

Social transmission of a novel foraging trait in yellow-bellied marmots

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Abstract

Social transmission of novel behaviors can be an adaptive technique to rapidly and flexibly change responses to the surrounding environment. Although the dynamics of social transmission have been studied in highly social birds, primates, otters, and bats, we lack a solid understanding of the dynamics of social transmission in less social species, for which weaker social relationships may be less conducive for social transmission. To explore this knowledge gap, we tested a facultatively social species, yellow-bellied marmots (*Marmota flaviventer*), for presence of social transmission in a novel foraging task. We introduced a novel foraging behavior into a wild population with a 2-action puzzle box and studied the diffusion of this trait through the colonies' social network with network-based diffusion analysis (NBDA). In two out of four successful diffusion we found that a social transmission model fit better than an asocial model. From this we infer that social transmission is conditionally used by certain marmot groups and may thus be a cognitive ability used by wild groups of less social species.

Introduction

Many animals live in social groups despite possible costs of increased visibility to predators (Ruxton and Johnsen 2016), competition for resources (Wiklund and Andersson 1994), and disease transmission (Brown and Brown 2004), a fact that has perplexed evolutionary biologists for decades (Alexander 1974). In addition to other recognized benefits of sociality, including the dilution effect (Hamilton 1971), reduced vigilance (Pulliam 1973), mobbing behaviors (Smith and Graves 1978; Gross and MacMillan 1981), reciprocity of resource sharing (Carter and Wilkinson 2013), and cooperative hunting (Blundell et al. 2002), social groups can act as “information centers,” where conspecifics share knowledge of novel predators (Griffin

2004) and ideal foraging sites (Ward and Zahavi 1973). When individuals are uncertain of their environment, have been unsuccessful in completing a task, or when they are surrounded by successful individuals and kin, sharing information provides individuals with greater access to resources and behaviors than they would have had alone (Laland 2004).

Innovation and social learning are important cognitive abilities for animals living in complex and variable environments (Maynard Smith 1989; Laland 1992; Sayol et al. 2016). Naïve individuals may innovate and produce a novel behavioral trait asocially by trial-and-error learning; a potentially time-consuming process, exposing them to predators, and reducing their time available to mate and forage. However, naïve individuals may also reduce the costs by observing experienced individuals and copying their actions, using a variety of social learning strategies (Barnard and Sibly 1981; Galef and Laland 2005). The process of scrounging new innovations constitutes social transmission, which can efficiently diffuse novel traits through a population by social transmission (Hoppitt and Laland 2013), leading to unique diets (Kawaguchi et al. 2006), foraging tactics (Safi and Kerth 2007; Hobaiter et al. 2014), and courtship behaviors (Freeberg 2000). Therefore, innovation and social transmission can create culturally distinct “traditions” in different populations of the same species, conserved across generations, and allow populations to adapt to novel features in a changing environment.

Diffusion and social transmission analysis can illuminate the dynamics and detailed paths through which knowledge or abilities are shared. By comparing behavioral diffusion to social structure, we can identify who learns from whom, who demonstrates to whom, and under what conditions social learning may occur. Previous studies have explored the patterns of behavioral social transmission in highly social species such as otters (*Lutrogale perspicillata* and *Aonyx cinereus*; Ladds, Hoppitt, & Boogert, 2017), chimpanzees (*Pan troglodytes*; Hobaiter et al.,

2014), meerkats (*Suricata suricatta*; Thornton & Malapert, 2009), bats (*Trachops cirrhosus*; Page & Ryan, 2006), magpie jays (*Calocitta formosa*; Langen, 1996), and pigeons (*Columba livia*; Giraldeau & Lefebvre, 1987). Overall, social learning studies assume that more connected individuals are more likely to learn a novel behavior from other individuals than socially isolated individuals, since they have a greater opportunity to observe and learn from others' behaviors (Hoppitt and Laland 2013). However, social transmission can depend on other characteristics such as individual age (Thornton and Malapert 2009), sex (Choleris and Kavaliers 1999), kinship (Lamon et al. 2017), group foraging dynamics (Ladds et al. 2017), the type of interaction (Coussi-Korbel and Frigaszy 1995), and the difficulty of the novel behavior (Laland 2004; Ladds et al. 2017).

