



Producer–scrounger relationships in yellow-bellied marmots

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When social animals forage together, they may engage in frequency-dependent strategies either as producers, those who acquire food with their own energy, or as scroungers, those who feed on what the producers discover. An individual's choice of strategy may depend on the frequency of strategies within the group, or it may depend on the individual's own traits. Most of our understanding of producer–scrounger relationships comes from highly social species, but we may gain different insights by studying less social species. We used novel puzzle box experiments to study social foraging relationships and identify the traits associated with strategy choice in facultatively social yellow-bellied marmots, *Marmota flaviventris*. We found that marmots had consistent strategies as either producers or scroungers. Furthermore, several individuals specialized as scroungers, following the producers to the puzzle box before other scroungers. However, their roles were only associated with sex (males were more likely to produce), and not with age, boldness or dominance rank. Marmots' lack of trait-regulated foraging roles may be associated with their relatively abundant and not-entirely defensible food, or may emerge from their lack of obligate social structure. We discuss how multiple factors may explain variation in social foraging behaviour.

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Individuals acquire a variety of benefits from aggregating with others (Hamilton, 1971; Smith & Graves, 1978), including the benefits of social foraging. Animals forage in groups to secure food resources or to ensure protection from predators (Giraldeau & Caraco, 2000; Pulliam, 1973). When animals engage in group foraging, individuals increase their feeding opportunities in a way that reduces initial energetic costs but introduces the costs of sharing and competing for resources. Because of these contrasting costs and benefits, individuals often specialize in different social foraging strategies to maximize their personal fitness (Giraldeau & Caraco, 2000; Maynard Smith, 1979).

For social foragers, individuals may adopt a specific role as a producer or as a scrounger. Producers find, acquire or hunt food for themselves and, therefore, suffer energetic costs. Scroungers steal food from others and, by doing so, save time and energy that would otherwise be devoted to finding and acquiring their own food. However, there are costs to being a scrounger, including reduced access to food and a chance of being the recipient of aggression from the producer (Giraldeau & Caraco, 2000). The benefits of each

strategy depend on the prevalence of the different strategies in the present group assemblage (Kim, Toyokawa, & Kameda, 2019). When there is a high ratio of producers in a group, scroungers have a greater cheater's benefit (Carter & Wilkinson, 2013; Scheel & Packer, 1991) in which they may gain a reward with little cost. However, when there is a high ratio of scroungers in a group, there are fewer producers from which they can scrounge, and the reward for scrounging is split between more individuals. Thus, the optimal social foraging strategy is frequency dependent.

An individual's traits may influence their choice in being a producer or a scrounger. Recent insights show that larger (coho salmon, *Oncorhynchus kisutch*: Phillips et al., 2018), more dominant (transvolcanic jay, *Aphelocoma ultramarina*: McCormack, Jablonski, & Brown, 2007; chacma baboon, *Papio ursinus*: King, Isaac, & Cowlshaw, 2009), more vigilant (Egyptian fruit bats, *Rousettus aegyptiacus*: Harten et al., 2018) individuals and more exploratory females (Eurasian tree sparrow, *Passer montanus*: Fülöp et al., 2019) tend to scrounge more, and that smaller individuals (coho salmon: Phillips et al., 2018) and juveniles (great tit, *Parus major*: Aplin & Morand-Ferron, 2017) tend to be producers. These traits suggest that scroungers are often individuals who can socially displace others or who would otherwise be unwilling to expose themselves to predation risk by producing at an unknown food source. Some individuals change strategies to satisfy changing energetic

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requirements, such as changing energetic costs as a function of reproductive status (Harten & Dor, 2019; Harten et al., 2018; King et al., 2009). However, when traits are static, such as for sex or personality, individuals typically do not change strategies (rock dove, *Columba livia*: Giraldeau & Lefebvre, 1987; Egyptian fruit bats: Harten et al., 2018). Thus, an individual's traits influence their decision to produce or scrounge, and, because foraging strategies are frequency dependent, these traits may also influence an entire group's foraging dynamics.

