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

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Highlights

• Goats only joined patches during the wet season when feed was readily available.

• Goat herds split into subherds more frequently in the dry season.

• Interindividual distance increased in the dry season.

• Individuals in large herds reduced competition more than those in small herds.

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 owner-determined 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.

Key words: goats, interindividual distances, season, herd splitting, subherds

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 & 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 & 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 & 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 & 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 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 & 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 & 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 & 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° 44' 0" South, 30° 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 landscape covered with rocky surfaces and a sparse grass layer (Fowler 2011). The region receives an annual rainfall ranging between 600-700 mm, with the majority of the rain falling during summer (December to February) (Cousins *et al*. 2009). Summer temperatures range between 25 and 44 ^{0}C (Mucina & Rutherford 2006; Cousins *et al*. 2009), while winter (May to July) temperatures are between -4 and 26 ^{0}C (Mucina & 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 & 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 to 28; mean= 19.3 $\pm$ 6.3 (SD) goats) and two large (N= 60 to 83; mean= 60.4 $\pm$ 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 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 ± 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 estimated the IID, to the nearest metre, that individuals kept between themselves as soon as they started feeding (unsplit herd), as well as after splitting into subherds. This was done using the scan sampling method (Gilby *et al.* 2010), with samples taken every 10 minutes. Due to the goats being habituated to our presence, we were able to record these data while standing 5 m away. However, errors in the estimation of IID are more prevalent from ground observers working with large herds (Lehner 1998). In an attempt to reduce this error, we limited IID estimates to individuals that were within 10 m of the observers and not obstructed by other goats or vegetation. This resulted in ca. 72% and 55% of the potential IIDs being recorded in the small and large herds, respectively. We then generated a mean IID for each herd using these values, and a seasonal mean using the IID values of the herds recorded in each season (wet, dry).

2.5 Statistical Analysis

We used a Pearson Chi-Square (χ^2) test to determine if there was a difference in the number of patch-joining events in small and large herds in the wet season. We did not analyse data from the dry season, as the goats did not join the patches of other herd members during this season (see results). To determine if the number of subherds formed when a herd split (dependant variable) varied with herd size (small, large) and season (wet, dry) (independent variables), we used a 2-way ANOVA. We then used a second 2-way ANOVA to determine if the number of individuals per subherd was influenced by season (wet, dry) and/or herd size (small, large). Lastly, as we recorded data from the same herds on multiple occasions, we used a repeated measures ANOVA to determine if IID (dependent variable) was influenced by herd type (unsplit herds, subherds), unsplit herd size (small, large), and season (wet, dry) (independent variables). To determine where the significant differences

existed in each of these ANOVAs, we ran Fisher's least significant difference (LSD) post hoc tests. We analysed all the data using SPSS version 23. Means ± standard deviation of the mean are reported.

2.6 Data statement

Data have not been deposited into a public repository as the study forms part of a PhD that has not yet been examined. However, the corresponding author will happily provide the data upon request.

3. Results

3.1 Patch joining

For both small and large herds, patch-joining events only took place during the wet season. Yet, the number of joining events did not differ between the different sized herds (small, mean = 16.5 ± 3 joining events; large, mean = 27.5 ± 5 joining events; $\chi^2 = 2$, df = 1, P = 0.157). Moreover, none of the joining events resulted in aggressive interactions.

3.2 Herd splits

While foraging, large herds split into subherds 58% of the time during the wet season and 100% of the time during the dry season (N= 24 observations). Small herds showed a similar pattern (25% wet season, 67% dry season), but not all the small herds split into subherds during the dry season (N= 24 observations). The number of subherds the goat herds split into was significantly influenced by season, herd size, and the interaction of season and herd size (Table 1). In both the wet and dry seasons, large herds split into more subherds when foraging, than did the small herds (Table 1). During the dry season, both small and large herds significantly increased the number of subherds in which they split into, but large herds (N= 40 subherds) still split into more subherds than small herds (N= 26 subherds) (Table 1; Fig. 1).