The effects of the weaker connections in less social species is not as studied as in highly social species (Künstner 2010). Therefore, we studied the presence of social learning in facultatively social yellow-bellied marmots (*Marmota flaviventer*). Marmots live in different size groups (Blumstein 2013; Armitage 2014) and social behavior varies most noticeably between age classes: as marmots age they become less connected with others and females engage in more agonistic interactions (Wey and Blumstein 2010). Social behavior also varies between sexes: males obligately disperse, while females often remain in socially tight-knit matriline (Armitage 2014). Thus, females' social cohesiveness in comparison to males should allow females to participate in social transmission more than males. These sexually dimorphic social behaviors can create sex-based effects on social transmission. This is demonstrated by female-dominated tool-use diffusions in chimpanzees (Lonsdorf 2005) and bottle-nosed dolphins (*Tursiops sp.*) (Krützen et al. 2005). At the same time, maternal care and maternal demonstration has been linked to greater social learning in offspring (Lévy et al. 2003; Rymer et al. 2008; Lindeyer et al.

2013).

The presence of social learning is likely to be context specific, varying with the type of activity and the social interactions involved. For example, a cooperatively foraging otter species showed evidence for social transmission of a novel foraging innovation, while a solitarily foraging otter species showed asocial learning (Ladds et al. 2017), suggesting that social species may be relatively primed for social learning. Although marmots do not cooperatively forage, like carnivorous otters, they do have selective preferences for foraging areas (Carey 1985) and often forage near kin and other members of their social group (Frase and Armitage 1984; Barash 1989). Consequently, an individual may benefit from local enhancement (Thorpe 1958; Heyes 1994) and use social cues to determine a suitable location to forage, but the individual may not use social clues to actively acquire the food and feed, once the patch is identified—particularly if the food is vegetation that does not require much manipulation to consume. Therefore, social learning may be important to identify foraging patches, but not for behaviors used in food manipulation.

In testing social transmission and exploring the contexts and factors that influence it, Network Based Diffusion Analysis (NBDA) is commonly used. NBDA quantifies the effects of social learning within a study population by comparing the observed pattern of innovation with a model of the expected pattern given purely asocial learning and a model of the expected pattern given asocial learning enhanced by social transmission (Franz and Nunn 2009; Hoppitt 2017). Thus, NBDA will permit us to infer the extent to which social relationships influence observed diffusion patterns, and whether diffusion patterns are affected by age and sex.

Given that the marmots' social variation is largely explained by age and sex (Armitage 2014), we expect that social transmission will be stronger among younger individuals (younger

marmots are more affiliatively social than adults; Wey and Blumstein 2010), specifically between pups and mothers by vertical transmission (social transmission often occurs between females in a matriline; Krützen et al. 2005; Lonsdorf 2005), but weaker among older individuals (marmots become more socially isolated with age; Wey and Blumstein 2010; Armitage 2014). We also predict that females may depend more on social transmission than males (females are more socially connected than males in a colony; Armitage 2014) and may act as key demonstrators.

Methods

Subjects and Study Site

In June and July in 2018 and 2019, we studied wild populations of yellow-bellied marmots in and around the Rocky Mountain Biological Laboratory in Gothic, Colorado, USA. All marmots were live-trapped and individually marked with ear tags for permanent identification, and their dorsal pelage was seasonally marked with a unique pictograph with nontoxic black fur dye to permit identification from afar (Blumstein 2013). We focused on seven marmot colonies which in these years were comprised of six marmot social groups (Fig. 1). The North Picnic, Picnic, and Marmot Meadow colonies live in fully-natural talus/meadow burrows. Individuals of the Gothic Town colony live in burrows among the cabins and buildings of the Gothic townsite. The Bench and River Mound colonies are socially connected and are split between urban burrows beneath cabins and natural meadow and rock burrows. River Annex is geographically isolated from Bench and River Mound and consists of a single rock burrow.

