural equation modeling · Yellow-bellied marmots · Problem-solving · Cognition · innovation

Background

Animals encounter numerous novel physical or social environments throughout their lives that may be due to dispersal, migration, social upheavals or catastrophic environmental events. To prosper, individuals must be able to flexibly adjust to these novel environments. Innovation, or problem-solving, is one way by which animals are able to adapt to these changes. Innovation is the ability to devise a novel solution to a novel or existing problem (Reader and Laland 2003) and this ability often carries fitness benefits. Birds with larger brain size, a correlate of innovation, are better at establishing populations in novel environments (Sol et al. 2005a). In Palearctic birds, innovation allows overwinter residents to utilize novel food sources, a skill that their migratory counterparts lack (Sol et al. 2005b). 'Nuisance' species, such as racoons (*Procyon lotor*), are enthusiastic problem-solvers, a skill that seems to aid them in the settlement of human-altered habitats and sometimes bring them into conflict with humans (Barrett et al. 2019). With human impacts rapidly altering environments physically, chemically and behaviorally (e.g., Sih et al. 2016), there is an increasing need to understand which animals will be able to behaviorally adapt to these challenges and how they will do so.

Problem-solving ability varies greatly across species (chimpanzees *Pan troglodytes* Reader and Laland 2001; black-throated monitor lizards *Varanus albigularis albigularis* Manrod et al. 2008; spotted hyenas *Crocuta crocuta* Benson-Amram and Holekamp 2012) and individuals (Johnson-Ulrich et al. 2020; Rowell and Rymar 2019). Innovation and problem-solving are difficult to study in the wild as they require a breadth of knowledge on a species behavior.

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Instead, many researchers study problem-solving through the introduction of novel tasks, such as puzzle boxes (Griffin and Guez 2014). These puzzle boxes have helped researchers experimentally test why these variations arise. Across species, traits like brain size (Benson-Amram et al. 2016) and being a habitat generalist (Overington et al. 2011) seem to drive problem-solving ability. Some life history traits, such as age, where older individuals are more likely to innovate (Kendal et al. 2005), or dominance rank, where lower-ranked individuals lack access to normal food sources and are forced to innovate (Thornton and Samson 2012) may correlate with individual variation. However, individual variation is most frequently predicted by behavioral traits, defined by their consistency—which may be traits such as persistence or personality traits such as boldness (Amici et al. 2019). The relationships between problem-solving and some behavioral traits are straightforward. *Neophobia*, defined as an aversion to new stimuli, may compromise an animal's ability to problem-solve by preventing them from interacting with a novel object (Benson-Amram and Holekamp 2012; Benson-Amram et al. 2013). By contrast, *persistence*, defined as engaging in multiple attempts or spending more time trying to solve a puzzle, is frequently associated with problem-solving success with more persistent individuals being more successful (Keagy et al. 2009; Overington et al. 2011; Thornton and Samson 2012; Benson-Amram and Holekamp 2012; Cole et al. 2012; Chow et al. 2016; Loepelt et al. 2016). Similarly, individuals who attempt a large number of behaviors, referred to as being exploratory or engaging in *behavioral diversity*, are more likely to generate an innovative solution to a problem (Benson-Amram et al. 2013; Griffin et al. 2014; Griffin and Diquelou 2015; Daniels et al. 2019) because they are able to gather more information about an object (Reader and Laland 2003). The relationship between problem-solving and other behavioral traits is less clear-cut. *Behavioral selectivity*, engaging in behaviors most likely to successfully solve a problem, such as manipulating a handle to release a door rather than chewing on the bottom, minimizes energy and opportunity costs of problem-solving by engaging in efficient activities (Benson-Amram and Holekamp 2012; Chow et al. 2016; Daniels et al. 2019). Behavioral selectivity, however, requires trade-offs so that an individual cannot have both high behavioral diversity and high behavioral selectivity (Chow et al. 2016). The question is then, what drives individuals to use different behavioral traits when they solve a problem?

Context is often important to understand an individuals' decision-making and problem-solving and is likely influenced by an individuals' life history and current physiological, environmental and social circumstances (Boogert et al. 2018). Captive pack-living dogs (*Canis familiaris*) and pet dogs were more persistent and manipulative when interacting with a puzzle solving task than were free-ranging dogs. Free-ranging dogs lack a consistent food source and were likely less persistent as a means of conserving energy. Additionally, captive and pet dogs live in an environment where humans encourage and reward interaction with novel objects, which may increase both their motivation and persistence (Lazzaroni et al. 2019). In spotted hyenas (*Crocuta crocuta*), captive individuals had greater initial exploratory behavior and lower neophobia, making them better puzzle solvers than their wild counterparts (Benson-Amram et al. 2013). Subordinate black-capped chickadees (*Poecile atricapillus*) were more successful problem-solvers because dominant individuals guard easily accessible food resources, forcing subordinates to forage on more difficult to access resources. Subordinates subsequently also exhibited less neophobia (MacDougall-Shackleton et al. 2011). Thus, different physical or social environments alter the behaviors that individuals use when confronted with novel problems and, in turn, these changes can alter their problem-solving success.

The interaction of the physical/social environment and behavior is, however, complex and may involve multiple simultaneous interacting factors as well as both indirect and direct effects. This is particularly true for an individuals' social interactions, which can include hierarchies, different styles of relationships and indirect influences from the broader group. Social networks (Wey et al. 2008) quantitatively measure all of an individual's relationships with other members of their group and can be analyzed to extract information such as how many individuals a focal individual interacts with or how much influence they hold over the rest of the group. While most prior studies of social influences of problem-solving focused on dominance rank, social networks allow for more precise questions to be asked about how measures of an individuals' position in their social network might influence their behavior. Additionally, an individuals' social network may influence problem-solving in both direct and indirect ways. Directly, an individuals' social network position may determine how much information about the task they have access to through their close contacts or whether they are targets of aggression and thus, have increased motivation to open the box. An individuals' social network position may also influence which behavioral trait they are most likely to use. For example, an individual who is a frequent target of aggression may not be very persistent while attempting to solve the box. These complex multivariate interactions can be modeled with structural equation modeling, which accounts for the indirect and direct effects of multiple factors on a single outcome (Shipley 2000).

