



Cohesiveness reduces foraging efficiency in a social herbivore

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For social foragers, movement as a group could increase foraging efficiency through collective discovery of high-quality food sources. This would require an efficient mechanism for transferring information about food quality between individuals. Conversely, the constraints of foraging as a cohesive group could decrease efficiency; grouping may persist to serve other functions such as protection from predators. To test what drives cohesion in herbivores, we manipulated patch shape and within-patch pattern of food quality and quantified the effects on group level diet selection by a social herbivore, the fallow deer, *Dama dama*. We arranged feeders containing fodder in lines or blocks, and manipulated the pattern of food quality within patches by adding tannin, a plant secondary compound that decreases palatability. We quantified the relative consumption of low- and high-tannin food to compare diet selectivity at the group level between patch treatments. If group foraging evolved to increase foraging efficiency, altering the spatial arrangement of food should not affect diet selectivity because information about food location and quality is shared. We found, however, that the herd expressed different levels of selectivity between both patch shapes and food quality patterns. Deer selected better diets in blocks than lines. In lines, the herd selected better diets when quality varied between alternate feeders rather than between the two halves of the patch, suggesting a reliance on personal rather than group information. Deer consumed the most at patch centres in all treatments except in blocks with high-tannin centres, but diet selection was poorer in the latter compared to blocks with low-tannin centres. Aggregation at the centre of patches appears to have restricted exploitation of the best food. Predation pressure and/or resource variability may have favoured the evolution of a foraging strategy that prioritizes social cohesion over effective diet selection.

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Foraging is a critical aspect of an animal's life that ultimately affects its fitness. For most large generalist herbivores, the optimal foraging strategy involves selecting relatively high-quality food from among abundant low-quality food (Westoby, 1974). Quality, and thus preference, is defined by the nutrient content, chemical and physical defences and morphology of plants, as well as by the nutritional needs and detoxification abilities of herbivores at a particular point in time (Freeland & Janzen, 1974; Kimball & Provenza, 2003; McArthur, Hagerman, & Robbins, 1991). It is further modified by the availability of foods, which may change seasonally and with environmental disturbances (Di Stefano & Newell, 2008; Shipley, Blomquist, & Danell, 1998). Herbivores must therefore negotiate a mosaic of food quality that is both

temporally and spatially variable. The expression of these preferences often results in the consumption of plants in proportions differing from their availability, and thus diet selection is important not only from the herbivore perspective but also because it can alter the composition of plant communities (Augustine & McNaughton, 1998).

Understanding diet selection by large herbivores is, however, complicated by a plethora of factors external to plant quality. Herbivores must make trade-offs between the benefits of selecting the highest quality plants and the costs incurred to do so. These costs include the time and energy invested in searching for and assessing the quality of plants relative to the available vegetation, involving the use of visual and olfactory cues, or direct sampling of plants (Fortin, 2003; Freidin & Kacelnik, 2011; Stutz, Banks, Dexter, & McArthur, 2015; Stutz, Croak, Proschogo, Banks, & McArthur, 2017). How efficiently herbivores detect and choose between available plants depends not only on their sensory abilities but also on the spatial distribution of plants (Bell, 1990; Bergvall, Rautio, Sirén, Tuomi, & Leimar, 2008; Etzenhouser, Owens, Spalinger, & Murden, 1998; Kotliar & Wiens, 1990). It follows that investment

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in search and assessment behaviours would require either reduced quantitative intake or more time spent foraging at the cost of other activities. Importantly, there is mounting evidence across a variety of taxa for a trade-off between diet selectivity and behaviours that minimize predation risk (Lima & Dill, 1990). In some cases, foragers accept greater perceived risk to obtain higher quality food, while in other scenarios, predator-induced vigilance has resulted in reduced selectivity between food items, presumably depending on the costs and benefits of predator avoidance and selectivity (Lima, 1988; Lima & Valone, 1986; McArthur, Orlando, Banks, & Brown, 2012; Metcalfe, Huntingford, & Thorpe, 1987). Suboptimal diet selection can therefore result when the cost of maximizing plant quality outweighs the benefits.

Animals that forage in groups can reduce some of the costs of diet selection compared to their solitary counterparts. Group-living animals can enhance their foraging efficiency by using social information from conspecifics, such as the location and quality of a resource patch (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Rieucou & Giraldeau, 2011). Individuals may be attracted to a patch due to the presence of conspecifics (local enhancement; Pöysä, 1992), and the outcomes of foraging and behavioural decisions of other individuals can inform about patch quality once there (public information; Valone & Templeton, 2002). This information can be efficiently transferred without using specific signals or mutual recognition of informed and naïve individuals (Couzín, Krause, Franks, & Levin, 2005). In addition, shared vigilance can reduce individual investment in vigilance behaviour, freeing up more time to forage (Dias, 2006; Elgar, 1989). Foraging in groups can also provide protection from predation via earlier detection of potential predators (Powell, 1974; Pulliam, 1973), reduced individual predation risk via the dilution effect (Foster & Treherne, 1981), predator confusion (Milinski, 1984), and the use of other group members as buffers from predators (Hamilton, 1971). Any of these mechanisms could lead an individual to perceive a lower risk of predation when foraging among conspecifics.