Social Observations

Trained observers quantified social interactions during peak hours of marmot activity, from 07:00 to 11:00 and 16:00 to 18:00 with 10x40 binoculars and 15-45x spotting scopes (Blumstein et al. 2009; Blumstein 2013). Social interactions were categorized as affiliative—which included play, greet, allogroom, cheek rub, sit within one meter, sit with body contact, and forage together, or as agonistic—which included aggression, simple displacement, and proximity displacement. Observed affiliative and agonistic interactions were used to create separate affiliative and agonistic social networks for each marmot social group each year.

The Gothic Town 2019 social network was incomplete at the time of analysis, so we used the social network for Gothic Town 2018, including pups (2019 yearlings), for Gothic Town 2019 diffusion analysis. 2019 analyses will ultimately have to be recalculated with 2019 social network data.

Puzzle Box Experiment

To study putative diffusion, we deployed a novel puzzle box to each colony and filmed all marmot interactions with it. The 30.84 x 30.84 x 30.84 cm puzzle boxes were made of clear plexiglass attached to a wooden frame of 5.08 cm wooden strips. A plexiglass tab was attached to the hinged lid and a metal knob was attached to the hinged door. Both the lid and the door were held close with Velcro strips. Each puzzle box was bolted to a 60.7 x 50.8 cm plywood board (Fig. 2). Each day between 3 June and 18 July 2018 and between 16 June and 23 July 2019, from 07:00 to 11:00, the puzzle-box-plywood setup was placed between two motion-sensing camera traps (Browning Strike Force HD or Browning Spec Ops FHD cameras; Browning Trail Cameras) strapped to PVC stakes. One cup of horse feed bait (Omolene 200; Purina Animal Nutrition LLC) was placed inside each puzzle box and one pinch of bait on the surrounding plywood base at the beginning of each sampling period. Throughout the sampling

period, the marmots were able to freely access the plywood, interact with the surrounding bait, interact with the box, and interact with the bait inside, and were able to freely leave at any time. We scored an innovation as successful if an individual opened the box and accessed the bait. In this analysis, we excluded colonies containing fewer than three individuals and diffusions with one or no innovation event as they lacked the power to detect social transmission with NBDA.

Statistical Analysis

To determine order of innovation within a colony, we extracted information on individual innovations: the date and time each individual innovated and the individual's innovation order in its group. The times and order of innovations were separately compiled into a time-ordered and an order of acquisition list.

We used NBDA to assess the diffusion data for each colony, given the established social network. Diffusion can be modeled by the simplified order of the first instance of each individual's innovation (order of acquisition diffusion analysis, OADA; Hoppitt et al. 2010). OADA models consist of a pre-determined asocial factor of learning multiplied by a social transmission factor, incorporating the probability of transmission between a naïve and an informed individual, assumed from their social connectivity. OADA then compares the social transmission model with the predicted model given purely asocial innovation (the model without the social transmission factor). For colonies with successful evidence for social transmission, we proceeded to test models incorporating sex and age, to understand their influence on any social transmission. Sex and age were incorporated into OADA by a multiplicative model, where the characteristics factor a constant ratio with increased sociality, determined by fitting multiple randomly generated models with varying effect estimates (Hoppitt and Laland 2013). The model with the lowest AICc output provides a better fit, and the fit will be considered significantly different if the difference in AICc > 2 .

To assess evidence of vertical transmission in colonies with evidence of social transmission, we isolated the social networks of individual family groups (mother, father, and yearling offspring). We used OADA to assess whether any social transmission still exists in the isolated family group. If social transmission persists, we tested models with the effect of age: if social transmission favors young individuals, that would imply the offspring learn from their parents, and if social transmission favors adults, that would imply the parents learn from their offspring.

We used the R script model for NBDA Version 1.2.13 available at <http://lalandlab.st-andrews.ac.uk/freeware.html>.