Table 1. Analysis of variance of the number of subherds in each herd size, number of individuals in

subherds, and interindividual distances (IID) of small and large herds in the wet and dry seasons.

| Dependent	Independent	Sum of Squares	df	Mean Squares	F-ratio	P-value
Number of subherds	Season	12.96	1	12.96	14.12	0.002
	Herd	17.27	1	17.27	21.78	0.004
	Season*herd	33.33	1	33.33	37.36	<0.0001
Error			15			
Individuals in subherd	Season	133.68	1	133.68	12.28	0.001
	Herd	1306.43	1	1306.43	120.01	<0.0001
	Season*herd	228.66	1	228.66	21.01	<0.0001
Error			104			
IID	Season	579.30	1	579.30	52.72	<0.0001
	Herd	475.00	3	237.50	17.01	<0.0001
	Time	422.02	3	140.67	12.80	<0.0001
	Season*herd	142.14	3	113.69	15.81	<0.0001
	Season*time	106.66	3	35.55	3.24	0.024
	Herd*time	11.10	3	11.10	1.09	0.009
	Season*herd*time	96.54	3	69.50	10.58	<0.0001
Error			182			
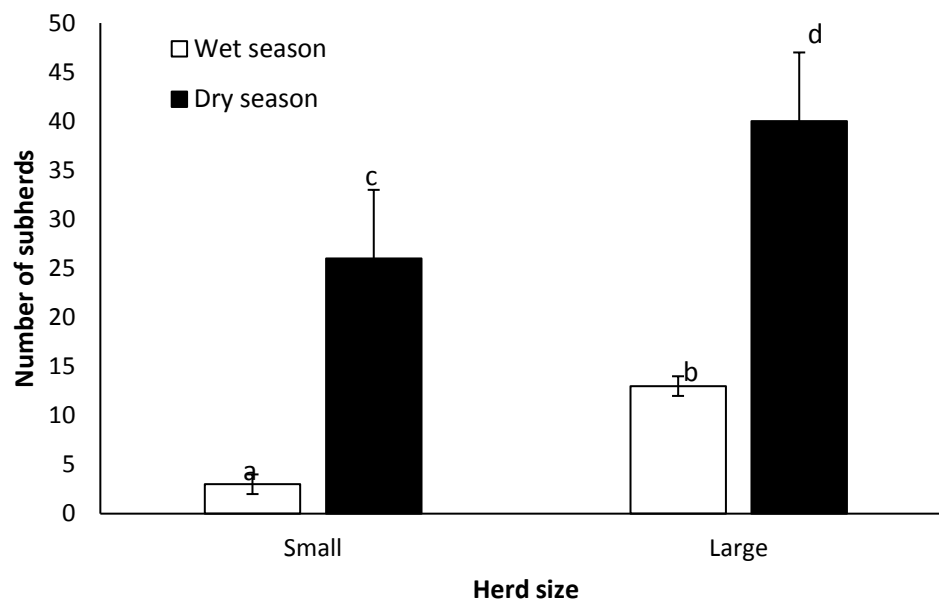
Fig. 1. Number of subherds in both small and large herds in the wet and dry seasons. Different letters

indicate significant differences (P<0.001).