Here, we sought a more comprehensive understanding of how social factors and behavioral traits influence problem-solving success at a novel puzzle box in yellow-bellied marmots (*Marmota flaviventer*). To do this, we adopted a multistep approach using both correlative analyses and causal confirmatory path analysis to account for both direct and indirect pathways to successful problem solving. We first tested for associations between our 11 factors (four behavioral traits measured from interactions with a puzzle box: behavioral diversity, behavioral selectivity, neophobia and persistence, and six social measures: three affiliative PCAs, three agonistic PCAs and relative dominance rank) and problem-solving success using generalized linear mixed effects models and general linear models (summarized in Fig. 1a). We then used confirmatory path analysis (Shipley 2000) to test 24 hypothesized causal path diagrams of how social factors directly and indirectly effect problem-solving success via behavioral trait (summarized in Fig. 1b). We hypothesized that individuals with different social measures would use different behavioral traits to successfully solve the novel puzzle box.

Yellow-bellied marmots are a facultatively social, hibernating rodent species that have been studied at the Rocky Mountain Biological Laboratory since 1962 (Armitage 2014). While rodents are frequently used in cognition research, innovation and problem-solving have never been studied within the genus *Marmota*. Marmots are generalist herbivores that do not typically engage in extractive foraging (Armitage 2014), although they do occasionally manipulate objects in their environment (i.e., moving rocks, playing with sticks, pers. obs.). Problem-solving ability is often tested in species that regularly engage in extractive foraging, yet we believe that 'absence of evidence is not evidence of absence', and marmots permit us to test whether these problem-solving abilities exist, and indeed operate in similar ways in species that may not have an immediate benefit from them.

Additionally, marmots have a wide range of social structures available to be studied within a single population which makes them particularly suitable to test our question of the indirect effects of social networks on problem-solving. Marmots live in harem-polygynous matrilineal colonies composed of one to several related females, their pups, yearlings and one to two dominant males (Blumstein 2013; Armitage 2014). Considerable prior work has shown that, in contrast to many species, yellow-bellied marmots suffer costs of engaging in affiliative behavior and receive some benefits from agonistic behavior. Affiliative social measures are frequently associated with negative fitness outcomes, including individuals with stronger affiliative relationships were more likely to die during hibernation (Yang et al. 2016), live shorter lives (Blumstein et al. 2018) and suffer decreased reproductive success (Wey and Blumstein 2012). Additionally, individuals with more affiliative interaction partners, who had fewer degrees of separation from others in their affiliative network, died younger (Blumstein et al. 2018). Yearling females seem to be the only ones to benefit from strong affiliative relationships, which may protect them from predators (Montero et al. 2020). Meanwhile, males who are more aggressive towards others have higher reproductive success (Wey and Blumstein 2012). Females become more agonistic with age (Wey and Blumstein 2010), which can serve to reproductively suppress younger females and

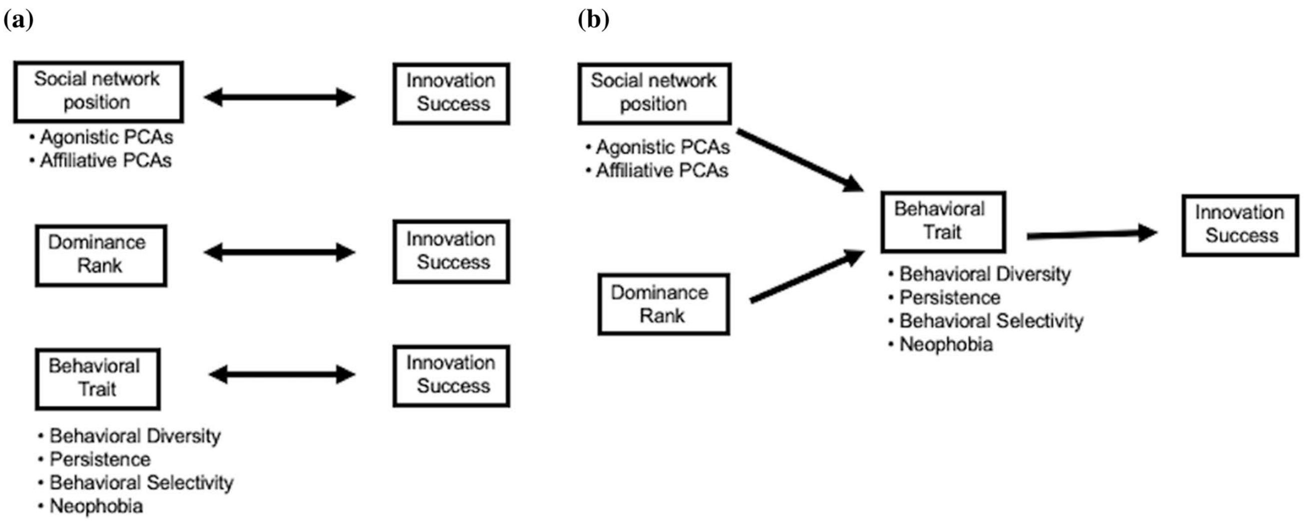

Fig. 1 Illustration of alternative model fitting approaches. **a** Correlative model testing the association between 12 different traits and problem-solving success. Traits have been consolidated into three categories for clarity: behavioral traits (four strategies: behavioral diversity, behavioral selectivity, persistence, and neophobia), social measures (three affiliative PCAs and three agonistic PCAs outlined in Tables 2 and 3) and dominance rank (measured as relative rank). **b** Causal model (SEM) testing the hypothesized link between social position (controlling for dominance) and problem-solving success mediated by behavioral trait. Traits have been consolidated into three categories for clarity (see above for descriptions). All possible combinations of these traits were tested in a series of twenty-eight separate models

concentrate resources for an aggressive females' offspring (Armitage 1991, 2003). Social dominance in pups correlates with higher dominance rank as adults (Huang et al. 2011), which is also correlated with higher body mass (a key factor associated with reproductive success) (Huang et al. 2011). This interesting pattern of negative affiliative relationships and some positive agonistic relationships allows us to test whether sociality affects problem-solving differently in species with less frequent social interactions where affiliative relationships, typically important to problem-solving, are costly.