Results

Diffusions and Evidence for Social Transmission

Two successful diffusions occurred in 2018 at Gothic Town and Marmot Meadow 2018, and one successful diffusion for each of the lid and door-entry methods occurred in 2019 at Gothic Town. Both Marmot Meadow and Gothic Town in 2018 had a total of two individuals innovate. Gothic Town in 2019 had a total of five individuals innovate for each of the lid and door-entry methods.

Gothic Town 2018

In the Gothic Town 2018 diffusion (Fig. 3a), two of nine individuals who interacted with the box successfully innovated, and the model with social transmission provided a better fit ($AICc = 31.621$) than the model without social transmission ($AICc = 40.994$; $p < 0.001$). Social transmission better described the data when adding the effect of age ($AICc = 36.323$; $p < 0.001$),

but with a nonsignificant age estimate (-0.509; 0.585). When the matriline of individual 6612_6640 was isolated, two of three individuals successfully innovated, and neither the model with social transmission (AICc = 22.024) or the model without social transmission (AICc = 22.020; $p = 0.083$) provided a better fit. Both innovators were female, so the effect of sex could not be analyzed.

Marmot Meadow 2018

In the Marmot Meadow 2019 diffusion (Fig. 3b), two of twelve individuals who interacted with the box successfully innovated, and the model without social transmission provided a better fit (AICc = 42.123) than the model with social transmission (AICc = 45.123; $p = 1$).

Gothic Town 2019 Lid-Entry

In the Gothic Town 2019 lid-entry diffusion (Fig. 3c), five of seventeen individuals who interacted with the box successfully innovated, and neither the model with social transmission (AICc = 142.85) or the model without social transmission (AICc = 142.59; $p = 0.153$) provided a better fit.

Gothic Town 2019 Door-Entry

In the Gothic Town 2019 door-entry diffusion (Fig. 3d), five of seventeen individuals who interacted with the box successfully innovated, and neither the model with social transmission (AICc = 141.88) or the model without social transmission (AICc = 142.59; $p = 0.082$) provided a better fit.

Marmot Meadow 2018 Plywood-Chewing

After observing Marmot Meadow 2018 individuals spontaneously chewing on the puzzle box plywood, we performed an OADA on the diffusion of plywood-chewing. With six of twelve

individuals chewing on the plywood (Fig. 3e), the model with social transmission provided a better fit ($AICc = 114.84$) than the model without social transmission ($AICc = 118.65$; $p = 0.014$). Social transmission better described the data when adding both the effects of sex ($AICc = 103.13$; $p < 0.001$) and age ($AICc = 116.43$; $p = 0.009$), with a sex estimate of 2.44 ($p < 0.001$) and a nonsignificant age estimate (0.610; $p = 0.249$). In the isolated matriline of individual 6385_6342, six of nine individuals successfully innovated, and the model without social transmission provided a better fit ($AICc = 103.51$) than the model with social transmission ($AICc = 105.50$; $p = 0.606$).

Discussion

We found that an OADA social transmission model described the behavioral diffusion in Gothic Town in 2018 and the plywood-chewing diffusion in Marmot Meadow in 2018 extremely well and described the door-entry diffusion in Gothic Town in 2019 poorly, while the asocial model described the lid-entry diffusion in Gothic Town in 2019 poorly and described the diffusion in Marmot Meadow in 2018 extremely well. From this we can infer that it is, indeed, possible for marmots to socially learn a foraging task, but social learning is not ubiquitous, occurring only at certain sites and with certain activities. Despite a successful puzzle box transmission, the Gothic Town 2018 diffusion did not show any significant effect of sex or age. Thus, we do not have strong support for the expected diffusion among females and younger animals. Similarly, there was no strong difference between the lid and door diffusions in Gothic Town in 2019, contrasting our original predictions that the difficult door-entry task would show more evidence of social transmission. Although the innovations seem localized within family groups within Gothic Town in 2018 and Marmot Meadow's plywood chewing in 2018, when we

isolated the family networks for the originally socially transmitted diffusions, we no longer could conclude that they were socially transmitted. This may suggest that the diffusions did not occur by within-family transmission, or that excluding network interactions decreased the power of our models. Overall, none of our tested factors had any effect on the social transmission within our successful diffusions.