Most previous studies have primarily focused on social foraging in highly social species, but this limits our understanding of social foraging to contexts where there are only strong, dependable social relationships. For example, Egyptian fruit bats live within large roosts (Kwiecinski & Griffiths, 1999), yet form smaller, consistent social foraging relationships with preferred group members. Within these established social foraging relationships, males tend to produce, sometimes in exchange for sex (Harten & Dor, 2019), while females can flexibly adjust their foraging role to accommodate the energetic demands of lactation (Harten et al., 2018). In this way, social foraging roles among highly social animals are both determined and stabilized by their social relationships.

In contrast, the reduced social relationships among less social species may hinder or alter any emergent social foraging relationships, yet this possibility has remained unexplored. Less social species are less dependent on social interactions overall, making them less cohesive, and they sometimes even face costs of living with others (Blumstein, Williams, Lim, Kroeger, & Martin, 2018; Thompson & Cords, 2018; Wey & Blumstein, 2012). A lack of social structure may cause foraging strategies to be unstable and flexible, or it may support stable foraging strategies that are determined by traits, similar to highly social species. Egyptian vultures, *Neophron percnopterus majorensis*, are a less social species that aggregate only around feeding sites and otherwise live and forage in solitary breeding pairs. From a study on vultures' social foraging behaviour, it is evident that they engage in dominance and aggressive displacement to facilitate and limit access to carrion, reminiscent of scrounging by dominants from subordinates (van Overveld et al., 2020).

While the presence of any producer–scrounger roles or relationships has yet to be formally investigated in less social species, we can envision plausible scenarios in both less social and highly social species. For vultures, producers might discover, land at and feed from exposed carrion, and scroungers might follow familiar producers to feeding sites. A scrounging vulture could also use its previously established dominance rank to displace a producer from the carrion upon which they were actively feeding. Although these less social individuals may still have consistent foraging roles, their roles may be much more flexible than those held by highly social species. But scrounging may not be restricted to species that feed on defensible, limited resources. Thus, a grazing herbivore may engage in social foraging through local enhancement, where a producer attracts scrounging individuals to a patch that can be shared with others (Giraldeau & Caraco, 2000). Highly social animals, such as Egyptian fruit bats or scavenging spotted hyaenas, *Crocuta crocuta*, have well-developed foraging relationships in their close-knit groups. In this way, producer–scrounger roles may be enforced by an individual's social relationships with others and lead to a breakdown of roles in less social species or, otherwise take a more flexible form. However, less social species are rarely studied in this context and their foraging roles have yet to be clarified.

To test whether social foraging roles exist in a less social, free-grazing species, and in what way individual traits influence foraging roles, we investigated the social foraging strategies of a wild population of yellow-bellied marmots, *Marmota flaviventris*. Marmots are facultatively social ground squirrels where individuals

may live in variable-sized groups. Their groups consist of females and their descendants (Armitage, 2014) whose social relationships are structured by age and kinship (Wey & Blumstein, 2010). Marmots are generalist herbivores, share foraging areas with related kin (Fraser & Armitage, 1984) and may forage near others, but nothing is known about how their foraging behaviour translates to formal social foraging roles. Additionally, only a few studies have investigated producer–scrounger relationships in the wild (Aplin & Morand-Ferron, 2017; King et al., 2009; McCormack et al., 2007; Morand-Ferron, Giraldeau, & Lefebvre, 2007). Studying wild populations of marmots allows us to best understand strategies in relation to the ecological context in which these strategies evolved.

