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How do free-ranging domestic herbivores reduce competition within ownerdetermined herds?

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ABSTRACT

Group size and competition are key drivers of foraging behaviour in social animals. With seasonal changes in food quality and availability, comes changes in the type (scramble or interference) and degree of competition (aggression or none). One way that animals can deal with these variations is by living in groups where the benefits of the group size outweigh the costs. However, this is generally not possible with domesticated animals, as group sizes are determined by owners. Thus, within these groups, animals have to make behavioural adjustments to reduce competition. To determine how domestic indigenous veld goats (Capra hircus), living in different sized owner-determined groups, dealt with seasonal variations in food availability and quality, and thus competition, we recorded their foraging behaviour. Specifically, we documented patch-joining events, herd splits, and interindividual distances (IID). We found that goats only joined the patches of other herd members during the wet season, when food was more readily available. In addition, we found that large herds split into a number of smaller subherds (comprising ca. 15 individuals) that were similar in size to the unsplit small herds. Furthermore, these splits primarily happened during the dry season and were more frequent in large herds compared to small herds. Finally, IID increased in the dry season for both small and large herds, likely as a way to reduce interactions while feeding. Yet, individuals in large herds maintained larger IID than individuals in small herds, suggesting a greater attempt to reduce interactions in large herds. The fact that the large ownerdetermined herds had to elicit a greater number of behaviours, suggests greater levels of competition in these herds in the arid savanna system. These results suggest that by using behavioural indicators such as IID or herd splits, owners could monitor competition within their herds and determine when it would be better to keep their goats in smaller herd sizes.

1. Introduction

One of the main benefits of group-living is increased foraging efficiency (Valone, 1989; Baciadonna et al., 2013). This happens via individuals observing the foraging of other group members and thus obtaining social information (Valone and Templeton, 2002; Shrader et al., 2007). By doing this, individuals can find food patches (local enhancement; Pöysä, 1992) and assess the quality and availability of food over a wider area, quicker and more efficiently than they could on their own (Valone and Templeton, 2002; Fraser et al., 2006). Moreover, these benefits may be enhanced by group size with individuals in large groups assessing food quality and availability over a wider area than individuals in small groups (Valone, 1989).

There are, however, also costs to living in groups such as competition and disease transmission (Majolo et al., 2009; Kappeler et al., 2015). By monitoring the foraging of group members and then joining them at their feeding patches (termed scrounging), individuals increase competition for food via intra-group competition (Isbell, 1991; Beauchamp and Giraldeau, 1996; Sirot et al., 2012). Within these groups, competition can present itself in two forms, scramble and interference. Scramble competition occurs when an individual eats a food item, thus preventing other group members from gaining access (Van Schaik and Van Noordwijk, 1988; Koenig, 2002). The extent of scramble competition may be influenced by group size, with larger groups experiencing greater levels (Robbins, 2008). In contrast, interference competition occurs when an individual is interrupted and/or displaced by another group member before, or while feeding (Amarasekare, 2002; Valeix et al., 2007; Zhang et al., 2015). If the patch-holder (producer) is chased away, then the individual joining the patch (scrounger) can monopolise the resources in the patch (King et al., 2009).

The intensity of interference, however, is likely affected by food

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availability (Stillman et al., 1996; Rands et al., 2006), with greater levels of aggression during periods when food is limited (Isbell 1991; Barroso et al., 2000; Fokidis et al., 2013). For herbivores, this is during the dry season when the availability and quality of vegetation declines due to utilisation and senescence (Teague, 1988; Owen-Smith, 1994). Thus, competition for food between group-living herbivores likely increases during this critical time (Ranta et al., 1996; Wittemyer and Getz, 2007; Majolo et al., 2009).

For wild group-living animals, group size is determined by the trade-off between the costs and benefits of group living (Roberts, 1996; Kappeler et al., 2015). In contrast, domesticated animals are put into groups where group size is determined by their owners. This may be detrimental especially considering that potential costs of group size are rarely considered by livestock owners (Borries et al., 2008). When food is scarce, the benefit of staying in a group (e.g. greater foraging efficiency) may be lower than the costs (e.g. increased competition and aggression; Isvaran, 2007). Thus, during these periods, it may be better for individuals to move in smaller groups. Wild, and free-ranging domestic herbivores, have an advantage over herded domestic livestock, as they can change the size and structure of foraging groups in response to variation in resources (Yang et al., 2015). For example, when the availability and quality of food declines, wild herbivores can reduce competition by temporarily or permanently splitting into smaller subgroups (Smith et al., 2010). In contrast, herded livestock cannot (Estévez et al., 2007).

Within herds, one factor that influences aggression and competition between individuals is the distance they keep between themselves while foraging, termed interindividual distance (IID). When individuals forage close together, they tend to compete more, which can result in increased aggression (Estévez et al., 2007; Aschwanden et al., 2009). They can, however, reduce these costs by increasing their IIDs (Van Schaik and Van Noordwijk, 1988; Rands et al., 2006). For example, female kangaroos maintained greater IID in winter compared to spring due to competition for limited food (Jaremovic and Croft, 1991). As domestic livestock tend not to be able to adjust their herd sizes, adjusting IID is likely an important way in which they can reduce interference and scramble competition (Grueter et al., 2016).