Once split, the number of individuals in the subherds differed significantly in relation to season, the size of the unsplit herd (small, large), and the interaction of season and herd size (Table 1). Small herds that split (N= 18-21 individuals) tended to divide into 3 subherds of ca. 4 individuals in both the wet (3.0 ± 3.6 individuals) and dry (3.9 ± 3.6 individuals) seasons. In contrast, in the wet season, large herds split into four subherds (N= 14.6 ± 3.1 individuals) that were similar in size to the unsplit small herds (N= 19.5 ± 5.8 individuals). In the dry season, large herds split into smaller subherds of ca. 9 individuals (8.6 ± 2.9). This resulted in a significant drop in the number of individuals within the subherds of the large herds from the wet to dry season (Table 1; Fig. 2).
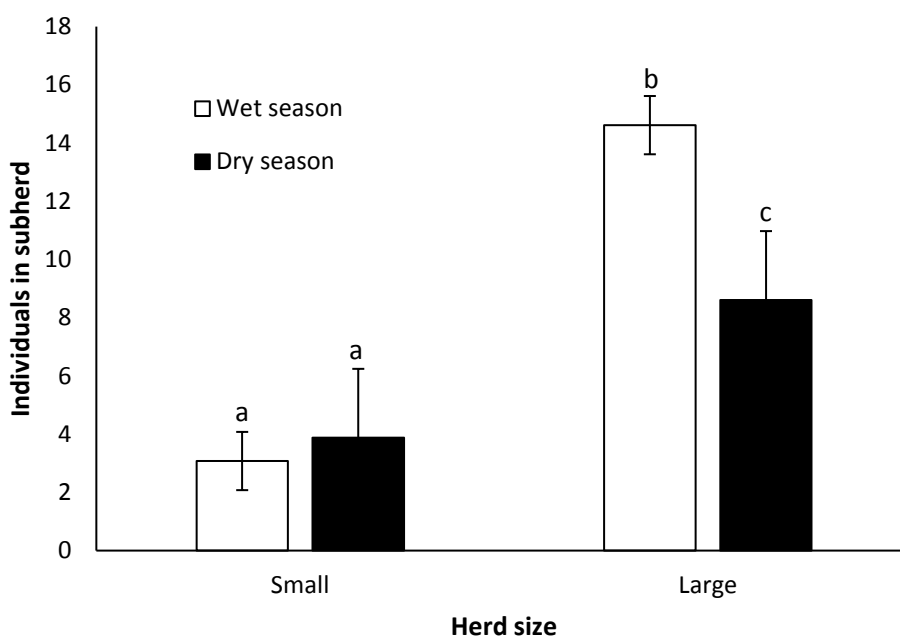

Fig. 2. Number of individuals in the subherds of both small and large herds in the wet and dry seasons. Different letters indicate significant differences (P<0.001).

3.3 Interindividual distance (IID)

The IID of the goats differed with herd type (unsplit herd, subherd), herd size, season, and the interaction of these variables (Table 1). The IID maintained by individuals in both small and large herds in both seasons differed between the unsplit herds and the resulting subherds (Table 1; Fig. 3). During the wet season, the IID before the small herds split was 1.7 ± 1.4 m, but then increased to 5.1 ± 2.2 m in the subherds (P = 0.004). Likewise, the mean IID in the large herds before splitting was 1.1

$\pm$ 0.9 m and increased to 4.4 $\pm$ 1.8 m in the subherds (P = 0.005). Similar patterns were found during

the dry seasons, but the IIDs were greater. Specifically, in small herds, IID increased from 4.4 $\pm$ 2.4 to

7.8 $\pm$ 4.4 m (P = 0.0001) as individuals shifted from moving in the unsplit herd to moving in

subherds. Similarly, in large herds, IIDs increased from 4.5 $\pm$ 2.2 in the unsplit herd to 12.1 $\pm$ 4.2 m

(P = 0.0001) in the subherd. Overall, the IID between individuals in the small and large herds were

similar in the different seasons and herd types. The only exception was during the dry season where

individuals in the subherds of the large herds maintained significantly greater IIDs compared to