We studied the relationships of marmot producer–scrounger foraging using novel puzzle boxes that required individuals to perform an extractive foraging task. We first tested whether individuals consistently exhibited a single social foraging strategy (producer or scrounger) when interacting with the box over a 2-week period. We then asked whether scroungers engaged in social foraging by learning to follow producers rather than performing opportunistic scrounging. To do this, we observed whether certain individuals were consistently first to scrounge at the box each day and whether individuals scrounged shortly after the producer opened the box. We then asked whether individual or social traits (sex, age, boldness, dominance) were associated with an individual's role as a producer or scrounger. Based on findings from other species (Aplin & Morand-Ferron, 2017; Fülöp et al., 2019; Harten & Dor, 2019; Harten et al., 2018; King et al., 2009; McCormack et al., 2007; Phillips et al., 2018; van Overveld et al., 2020), we predicted that marmots would have weaker and possibly inconsistent producer–scrounger relationships. Even so, if they had consistent strategies, we predicted that certain individual traits would influence strategy choice: we predicted that yearlings and bold individuals would produce, while females and dominant individuals would be scroungers.

METHODS

Field Methods

In June and July of 2019, we studied wild populations of yellow-bellied marmots in and around the Rocky Mountain Biological Laboratory (38°57'29"N, 106°59'06"W, elevation ~2890 m) in Gunnison County, Colorado, U.S.A. All marmots were live-trapped and individually marked with eartags for permanent unique identification (UIDs), and their dorsal pelage was seasonally marked with a unique pictograph with nontoxic black Nyanzol-D fur dye (Albanil Dyestuffs, New Brunswick, NJ, U.S.A.) to permit identification from video footage (Blumstein, 2013). We observed the social interactions across 11 colonies during peak hours (0700–1100 hours and 1600–1800 hours) using 10 × 40 binoculars and 15–45× spotting scopes (Blumstein, 2013). During observations we recorded all visible social interactions following an established ethogram (Blumstein, Wey, & Tang, 2009) and recorded which individual initiated the interaction, which individual 'won' the interaction (the loser moved away) and whether the interaction was agonistic or affiliative.

Puzzle Box Experiments

We deployed a series of two-action puzzle boxes, representing a novel extractive foraging task originally created to test patterns of innovation, to six of the 11 studied colony groups and filmed all marmot interactions with the box (Williams, Wu, & Blumstein, 2020). Instead of mimicking a natural foraging task, we created an entirely novel task to observe social foraging relationships

unfold initially following a novel innovation. Given that some colonies consisted of multiple smaller social groups (often linked by only one or two crossing individuals), a puzzle box was deployed for each social group. Following this, we observed nine puzzle boxes presented to nine social groups within the six colonies: three boxes were placed at Gothic Town (one for each noninteracting social group), two boxes were placed at Picnic (due to large group size, but both were within the same social group), and one puzzle box was placed at each of the colonies, Bench, Marmot Meadow, Boulder and North Picnic. The $30.84 \times 30.84 \times 30.84$ cm puzzle boxes were made of clear Plexiglas attached to a wooden frame of 5.08 cm wooden strips. A Plexiglas 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 closed with Velcro strips. Each puzzle box was bolted to a 60.7×50.8 cm plywood board (Fig. 1). Each day between 16 June and 22 July 2019, from 0700 hours to 1100 hours, the puzzle-box set-up was placed between two motion-sensing camera traps (Browning Strike Force HD or Browning Spec Ops FHD cameras; Browning Trail Cameras, Morgan, UT, U.S.A.) strapped to PVC stakes. One cup of horse feed bait (Omolene 200; Purina Animal Nutrition LLC, Gray Summit, MO, U.S.A.) was placed inside each puzzle box and one pinch of bait was placed 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, interact with the bait inside and freely leave at any time. The camera traps recorded only the puzzle box, the plywood and the immediately adjacent groundcover and did not allow us to directly observe individuals observing each other. Therefore, we estimated the individuals' interaction with the box and with each other by their pattern of arriving at the box.

