

THE EFFECTS OF MORPHOLOGICAL AND ENVIRONMENTAL CONDITIONS ON VIGILANCE BEHAVIOUR IN THE FERAL GOAT (*CAPRA HIRCUS*)

by

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ABSTRACT

Studying the complex relationships and structure of the feral goat on Lundy facilitates the understanding of sociality. Vigilance behaviour and behaviour repertoires were assessed using continuous and instantaneous focal sampling. Correlations and regression models found that vigilance behaviour was associated with grazing and mobility and dependant on age, time, location, sex and colour. Social network analysis highlighted specific cliques of both sexually segregated and mixed groups that, with time, diffused. To our knowledge this is the first study of its kind to assess the social complexities of the feral goats on Lundy. The results in conjunction with further research could give guidance on culling and may have beneficial implications for both the welfare and production of goats used for meat and dairy products.

Keywords: *Behavioural repertoire, Capra hircus, Lundy, Social networks, Vigilance*

INTRODUCTION

Studying the complex relationships and structure of social animals facilitates the understanding of causes and consequences of sociality (Hinde, 1976). Particularly in small isolated populations, knowledge of social dynamics will aid in the crucial understanding of disease and information transfer (Wright *et al.*, 2006). A deeper understanding of social complexity can be measured directly using social network analysis (Wey *et al.*, 2008), which incorporates interactions of nodes (component of the network with a known relationship to others in the network) and their ties (association between two nodes). Once constructed, a social network describes the influence individual animals have upon their local group and further, how group dynamics influence population level processes.

Group members acquire social information from conspecifics (sheep; Clark & Mangel, 1986) and individuals therefore benefit by monitoring the foraging of others (goats; Shrader *et al.*, 2007), through local enhancement (Sherry & Galef, 1990), social facilitation (goats; Arnold & Dubzinski, 1978) or by having better assessment of resource patches (Valone, 1989). Similarly, group living has many other associated benefits such as

increased mate availability, offspring security (goats; O'Brien, 1988) and decreased predation risk (zebrafish; Wright *et al.*, 2006). Although benefits from group living are high, associated costs include increased competition and disease transmission (Wright *et al.*, 2006). Group living is therefore a trade-off and will result in increased fission events when the associated costs become too high (Wright *et al.*, 2006). Living in a social group often permits individuals to increase foraging effort, as the safety of an individual can increase with group size through the dilution effect (Pulliam & Caraco, 1984), selfish herd hypothesis (Hamilton, 1971) and/or the 'many eyes' hypothesis (birds; Pulliam, 1973).

Goats were domesticated over 10,000 years ago (Mason, 1984) and selectively bred for both morphological and behavioural traits (O'Brien, 1988). They are highly gregarious animals which have anecdotally been sighted in groups of 200 and are seldom seen alone (Ross & Berg, 1956), however model group size has been reported as three (Shi *et al.*, 2005). Goats use auditory, visual and olfactory cues in order to remain within a social group. When isolated, studies have shown that cortisol levels rise, indicating emotional stress (Kannan *et al.*, 2002). However individuals are free to join and leave groups with no social consequence (Shi *et al.*, 2005). Although some populations deviate (O'Brien, 1988) generally feral goats form sexually segregated groups in response to the females reproductive cycle (Shi *et al.*, 2005) with the males' home ranges overlapping (O'Brien, 1988) with that of larger female groups (Shi *et al.*, 2005). This segregation is thought to arise as the ecological needs of individuals differ between the sexes (O'Brien, 1988). On closer inspection larger female groups may arise due to the increased number of offspring within a group (Shi *et al.*, 2005). Interestingly however, compared to other ungulates segregation is relatively low (Shi *et al.*, 2005).

Goats spend 58% of daylight hours grazing (Animut *et al.*, 2005) and therefore require a trade-off between grazing and being vigilant. Reducing vigilance will increase the likelihood of being detected by predators (Quenette, 1990), reduce social contact (Beauchamp, 2003), and can result in missed food locations (Barbosa, 2002).