Despite the lack of complex effects of social transmission, we conclude that social learning is not restricted to obligately social species. Even though the wild marmots do not rely on social interactions for foraging, we found simple social transmission in our foraging task. However, a task the marmots invented themselves, chewing plywood, also was socially transmitted and in a more complex way, with more individuals innovating and a strong effect of sex. From this we can infer that social learning is not an umbrella mechanism, but rather used with select tasks. Perhaps a chemical present in plywood glue is sufficiently desirable that individuals depend on others to acquire it. Chewing plywood may also help categorize marmots' social transmission as local enhancement, where individuals are attracted to the plywood and puzzle box simply by others being present, instead of a transmission of the actual manipulating task.

Our results suggest that social learning is conditional in marmots. A *copy-if-dissatisfied* strategy claims that individuals will observe and learn from others more when they are dissatisfied with their own established behavioral trait. A *copy-successful-individuals* suggests that individuals will adopt behaviors only from successful individuals. Meanwhile a *copy-when-established-behavior-is-unproductive* claims that individuals will be willing to observe others after their trial-and-error efforts are unsuccessful (Laland 2004). Any of these strategies, or any combination, could describe the variance in social learning use in marmots, but further research

of which circumstances and which environmental cues support social learning is still needed to clarify the dynamics of this and other systems.

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Fig. 1 A map of the marmot colonies in the East River Valley. One puzzle box was placed at North Picnic, two at Picnic, two at Marmot Meadow in 2018, one at Marmot Meadow in 2019, three at Gothic Town, one at Bench, one at River Mound, and one at River Annex.

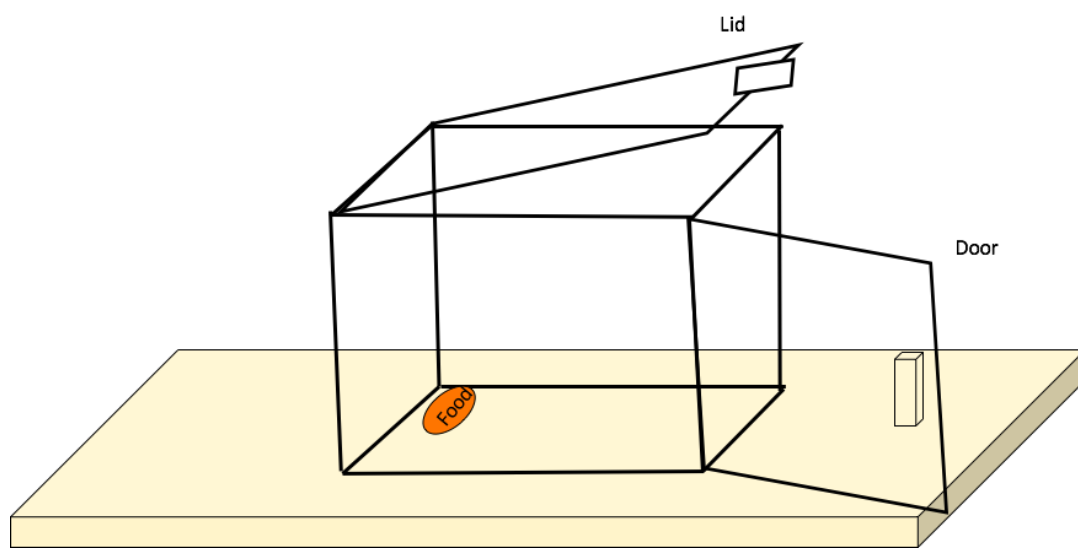


Fig. 2 Schematic of the two-action puzzle box.