Materials and methods

Study site and system

We presented puzzle boxes to yellow-bellied marmots at eight colony sites in and around the Rocky Mountain Biological Laboratory located in Gothic, CO. Each colony was a geographically distinct area (colony size range: 2–44 individuals, average: 21 individuals) that contained one or more social groups, which were socially isolated groups of interacting individuals within a colony. Colonies ranged from 0.52 km (the two nearest colonies) to 5 km apart (colonies at the opposite ends of the valley) and while marmots can travel this distance, dispersal from one colony to another is rare. We observed no inter-colony movement during this study period. These marmots are part of a long-term study (Blumstein 2013; Armitage 2014) and individuals are regularly trapped and individually marked with numbered ear tags and unique pictograms are dyed on their dorsal pelage for identification from afar (Blumstein et al. 2009). Observers use binoculars and 15–45 × spotting scopes to record social interactions with all occurrence behavioral sampling. Recorded behaviors follow a defined ethogram of affiliative (sit together, play, greet, allogroom, follow, forage together) and agonistic (aggressive bite, box, chase, grab/slap/push, mouth spar, pounce, snap/snarl/hiss, displacement) behaviors (full ethogram with descriptions in Table 1 in Online Resource 1). Observers are positioned at distances chosen so as to not interfere with normal behavior (Blumstein et al. 2009). Social interactions were recorded from mid-April, when marmots emerge, until mid-September when they begin to enter hibernation. During this period, behavioral observations are conducted on most days, weather permitting, during hours of peak activity (7–10 h in the morning and 16–19 h in the afternoon, (Blumstein et al. 2009).

Puzzle box

We constructed and deployed eight, wood-framed, plexiglass puzzle boxes (30.84 × 30.84 × 30.84 cm, Fig. 2). Each box had two hinged sides that an individual could interact with and open to obtain food. The first solution was the lid of the box, which had a plexiglass protrusion, and marmots could use any part of their body to lift the lid by the protrusion or by gripping the lid itself and pushing it up. The second solution was a door on one side of the box, which marmots could use any part of their body to pull open. Both solutions were held shut by two 5.08 cm Velcro strips placed on either side of the plexiglass projection (lid) or a small metal knob (door) (Video of solutions provided in Online Resource 2). The solutions were designed so that the behaviors required to open the boxes were already in the marmots' repertoires (i.e., pushing and pulling objects, manipulating objects with their mouths). A marmot was considered to have 'successfully innovated' if they approached a closed puzzle box and

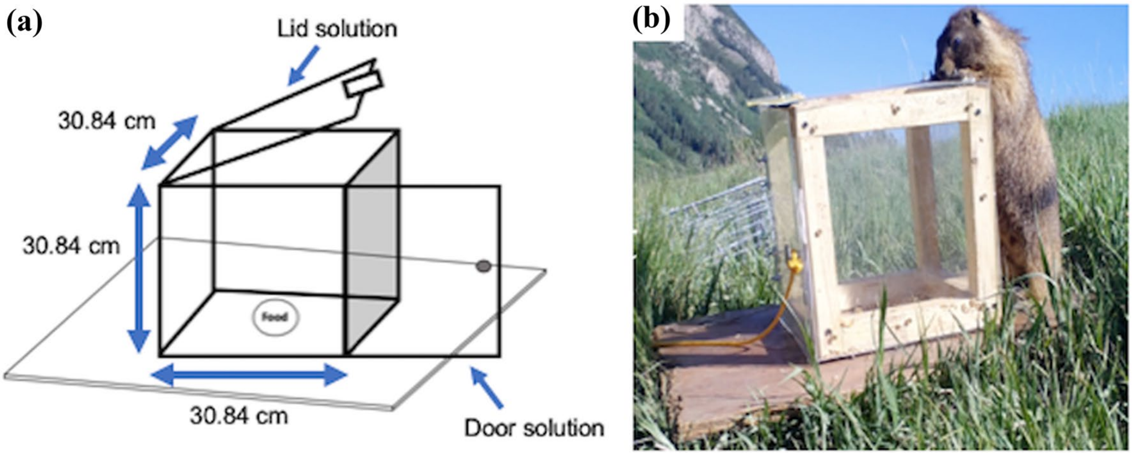

Fig. 2 Puzzle box. **a** Diagram of experimental puzzle box. The puzzle box is made of a 30.84 × 30.84 × 30.84 cm wooden frame covered in plexiglass with a hinged door and hinged lid to provide access. The whole apparatus was affixed to a piece of plywood to prevent the box from being flipped. Not marked: The plywood base is 60.7 × 50.8 cm. **b** Photograph of actual puzzle box

proceeded to open it using either of the two solutions and obtained the food inside, which was determined by seeing them chewing or eating. Although both box solutions were given equal resistance, the marmots overwhelmingly preferred the lid solution, which may reflect that marmots are used to pushing objects with their nose rather than pulling or that marmots may have more leverage pushing up than pulling out. Due to small sample size of the individuals using the door solution, either solution was considered as a successful innovation. To prevent marmots from flipping the apparatus, each box was secured to a 60.7 × 50.8 cm plywood platform. Both the wooden frame and plywood were sealed with two coats of polyurethane to prevent water damage and to permit cleaning (with concentrated acetic acid) between deployments to different colonies.

Puzzle boxes were deployed from 3 June to 1 July 2018. Boxes were set out at eight colonies with multiple boxes placed at social groups within colonies depending on group size and distribution of individuals. Each box was set out for a total of 2 weeks at each colony. Weeks were separated into two rotations: a down-valley rotation where the boxes were set out at four lower-elevation colonies: Gothic Townsite, River Annex, River Mound/Bench, Avalanche and an up-valley rotation where boxes were set out at four higher-elevation colonies: Marmot Meadow, Picnic, Boulder and North Picnic. Gothic Townsite had three puzzle boxes set at three distinct social groups that do not interact or overlap in physical space. River Mound and Bench had two puzzle boxes due to physical distance of the two burrows (200 m) that the individuals of the colony moved between. Picnic had two puzzle boxes due to group size (33 individuals). Marmot Meadow previously had two distinct non-interacting social sub-groups and were given two puzzle boxes. However, during the 2018 season, the individuals had significant social overlap and were considered as one social group for this experiment. Boulder, North Picnic, River Annex and Avalanche all had one puzzle box due to low group size and centralized location. Boulder and River Annex did not have enough observations and were dropped from subsequent analysis. The lack of movement of individuals between colonies precluded any potential transfer of knowledge between colonies. Puzzle boxes were placed within 1 m of an active marmot burrow. Marmots tend to be philopatric to their burrows and an active burrow was identified if observers had seen activity there over the past three days.

