

Can yellow-bellied marmots (*Marmota flaviventer*) learn
foraging innovations?

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Abstract

Innovation is widespread in animals and may help them modify their behavior to changes in the environment. A common method to determine whether a species possesses innovative abilities is to present them with a novel foraging problem and then to explain the traits that may predict success. Individuals differ in their innovative propensity and factors that have been linked to such differences include age, sex, rank, and personality. Yellow-bellied marmots (*Marmota flaviventer*) are 3-5 kg ground dwelling squirrels that live in female kin groups at predictable locations, making them an ideal subject of an innovation study. Here we asked whether yellow-bellied marmots can learn foraging innovations and how the factors of age, sex, and sociality affect an individual's innovative propensity. We presented individuals with a two-action puzzle box and began by determining who was able to solve it, and who was not. We used logistic regression to study characteristics associated with success and our preliminary data suggest that the social group to which an individual belongs to was an important predictor of innovative success. To determine whether innovative success illustrated learning, we asked whether marmots' latency to open the box declined over repeated exposures. We also asked whether the diversity of behaviors used to open the box decreased with successive experience. Surprisingly, we found no evidence that marmots learned to open the box either faster or more efficiently with more experience. In order to better study innovation, larger sample sizes will be needed. In addition, future studies will ask whether innovation can be socially transmitted through marmot groups.

Keywords: yellow-bellied marmot, innovation, puzzle box, behavioral flexibility

Introduction

Humans, in part, owe our success as a species to our innovative abilities. While human achievements are highly emphasized, innovative abilities are not restricted to mankind and instances of innovation in the animal kingdom are numerous and taxonomically widespread (Reader, Morand-Ferron & Flynn, 2016). Innovation is defined as “a process that results in new or modified learned behaviour and that introduces novel behavioural variants into a population’s repertoire” (Reader & Laland, 2003, p. 14). For instance, African grey parrots (*Psittacus erithacus*) use elements of human speech (Pepperberg, Gardiner & Luttrell, 1999) and display innovation through the recombination of utterances to which they have been exposed to form novel ones (Pepperberg, 1981). Orangutans (*Pongo abelii*) repeatedly added water to a tube to get access to a floating peanut, using a tool (water) that was not physically visible inside the drinker, suggesting they were forced to think at an abstract level (Mendes, Hanus, & Call, 2007). Based on the prevalence of innovative tendencies in animal taxa, it is not surprising that studies suggest innovation affects many aspects of a species’ ecology and is adaptive in certain situations, including facilitation of subspecies diversification, range expansion, and tolerance of harsh environments (Lefebvre, Ducatez & Audet, 2016; Sol, Stirling, & Lefebvre, 2005; Sol, Lefebvre, & Rodríguez-Teijeiro, 2005; Sol & Lefebvre, 2000).

It is difficult to accurately identify whether a species has the ability to innovate. Two methods are commonly used to assess a population’s innovative propensity. The first is naturalistic observational study, where a group or population is observed and spontaneous innovations are recorded. In a study of Neotropical bird feeding innovations, 352 innovations were identified in 256 species, ranging from feeding on a newly available food source, to baiting

fish with bread by rufescent tiger herons (*Tigrisoma lineatum*), to drinking elephant seal (*Mirounga leonina*) blood (Ruxton & Hansell, 2011). Comparative methods require many long-term field studies and rely heavily on anecdotal reports, making it somewhat difficult to determine with confidence the novelty of a given behavior (Thornton & Sampson, 2012).

The second method involves the presentation of a novel problem, usually a food acquisition test, such as a two-action puzzle box. Captive hyenas (*Crocuta crocuta*) performed substantially better than their wild counterparts in a novel problem solving task, in part because they were less neophobic, making them more likely to explore novel objects (Benson-Amram, Weldele, & Holekamp, 2013). However, eliciting innovations by presenting captive populations or even wild populations in captivity with novel problem solving tasks may not accurately demonstrate a populations' propensity or reflect natural scenarios that would foster innovation in the wild (Ramsey, Bastian & van Schaik, 2007). The presentation of a novel problem to wild populations in their natural habitat may be the most robust approach for assessing a species innovativeness.