Inevitably, group foraging is also associated with costs. Individuals in groups may experience reduced foraging efficiency in terms of both the amount and quality of food ingested via competition and interference with conspecifics (Giraldeau, Valone, & Templeton, 2002; Krause & Ruxton, 2002; Valone, 1993). As group size increases, there is less food available per individual foraging in a patch and it is likely that some will be forced to eat lower quality food. Under competitive conditions, individuals may sacrifice selectiveness to maximize intake of a depleting resource. Unless the resources in a patch are abundant, the costs of sharing them are rarely offset by a heightened ability to find resource patches because individual search areas will overlap; it is, however, likely to reduce individual variance in intake (Ruxton, 1995). Interference between individuals foraging in a group can lead to the consumption of poorer diets by restricting the ability to move about in a patch and increasing aggressive interactions and theft of discovered food (Free, Beddington, & Lawton, 1977; Molvar & Bowyer, 1994). The effects of competition and interference thus limit the freedom of an individual to choose food with high quality within a mosaic of abundant low-quality food.

Use of shared information can also be detrimental to diet selection. Poor decisions by a single individual can be perpetuated throughout the group; it may not be possible to use personal and social information simultaneously, so observers may only be informed by behavioural decisions (not the cue used by the observed) leading to informational cascades (Giraldeau et al., 2002). Such processes may decrease individual fitness, not only as a result of the poor diet selection but also as a result of increased direct mortality due to predation. For example, by following conspecifics experienced with agricultural patches, bison, *Bison bison*,

increased their exposure to hunters, resulting in a dramatic population decline in Prince Albert National Park, Canada (Sigaud et al., 2017). In addition, herbivores may choose lower quality food patches or leave good patches early to stay together (Dumont & Boissy, 2000; Scott, Provenza, & Banner, 1995; Valone, 1993). To avoid this, individuals must effectively balance interdependence and independence (List, Elsholtz, & Seeley, 2009). If interdependence is too low, animals fail to reach consensus, and group cohesion and behavioural synchronization can be weak, resulting in the group splitting up (e.g. subgroups of sheep, *Ovis aries*; Howery, Provenza, Banner, & Scott, 1996; Roath & Krueger, 1982). On the other hand, if independence is too low, choices can be suboptimal (List et al., 2009). Relatively little is known about how the costs of competition when foraging in a group interact with group cohesiveness, even though these costs lie at the root of group splitting.

Few empirical studies have examined the influence of collective behaviour and spatial pattern of food on foraging decisions in a group-living mammalian herbivore. Here, we used the fallow deer, *Dama dama*, as a model organism to test how the shape of a food patch and the distribution of food quality within it affect group level diet selection by a herd of social foragers. Fallow deer are appropriate models for testing this because their foraging behaviour is known to be influenced by both social factors and the spatial arrangement of food. Fallow deer herds are nonpermanent units that split up and fuse, with larger groups showing reduced foraging success (Focardi & Pecchioli, 2005; Gerard, Bideau, Maublanc, Loisel, & Marchal, 2002). Documented patterns of feeding behaviour by fallow deer herds suggest that they prioritize cohesion over food quality. Consumption of nonpreferred Norway spruce, *Picea abies*, probably by lower-ranked peripheral individuals, was greater in close proximity to supplemental feeding sites with high-quality food (Garrido, Lindqvist, & Kjellander, 2014). Also, in an experiment using feeders of high- and low-tannin pellets, fallow deer foraging in groups consumed more tannins than fallow deer foraging alone; that is, they were less selective in groups (Bergvall, Rautio, Kesti, Tuomi, & Leimar, 2006). Thus, group cohesion seems to be a priority for fallow deer, probably because nonforaging functions such as reduced predation risk outweigh the costs of foraging together (Beecham & Farnsworth, 1999). How the prioritization of cohesion interacts with the spatial distribution of food resources is not well understood.

To test the group level feeding response of fallow deer to patch shape, we used bowls of pelleted food (feeders) arranged in lines and blocks to create elongated and compact patches. In a scenario where information is transmitted efficiently between individuals and there are no competing factors determining their distribution within patches, deer should be equally selective in food patches of different shapes. However, when foraging collectively, fallow deer tend to form rounded groups in exposed areas, possibly in response to predation risk (Focardi & Pecchioli, 2005). We therefore hypothesized that selecting the highest quality food as a cohesive group would be easier in block rather than line patches.

Information transmission may also play a role in how the distribution of food quality within patches influences diet selectivity. We manipulated food quality within patches by applying a tannin-rich plant extract to the food pellets; tannins are plant secondary metabolites that reduce palatability and hence food preference (Bergvall, Rautio, Luotola, & Leimar, 2007; Bernays, Driver, & Bilgener, 1989). If deer make efficient use of group information, they should consume more of the high-quality (low-tannin) food when quality differs between the two sides of a patch (i.e. a single contrast at the patch centre) than when quality alternates between neighbouring feeders. This is because the group should use shared information about the distribution of food quality to move to the

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