The extent to which free-ranging domestic herbivores may adjust their intra-herd dynamics as a way to reduce competition and aggression is poorly understood. To explore this, we focused on the foraging interactions of free-ranging indigenous veld goats (*Capra hircus*) living in different sized owner-determined herds. Due to the reduction in food quality and availability during the dry season, we predicted that within these herds, 1) competition and aggressive behaviour would increase, 2) the frequency of patch-joining events would decline, 3) herds would try to reduce competition by splitting into smaller subherds, 4) the number of subherds the goats split into would increase, and 5) IID would increase within both unsplit herds and subherds. Moreover, we expected that these changes would be more marked in large herds (due to increased resource demand).

2. Materials and methods

2.1. Study sites

The study was conducted at three sites (Ncunjane, Jolwayo and Ngubo), around Msinga, KwaZulu-Natal, South Africa ($28^{\circ}44' 0''$ South, $30^{\circ} 27' 0''$ East). Jolwayo and Ngubo are located on the East and West side of the Tugela River respectively, while Ncunjane is located approximately 5 km West of the river. Msinga is an arid savanna land-scape covered with rocky surfaces and a sparse grass layer (Fowler, 2011). The region receives an annual rainfall ranging between 600 and 700 mm, with the majority of the rain falling during summer (December to February) (Cousins et al., 2009). Summer temperatures range between 25 and 44 °C (Mucina and Rutherford, 2006; Cousins et al., 2009), while winter (May to July) temperatures are between -4 and

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26 °C (Mucina and Rutherford, 2006). Due to limited clay soils, the area is largely unsuitable for crop farming (Fowler, 2011), thus residents generally rely on livestock (goats, cattle, sheep and chickens) for their livelihoods. The landscape contains a variety of savanna tree species including deciduous *Vachellia tortilis, Vachellia karroo, Vachellia nilotica, Spirostachys africana* and evergreen *Euclea crispa, Boscia albitrunca*, and *Olea europaea africana*. Succulent species present include *Aloe* spp. and *Euphorbia* spp. (Mucina and Rutherford, 2006).

To determine how goats in owner-determined herds reduced competition, we collected observational data in both the wet (January and February 2015) and dry (September and October 2014) seasons from two small (N = 12-28; mean = 19.3 + 6.3 (SD) goats) and two large (N = 60-83; mean = 60.4 + 14.8 goats) herds at each of the three sites (N = 12 herds). Each herd was observed for two days, which resulted in 24 observations per season. Data were collected by two observes (a main observer and assistant) continuously scanning back and forth across the herd/subherd being observed. Despite the large number of individuals within the big herds, the small interindividual distances (IID) within these herds (see results) meant that these herds covered relatively small areas (ca. $60-180 \text{ m}^2$), which facilitated data collection. As the colours and coat pattern of indigenous veld goats are not uniform, we were able to identify individuals via each individual's unique coat pattern and colour, body size, sex, and the presence or absence of horns. The experimental design was approved by the University of KwaZulu-Natal Animal Ethics Committee (clearance number 208/15/ Animal). Moreover, no animals were adversely affected by the observations carried out during the study.

2.2. Patch joining and aggression

To record the degree to which goats joined the patches of other individuals while foraging, we continuously scanned back and forth across the herd and recorded all patch-joining events in the different seasons, and whether these events resulted in aggressive interactions such as head-butting and charging. To do this, we followed a single herd for two days at each site per sampling season. Observations started once the goats left their kraal (also called a corral) in the morning (at 07:45 h in the wet season and 07:00 h in the dry season) and carried on until the point when they started heading back to the kraal (at 12:15 h in the wet season and 15:30 h in the dry season). Once the goats had arrived at the feeding site, we recorded the tree species on which the joining events took place, the number, age, and sex of the goats that were feeding from the particular tree, and any aggressive interactions between the patch joiners and holders.

Upon arrival at feeding sites, the goat herds split into small subherds before feeding. To ensure that we were able to obtain data from a number of different individuals, we followed and recorded data from individuals in the largest of these subherds ($N = 3-16 \pm 3$ individuals). In addition, we determined the proportion of patch holders and patch joiners in each herd. Finally, we calculated the mean number of patch-joining events for the different herd sizes in the different seasons to determine whether these events varied with herd size.

2.3. Herd splits

To determine if the different sized goat herds at all three sites split into smaller subherds as a way to reduce competition while feeding, we recorded 1) if the herd split, 2) the number of subherds the herd split into, and 3) the number of individuals in each subherd. We defined a herd as being split when the individuals on the periphery of the potential subherds were more than 20 m apart. Individuals less than 20 m apart were considered as part of the same herd.

2.4. Interindividual distances (IID)

When goats arrived at a feeding site and started feeding, we

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