Factors that affect individual differences in innovative propensity are largely unknown and beg more study in a wider scope of taxa. Innovative problem-solving-propensity (PSP) in wild great tits was linked to factors such as age, personality and whether the individual was an immigrant or native born (Quinn, Cole, Reed, & Morand-Ferron, 2016). Wild meerkats (*Suricata suricatta*) showed differences in innovative tendencies with age, sex and rank and while juveniles attempted to solve food acquisition tasks more frequently, adult subordinates had the highest rate of innovation (Thornton & Samson, 2012). Reader and Laland (2000) found that female guppies (*Poecilia reticulata*) were more likely to both discover and transmit information about a foraging path. Additionally, they found that innovation in primates was more likely in

subordinates than dominants, providing evidence to support the notion that exclusion from resources creates greater necessity for innovation (Reader & Laland, 2001). While much research is still needed to define factors that affect innovation and how they might interact, it is clear that members of a population will almost certainly have different innovative propensities.

Yellow-bellied marmots (*Marmota flaviventer*) are large ground-dwelling squirrels, found in a variety of alpine and riparian environments (Armitage, 1982). Most marmots are found in female kin groups, composed of a territorial male defending one or more matriline, which are comprised of mothers, daughters and sisters (Armitage, 1996; Blumstein and Armitage, 1999; Armitage & Schwartz, 2000; Armitage and Blumstein, 2002). Marmots are ideally suited for a study of innovation because they live in burrows in predictable locations and because their level of sociality varies, which ultimately permits us to test whether or not degree of sociality influences innovation ability. In addition, there are unpublished observations from our study site, conducted over the past 55 years, that suggest some marmots learn to roll traps to access bait, potentially indicating that new ways to acquire food have already been discovered and have simply not been studied thus far.

Here, we aimed to identify traits and contexts associated with innovation. We used a two-action puzzle box with a food reward where individuals had to either push open a lid or pull open a door, both natural behaviors in a novel context, in order to retrieve the reward. To identify innovators, we scored individuals who solved the problem by opening the puzzle box and then used logistic regression to ask whether age, sex and colony explained any variation in the probability of innovation. To demonstrate innovative learning, we examined the latency to acquire food and variability and diversity of behaviors used to access the food. We expected that both would decrease with experience and such a decrease would be consistent with learning. To

determine if this population of yellow-bellied marmots were neophobic, we examined the latency to touch the puzzle box.

Methods

Subjects

We studied marmots between June and August 2017 at the Rocky Mountain Biological Laboratory, located in the Upper East River Valley in Gothic, Colorado (38° 77'N, 106° 59'W) (Blumstein 2013; Armitage 2014). Individuals were trapped in Tomahawk-live traps placed outside their burrows baited with Purina Omolene horse feed every two weeks to obtain mass estimates, collect biological samples (blood, hair, feces) and to mark or re-mark animals.

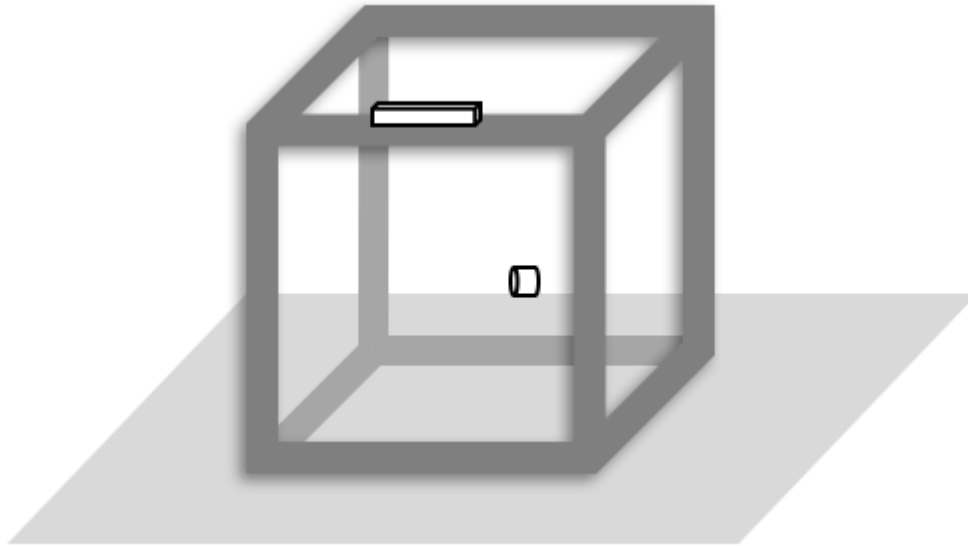
Marmots are permanently marked with numbered ear tags and their dorsal pelage is marked with Nyanzol fur dye for identification from afar (Blumstein 2013). Marmots were observed in the morning and afternoon, during periods of peak activity where we recorded their location and any social interactions. For our experiment we selected subjects that were predictably seen at specific burrow locations. None of the marmots who participated in this study had ever been exposed to a puzzle box.