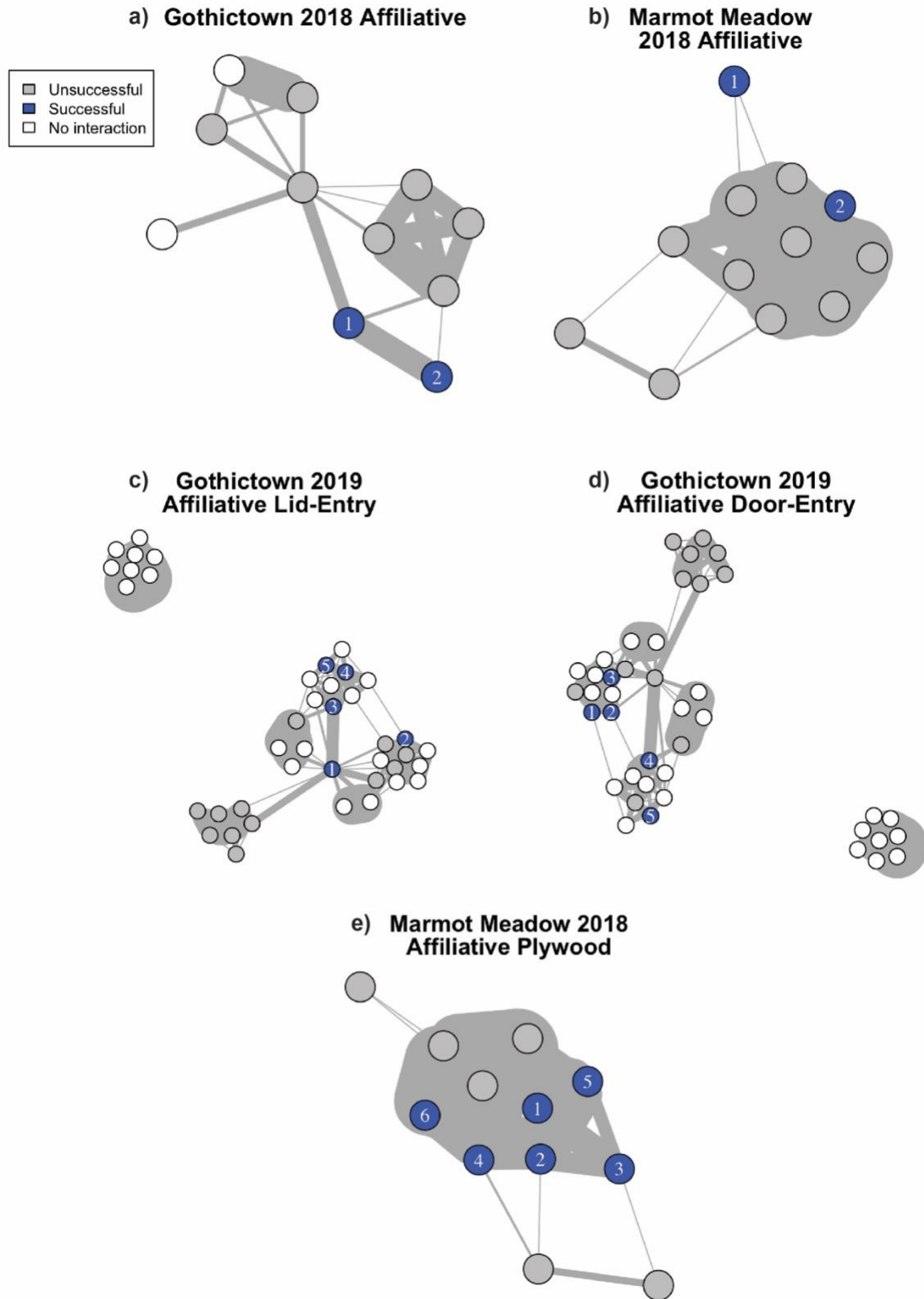


Fig. 3 Puzzle box diffusions mapped onto social networks for each colony. Node colors signify an individual's interaction with the puzzle box. Node numbers represent the order in which the individuals innovated.