Aim

To use social network analysis to assess how environmental and morphological conditions affect vigilance behaviour to confirm the following hypotheses:

H₁: Vigilance behaviour will differ with both environmental (group number, time, vegetation quality and location) and morphological (age, sex and colouration) conditions.

H₂: The feral goats on Lundy are structured by non-random social interactions.

METHODS

Study population

This study was conducted on Lundy in the Bristol Channel (51°10' N 4°40' W) from 17 April 2010 until 23 April 2010. Lundy is approximately 5km long and 1.2km wide with steep slopes and cliffs surrounding its coastline, presenting ideal conditions for feral goats (O'Brien, 1988). Therefore Lundy offers an exemplary environment in which a manageable number (N=38) of feral goats can be observed repeatedly in the wild to assess social behaviour.

Data Collection

Observations were taken throughout the day and preliminary recordings allowed the assessment of inter-observer reliability, in which variation was minimal. Goat location involved trekking around the coastal paths while scanning the cliffs and basins through binoculars. On first encounter goats were sexed, numbered, photographed and assigned an age category of either juvenile (still suckling from its mother) or adult for repeated identification (full key available at www.lundy.org.uk/resources).

Social network

On finding a group of goats an initial scan was taken through binoculars to assess which individuals were in the group and who their nearest neighbours were. Simultaneously the group was photographed to keep both a hard copy of the finding and to ensure identifications were accurate. Group membership was based on an arbitrary but consistent inter-individual distance that was never greater than 50m (Shi *et al.*, 2010). Group membership was also based on the conditions of the presence of social interactions and visual contact with at least one other member of the group. For this study social interactions were present when individuals were either influenced or had influence on group movement. To increase sample size associates also took photographs of entire groups of goats as they were encountered. To maintain independence of samples no groups were recorded twice in six hours.

Vigilance and behavioural repertoire

Once the social network data had been collected a focal animal was strategically selected to ensure an equal representation of the population was sampled and that no animal was sampled twice. Observers worked in pairs at a distance of approximately 30m (Hopewell *et al.*, 2000) in order to achieve the most reliable results. Observer A used 20 one-minute instantaneous focal samples to ascertain the behavioural repertoire of the individual using an ethogram (Table 1), while observer B recorded the number of vigilance bouts (Table 1) and the cumulative duration of said bouts over the 20-minute period. In the event that the focal animal was out of sight for over 10 minutes the sample was disregarded. *Ad libitum* recordings were taken of dyadic interactions with the intention of constructing a dominance hierarchy but unfortunately insufficient data was collected due to difficulties locating goats and the short time frame available for this study. After an observation had been conducted, vegetation was subjectively rated on a scale of 0-5, where zero indicated that the animals were found on bare rock, one indicated pioneer plants were sparsely present, two indicated coverage of pioneer plants with small areas of shrubbery, three indicated full shrubbery coverage, four indicated loosely cultivated land and five indicated lush pasture grass. This scale was not indicative of vegetation quality but served to give a nominal value to categorise vegetation type. Similarly geographic location, weather and time of day were documented.

Ethics

No behavioural manipulations were used in this study, only observations, and all observations were conducted from 30m causing minimal disturbance (Hopewell *et al.*, 2000) deeming this study ethically sound.