Puzzle boxes

We constructed eight, 30.84 x 30.84 cm, puzzle boxes. Boxes were designed so that the behaviors required to open them were already in the marmots' repertoires. Each box had a wooden frame made with 5.08 x 5.08 cm wood bars, to which we affixed plexiglass that permitted marmots to see the food reward inside. There were two ways to open the box. First, the lid had a small plexiglass projection that marmots could push up to open. Second, one of the sides was a door with a small metal knob. The door was held closed with two 5.08 cm Velcro strips, while the lid was held closed by gravity. Boxes were secured to a 60.7 x 50.8 cm plywood

platform to prevent marmots from flipping them. Both the wooden frame and plywood were coated with polyurethane to prevent water damage.

Figure 1. *Puzzle box.*



The platform has dimensions of 60.96x50.80 cm. The box is 30.84x30.84 cm, constructed of square wood planks with dimensions of 5.08x5.08 cm.

Procedures

Puzzle boxes, baited with half a cup of Purina Omolene horse feed, were placed outside subjects' burrows during peak hours of activity -- for four hours in the morning, roughly 7:00 – 11:00, and for two hours in the afternoon, 16:00 – 18:00. 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. The cameras captured any animal movement and were set to record two minute videos with a five second recovery time. Boxes were placed opportunistically where animals were observed, as individuals usually switched between several burrow locations during a day.

Quantifying innovation

We calculated the total time each individual was filmed. A trial was said to begin every time an individual stepped onto the puzzle box platform. Successful trials were ones in which an individual opened the puzzle box; unsuccessful trials were ones in which the individual either touched and failed to open or did not touch the box at all. We scored innovation as the first trial in which an individual opened the box. We defined “opening” the box as lifting the lid or opening the door but did not consider acquiring the food reward a requirement, because individuals sometimes did not enter the box fully after opening it, or the bait had already been consumed by that or another individual. In addition, we scored, using JWatcher (Blumstein and Daniel 200x), behaviors marmots employed during trials when opening the box (ethogram in Table 1).

Statistical analysis

To determine if the probability of innovation was influenced by a marmot’s age, sex, level of sociality or the colony it lived in, we tabulated successful and unsuccessful trials and fit logistic regression models to these data. We defined an animals’ level of sociality, as either low, medium, or high, based on the observed number of individuals they interacted with. Age was defined as yearling if they were in their second year of life, or adult if they were anywhere past their second year. Some individuals were observed at more than one colony throughout the study and in these cases colony was determined by the location at which they spent the majority of their time. We fitted six models to these data with different combinations our four independent variables to determine how our binary dependent variable would be affected. To compare our six models, we looked at the Nagelkerke R^2 values and the percentage accuracy in classification (PAC) of trials as successful or unsuccessful.

To determine if innovation involved learning, we focused on individuals that successfully innovated and asked whether the latency to open the box declined over time and whether the diversity of behaviors that were used to open the box decreased over time. We analyzed latencies calculated from the footage captured during successful trials using both a paired t-test (to see if the second latency was systematically shorter than the first latency) and a linear mixed effect model to determine how and if latencies decreased as trial number increased. The linear mixed effect model allowed us compare individuals with differences in the number of trials they had.

To determine if marmots became more efficient in opening boxes with experience, we used information theory and calculated the $H(x)$ using the standard formula:

$$H(x) \equiv \sum_{x \in \mathcal{X}} p(x) \log_2 p(x) = \mathbb{E} \log_2 \left[\frac{1}{p(x)} \right]$$

We then plotted successful trials with $H(x)$ as a function of trial number. We also plotted the first and second successful trials of individuals who solved the box more than once with $H(x)$ as a function of trial number, to determine how $H(x)$ changed from the first to the second success.

