



Does the removal of finder's share influence the scrounging decisions of herbivores?



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Group-living animals use social information when making patch-joining/scrounging decisions. However, the extent to which they use finder's share (i.e. amount of food eaten in a patch before other individuals arrive) as a cue when making these decisions is unknown. It is likely that the removal of finder's share decreases patch attractiveness to scroungers. However, it is unclear how large a finder's share must be to reduce attractiveness, or how this varies with food availability. To answer these questions, we recorded the patch-joining decisions of dominant goats, *Capra hircus*, when presented with a choice between an artificial patch where finder's share had been removed by a subordinate patch holder (producer), and one where the patch holder had just started eating. We used time spent feeding by a patch holder (10, 30, 60 and 120 s) as an index of finder's share size, and tested this using three food availabilities (40 g, 100 g and 300 g). At low (40 g) and intermediate (100 g) food availabilities, scrounging goats avoided the finder's share patch once the patch holder had fed for ≥ 30 s (i.e. 25% and 17% of the food removed, respectively). However, at the highest food availability (300 g), these goats continued to join the finder's share patch even after the patch holder had fed for 120 s (18% removed). Ultimately, our results indicate that goats weigh up both food availability and the finder's share when making scrounging decisions. Nevertheless, finder's share removal was less important in patches with more food.

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There are both benefits and costs to group living (Krause & Ruxton, 2002). Benefits include reduced predation risk (Lima, 1990; Schmitt, Stears, & Shrader, 2016; Schmitt, Stears, Wilmers, & Shrader, 2014), and greater feeding efficiency due to social information (Shrader, Kerley, Kotler, & Brown, 2007; Valone & Templeton, 2002; Valone, 1989). For example, by watching other group members, individuals can gain a greater understanding about the environment beyond their own personal information (Giraldeau, Valone, & Templeton, 2002; Valone & Templeton, 2002). This allows group members to feed more efficiently and have greater access to high-quality patches (Shrader et al., 2007). Moreover, individuals can use social information to locate feeding group members and then join them at their patches (Giraldeau et al., 2002). However, this can result in the cost of increased competition within these patches.

One way to explore patch-joining decisions of individuals is by using game theory in the form of producer – scrounger games (Barnard & Sibley, 1981; Giraldeau & Beauchamp, 1999). In these games, an individual can either search for food patches (produce) or join other individuals at their patches (scrounge; Beauchamp, 2008; Ohtsuka & Toquenaga, 2009). When making scrounging decisions, individuals weigh up a range of factors including the quantity and quality of food in a patch, and the dominance status of the patch holder (Barnard, 1984; Stears, Kerley, & Shrader, 2014). Generally, dominant individuals join subordinates at feeding patches (King, Isaac, & Cowlshaw, 2009; Liker & Barta, 2002). In response, subordinate individuals can increase their intake rate to ensure they obtain a greater proportion of food in a patch prior to scroungers joining them (i.e. the finder's share; Vickery, Giraldeau, Templeton, Kramer, & Chapman, 1991; Shrader et al., 2007).

Key factors that affect finder's share include the amount of food in the patch (Di Bitetti & Janson, 2001) and the amount of time available to the patch holder to eat before a competitor arrives (Vickery et al., 1991). To date, theoretical and empirical exploration of the impact of finder's share on the foraging decisions of group-living animals have focused mainly on how the size of the finder's share removed influences the overall foraging strategies of

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group members; for example, how increasing finder's share obtained by producers (i.e. individuals that find food patches) decreases the benefits of scrounging (e.g. Caraco & Giraldeau, 1991; Giraldeau & Livoreil, 1998; Hamilton, 2002). In response to this increasing finder's share, individuals are predicted to change their overall foraging strategy and search for their own patches (i.e. shift from acting as scroungers to acting as producers; Giraldeau & Caraco, 2000). However, one aspect that has not been considered is that individuals may not change their overall foraging strategy in response to changing finder's share. Rather, they may simply scrounge from a different individual within the group at a patch where less food has been removed (i.e. smaller finder's share). If this is the case, then variability in finder's share may play a large role in influencing the patch choice decisions of scrounging individuals.

With many group members feeding simultaneously (Valone & Templeton, 2002; Valone, 1989), it is likely that the time each of these individuals started feeding in a patch, and thus the amount of food they have removed at any specific point in time, varies. Hence, it may be more beneficial to join certain patches rather than switch foraging strategies and incur the costs of searching for a new patch. If this is the case, then how do scroungers determine which patch to join? Food availability within patches is not constant across the landscape. Thus, the impact of the removal of the finder's share will probably vary with the amount of food in the patch. As a result, the size of the finder's share removed should ultimately influence the patch-joining decisions of scroungers across a range of different patches. However, the degree to which herbivores use finder's share as a cue for making patch-joining decisions has not been explored (Di Bitetti & Janson, 2001).

