

Behavioral correlates of innovation success in facultatively social marmots

(Marmota flaviventer)

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Abstract

Innovation has transformed ecology and evolution, and understanding behaviors that lead to innovation success can have profound implications and applications in animal populations and human society. In past research, persistence, behavioral selectivity, and neophobia have influenced an individual's ability to innovate, however the traits that lead to innovation success are not well understood. Exploring these subjects in the socially flexible yellow-bellied marmot can disentangle these factors and reveal which one, if any, influences innovation success. To test innovation correlates in marmots, we will present them with a two-action puzzle box from which they can obtain a food reward, and video their interactions with the box. These videos will be scored for individual behaviors, and the interactions of innovation success, behavioral interactions with the box, and social metrics will be examined. We predict that high degrees of persistence, behavioral selectivity, and neophilia will correlate with innovation success. Previous studies have found correlations between success in novel habitats and innovation success, and because climate change will cause novel habitats, the results of this study can guide conservation management.

Introduction

Innovation has been a cornerstone to anthropogenic history, and more recently has been under study in non-human animals (Reader et al. 2016). Innovation is defined as any new behavior resulting in problem-solving success that arises within a population, and research on innovation in the animal kingdom continues to reveal profound impacts in

sociality, ecology, evolution, and intelligence (Reader and Laland 2003 p.14, Ramsey et al. 2007, Reader et al. 2016). Intraspecies sociality is a predictor of innovation success. Social animals participate in a social network, defined as social groups that are linked by social interactions (Wey et al. 2007). Individuals keep track of not only others in the group, but also members' relationships with each other, which begets greater intellectual capacity (Kudo and Dunbar 2001, Lefebvre et al. 2004). The intelligence and brain size of a species shapes a species' ecological niche and rate of macroevolution (Reader and Laland 2002, Lefebvre et al. 2004, Ramsey et al. 2007). Innovation can ease niche construction, as birds with bigger brains and greater innovative ability were more successful in novel environments (Odling-Smee et al. 2003, Sol et al. 2005). While innovative niche construction may slow evolution on a grand scale, innovation may accelerate macroevolution because innovative individuals who are exposed to different selective pressures may speciate at a different rate. Thus, the study of innovation can predict a species' success in response to changing conditions, such as the rapid range shifts resulting from climate change, and ultimately guide effective conservation management (Sol 2003, Sol et al. 2005, Ramsey et al 2007, Chen et al. 2011, Hoffman and Sgrò 2011, Pecl et al. 2017). Studies of animal innovation have shed light on patterns and processes of the natural world and continue to shape human understanding and decision-making.

Both cognition and fitness have been linked to innovation success, and recently, scientists have focused on behavioral traits to lead to innovation. (Cole et al. 2012, Keagy et al. 2009, Chow et al. 2016). In particular, behavioral traits, such as persistence,

behavioral selectivity, and neophobia, vary in effectiveness when overcoming unfamiliar challenges. Persistent individuals attempt a problem multiple times, which increases the likelihood of solving complex problems. This trait correlates positively with problem-solving success in eastern grey squirrels, hyenas, carib grackles, great tits, and meerkats (Chow et al. 2016, Benson-Amram and Holekamp 2012, Overington et al. 2013, Thorton and Samson 2012). Likewise, behavioral selectivity can improve problem-solving success because individuals who choose specific, advantageous behaviors may discover more efficient solutions, exemplified in eastern grey squirrels (Chow et al. 2016, 2017). Neophobia is a character trait defined as the aversion of new stimuli (Greenberg 2003). This fear may compromise an animal's ability to innovate and successfully solve novel problems, as demonstrated in hyenas (Benson-Amram and Holekamp 2012, Benson-Amram et al. 2012).

Although persistence, behavioral selectivity, and neophilia have been previously associated with innovation success, the effectiveness of these factors rely on the tradeoff between costs and benefits. The more an individual manifests these behavioral traits, the more time and energy is spent on a particular problem. Consequently, the reward from solving the problem decreases with greater time and energy expenditure, as does safety from predation (Chow et al. 2016). While these three traits can multiplicatively enhance innovation success, the opposite can also be true. For example, an individual who persistently engages in an ineffectual behavior would have a high score of persistence, but a low score of behavioral selectivity (Chow et al. 2016). That is, strategies employed

to address problems vary in effectiveness and require further study to understand how these behavioral qualities are linked to innovation success.