To determine if marmots were neophobic, we analyzed their latency to touch the box using a mixed linear effects model to determine whether their latencies decreased over successive trials.

Results

None of the logistic regression models we fitted to explain innovation propensity were significant (Table 2). However, the colony that the marmot lived in explained the most variation in innovation propensity. In addition, while all other models successfully predicted 75% of the innovation propensities, none had a positive predicted value (a measure of the percentage of

cases in which the box was solved that were accurately predicted by the model) except the model with colony, which had a positive predicted value of 14.286% (it predicted that two individuals would solve the puzzle box while we found seven cases where the puzzle box was solved). The results of our paired t-test showed no significant change in latency between the first and second successful trials; $t(18)=0.366$, $p=0.719$. The linear mixed-effects models used to identify independent variables explaining variance in latency to open showed that neither sex, age, (log)trial number or an interaction between age and (log)trial number significantly explained the variance (Table 3 & 4). As an overall trend, we found an increase in the $H(x)$ value as trial number of success increased (Figure 1). For individuals who solved the puzzle box more than once, we found a decrease in their $H(x)$ values from the first to second successful trial, indicating that the frequency of unnecessary behaviors decreased (Figure 2). The linear mixed-effects model used to determine if marmots were neophobic showed that trial number did not explain the variance in time to touch over trials (Table 5).

Due to a hard drive malfunction, a substantial amount of video footage was lost, some of which had not been analyzed for latency information yet. Many trials were known to be missing and therefore accurate information regarding some individuals prior exposure and experience with the puzzle box was unattainable. We were therefore not able to analyze the behaviors and latency of one individual who we know solved the box at least one time.

Discussion

We have shown evidence that yellow-bellied marmots may learn foraging innovations, as well as identifying factors which may affect an individual's innovative propensity. We found that colony, while not statistically significant, explained more variation in the likelihood of innovation than the factors of age, sex or one measure of sociality. It is well established that

marmots are facultatively social (Blumstein, 2013) and thus each colony differs the baseline level of sociality, as well as having a distinct social network. Based on this, it is suggestive that an individuals' position in the social network may affect their innovative propensity. Individuals who are subordinate and therefore potentially less able to compete with others might be more likely to attempt to enhance their fitness through innovation, a theory which has support from studies on other species such as fish (Laland & Reader, 1999) and primates (Reader & Laland, 2001). Other studies contradict this idea, suggesting that high-ranking individuals achieved their high competitive status *by* being innovative (Boogert et al. 2006; Bouchard et al. 2007). Incorporating social network analysis into future studies on innovation in yellow-bellied marmots would potentially reveal which individuals may benefit most from innovative behavior. Additionally, an individual's position in the social network may make them more or less likely to socially learn or transmit an innovation. Social transmission of innovations is a direction this study will likely take in the future. A larger sample size will conceivably increase our ability to find trends regarding innovative propensity and the factors that may influence, as well as allow us to analyze it in the context of social networks. Our findings regarding the decrease in frequency of random, unnecessary behaviors directed towards the puzzle box over successive trials is indicative of learning. Once again, our small sample size did not allow us to analyze the decrease over trials in any significant way.

We believe that the continuation of this study in future years, armed with the knowledge that colony likely effects innovation, the preliminary results regarding learning and a larger sample size, will certainly lead to stronger verdict regarding variation in innovative propensity in the yellow-bellied marmot

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Table 1. Ethogram of behaviors interacting with puzzle boxes

Behavior	Operant Definition
Stand look	Quadrupedally standing with head up
Stand Forage	Individual is foraging on bait inside the puzzle box
Rear look	Bipedally standing, head up off ground
Stand Forage near	Individual is foraging near puzzle box but not from bait
Stand Forage at	Individual is foraging on the bait provided outside the puzzle box
Walk	Individual moves around box while looking at it (i.e. clearly engaged with the box and not moving past it as an obstacle). Individual may stop briefly at each side and attempt to get into box.
Nose nudge	Individual uses nose to push or nudge at box
Chew plywood	Individual chews plywood base
Paw	Quadrupedal individual places paw on box or attempts to scratch at box
Contact	First touch to puzzle box during each continuous bout of interaction
Rear paw	Bipedally standing with paws on box
Bite	Take piece in teeth and move
Sit on top	Individual sits on top of the box
Chew (part)	Individual chews on piece of puzzle box, (i.e. hinge, lid, plywood, etc.)
In/Out of sight	Individual momentarily not visible