Each puzzle box was baited with half a cup of Omalene horse feed (Purina® Omolene 100, Purina Mills, LLC, St. Louis, MO, USA), which is a desirable food source also used to bait traps (Fuong et al. 2015). The boxes were all set up before 07:00 h and were freely accessible to the marmots throughout the morning. Individuals started a trial when they stepped with at least one paw onto the plywood and were considered ‘interacting’ with the box from when they first made physical contact with the box with any part of their body until they no longer had physical contact with the plywood or box for over 5 s, when the trial was considered over. Individuals engaged in 1 to 48 trials a day with an average of 7.5 daily trials and spent 5 s to 896 s at the box with an average visit lasting 80.9 s (standard error ± 3.75). Two Browning Strike Force HD or Browning Spec Ops FHD cameras were placed approximately 2.5 m from the box and aimed at opposite corners of the platform to capture activity from different perspectives. Cameras were movement activated and set to record 2-min videos with a 5-s recovery time.

Measures

Social measures

We used all occurrence behavior sampling to quantify social interactions recorded over the summer season to calculate two separate social networks for each colony from all affiliative or agonistic interactions between yearlings and adults (ethogram listed in Table 1 in Online Resource 1). All networks took into account direction of the interaction (initiator and recipient) and weight of the interaction (number of times the pair interacted). From these networks, we calculated nine social measures (in/out degree, in/out strength, in/out closeness, local clustering, betweenness centrality and eigenvector centrality), which characterize an individuals’ position in their social network (specific definitions are listed in Table 1). All calculations were made with the igraph package (Csárdi and Nepusz 2006) in R v. 3.6.1 (R Core Team 2019) and RStudio (RStudio Team 2020).

PCA

To account for correlation between social measures, we used principal component analysis to reduce these traits into three principal components (eigenvalues > 1.0) each for the affiliative and agonistic networks. Principal component analysis (PCA) was conducted with the psych package in R (Revelle 2018).

Principal component loadings are summarized in Tables 2 and 3. We interpreted the first affiliative component as describing *friendliness*; indegree, outdegree, instrength, outstrength and eigenvector centrality loaded heavily on it. Friendly individuals have many strong affiliative relationships. We interpreted the second affiliative component as *isolation*; negative betweenness loaded heavily on it. Isolated individuals did not link the group together. Since this variable was negative in the loadings, it indicates that an interpretation of high isolation indicates low connecting of disparate subgroups. We interpreted the third component as *initiated closeness*; outcloseness loaded heavily on it. These individuals initiated

Table 1 Social network attributes and their definitions

Attribute	Summary
Degree (In/Out)	Number of individuals with whom a focal individual interacted (Wasserman and Faust 1994)
Strength (In/Out)	Total number of interactions involving a focal individual (Barrat et al. 2004)
Closeness (In/Out)	Reciprocal of sum of shortest path lengths between focal and other individuals (Wasserman and Faust 1994; Wey et al. 2008; Fuong et al. 2015)
Betweenness	Number of shortest paths between pairs of individuals that pass through a focal individual's network (Wasserman and Faust 1994; Wey et al. 2008)
Eigenvector centrality	A measure of how well one's direct associates are connected with others (Bonacich 2007; Fuong et al. 2015)
Local Clustering	Fraction of ties to other individuals that a node has over all possible ties a node could form (Opsahl 2013; Watts and Strogatz 1998)

Out indicates interactions initiated by the focal individual and In indicates interactions received by the focal individual. All attributes were extracted from a weighted network, which accounts for the rate of interactions

Table 2 Principal component scores from principal component analysis of affiliative social network measures

	Friendliness	Isolation	Initiated closeness
Indegree	**0.94**	– 0.18	– 0.07
Outdegree	**0.93**	– 0.11	– 0.03
Betweenness	0.38	**– 0.78**	0.19
Local clustering	-0.27	0.44	0.53
Outstrength	**0.75**	0.55	– 0.05
Instrength	**0.76**	0.55	– 0.01
Outcloseness	0.03	0	**0.88**
Incloseness	0.33	– 0.46	0.15
Eigenvector centrality	**0.90**	0.01	0.14

Bolded values indicate high loading values included in the component

Table 3 Principal component scores from principal component analysis of agonistic social network measures

	Aggression	Received Aggression	Initiated aggression frequency
Indegree	0.69	**0.64**	– 0.11
Outdegree	**0.88**	– 0.31	0.19
Betweenness	**0.74**	– 0.37	– 0.34
Local clustering	– 0.49	0.18	0.14
Outstrength	0.40	– 0.24	**0.85**
Instrength	0.21	**0.67**	0.06
Outcloseness	**0.78**	– 0.24	– 0.43
Incloseness	**0.70**	0.45	0.06
Eigenvector centrality	**0.76**	0.03	0.23

Bolded values indicate high loading values included in the component

interactions directly with a large portion of other individuals in their network. We interpreted the first agonistic component as *Aggression*; outdegree, betweenness, eigenvector centrality, incloseness, outcloseness loaded heavily on it. Individuals who scored high in this category initiated aggression against a large proportion of others in their network. We interpreted the second agonistic component as *received aggression*; indegree and instrength loaded heavily on it. Individuals who scored high in this category received higher amounts of aggression from others. We interpreted the third agonistic component as *initiated aggression frequency*; outstrength loaded heavily on it. These individuals frequently initiated aggressive interactions towards others.

Dominance rank

To account for potential effects of dominance on innovation success, we used the Clutton-Brock index of social dominance (CBI, Clutton-brock et al. 1979) to calculate relative rank. We used CBI because it excludes rate of interaction from calculations, which is better suited to species with low-frequency interactions like marmots (Bang et al. 2010). The CBI was calculated from a ratio of wins and losses during agonistic events for each individual. The equation for CBI is $(B+b+1)/(L+l+1)$, where B is the total number of individuals 'beaten' who previously lost an interaction to the focal individual, b is the number of individuals who those individuals who were 'beaten' have won against, L is the number of individual 'winners' who have won an interaction with the focal individual, and l is the number of individuals to whom 'winners' have lost (Blumstein et al. 2016).

Relative rank was calculated to account for different numbers of individuals in a hierarchy, here defined as a colony. Each rank was standardized with respect to the total number of individuals present in the group (Huang et al. 2011). CBI values were ordered from lowest to highest to calculate an absolute rank value and then divided by the total number of individuals in the network to calculate relative rank. For each colony, the lowest ranked individual had a relative rank of zero and the highest ranked individual had a relative rank of one.