For this experiment, yellow-bellied marmots were exposed to a baited puzzle box to evaluate whether behavioral correlates, such as persistence, behavioral selectivity, and neophobia, influence innovation success. Innovation is often tested using puzzle boxes from which individuals may obtain a food reward if the puzzle is solved (Boogert et al. 2008; Benson-Amram and Holekamp 2012; Benson-Amram et al. 2013; Bókonyi et al. 2013; Chow et al. 2016, 2017). We scored marmot interactions with the puzzle boxes for persistence, behavioral selectivity, and neophobia. Persistence was defined as the number of behaviors directed at a test apparatus, behavioral selectivity as the proportion of successful behaviors when interacting with the apparatus, and neophobia as the latency between contact with the puzzle box platform and the puzzle box (Chow et al. 2016). These traits were measured in a similar manner to a comparable study on another sciurid rodent, the eastern grey squirrel (Chow et al. 2016).

Yellow-bellied marmots (*Marmota flaviventer*), a facultatively social ground squirrel, are ideal subjects to study innovation success in problem solving (Armitage 2014). Marmots are members of the family Sciuridae, characterized by a large brain size to body ratio relative to other rodents (Mace et al. 1981, Roth and Dicke 2005, Chow et al. 2016). Larger brain proportions are tied to successful invasions of novel environments, making marmots well-suited for innovation research (Sol et al. 2005, Amiel et al. 2011). Since 1962, the population of these diurnal rodents at the Rocky Mountain Biological Laboratory (RMBL) in Colorado has been the focus of many studies

as they are relatively easily trapped, marked, and are followed throughout life. Extensive data on births, deaths, and heritable social relationships exist for this facultatively social animal, as well as detailed analyses of their behavioral ecology (Armitage 1982).

Facultatively social individuals exhibit varying levels of social flexibility and cooperation within their unevenly distributed groups, so we can test whether a marmot's degree of sociality determines innovation success (Armitage 2014). We predicted that (1) more centrally located individuals who initiated more interactions than they received would have a greater propensity to innovate and (2) marmots who exhibited high degrees of persistence and behavioral selectivity, but low levels of neophobia, were more likely to innovate.

Methods

Subjects and Study Site

We studied the yellow-bellied marmots of East River Valley at the Rocky Mountain Biological Laboratory in Gothic, Colorado, U.S.A. June-July 2017 and 2018. These 53 free-living marmots live in one of 11 colonies, which are comprised of at least one social group, and include members of both sexes and a mix of adults, yearlings, and pups (Armitage 2014). The 7 colonies north of Gothic were in the up valley group, while the 4 southernmost colonies, including Gothic town site, were in the down valley group. Upon initial capture, we ear-tagged individuals for permanent identification and gave them a unique dorsal mark, re-dyed during routine trapping, for easy identification (Armitage 1982).

Puzzle Box Design

We constructed six 30.84 x 30.84 x 30.84 cm puzzle boxes made of clear plexiglass walls attached to a wooden frame, constructed from 5.08 cm wooden strips. A small plexiglass ledge was attached to the lid of the box with two 5.08 cm Velcro strips, while a hinged door with a metal knob and string attached was secured to one side using another pair of Velcro strips. The subjects could manipulate either the lid or the door to solve the puzzle and obtain the food reward inside the box, and both solutions were possible given the marmots' behavioral repertoire. Each puzzle box was stationed on a 60.7 x 50.8 cm plywood board, so marmots would be unable to upturn the box. All wooden pieces were protected from water damage with two coats of polyurethane, and each apparatus was cleaned prior to transport between colonies to minimize olfactory attraction to the puzzle box. This design allowed marmots to visually and olfactorily detect the food reward, thus motivating them to solve the puzzle box (Figure 1).

Experiment

Puzzle boxes were situated near recently occupied burrows within each colony, and two motion sensing trail cameras (Browning Strike Force HD or Browning Spec Ops FHD cameras) captured marmot interactions at each puzzle box site. Marmots could solve the puzzle box using one of two solutions, opening the lid or the door. During two, nonsequential testing periods, puzzle boxes were placed at each of the 11 colonies for one week at a time, from approximately 07:00 to 11:00 each morning. We alternated puzzle box placement weekly between the up valley and down valley colonies. Larger colonies,

defined by area and the number of individuals, had two or three puzzle boxes, while smaller colonies had one puzzle box.