To address this, we asked the following. (1) What is the relationship between food availability, feeding time and the finder's share? (2) Do scrounging herbivores use the finder's share obtained by a patch holder (i.e. producer) as a cue for making patch-joining decisions (i.e. patch attractiveness)? (3) If so, how does the influence of finder's share on patch-joining decisions vary with food availability in a patch? If scrounging herbivores do not utilize finder's share as a cue, then we would expect that the amount of time a patch holder feeds within a patch (i.e. an index of finder's share) should not influence patch choice by scrounging individuals. In contrast, if finder's share does play a role, individuals should prefer to join patches where the patch holder has fed for less time, and thus obtained less food (i.e. small finder's share; Giraldeau, Hogan, & Clinchy, 1990). In addition, as feeding in a patch reduces food availability, the influence of finder's share removal on patch-joining decisions should be greater in patches with less food. This is because by feeding in these patches, patch holders remove a greater proportion of the available food, and thus reduce food availability and probably patch attractiveness for scroungers. Therefore, we predicted that scrounging herbivores should tolerate larger finder's shares being removed (i.e. patch holder feeding for longer) in patches with greater food availability compared to patches with lower food availability.

METHODS

We ran the study during May–July 2013 at Ukulinga Research Farm, Pietermaritzburg, South Africa. The University animal ethics committee cleared the experimental procedures (reference number 015/13/Animal), and no animals were hurt during the experiments.

To explore how the removal of the finder's share affected the patch-joining decisions of scrounging herbivores, we recorded the patch-joining decisions of 19 (11 male, eight female) dominant indigenous veld goats, *Capra hircus*, from a single herd of 43 individuals. Prior to these experiments, we trained these dominant

goats to associate the different colours and shapes of artificial patches with different food quantities. Thus, their patch-joining decisions were based on this prior knowledge. All individuals in the herd were familiar with each other prior to the start of our experiment, and none of the females in the herd were lactating. We focused on the scrounging choices of dominant individuals because they are more likely to join patches of other group members (Barta & Giraldeau, 1998; Liker & Barta, 2002). Goats provide a good model to test our predictions because they learn quickly (Cote, 2000), and use social information and the availability of food in a patch when making patch-joining decisions (Shrader et al., 2007; Stears et al., 2014).

In line with standard practices in South Africa (see Shrader, Kerley, Brown, & Kotler, 2012), the goats were held in a barn (30 × 12 m) overnight where they had ad libitum access to water, but no food. In the mornings prior to the experiments, we moved the goats into a rye grass paddock and allowed them to feed for 30 min. This allowed them to become partially sated and thus reduce the effect of hunger on the results. We then ran experiments from 0700 hours to 1100 hours. After the experiments, we released the goats into a natural grassland where they fed for ca. 6 h before returning to the barn.

Dominance Relationships

To identify dominant individuals in the herd (Table 1), we followed the same procedure outlined in Stears et al. (2014) to establish a dominance hierarchy for the goat herd (for details, see Stears et al., 2014). As with Stears et al. (2014), we determined dominance by staging interactions between two individuals. We did this by providing an artificial food patch (57.0 × 36.5 cm and 23.0 cm deep) containing 200 g of commercial sheep food (Complete Sheep Finisher, Meadow Feeds, South Africa) to the two goats. To reduce the risk of injury, we staged the interactions within a 700 × 450 cm pen, which provided enough space for subordinate individuals to move away from aggressive dominant individuals. We released the goats from opposite sides of the food patch and determined dominance by observing the behavioural interactions of the two goats over a 1 min period (see Stears et al., 2014). We did this, as all interactions tended to take place within the first 30 s. We classified goats that initiated aggressive behaviours (e.g. horning, head butting) and/or monopolized the patch as being dominant. In contrast, those that moved away from or refused to join the patch were classified as subordinate. We then used this information to calculate a win – loss matrix and goats were ranked according to David's score (Bang, Deshpande, Sumana, & Gadagkar, 2010; Gammell, De Vries, Jennings, Carlin, & Hayden, 2003).

Three factors that could potentially influence our experiments were (1) the relatedness of individuals, (2) the sex of patch joiners and patch holders and (3) whether individuals had horns or not. The genetic relatedness of all individuals in the goat herd was not available, thus it is likely that we tested dominance between related individuals. When we staged interactions between individuals that we knew to be related, aggressive interactions took place and a dominant individual was always identified. Despite this, we never directly tested individuals that we knew to be related in the patch-joining experiments (see below). Stears et al. (2014) found that the sex of the joining individual, as well as the sex of the patch-holding individual, did not influence patch-joining behaviour. In our study, the dominant and subordinate groups comprised individuals of both sexes (Table 1). Thus, neither patch joining nor patch holding was restricted to a specific sex. Lastly, the presence of horns was randomly distributed throughout the goats' hierarchy (Table 1). This observation was similar to that of Aschwanden, Gyax, Wechsler, and Keil (2008) who found no correlation between the

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