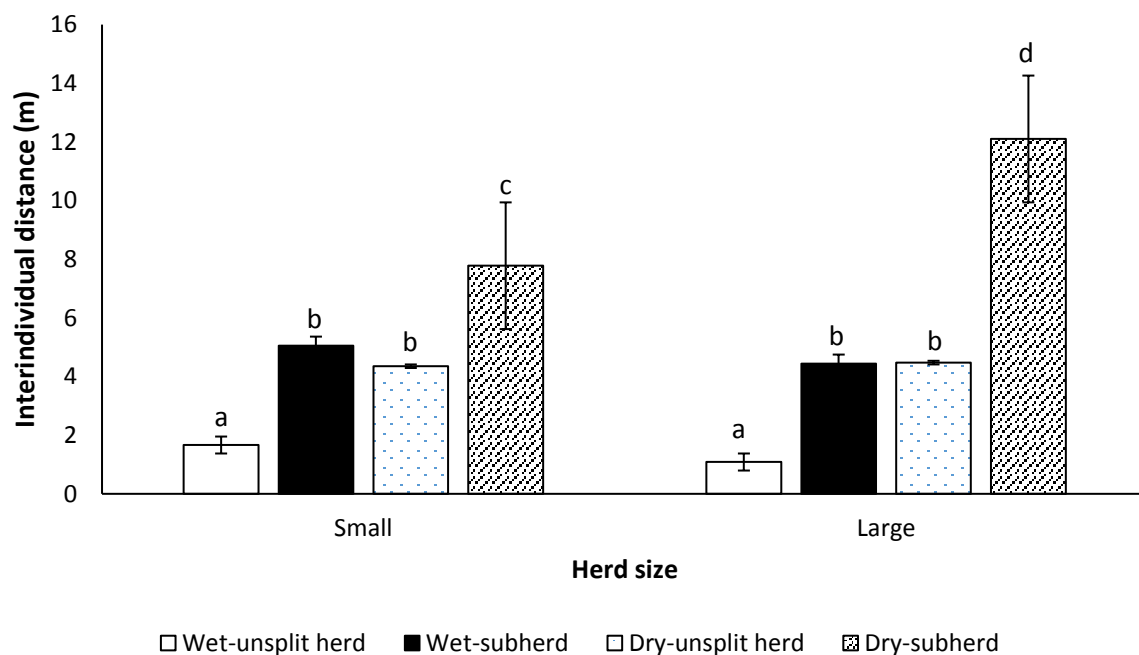individuals in the subherds of the small herds (Fig. 3; P = 0.0001).

Fig. 3. Interindividual distances of unsplit and subherds of both large and small herds during the wet

and dry seasons. Different letters indicate significant differences (P<0.05).

4. Discussion

For herbivores, living in groups can result in greater feeding efficiency, but also greater

competition as group members join individuals at food patches (Chapman *et al*. 1995; Isvaran 2007).

This is especially true during the dry season when food availability and quality is poor (Jaremovic &

Croft 1991; Owen-Smith 1994). Free-ranging herbivores, can reduce these costs by utilising a suite of

behaviours such as adjusting herd sizes and IID within herds. However, the options available to

domestic herbivores living in owner-determined herds may be more limited. When focussing on goats in owner-determined herds that free-ranged when feeding, we found that patch-joining events, in both large and small herds, only took place during the wet season when high quality food is readily available. Moreover, these events did not involve aggressive interactions. However, in both seasons, small and large goat herds split into smaller subherds. Yet, larger herds split more often, and interestingly when they split, they formed subherds that were similar in size to the unsplit small herds. Finally, individuals in both large and small herds maintained similar IIDs in both unsplit herds and subherds. The only exception was during the dry season, when individuals in the subherds of large herds maintained greater IIDs than individuals in the subherds of small herds.

Within groups, individuals can compete via both scramble and interference competition by individuals joining the patches of other group members (Robbins 2008; Sirot *et al*. 2012; Zhang *et al*. 2015). With declines in food availability and quality during the dry season, we expected more patch-joining events as a way of reducing search time and thus increasing foraging efficiency, especially in larger herds. This, however, did not happen. In contrast, the goats completely avoided the patches of other group members during the dry season and only joined during the wet season. A possible reason for this, is that the amount of food available in the different patches was so low that the potential food that could be obtained by a scrounging individual, after the finder's share (i.e. the amount of food eaten by the patch holder prior to other individuals joining the patch; Vickery *et al*. 1991) had been removed, was lower than what could be obtained by an individual searching for its own patch. For example, Kok *et al*. (2017) found when food availability was low (40 & 100 g), that individuals would avoid patches in which patch holders had fed for as little as 30 seconds. They suggested that this was likely due to the patch holders extensively reducing food availability, and thus patch attractiveness to potential joiners. It is possible that due to the poor-quality environment in which our study was conducted, that the goats in the different herds faced a similar situation. As a result, they did not increase competition during this time of the year by joining patches, but rather looked for their own patches in which to feed (Beauchamp & Giraldeau 1996).