Table 1: A table, using modified descriptions from Barroso *et al.* (2000) and Hopewell *et al.* (2005), describing the common behaviours expressed by the feral goats on Lundy (*Capra hircus*)

Behaviour	Description
Vigilance	Standing or sitting with head raised above shoulder height and eyes open
Grazing	Standing, with head below shoulder level, biting or chewing vegetation
Mobile Grazing	Walking, with muzzle close to the ground, biting or chewing vegetation
Sitting and grazing	Biting or chewing vegetation whilst laying down
Sitting and ruminating	Chewing cud whilst laying down
Standing and ruminating	Chewing cud whilst laying down
Locomotion	Walking or running
Sitting and resting	Sitting whilst doing no other behaviour with head below shoulder level
Standing and resting	Standing with eyes closed
Yawning	Neck stretched outwards with an open mouth
Stretching	Extension of limbs
Vocal	Bleating
Retreat	The individual moves away at the approach of another
Displacement	The individual approaches another which results in the other individual retreating
Supplant	The individual takes away another's resource
Threat	The individual directs its horns or nose towards another individual but no contact is made
Aggression	The individual directs its horns or nose towards another individual and contact is made
Hoof stamping	The individual hits its hoof on the ground whilst interacting with another
Self grooming	Any act of grooming oneself with either the mouth, horns or hooves
Object-directed grooming	Any act of grooming which involves use of an object (e.g. fence or tree)
Allogrooming	Any act of social grooming either being accepted or directed towards another individual
Defecating	Excreting solid waste from the anogenital area
Urinating	Excreting fluid waste from the anogenital area
Out of sight	Individual not visible to the observer

Statistical analysis

To facilitate statistical analysis the following vigilance measures were transposed: Bouts, the number of vigilance bouts performed; Bouts per second, number of bouts performed over the observation divided by the duration of the observation; Duration, cumulative time spent being vigilant; Average duration, the cumulative duration divided by the number of bouts; vigilance percentage, the percentage of time spent being vigilant over

the observation period. Behavioural repertoire data was selectively pooled to create two new variables for analysis. The total proportion of time grazing was calculated using the sum of all three grazing behaviours (Table 1). Similarly the proportion of time the animal was mobile was calculated using the sum of locomotion and mobile grazing. Both variables were tested against each vigilance measure using a Spearman's rank correlation as parametric assumptions were not met. However, to assess the effects of environmental and morphological characteristics on vigilance behaviour two regression models were constructed to predict both bout rate and percentage of time spent being vigilant. All data was analysed using SPSS 16. However group membership and an individual's nearest neighbour data were inserted into separate matrices in Microsoft Excel and social networks diagrams were constructed using UCINET. The diagrams were then spring embedded to give a more accurate visual representation of the data allowing the reader to highlight possible trends within the population. Spring embedding treats nodes (individual goats) as masses and their ties (number of times individuals are seen together) as springs and pulls together individuals that have the strongest ties while allowing individuals with weaker ties to drift towards the fringe of the clique. It is important to note that spring embedding can only highlight possible associations which need to be statistically tested in order to conclusively state a finding.

RESULTS

Does total grazing time have an effect on vigilance behaviour?

Results from a Spearman's rank correlation indicate a significant negative association between the proportion of time a goat was grazing and the average vigilance bout duration per goat, $r=-0.48$, $N=21$, $p=0.026$ with bout length decreasing as an animal grazed more. No other significant associations were found between the vigilant measures and grazing.

Does mobility have an effect on vigilance behaviour?

Results from a Spearman's rank correlation indicate a significant positive association between the proportion of time a goat was mobile and the number of vigilance bouts performed, $r=0.64$, $N=21$, $p=0.002$ with vigilance increasing as an animal got progressively more mobile. This was expected as a more mobile animal will need to find new food sources, maintain visual contact with other group members, avoid obstacles and maintain its anti-predatory behaviour. A similar association was found between mobility and the rate of bouts performed, vigilance duration and percentage of time spent being vigilant. However only bout rate was significant: $r=0.57$, $N=21$, $p=0.007$; $r=0.42$, $N=21$, $p=0.056$ N.S. and $r=0.38$, $N=21$, $p=0.089$ N.S. respectively. In contrast the average bout duration per goat approached a significant negative association with mobility, $r=-0.39$, $N=21$, $p=0.079$ N.S. suggesting that when still the duration of each bout increases.

Does vigilance behaviour change with an individual's morphology and environment?