Table 2. Summary of logistic regression analyses for variables predicting likelihood to solve the puzzle box

<i>Model</i>	<i>Independent Variable(s)</i>	<i>R² (Nagelkerke)</i>	<i>PAC</i>	<i>Positive Predicted Value</i>
<i>Model 1</i>	Age	0.000	75.0	0.00
<i>Model 2</i>	Sex	0.011	75.0	0.00
<i>Model 3</i>	Sociality	0.064	75.0	0.00
<i>Model 4</i>	Sex*Sociality	0.066	75.0	0.00
<i>Model 5</i>	Sex*Age* Sociality	0.068	75.0	0.00
<i>Model 6</i>	Colony	0.207	75.0	14.286

Table 3. Results of linear mixed-effects model to identify variables predicting change in latency to open with fixed effects of sex and trial and random effect of UID

<i>Fixed-effects</i>	<i>Estimate</i>	<i>Std. error</i>	<i>df</i>	<i>t-value</i>	<i>p-value</i>
Intercept	2.928	0.567	3.331	5.163	0.011
Sex(M)	-0.623	0.407	2.994	-1.534	0.223
(log)Trial	0.441	0.187	3.394	2.351	0.090

Table 4. Results of linear mixed-effects model to identify variables predicting change in latency to open with fixed effects of age, trial and interaction between age and trial, and random effect of UID

<i>Fixed-effects</i>	<i>Estimate</i>	<i>Std. error</i>	<i>df</i>	<i>t-value</i>	<i>p-value</i>
Intercept	1.821	0.392	70.640	4.649	1.51e-05*
Age(Y)	0.988	0.583	91.060	1.694	0.094
(log)Trial	0.0434	0.181	31.790	0.813	0.813
Age(Y):(log)Trial	-0.455	0.249	52.190	-1.827	0.073

Table 5. Results of linear mixed-effects model to identify how trial number predicted change in latency to touch with random effect of UID

<i>Fixed-effects</i>	<i>Estimate</i>	<i>Std. error</i>	<i>df</i>	<i>t-value</i>	<i>p-value</i>
Intercept	2.252	0.278	101.960	8.095	1.27e-12
(Log)Trial	-0.170	0.115	46.030	-1.482	0.145