Behavioral traits

We extracted innovation success and four behavioral traits (persistence, behavioral selectivity, behavioral diversity and neophobia) from video recordings of the marmots at the puzzle box using JWatcher 1.0 (Blumstein and Daniel 2007). After the start of each trial (when a marmot first physically contacted the plywood platform), we recorded the onset of all behaviors an individual engaged in (full ethogram in Table 2 in Online Resource 1) until the end of the trial when the marmot was no longer in physical contact with the plywood platform for longer than 5 s. Behaviors were separated based on which section of the puzzle box the individual touched (door, lid, other part of box) and how they interacted with it (nose, paw, bite, other).

Successful marmots manipulated either one of the two solutions, the door or the lid, to enter the box and thus obtained the food reward (which was confirmed by seeing them chew). All other marmots who initiated trials but did not open the box were considered not successful, even if they obtained the food reward through scrounging. We formally studied scrounging in marmots in a companion paper, although this analysis was conducted on a dataset from 2019 (Evans et al. 2021). Trials in which marmots engaged in no other behaviors than chewing on the plywood for extended periods of time were also removed from the analysis. Only one of the two puzzle box cameras was scored and included in the analysis to prevent repeated observations. Scorers were trained to have repeatable ≥ 0.95 interobserver correlation on test videos before collecting data.

We quantified four behavioral traits commonly measured in relation to innovation success: persistence, behavioral selectivity, behavioral diversity and neophobia. We quantified persistence as the proportion of time in sight that the focal marmot spent interacting with the box during a trial (hereafter, proportion of time). Behavioral selectivity was calculated as the sum of the proportion of time in sight devoted to effective behaviors, defined as actions directed at the door or the lid of the box. For persistence and behavioral selectivity, we excluded all trials during which marmots were on the plywood but did not interact with the puzzle box in order to avoid inflating the dataset with zeros for non-interacting marmots. To account for different trial lengths and number of observations of each behavior per trial, we calculated behavioral diversity with a Shannon index $H = -\sum_{i=1}^{R} (p_i \bullet \log p_i)$ (Pielou 1975), for each individual across each trial. Here, p_i = the proportion of time spent enacting behaviors, such as manipulating the door with their mouth or manipulating the lid with their paw (full ethogram defined in Table 2 Online Resource 1), out of the total time spent in sight on the plywood. The behaviors ‘on’ and ‘off’ plywood were excluded from analysis because these behaviors marked the start or end of the trial. To assess an individual’s degree of neophobia, we measured the latency to touch the box from stepping onto the platform for the first trial of each day an individual interacted with the box. To account for potential habituation to the box over each day, neophobia was measured only on the first trial of each day that a marmot interacted with the puzzle box. Neophobia could not be calculated for marmots that touched the plywood but did not touch the box and they were removed for these days in the dataset. The neophobia dataset were smaller than those of the other behavioral traits as it was measured a different level (day).

Data analysis

Traits associated with problem-solving success

To test whether social measures or a specific behavioral trait was associated with innovation success (Fig. 1a), we created a series of generalized linear mixed models for behavioral traits and generalized linear models for social measures. All models had a binary measure of problem-solving (success or failure) as the dependent variable. Eleven total models were fitted on six different datasets due to data being measured at different level and are outlined below. The six datasets were behavioral diversity ($N = 547$ observations on 34 individuals), behavioral selectivity and persistence ($N = 365$ observations on 33 individuals), neophobia ($N = 155$ observations on 35 individuals), affiliative attributes ($N = 38$ observations on 38 individuals), agonistic attributes ($N = 26$ observations on 26 individuals) and relative rank ($N = 32$ observations on 32 individuals). Dominance and both social network attributes were measured as a once yearly value and tested against a yearly measure of problem-solving success (individual solved the puzzle at least once over the season = 1, individual did not solve the puzzle over the season = 0). These three variables created three separate datasets due to sample size differences between them. Neophobia was measured for the first trial of each day that an individual interacted with the box and so it was tested against a daily measure of problem-solving success (individual solved the puzzle at least once during that day = 1, individual did not solve the puzzle that day = 0). Behavioral diversity, behavioral selectivity and persistence were measured per trial and were tested against trial-level problem-solving success (individual solved the puzzle during that trial = 1, individual did not solve the puzzle during that trial = 0). However, they were separated into two separate datasets because sample size differences due to the individuals dropped from persistence and behavioral selectivity. These separate datasets were created to avoid statistical issues associated with multiple levels in statistical models (Preacher et al. 2010) and small sample sizes.

Four generalized linear mixed effects models were fitted to test the association of each behavioral trait with problem-solving success. Each model had one fixed effect (behavioral diversity, behavioral selectivity, persistence and neophobia) and individual identity as a random effect to account for repeated measures in each of the behavioral traits. Six generalized linear models were fitted to test the association of social measures and problem-solving success. Three models were fitted with one fixed effect of affiliative PCA (Friendliness, Isolation, Initiated Closeness) and three other models had one fixed effect of agonistic PCA (Aggression, Received Aggression, Initiated Aggression Frequency). One generalized linear model tested the correlation of dominance rank and problem-solving success with a fixed effect of relative rank.

All other model variables (behavioral traits, dominance rank) were centered by subtracting column means and scaled by dividing the centered columns by their standard deviations using the scale function in R to ensure comparability of effect sizes (R Core Team 2019). To account for the binomial nature of success, models had a binomial distribution with link = logit function and to promote convergence, we used the optimizer bobyqa on all models that were unable to converge (Bates et al. 2015b). All models were fitted in the lme4 package (Bates et al. 2015a) in *R* and *p* values (significance level ≤ 0.05) were extracted with the lmerTest package (Kuznetsova et al. 2017).

Evaluation of structural equation models

To test whether social structure acted directly or indirectly through behavioral traits to affect problem-solving success, we used confirmatory path analysis using the directed separation (d-sep) method (Shipley 2000). Structural equation models use path diagrams to incorporate multiple hypothesized causal relationships between variables, which can appear as both predictor and response variables, into a single causal network (Lefcheck 2016). A piecewise approach translates the path diagram into a series of linear equations that can be individually evaluated in a stepwise manner. Directed separation tests are used to determine goodness-of-fit and whether variables are conditionally independent, meaning there are no missing relationships between unconnected variables in the hypothesized model (Shipley 2000). This method allows for more flexibility in fitting non-normal data by incorporating multiple modeling methods, such as the inclusion of random effects (Lefcheck 2016) and binomial dependent variables.