Bouts per second: A backwards procedure within a multiple regression analysis was carried out to test the relationships between variables and establish predictor variables.

The variables used encompass both morphological (age, sex and colouration) and environmental (group number, time, vegetation quality and location) characteristics. The residuals were normally distributed and the assumption of independent errors was met (Durban-Watson=1.40). *Note: The following predictor coefficients are reported to three decimal places due to the sensitivity of the dependent variable, bouts per second (M=0.014).*

$$y=b_1x_1+b_2x_2+b_3x_3+b_4x_4+a$$

$$\text{Bouts per second} = (-0.012 \times \text{age}) + (-0.005 \times \text{colour}) + (0.008 \times \text{location}) + (0.005 \times \text{time}) - 0.012$$

The regression was highly significant ($F_{4,16}=12.23$, $p<0.001$) and a very good fit, describing 75.3% of the variance in vigilance bouts per second ($R^2_{\text{adj}}=69.2\%$). With other variables held constant vigilance bouts per second were negatively related to age ($t_{4,16}=-3.55$, $p=0.003$), increasing by 0.012 extra bouts per second when juvenile as opposed to adult, negatively related to colour ($t_{4,16}=-2.20$, $p=0.043$), increasing by 0.005 extra bouts per second when white as opposed to not-white, positively related to location ($t_{4,16}=3.04$, $p=0.008$), increasing by 0.008 extra bouts per second when situated north of Halfway Wall as opposed to the south and positively related to time ($t_{4,16}=1.85$, $p=0.083$ N.S.), increasing by 0.005 extra bouts per second during the afternoon (>1200h) as opposed to the morning (≤ 1200 h). All other variables were excluded from analysis.

Percentage of time spent being vigilant: A backwards procedure within a multiple regression analysis was carried out to test the relationships between variables and establish predictor variables. Again the variables used encompass both morphological and environmental characteristics. The residuals were normally distributed and the assumption of independent errors was met (Durban-Watson=2.12).

A casewise diagnostic analysis identified goat D as having vigilance scores greater than two standard deviations from the residual mean. Although by definition this score qualifies as an outlier there was no reasonable justification to exclude it from the analysis.

$$y=b_1x_1+b_2x_2+b_3x_3+b_4x_4+a$$

$$\text{Vigilance percentage} = (-5.56 \times \text{age}) + (-3.13 \times \text{colour}) + (-1.55 \times \text{sex}) + (2.20 \times \text{time}) + 0.15$$

The regression was highly significant ($F_{4,16}=9.18$, $p<0.001$) and a good fit, describing 69.7% of the variance in the percentage of time spent being vigilant ($R^2_{\text{adj}}=62.1\%$). With other variables held constant the percentage of time spent being vigilant was negatively related to age ($t_{4,16}=-5.32$, $p<0.001$), increasing by 5.56% when juvenile as opposed to adult, negatively related to colour ($t_{4,16}=-3.62$, $p=0.002$), increasing by 3.13% when white as opposed to not-white, negatively related to sex ($t_{4,16}=-1.98$, $p=0.065$ N.S.), increasing by 1.55% when male as opposed to female and positively related to time ($t_{4,16}=2.32$, $p=0.034$), increasing by 2.20% during the afternoon (>1200h) as opposed to the morning (≤ 1200 h). All other variables were excluded from analysis.

Given the above two regression models suggest a consistent effect of age on vigilance behaviour, independent-samples t-tests were conducted on each vigilance measure. Results indicate that compared to adults, juveniles spend a significantly higher percentage of their time being vigilant and conduct longer and more frequent bouts (Table 2).