Video Data

We measured individual interactions with the puzzle box through trials, which were initiated when the focal individual stepped on the puzzle box's plywood platform and were terminated when the individual completely stepped off the plywood and no longer had physical contact with the puzzle box for more than 5 s. If a trial extended beyond one recorded video, we synced the original video with the subsequent video from the same camera or the concurrent video from the opposite camera and measured the continuous trial time. If there was a time lapse of over 5 s, we considered the trial terminated with an unknown trial end-time. Likewise, if a video began with an individual already on the plywood, we assigned an unknown trial start time. An individual was considered a producer if it opened the lid or door itself and

accessed the bait. An individual was considered a scrounger if it entered an already-opened box and accessed the bait. It was possible for a producer to open the box and have the lid return to a closed position, allowing multiple individuals the opportunity to produce within a day. However, if the lid or door remained open, the box was not closed by experimenters, and additional bait was not added within a day's experimental period. To account for a producer scrounging from a box it had previously opened, we removed each individual's scrounging trials following their first production of that day. To focus on biologically relevant data, we removed all trials in which the individual interacted with the box but did not enter it (i.e. they were neither producers, nor scroungers) from our analysis.

Producer–Scrounger Index

To describe each individual's daily strategy, we calculated the producer index (PI), used by Harten et al. (2018) from all of the focal individuals' trials (441 total trials, 32 individuals) over the course of each day (Eq. (1)). For a given individual, i , the index subtracts the number of scrounger trials (s_i) from the number of producer trials (p_i) and divides this difference by the total combined number of trials ($p_i + s_i$):

$$PI_i = (p_i - s_i)/(p_i + s_i) \quad (1)$$

The PI ranges between 1 and -1 , where a positive PI represents a producer, and a negative PI represents a scrounger. We considered PI values between -0.5 and 0.5 to represent an intermediate 'opportunist' strategy. Daily PI values were used to test the consistency of each individual's strategy. Consistent strategies were considered social strategies (strategies that suggest a social interplay) if each group had individuals that were solely producers and scroungers with relatively few opportunists. We additionally tested an individuals' strategy over the entire active season by creating a PI index that included all focal individuals' trials over the course of the 2-week experimental period.

Quantifying Boldness with Flight Initiation Distance

Following Petelle, McCoy, Alejandro, Martin, and Blumstein (2013), we quantified boldness using flight initiation distance (FID) measurements collected throughout 2019. Flight initiation distance is the distance at which an individual flees an approaching threat (Ydenberg & Dill, 1986). Bold animals, those with shorter FIDs, tolerate closer approaches. To measure FID, an observer identified a focal marmot and waited at least 5 min at the starting location to ensure individuals were not obviously alarmed before the start of the experimental approach. The observer then approached at a consistent pace of 0.5 m/s, dropping a flag three times: at the observer's starting position, at the observer's position once the focal individual became alert and at the observer's position once the focal individual fled. Following the completed flush, the observer used a measuring tape to measure the distance from each of these positions to the focal individual's initial location (Runyan & Blumstein, 2004). FIDs were collected no more than once per day per individual. We calculated the best linear unbiased predictor (BLUP) of FID ($N = 165$) for each individual ($N = 74$) using the fixed effects of the observer's start distance, the focal individual's alert distance, the focal individual's distance from the nearest burrow, the focal individual's total number of trials measured throughout the season, the time since the individual's last trial and the total number of trials performed at the colony each day, while using the random effect of marmot ID. To ease interpretation, we took the inverse of each individual's predicted FID



Figure 1. The two-action puzzle box with plywood and camera trap set-up. Marmots could solve the box by opening the lid or opening the door. Either solution could remain open after first production.

value to define 'boldness'. Thus, individuals with small FIDs were converted to have a large boldness value, and those with large FIDs were converted to have a small boldness value. Only 29 of the 74 individuals were subjects of the puzzle box experiments.

Quantifying Social Dominance with Interaction Data

We used the Clutton-Brock index (CBI) to quantify dominance hierarchies in each marmot social group (Blumstein, Keeley, & Smith, 2016; Clutton-Brock, Albon, Gibson, & Guinness, 1979). The dominance index (Eq. (2)) is calculated from the agonistic interactions in our social interaction data:

$$\text{CBI} = (B + \Sigma_b + 1) / (L + \Sigma_l + 1) \quad (2)$$

For each focal individual, B is the total number of other individuals against which the individual won, Σ_b is the total number of individuals against which each of those beaten individuals won, excluding the focal individual, L is the number of individuals our focal individual lost to, while Σ_l is the number of individuals those winners lost to, excluding the focal individual. From the CBI, we calculated each individual's relative dominance rank, which standardizes the CBI for the number of individuals in each colony (Blumstein et al., 2016); we ordered each colony's CBI values from lowest to highest, then divided the absolute ranks by the total number of individuals in the group. The highest subsequent ranking is always 1.0 for each group, and the lowest is always 0.