Quantifying behaviors

We used JWatcher v1.0 (Blumstein and Daniel 2007), a program designed to quantify behavior, to measure innovation success. Each trial began when a marmot touched the puzzle box and ended when the marmot stepped off the plywood platform. Successful marmots manipulated either the door or the lid and foraged on the food reward. On the contrary, marmots who contacted the puzzle box but did not obtain the bait failed to innovate. We scored videos for behavioral diversity, latency between contact with plywood and the puzzle box, and rate of innovation success (Table 1).

Statistical Analysis

We fitted logistic regressions and generalized linear mixed models to explain variation in innovation success as a function of social metrics including group size, social network statistics that characterize an individual's position in the network as well as age and sex. The number of unique behaviors directed at the puzzle box and the total time spent on each behavior were compared against an individual's number of trials and problem-solving success.

Results

We completed logistic regression analyses on the following social network statistics: in degree, out degree, betweenness, in closeness, outcloseness, local clustering, global clustering, group size, average shortest path, and eigenvector centrality. The p-

values for all of these metrics were above 0.05, so sociality did not explain the likelihood of innovation.

Discussion

Our results disprove our hypothesis that central individuals who are more likely to initiate an interaction would be more likely to innovate. Because none of the social network metrics correlate with innovation, sociality does not influence innovation success. Marmots are facultatively social, so they may have minimal communication and be unlikely to share information with others in their social groups.

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Tables and Figures

Figure 1. A diagram of the two-action puzzle box.