Table 2: A table to show the independent-samples t-test results of age under each vigilance measure

	Percentage of time spent	Bouts	Bouts per second	Duration	Duration per bout
Significance	$t_{19}=3.70$ $p=0.002$	$t_{19}=12.12$ $p<0.001^*$	$t_{19}=10.21$ $p<0.001^*$	$t_{19}=3.81$ $p=0.001$	$t_{19}=-0.58$ $p=0.567$
Mean	Juvenile=8.19 Adult=3.48	Juvenile=33.00 Adult=12.33	Juvenile=0.03 Adult=0.01	Juvenile=98.27 Adult=38.72	Juvenile=2.99 Adult=4.38
Standard deviation	Juvenile=2.76 Adult=1.94	Juvenile=1.00 Adult=6.81	Juvenile=0.00 Adult=0.01	Juvenile=33.20 Adult=23.90	Juvenile=1.06 Adult=4.02

Key: *Levene's test indicates data deviates from the assumptions of equal variance

Social networks

From the UCINET social network diagrams (Figure 1a) it is clear that definite cliques are prevalent in the population. More so, these cliques are dynamic showing intergroup dispersion with time. The population comprises sexually segregated and mixed groups with many strong dyadic ties loosely associated to the remainder of the clique. Further analysis into nearest neighbour data (Figure 1b) shows how each group is maintained through associations with some but not all individuals within the group. Perhaps not surprisingly mother-offspring associations are strong and can, at times dissolve the associative strength between adults (e.g. T, U, V & W). Finally as colour was found to effect vigilance behaviour it is worth noting that when the data is spring embedded white individuals tend to aggregate centrally within cliques and show some of the strongest nearest neighbour ties. This may suggest assortment by colour in the feral goats on Lundy, but, further data collection and statistical testing would be needed to infer this behavioural pattern.

DISCUSSION

Does total grazing time have an effect on vigilance behaviour?

Total grazing time had a significant negative association with average bout length indicating that by decreasing grazing effort the duration of the vigilance bout increased, regardless of the number of bouts. Initial analysis of the results highlighted a possible anomaly, however its removal did not initiate a quantitative change in the results and therefore it remained in the analysis. In the presence of predators chipmunks, *Tamias striatus*, show a similar pattern. Trouilloud *et al.*, (2004) showed that head raising significantly reduced the time spent foraging. Although this is a reliable result caution must be taken as with any behavioural repertoire data because the two measures are not completely independent.

Does mobility have an effect on vigilance behaviour?

Contrary to the earlier finding of Trouilloud *et al.* (2004) the results indicate that movement will increase the number of bouts and the rate of bouts per observation. However comparisons to the chipmunk study should be made with caution. The vigilance

behaviour expressed by the chipmunk was believed to be that of an anti-predatory response, whereas there is reason to believe the increased vigilance in the goats during locomotion may have been to maintain social contact with group members (Kannan *et al.*, 2002), find new food sources, avoid obstacles and maintain its anti-predatory behaviour. Maintaining social contact is the most plausible explanation as both the group membership and nearest neighbour social networks (Figure 1) indicated definite social cliques with strong associations occurring between many pairs of individuals.