We created twenty-four path models (Fig. 1b), one for each combination of the six social measures and the four behavioral traits. Relative rank was included as a covariate in each model to account for the potential effects of social dominance. Each structural equation model (SEM) contained two models. The first linear model tested was a linear mixed effects model of the relationship between social measures and behavioral trait, which included relative rank as a fixed effect to account for potential dominance effects and a random effect of individual identity (nlme, Pinheiro 2019). The second linear model was a generalized logistic mixed effects model of the relationship between behavioral trait and problem-solving success with a random effect of individual identity (lme4, (Bates et al. 2015a).

Each model was evaluated with the d-sep method to test for missing causal links. This was measured by Fischer's *C*, a combination of all *p*-values for each independence claim, compared with a X^2 distribution with $2*k$ degrees of freedom. The proposed causal pathway is supported when there is low conditional independence. This occurs when C could have happened by chance and where X^2 is greater than 0.05 (Lefcheck 2016).

Problem-solving success was modeled with a binomial distribution with link = logit function and the optimizer bobyqa was included to promote convergence (Bates et al. 2015b). All variables were scaled to standardize them and thus their magnitudes are directly comparable. All tests were run in the piecewiseSEM R package (Lefcheck 2016), which allows each path to be modelled separately using appropriate methods for the variables involved in that relationship.

Analyses were again conducted on six different datasets. Affiliative behavioral selectivity/persistence ($N = 282$ observations on 27 individuals), affiliative behavioral diversity ($N = 404$ observations on 28 individuals), affiliative neophobia ($N = 102$ observations on 27 individuals), agonistic behavioral selectivity/persistence ($N = 265$ observations on 21 individuals), agonistic behavioral diversity ($N = 377$ observations on 22 individuals) and agonistic neophobia ($N = 88$ observations on 22 individuals). Given the number of analyses (even though they were conducted on multiple data sets), we are most confident in results that are highly significant (i.e., $p < 0.001$). We considered strong effects to be those with $p < 0.05$ and weak effects to be those with $0.05 < p < 0.08$.

Results

Thirty-nine unique individuals interacted with the puzzle box. This included 19 adults and 20 yearlings, of which 24 were females and 15 were males. Seven individuals (18%) successfully solved the puzzle box, four of which only ever used the lid and the other three individuals used both the lid and the door. Out of 47 successful trials, the lid was used 36 times (77%) and the door was used 9 times (19%), with 8 door uses being a marmot entering the box through the lid and exiting through the door and returning to eat through the door. Datasets on which statistics were calculated consisted of smaller groupings of these individuals based on limitations of behavioral or social data.

Table 4 GLM results of direct models of social measures and innovation success and GLMM results of direct models of behavioral traits on innovation success

	Effect size	Standard error	*p* value
Behavioral traits			
Persistence	0.147	0.244	0.545
Behavioral diversity	**1.06**	**0.224**	**< 0.001****
Behavioral selectivity	0.290	0.231	0.210
Neophobia	− 0.011	0.630	0.986
Affiliative measures			
Friendliness	− 0.523	0.478	0.273
Isolation	− 0.214	0.386	0.580
Initiated closeness	− 0.285	0.442	0.519
Agonistic measures			
Aggression	0.002	0.504	0.997
Received aggression	**− 1.29**	**0.730**	**0.078***
Initiated aggression Frequency	0.479	0.425	0.260
Relative rank	0.295	0.472	0.532

*Indicates weak support ($p = 0.05–0.08$), ** indicates strong support ($p < 0.05$)

Bold values indicate significance

Behavioral traits associated with innovation success

We found a positive relationship between behavioral diversity (estimate(SE) = 1.06(0.224), $p < 0.001$) and innovation success. Innovation success was not associated with behavioral selectivity (estimate(SE) = 0.290(0.231), $p = 0.210$), persistence (estimate(SE) = 0.147(0.244), $p = 0.545$) or neophobia (estimate(SE) = − 0.011(0.630), p = 0.986). Received aggression had a negative, but weakly supported, relationship with innovation success (estimate(SE) = − 1.29(0.730), $p = 0.078$).

Neither affiliative social measures, nor relative rank, was correlated with innovation success (full results in Table 4).

Relationships between affiliative social measures and innovation success

After controlling for variation explained by relative rank, there was one path that was weakly supported. Individuals with low initiated closeness were more behaviorally diverse (estimate(SE) = − 0.196(0.097), $p = 0.054$) and more successful at solving the problem (Fig. 3a). Full results are presented in Table 5.