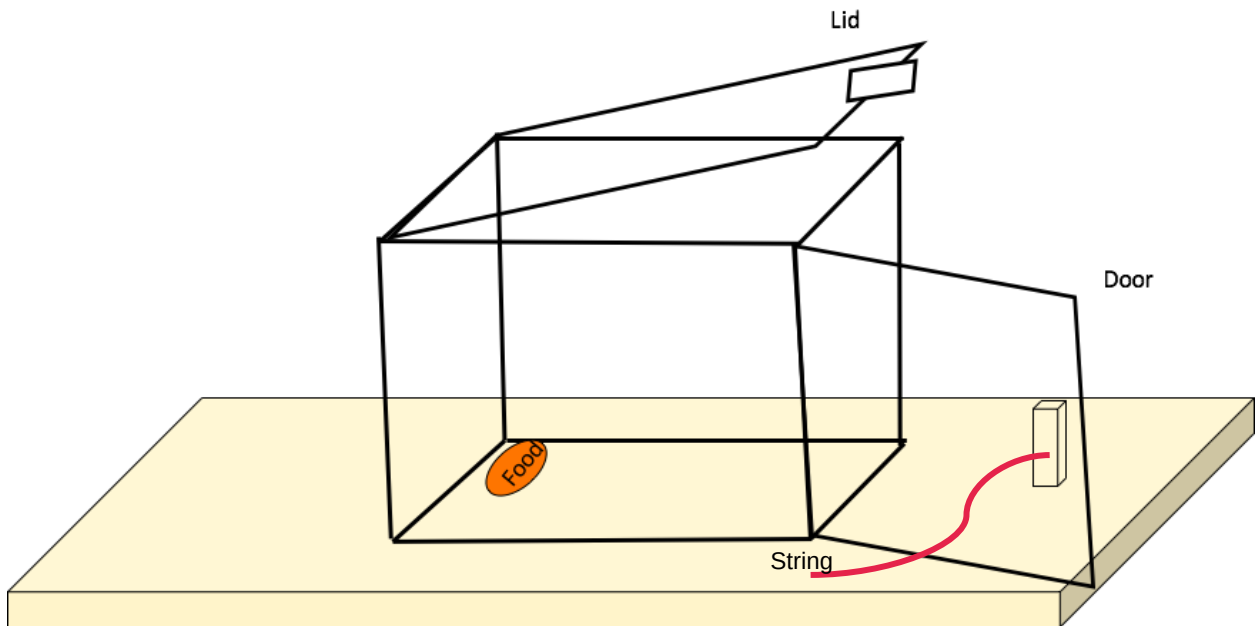
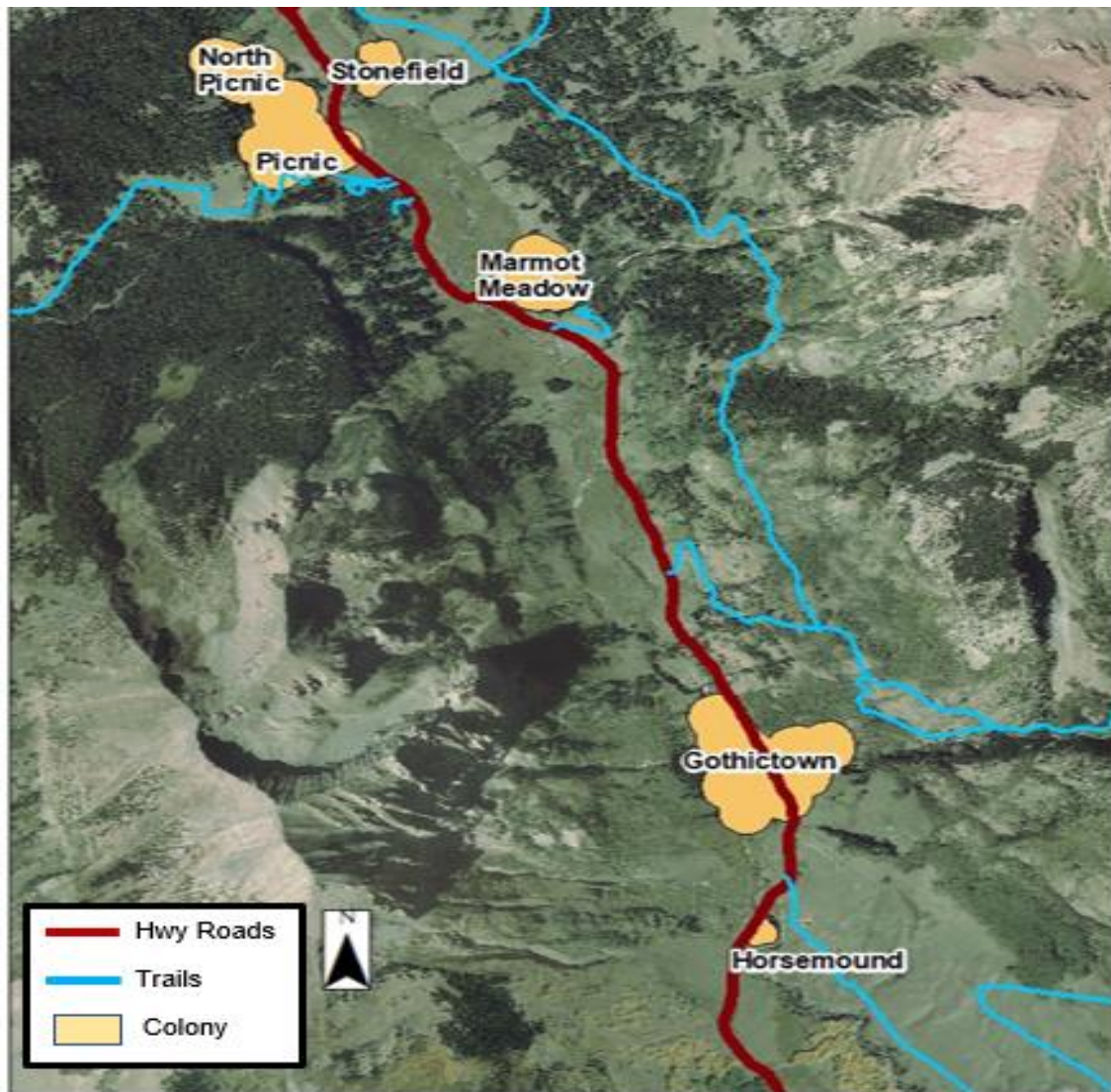


Table 1. A list of behaviors that will be scored and used as a measure of behavioral diversity.