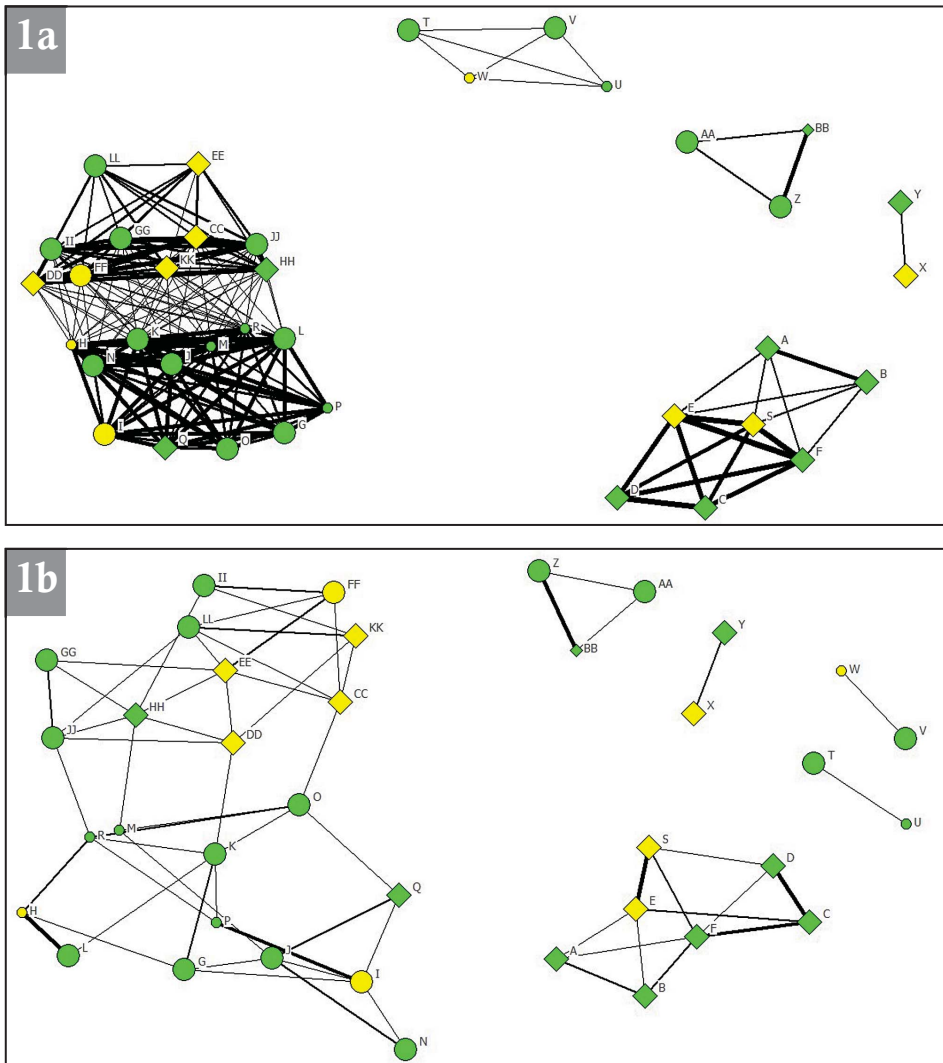


Figure 1. The spring embedded social network of the feral goat population of Lundy in relation to (a) group membership and (b) nearest neighbour. Lines relate to social ties with stronger ties represented as thicker lines; Node labels identify each individual; Node size relates to the animals age with small nodes representing juveniles and larger nodes representing adults; Node shape relates to sex with diamonds representing males and circles representing females; Node colour relates to fur colour with white representing white and grey representing not-white animals.

Does vigilance behaviour change with an individual's morphology and environment?

The effect of age was consistent across all but one vigilance measure (Table 2) indicating that juveniles perform significantly more vigilance behaviours than adults. This result is further demonstrated when viewing the nearest neighbour social network (Figure 1b). All juveniles within the population have very strong ties with at least one adult in their clique. This adult is generally believed to be the juveniles' mother and it is therefore important to maintain social contact with her. In accordance with the explanation of mobility, the vigilance behaviour reported here may not be exclusively anti-predatory but a strategy to avoid social isolation (Beauchamp, 2003). Loehr *et al.* (2005), however, found the opposite effect; their results suggested a positive association between age and vigilance behaviour in sheep. This discrepancy, however, could be due to differences in the methodologies between the two studies. Loehr *et al.* (2005) simulated a predators' presence whereas in the present study it has been suggested that the results may be due to the need for social contact (Beauchamp, 2003). The explanation produced by Loehr *et al.* (2005) cannot however be completely overlooked as there is reason to believe the annual culling of the feral goats on Lundy has in fact portrayed observers as potential predators (Shi *et al.*, 2005).

The resultant effect of sex in the regression models indicated that males are more vigilant than females. Li *et al.* (2009) would suggest that this result was due to the competition between males for dominance. Although a dominance hierarchy was beyond the scope of this investigation the prominence of the all-male clique (A, B, C, D, E, F & S in Figure 1a) would give the perfect opportunity for such an investigation to be carried out.