Since dominance was measured for social groups within a colony, there was one individual (UID = 0008) that was present in two different dominance hierarchies (the social groups in Gothic Town at North Pole and at Red Rock). In this instance, we calculated overall PI with puzzle box trials pooled from both social groups but only used the dominance ranking from their primary social group (North Pole; relative rank = 0.8) to analyse relationships between PI and dominance.

Statistical Analysis

To analyse the consistency of an individual's producer/scrounger strategy, we calculated the intraclass correlation coefficient (ICC) from its daily PI values ($N = 178$). ICC is a measure of repeatability and tests individual consistency of a continuous variable by comparing within-subject variation and between-subject variation (Johnson & Koch, 2011). From the ICC, we concluded whether marmots consistently differed in the strategies they adopted.

Once we confirmed individual consistency, we plotted the distribution of an individual's overall PI values to determine the specific strategies being used; we distinguished whether individuals acted consistently as producers, as scroungers, or with a consistent intermediate strategy.

Next, we analysed whether certain scroungers consistently arrived and scrounged before all others. We created a binary value for each scrounging individual that quantified whether they were the first to scrounge at that puzzle box that day (1) or not (0). We tested the overall consistency of scrounging first with Gwet's AC1 statistic (Gwet, 2019). Similar to ICC, Gwet's AC1 measures consistency by comparing within-subject variation and between-subject variation but allows for categorical variables and missing data. Once we confirmed whether individuals consistently arrived first, we quantitatively measured how often these individuals were first by calculating the percentage of days on which they were the first scrounger. We calculated the percentage using all of the days during which the puzzle box was opened for each colony, including

days where no individuals scrounged, despite a producer having opened the box.

We then tested whether scroungers followed producers to the box using the scroungers' latency to arrive at the box. For each individual each day, we calculated the time (scored as minutes from midnight) of their first scrounging trial and the time at which the first producer opened the box. We subtracted the producer's time from the scrounger's time. We then calculated individual average latencies over all days.

Finally, to analyse whether an individual's traits were associated with its propensity to produce or scrounge, we fitted a linear mixed effects model of the overall PI values ($N = 32$) with four potential predictor traits – age (yearling = 2 summers; adult = 3+ summers; reference level adult), sex (reference level female), dominance rank and boldness – as fixed effects. We used dominance rank to represent both the effects of dominance and the effects of body mass, since dominance rank tends to covary with body mass (Huang, Wey, & Blumstein, 2011). To ensure that our boldness and dominance rank values were not collinear, we calculated a correlation coefficient.

All analyses were performed in R v.3.5.2 (R Core Team, 2019). ICC was calculated using the ICC function in the 'psych' package (Revelle, 2019). Gwet's AC1 was calculated using the 'irrCAC' package (Gwet, 2019). All linear mixed-effects models were fitted with the 'lmer' function in the 'lme4' package (Bates, Maechler, Bolker, & Walker, 2019) and 'lmerTest' (Kuznetsova, Brockhoff, & Christensen, 2017). We checked the assumptions of our models using the 'check_model' function in the 'performance' package (Lüdtke, Makowski, Waggoner, & Patil, 2020); residuals were normally distributed and variances were homoscedastic.

Ethical Note

All procedures were approved under research protocol ARC 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 (TR-519). After trapping, individuals were released immediately at the trap location. Marmots were in traps no longer than 2–3 h, and typically for much less time. Traps were shaded with vegetation on warm days. Marmot handling was brief (typically 5–15 min depending upon the data to be collected), and marmots were not injured during handling. All marmots were handled while inside a conical cloth-handling bag to reduce stress. We swabbed ears with alcohol before tagging individuals to reduce the chance of infection. Observations were conducted at distances chosen to not overtly affect marmot behaviour. Interacting with puzzle boxes did not appear to overtly stress subjects.