Ethogram	
On plywood	Individual steps onto the plywood with one foot
Off plywood	Individual steps off plywood with four feet
Walk	Individual takes a step
Stand forage near	Individual forages on bait around box
Stand forage at	Individual forages on bait in box
Chew plywood	Individual chews on the plywood
Stand look	Individual stands quadrupedally and looks
Rear look	Individual stands bipedally and looks
Other	Individual does any other behavior

Sight bait	Individual sees bait inside puzzle box and reacts
Lid bite	Individual bites lid
Lid sniff	Individual sniffs lid
Lid paw	Individual paws lid or manipulates lid with paw
Lid nose	Individual noses lid or manipulates lid with nose
Lid other	Individual does other behavior at lid
Door bite	Individual bites door
Door sniff	Individual sniffs door
Door paw	Individual paws at door or manipulates door with paw
Door nose	Individual noses at door or manipulates door with paw
Door other	Individual does other behavior at door
Offside bite	Individual bites at any other side of box
Offside sniff	Individual sniffs at any other side of box
Offside paw	Individual paws at any other side of box
Offside nose	Individual noses at any other side of box
Offside other	Individual does other behavior at any other side of box

Figure 2. A map of the marmot colonies in the East River Valley at the Rocky Mountain Biological Laboratory.



Tables 2-10. Summary of of social network analysis.

	Estimate	Standard Error	Z Value	P Value
Intercept	-21.7392	5141.7451	- 0.004	0.997

In degree^{1/2}	0.2278	3.9709	0.057	0.954
Age	- 0.2153	1.5665	- 0.137	0.891
Sex	2.2788	1.5477	1.472	0.141
Valley Position	19.8316	5141.7447	0.004	0.997
	Estimate	Standard Error	Z Value	P Value
Intercept	- 25.1131	4502.8742	- 0.006	0.996
Out degree	6.5739	6.7918	0.968	0.333
Age	- 0.9818	1.6861	- 0.582	0.560
Sex	3.7473	2.5498	1.470	0.142
Valley Position	19.0746	4502.8715	0.004	0.997
	Estimate	Standard Error	Z Value	P Value
Intercept	- 33.497	4014.491	- 0.008	0.993
Betweenness	28.352	38.630	0.734	0.463
Age	1.212	1.975	0.614	0.539
Sex	2.324	1.967	1.181	0.238

Valley Position	29.916	4014.480	0.007	0.994
	Estimate	Standard Error	Z Value	P Value
Intercept	-21.61570	5147.19758	-0.004	0.997
In closeness	-0.01282	4.72078	-0.003	0.998
Age	-0.18586	1.65817	-0.112	0.911
Sex	2.25925	1.51638	1.490	0.136
Valley Position	19.87898	5147.19763	0.004	0.997
	Estimate	Standard Error	Z Value	P Value
Intercept	- 21.8407	5116.0438	- 0.004	0.997
Out closeness	0.8503	2.9873	0.285	0.776
Age	- 0.4325	1.7176	-0.252	0.801
Sex	2.3930	1.6121	1.484	0.138
Valley Position	19.6423	5116.0437	0.004	0.997
	Estimate	Standard Error	Z Value	P Value
Intercept	- 19.6758	4801.2054	- 0.004	0.997

Local

clustering	-18.3875	18.1199	-1.015	0.310
Age	0.7494	1.8770	0.399	0.690
Sex	2.6360	1.8204	1.448	0.148
Valley Position	20.9608	4801.2053	0.004	0.997

	Estimate	Standard Error	Z Value	P Value
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Intercept	-21.20233	21.20233	-0.004	0.997
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Global

clustering	-0.74149	5.17251	-0.143	0.886
Age	-0.05976	1.74217	-0.034	0.973
Sex	2.24825	1.51014	1.489	0.137
Valley Position	19.91800	5156.18033	0.004	0.997

	Estimate	Standard Error	Z Value	P Value
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Intercept	-2.555157	1.843710	-1.386	1.386
Group size	0.007247	0.050212	0.144	0.885
Age	-0.427201	1.102466	-0.387	0.387

Sex	0.375414	1.008788	0.372	0.710
Valley Position	1.783820	1.239582	1.439	0.150

	Estimate	Standard Error	Z Value	P Value
Intercept	-22.14454	5154.10304	-0.004	0.997
Average				
shortest path	0.22585	1.57547	0.143	0.886
Age	-0.05976	1.74217	-0.034	0.973
Sex	2.24825	1.51014	1.489	0.137
Valley Position	19.97493	5154.10170	0.004	0.997

	Estimate	Standard Error	Z Value	P Value
Intercept	-35.561	3857.668	-0.009	0.993
Eigenvector				
centrality	13.364	11.761	1.136	0.256
Age	1.360	2.107	0.645	0.519
Sex	4.109	2.564	1.603	0.109

Valley Position	20.780	3857.644	0.005	0.996
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