Figure 1. The relationship between trial number of first success and H(x) value

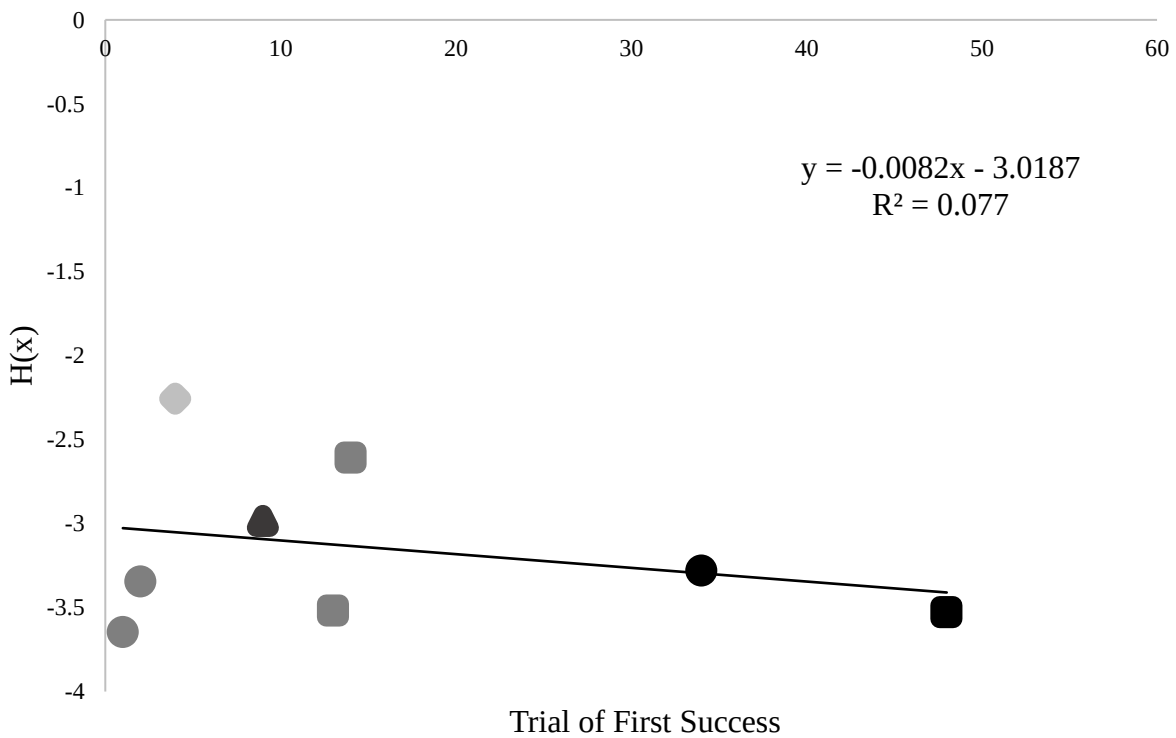


Figure 1. The relationship between the trial number of all successful trials and the H(x) value of each trial. Each individual who solved the puzzle box is represented by a unique marker. Two individuals had more than one successful trial, indicated by identical markers.

Figure 2. Relationship between the trial number of an individual's first two successes and $H(x)$ value

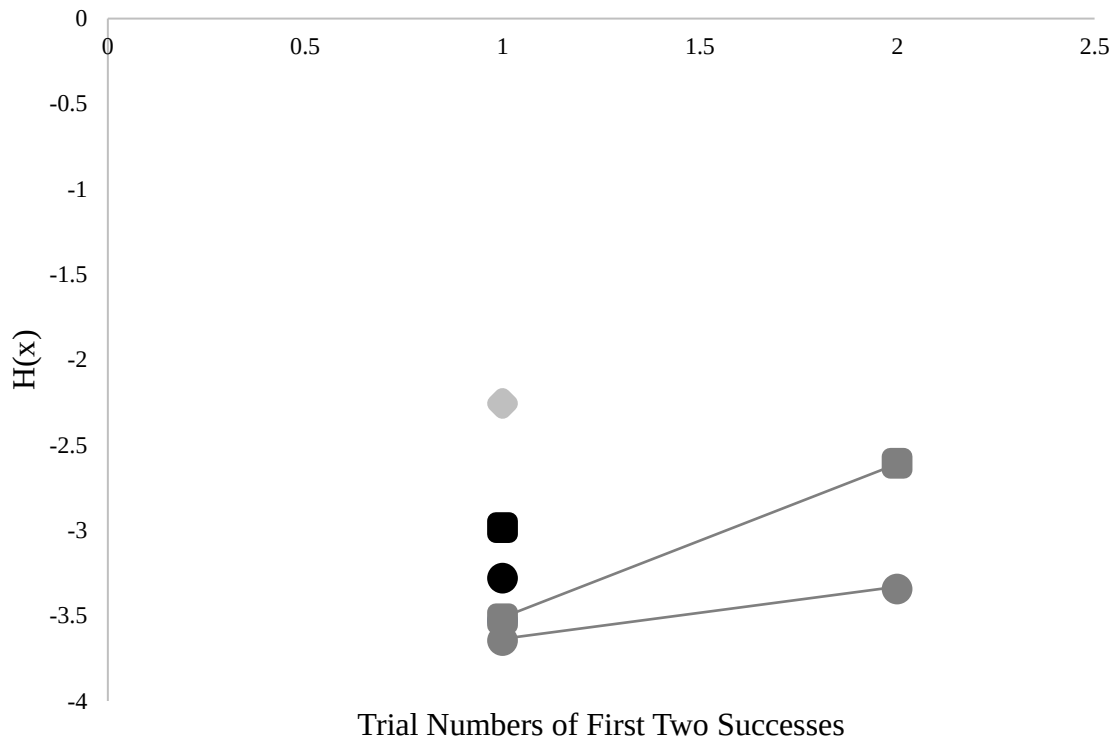


Figure 2. The relationship between the trial number an individuals first two successes and $H(x)$ value. Each individual is represented by a unique marker. In three out of the five individuals who solved the puzzle box more than once, both successes occurred in the same trial and thus the $H(x)$ value for both successes was the same, indicated by just one point on the graph.