RESULTS

Consistency of Individual Foraging Strategy

The ICC value for our producer–scrounger data showed that 41% ($F_{31,352} = 9.5, P < 0.001$) of variance in PI was explained by the individual, confirming that individuals exhibited consistent foraging roles. From our overall PI values, we saw that each colony tended to have one producer, a majority of scroungers and relatively few intermediate 'opportunists' (Fig. 2).

Consistency of First Scrounger

The Gwet's AC1 value for our first-scrounger data showed that 44% ($P = 0.013$) of variance in whether an individual scrounged first was explained by the individual, confirming that scrounging first

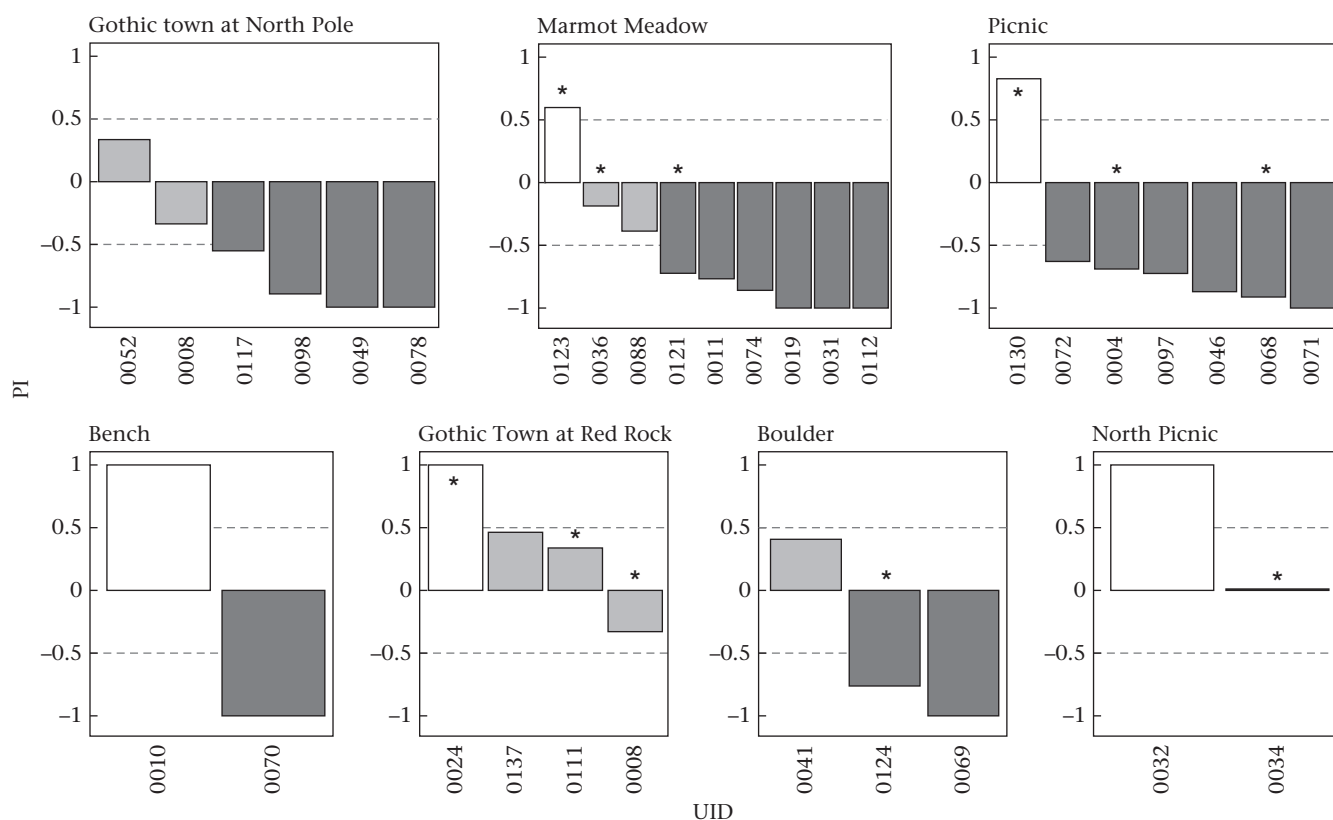


Figure 2. Overall producer index (PI) values for all individuals (UID: unique identity number) within their respective colonies. Individuals with negative PI values (dark grey bars) were consistent scroungers, while individuals with positive PI values (white bars) were consistent producers. We consider $0.5 > \text{PI} > -0.5$ to be opportunists (light grey bars). Dotted lines mark the PI cutoff for producers and scroungers. Asterisks mark males.

was consistent for individuals. Subsequent first-scrounger percentages showed that at most two individuals per colony, with the exception of Picnic, shared the majority of the first-scrounger observations. The most successful first scrounger was first in 67% of production events at their colony (Table 1).

Latency to Scrounge

When looking collectively at all first scroungers' average scrounging latencies, they scrounged a median of 13 min (range 0–187 min; Table 1) after the producer. In comparison, when looking collectively at all other scroungers' average scrounging latencies, they scrounged a median of 31 min (range 7–249 min) after the producer.

Individual Traits Correlated with Foraging Strategy

Our linear mixed effects model revealed that sex, but not age, boldness or dominance rank, explained variation in our PI (Table 2). Boldness and dominance rank were uncorrelated (Pearson correlation: $r_{20} = 0.223$, $P = 0.317$).

DISCUSSION