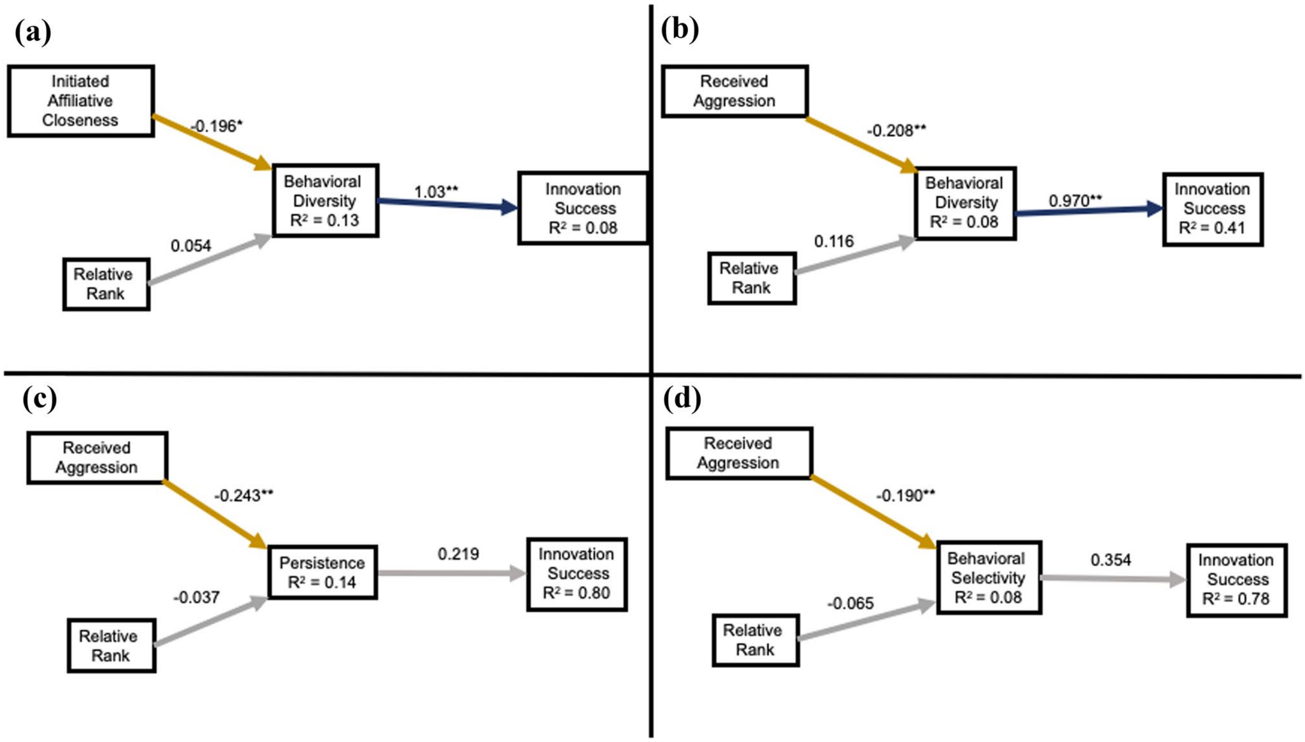

Fig. 3 SEM results. Path diagrams that included strongly or weakly supported effects of different social measures on behavioral traits and problem-solving success. **a** Affiliative initiated closeness and behavioral diversity, **b** received aggression and behavioral diversity, **c** received aggression and persistence, **d** received aggression and behavioral selectivity. Standardized path coefficients are interpreted in terms of standard deviation. Positive effects (+) are shown in dark blue. Negative effects (−) are shown in dark yellow. ** indicates the effect was strongly supported ($p < 0.05$), * indicates the effect was weakly supported ($p = 0.05–0.08$), no support ($p > 0.08$) are shown in grey. Conditional R^2 values are reported for each path

Table 5 Statistical output from path analysis of affiliative measures and behavioral traits

	Fischer's C		*p*	Estimate (PCA → Behavior)	*p*	Estimate (Behavior→ Success)	*p*
Persistence							
Friendliness	0.347	0.987		0.032	0.813	0.204	0.451
Isolation	1.01	0.909		− 0.092	0.370	0.204	0.451
Initiated closeness	1.66	0.798		− 0.042	0.730	0.204	0.451
Behavioral diversity							
Friendliness	0.285	0.991		0.029	0.800	**1.03**	**< 0.001****
Isolation	1.78	0.777		− 0.096	0.280	**1.03**	**< 0.001****
Initiated Closeness	1.52	0.823		**− 0.196**	**0.054***	**1.03**	**< 0.001****
Behavioral selectivity							
Friendliness	0.361	0.986		0.042	0.702	0.327	0.216
Isolation	1.01	0.908		− 0.117	0.153	0.327	0.216
Initiated closeness	1.66	0.799		− 0.144	0.127	0.327	0.216
Neophobia							
Friendliness	1.38	0.848		− 0.196	0.136	− 41.32	0.151
Isolation	1.42	0.84		− 0.037	0.723	− 41.32	0.151
Initiated closeness	0.977	0.813		0.078	0.586	− 41.32	0.151

*Indicates weak support ($p = 0.05–0.08$), ** indicates strong support ($p < 0.05$)

Significant Fischer's *C* value indicates that the hypothesized paths are inconsistent with the data and that the relationships could have occurred by chance

Bolded values are significant

Relationships between agonistic social measures and innovation success

Three models, which tested the causal effect of initiated aggression frequency on behavioral diversity, persistence and behavioral selectivity, had a high Fisher's *C* ($p < 0.05$, Table S4), indicating that the proposed causal path was not supported by the data.

After controlling for variation explained by relative rank, only a few paths were strongly supported. Individuals who received fewer aggressive interactions from their neighbors were more behaviorally diverse (estimate(SE) = − 0.208(0.071), $p = 0.009$) and more successful problem-solvers (Fig. 3b). Individuals who received fewer aggressive interactions were more persistent (estimate(SE) = − 0.243 (0.094), $p = 0.018$, Fig. 3c) and more behaviorally selective (estimate(SE) = -0.190(0.081), p = 0.031, Fig. 3d). However, neither of these paths influenced problem-solving success. Full results are presented in Table 6.

Discussion and conclusion

Taken together, we examined whether the propensity to solve a novel problem, a proxy for innovation, was driven by an individuals' behavioral traits, social measures, or dominance rank. We first examined the associations between our 11 variables and problem-solving success and then examined the causal direct and indirect effects of social structure (social measures, controlling for dominance rank) on behavioral traits and problem-solving success. From our correlative results, we found that individuals who are more behaviorally diverse were associated with more successful puzzle box solvers, while those who received more aggression were associated with less successful solvers. We additionally found that social structure affects which behavioral trait an individual uses and thus, indirectly affects problem-solving success. Individuals who initiated affiliative interactions with a greater proportion of their network were less behaviorally diverse, conversely suggesting that less friendly individuals are more successful problem-solvers.

Individuals who received more aggression were not only worse at problem-solving, but they also behaved differently. These individuals employed a less diverse set of behaviors, were less behaviorally selective and less persistent when exploring the box. Although problem-solving performance was only affected by decreased behavioral diversity, the effect of aggression on the other strategies indicates that there are multiple, indirect factors that influence perceived problem-solving ability. Recipients of aggression may be poor problem-solvers because they were prevented, physically or by stress, from engaging in the behavioral traits necessary to solve the problem. We would expect that

Table 6 Statistical output from path analysis of agonistic measures and behavioral traits