The lack of aggressive interactions and the fact that individuals were not displaced when herd members joined them at their patches during the wet season, indicates that the main form of

competition between goats during this period was via scramble competition, and not interference competition. This suggests that the availability of food in the patches during the wet season was high enough that patch joiners did not have to chase away the patch holders to ensure that they obtained adequate intake. Yet, competition for food may result in animals adjusting their intake rates. For example, Thomas's langur (*Presbytis thomasi*) females were reported to increase their intake rate when the group size increased (Steenbeek & van Schaik 2001). In addition, Shrader *et al.* (2007) found that goats increased their intake rates as the number of potential competitors increased. As we did not record intake rates, it may be possible that patch holders increased their intake rates when herd members joined them at their patches. If so, then this would increase the amount of food that they obtained from the patch. Yet, the lack of aggression in patch-joining events tends to suggest that even if patch holders did increase their intake rates, it was not enough to significantly reduce the potential intake of the patch joiners.

There are a number of reasons why groups may temporarily split into smaller subgroups. First, splitting may occur as a result of agonistic behaviour between group members, with the resulting subherds comprising individuals that show low levels of aggression towards each other (Gerard *et al.* 2002). We, however, did not record aggression between individuals in the unsplit herds, thus this is unlikely to be the main driver in this study. Second, it could be that groups split to limit competition for limited resources between group members. For example, feral goats were found to exhibit smaller group sizes in the dry season, when competition for food is highest (Shi *et al.* 2005). In addition, Arnold *et al.* (1981) found that as flock sizes increased, Dorset Horn sheep (*Ovis aries*) split into subgroups when foraging. Merino sheep (*Ovis aries*) also split into subherds, but only when food availability was low (Arnold *et al.* 1981).

In our study, the frequent splitting of herds into subherds, especially for large herds, in the dry season when food tends to be less abundant and of lower quality (Isvaran 2007; Yang *et al.* 2015), suggests that the key driver of herd splitting was increased competition between herd members. By moving in smaller herds, individuals were likely better able to locate unexploited food patches (Isvaran 2007; Morand-Ferron & Quinn 2011). Moreover, small groups are unlikely to experience high levels of competition (Steenbeek & van Schaik 2001). Interestingly, the large herds split into

subherds that were similar in size to the unsplit small herds. This, coupled with the lower splitting frequency in the small herds, suggests that the owner-determined herd sizes of between 12 and 28 individuals may be better suited to the arid environment of the study site.

If splitting into smaller subherds was the first strategy that the goats used to reduce potential intra-herd competition (likely scramble competition), it was apparently not enough. This is indicated by the fact that once they were in these subherds, individuals also increased their IID. Moreover, the greatest increase in IID was during the dry season in the subherds of the large herds. By maintaining greater IIDs, especially during the dry season, group members likely reduced competition. For example, large groups of female long-tailed macaques (*Macaca fascicularis*) maintained large IID distances as a way to reduce competition when feeding (van Schaik & van Noordwijk 1988). In addition, subordinate Japanese macaque (*Macaca fuscata*) females maintained large IID to avoid being displaced from food patches by dominant individuals (Saito 1996). Thus, it would seem that for the goats in our study, the way in which they reduced competition within the owner-determined herd sizes was to use a combination of splitting into smaller subherds, and then increasing their IIDs once in these subherds.

5. Conclusion

Overall, our results tend to suggest that for the goats in Msinga, the costs associated with living in the artificially determined large herds outweighed the benefits of being in these herds. As a result, it seems like these goats attempted to minimise competition once they were away from the kraal and livestock owner. They did this by splitting into small subherds when feeding, maintaining greater IIDs within these subherds, and not aggressively joining patches during the dry season when food availability and quality were likely low. In contrast, the seasonal stability of the small herds, and the lower formation of subherds tends to suggest that the cost:benefit trade-offs of group size were better for goats within the artificially determined small herds compared to the large herds. However, even the small herds divided into subherds. The results of our study suggest that livestock owners may be able to use behavioural indicators such as the frequency with which herds split into smaller subherds and/or IID as ways to monitor the degree of competition within their herds. The number of

behavioural adjustments made by the large herds could suggest that it would be better for livestock owners to keep their goats in small herds in this arid environment, or at least allow large herds to split into smaller subherds when feeding. By doing so, livestock owners may reduce competition and aggression within their goat herds, and possibly increase animal health, weight gain, and productivity (Nogueira *et al*. 2016).

Acknowledgements

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