Within groups of interacting marmots, individuals were consistent in their social foraging strategies. There was typically one consistent producer in a group, while most other individuals were consistent scroungers, and only a few individuals were intermediate opportunists. Furthermore, some individuals specialized as scroungers, arriving shortly after the producer, and consistently arriving before any other scrounger. From this, we can

conclude that marmots not only share foraging areas (Frase & Armitage, 1984), but they also have contrasting roles in a social foraging scheme. Specifically, scroungers actively followed producers to foraging sites to obtain food. It was common that a single producer supported their group's scrounging majority, and, therefore, possibly bore the energetic brunt of a community-wide social foraging effort. Therefore, marmots engaged in distinct foraging roles and social foraging relationships within their social group.

Social foraging strategies exist in marmots despite their lack of strong social relationships. This is supported by general theory, which assumes that social foraging requires only reoccurring group assemblages, not consistent and strong social relationships (Giraldeau & Caraco, 2000). Therefore, social foraging may occur among other less social species and asocial species, both experimentally and in wild contexts. For example, a species that lives a solitary lifestyle may inadvertently develop social foraging relationships around foraging sites, and these relationships may be shaped by ambivalent or aggressive behaviours towards others. Such 'asocial' social foraging may occur among Tasmanian devils, *Sarcophilus harrisii*, who live solitarily but share feeding sites with small groups (Pemberton & Renouf, 1993), possibly allowing unique, transient, and still unknown, producer–scrounger relationships. Meanwhile, species with strong social relationships may contribute to and support greater complexity in social foraging interactions: fruit bats live in large roosts, yet develop relationships with a smaller social foraging group, where producer–scrounger relationships may form (Harten & Dor, 2019).

However, sociality is not the only trait that may affect social foraging relationships. In addition to sociality, diet, foraging tactics and food availability are also crucial to shaping how individuals interact while foraging.

Table 1
The frequency of scrounging first and the average latency to scrounge for all first scroungers for each colony.