	Fischer's *C*	*p*	Estimate (PCA → Behavior)	*p*	Estimate (Behavior → success)	*p*
Persistence						
Aggression	2.29	0.682	0.050	0.652	0.219	0.421
Received aggression	4.31	0.366	**– 0.243**	**0.018****	0.219	0.421
Initiated aggression frequency	**10.8**	**0.029****	– 0.125	0.177	0.219	0.421
Behavioral diversity						
Aggression	4.69	0.320	0.032	0.743	**0.967**	**< 0.001****
Received aggression	6.55	0.162	**– 0.208**	**0.009****	**0.967**	**< 0.001****
Initiated aggression frequency	**23.0**	**0****	0.027	0.735	**0.967**	**< 0.001****
Behavioral selectivity						
Aggression	2.30	0.682	0.138	0.137	0.354	0.185
Received aggression	4.26	0.372	**– 0.190**	**0.031****	0.354	0.185
Initiated aggression frequency	**13.1**	**0.011****	– 0.090	0.256	0.354	0.185
Neophobia						
Aggression	1.48	0.831	– 0.023	0.835	– 12.9	0.289
Received neighbor aggression	2.43	0.656	0.021	0.843	– 12.9	0.289
Initiated aggression frequency	2.49	0.479	0.065	0.464	– 12.9	0.289

*Indicates weak support ($p = 0.05$–0.08), ** indicates strong support ($p < 0.05$)

Significant Fischer's *C* value indicates that the hypothesized paths are inconsistent with the data and that the relationships could have occurred by chance

Bolded values are significant

individuals who were excluded from the puzzle box by aggression would instead scrounge. However, in another study we found that dominance rank, which is calculated from aggressive interactions, was unrelated to whether an individual was a producer (an individual who obtains food for themselves) or a scrounger (an individual who relies on others to obtain food for them) (Evans et al. 2021). Thus, scrounging is unlikely related to social aggression. Interestingly, in this study, relative rank never directly explained variation in behavioral trait or problem-solving success, suggesting that the aggression referred to here is not related to competitive dominance.

Our correlative results were unsurprising given that both behavioral diversity and aggression are common factors considered when studying problem-solving ability. Behavioral diversity is consistently associated with problem-solving success in a number of species (Benson-Amram et al. 2013; Griffin et al. 2014; Daniels et al. 2019) and may be particularly important for generalist species, who are more likely to try different behaviors when searching for or exploiting novel resources (Benson-Amram et al. 2013). Marmots are generalist herbivores primarily feeding on surface level forbs and grasses and thus, they do not typically employ a wide range of foraging-related behaviors (Carey 1985). However, previous studies have found an association between generalist diets and novel object exploration (Bergman and Kitchen 2009; Tebbich et al. 2009), suggesting that for species that have a varied diet, it is advantageous to be more exploratory with potential novel food sources.

Our results on aggression are predicted by the social inhibition hypothesis, which states that problem-solving ability is inhibited in poor competitors because of their preoccupation with fear and risk avoidance in the presence of others (Griffin et al. 2013; Keynan et al. 2016). In Indian mynahs (*Acridotheres tristis*), individuals who were exposed to a novel foraging task in the presence of conspecifics were less likely to solve the task and, if they did, took longer to do so. The influence of conspecifics was context dependent where individuals in "high risk" situations (novel object nearby) were less likely to attempt the task when surrounded by conspecifics compared to a "low risk" situation (no object) (Griffin et al. 2013). In our population, less successful problem-solvers may be more sensitive to "risky" situations, but rather than this risk stemming from fear of a novel object, it comes from fear of receiving aggression from others. Aggression is known to be an important factor structuring marmot social groups (Blumstein et al. 2009; Wey and Blumstein 2010, 2012). While marmots will often share overlapping foraging territories with kin, mothers will exclude others from foraging areas; the propensity to share is shaped by individual behavior, age and reproductive status (Frase and Armitage 1984). Thus, aggressive marmots likely monopolized a desired foraging resource (the bait in the box), leading less aggressive marmots to forage on more easily accessible resources (freely available grass and forbs) to avoid aggression and stressful competition.

Some of our results were unexpected and contrary to findings in other species. Behavioral selectivity (i.e., employing only those behaviors that will be successful) is typically associated with problem-solving success (Benson-Amram and Holekamp 2012; Daniels et al. 2019) and indicates that animals learned effective strategies (Chow et al. 2016). We do not address learning here (exploration of learning in this system in Williams et al. in prep). However, behavioral selectivity measured as a proportion of time may yield different results than those in Chow et al. where it was measured as a proportion of behaviors because efficient behaviors may be inherently less time-consuming.

Interestingly, there was no significant effect of neophobia on problem-solving in any model, despite it typically being an important predictor of success in other species (MacDougall-Shackleton et al. 2011; Benson-Amram and Holekamp 2012; Daniels et al. 2019). Our population may have been less neophobic because they were habituated to man-made objects in their environment; they are exposed throughout their lives to livetraps used to trap them every other week. Alternatively, we may have measured neophobia in a way that did not capture the full trait variation within the population. We may have artificially excluded the more neophobic individuals of the population by only measuring those individuals who approached the box and truncated the approach latencies of other individuals, who could have seen the box upon exiting their burrows and were unafraid of the novel object by the time they stepped onto the plywood.

Our results demonstrate that social interactions can indirectly limit or change how an individual approaches a novel problem. In particular, we found that aggression, but not dominance rank, structures problem-solving and access to a novel food source within yellow-bellied marmot colonies. Thus, different types of social interactions may affect problem-solving in different and complex ways. When studying innovation in wild populations, it is difficult to exclude these numerous physical or social factors that directly or indirectly impact an individuals' interaction with a novel task. However, by not investigating these factors, we leave out important ecological context that frames innovation as a potential cognitive ability with fitness consequences. Structural equation modeling provides a statistical method through which to test these various indirect and direct effects and to model pathways between traits, sources of information, environmental conditions and innovation ability. Future studies of innovation would benefit from applying this approach.

Data and code availability

The Data and R code for this paper are available in Github repository: https://github.com/dmwilliams237/Marmot_SEM_Innovation.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10071-020-01464-2.

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Author contributions Conceptualization, DMW, DTB and CW; methodology DTB and DMW; investigation DMW and CW; formal analysis DTB, DMW and CW; writing-original draft DMW and CW; writing—review & editing DMW, DTB and CW; resources DMW and DTB.

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Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

Ethics approval The marmot study population is free-living and could freely interact with or leave the puzzle box as they desired. None were harmed by interacting with the box. Injuries are very rare during trapping and typically involves scrapes that are treated during handling. Marmots were studied under ARC protocol 2001-191-01 by the University of California Los Angeles Animal Care Committee on 13 May 2002, and renewed annually, as well as annual permits issued by the Colorado Division of Wildlife (TR519) and the Rocky Mountain Biological Laboratory's Animal Care Committee.

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