Colony	Total possible days ^a	Individual UID ^b	Percentage of days scrounged first	Average time to scrounge (min)	SD time to scrounge (min)
Bench	12	0070	42	40	33.21
Boulder	9	0124	67	8	2.49
		0069	11	10	0.71
Gothic Town at North Pole	5	0078	60	6	4.04
		0049	40	10	11.79
Gothic Town at Red Rock	5	0111	20	26	–
		0137	20	37	–
Marmot Meadow at Main Talus	12	0121	42	23	19.87
		0011	33	13	12.60
		0036	8	5	6.19
North Picnic	8	0034	12	144	–
Picnic	11	0046	27	23	23.60
		0097	18	62	78.66
		0072	18	66	41.34
		0071	9	57	7.07
		0004	9	64	13.87

^a Total days in which any individual produced at that colony for which the individual could have scrounged.

^b UID: unique identity number.

Table 2
Effects of age (reference: adult), sex (reference: female), boldness and dominance rank on explaining variation in overall producer index (PI) value.

Fixed effect	Estimate	SE	P
Intercept	–0.088	0.560	0.877
Age (yearling)	–0.507	0.354	0.170
Sex (male)	0.778	0.339	0.035
Boldness	2.734	3.208	0.406
Dominance rank	–0.638	0.552	0.264

Significant values are in bold.

Diet and foraging tactics direct social foraging relationships through the physical, physiological or intellectual requirements of the food source. For instance, lions, *Panthera leo*, depend on social cooperation to bring down large prey and may need greater experiential skill sets to hunt quality prey (Scheel & Packer, 1991). This creates trait-based skill sets that prioritize certain individuals over others in a foraging relationship, such as older individuals having more experience and skill to capture difficult prey. However, in free-grazing herbivores, there is no need for these skill sets because food is easy to obtain. Still, foraging in herds may lead them to engage in simple social foraging and producer–scrounger relationships through local enhancement.

We find support for this idea in our study where marmots exhibited consistent foraging strategies and only sex explained differences among individuals. For a wild marmot, the production of a food source may include finding a foraging patch, while scrounging may involve following another individual to a foraging patch, but neither of these roles require specialized skills or experience. Males are generally larger and therefore require more food. Thus, in the present study, it may have been easier for males, because of their size and strength, to reach the lid of the puzzle box and push against the Velcro to open the lid, but we find this hypothesis less convincing because females and yearlings were also physically able to open the lid. Males may also produce more, not because of any skills attributable to their sex, but rather because their obligate dispersal as yearlings may be associated with relatively more social independence (Armitage, 2014). However, our results might be an artefact of using an artificial puzzle box, introducing a more difficult, extractive task not commonly

encountered in the wild and where certain traits might have been required for success. Nevertheless, we found no support for age, boldness or dominance explaining patterns of production. This is consistent with the hypothesis that species with access to relatively easily acquired food may be freed from foraging roles associated with certain traits.

The distribution of food, specifically its ability to be monopolized, and its abundance may also influence social foraging relationships through intraspecific competition. When animals rely on resources scattered in time and space, producers may locate food patches and individuals may use dominance to regulate social foraging access, such as with the Egyptian vultures (van Overveld et al., 2020) and spotted hyaenas (Holekamp, Smale, Berg, & Cooper, 1997). It is possible that when food availability is infrequent and irregular, individuals can and must take advantage of established social dominance hierarchies to ensure access to food while also limiting others' access in their social foraging game. Yellow-bellied marmots eat grasses and forbs (Frase & Hoffmann, 1980), which are relatively abundant resources that should allow for unrestricted social foraging. Indeed, even at the novel puzzle box, marmots did not use dominance to either displace producers or defend food from scroungers and, instead, freely shared the available foraging space with all individuals that could fit into the box. Therefore, marmot behaviour supports the hypothesis that abundantly available food frees animals from dominance-based foraging roles.

We capitalized on the facultative social system of yellow-bellied marmots to explore the presence and limitations of social foraging strategies in a less social species, while illuminating the possible factors describing variation in social foraging systems. Subsequent research should further explore these different factors (sociality, diet and foraging tactics, food availability) and how they influence the structure of social foraging relationships in a variety of systems. In this way we can tease out how social foraging systems may assemble and may vary in response to their social and ecological environment.

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