The effect of time in the two regression models showed that during the afternoon vigilance behaviour increased. Shi *et al.* (2005) may explain this finding as a result of the gradual dispersal throughout the day by the goats resulting in smaller more vigilant groups in the evening. However, as the social networks (Figure 1a) suggest strong cliques exist with very few indications of fission events this explanation is unlikely. Similarly anecdotal observations from this study found that the larger groups were generally more prevalent in the evening. Unfortunately no data is available to test this observation. On the other hand increased vigilance may occur due to an increased perceived predation risk as dusk sets in or as the island becomes increasingly busy. O'Connor & Krause (2003) showed that guppies will cease shoaling under 'near night' light conditions and Orpwood *et al.* (2008) showed that by introducing a model predator anti-predatory behaviour will increase. Unfortunately human activity levels were not measured in this study. A similar explanation may also be useful when interpreting the effects of location. The north of the island is considerably quieter when compared to the south and so the presence of observers may unsettle the goats north of Halfway Wall more so than the possibly more habituated individuals in the south.

Group size was not found to have any effect on vigilance behaviour conflicting with evidence gathered by Shi *et al.* (2010) where the vigilance behaviour of goats decreased by 49% per unit increase of log group size. As the feral goats on Lundy did not show this trend we must ascertain that sociality allows other benefits more applicable to their ecology. These benefits may include increased foraging efficiency or offspring security

as the social network shows a selection of definite cliques. A possible explanation for this discrepancy is that the benefits attained by the feral goats on Lundy do not increase after a given threshold, which was described by Shi *et al.* (2005) as three. Not surprisingly vegetation did not affect vigilance behaviour. This challenges the findings of Shi *et al.* (2010) who suggested that the density and type of edible material may cause a decrease in feral goat vigilance. This deviation was probably because the feral goats on Lundy are so sparsely populated competition for grazing resources were minimal.

A particularly surprising result was that white goats were more likely to show vigilance behaviour than non-white goats. This can either be explained by assuming the goat has knowledge of self and others and therefore changes its behaviour accordingly (Delfour & Marten, 2001) or a more likely scenario is that the white genotype may have associated phenotypes that impose a predisposition for vigilant behaviour (Trut, 1999). A final scenario is that goats may be more likely to aggregate with individuals of a similar morphology (Wright *et al.*, 2006). If so, white goats with white nearest neighbours may acknowledge their neighbours' conspicuousness and perceive a greater predation risk and therefore be more prone to show vigilant behaviour (Orpwood *et al.*, 2008).

It is important to note that all the above effects may be confounded by the perceived predation risk of the observers' presence. This is not anticipated to be a significant issue as all observations were conducted from approximately 30m (Hopewell *et al.*, 2000) and any such confounds were constant throughout the study.

Due to time constraints and the affiliative nature of the goats (Schino, 1998) insufficient data was collected to construct a dominance hierarchy. This in turn hampered data analysis as relating dominance to the social network described above using randomisation models may have highlighted some important aspects of society. For example which social ranks are more vigilant and how that relates to the number of ties that individual possesses within a clique. That being said the results obtained have furthered the knowledge of goat social structure and behaviour by incorporating traditional ethological methods with more modern social network analysis. The results shed light on the multi-factorial effects of vigilance behaviour which may be adapted to decrease stress on captive animals which could increase the weight gain performance of commercial animals through better husbandry.

On a more localised scale, however, the information illustrated by the social network diagrams could aid decision making during the culling process. It would be advisable, in order to maintain social cohesion and reduce unnecessary stress associated with losing familiars and the reconstruction of a dominance hierarchy, to cull individuals with the lowest number of social ties. Individuals that would fit this criterion would be those with weak nearest neighbour ties, a low number of group membership ties and individuals that rarely participate in group fusion events. It may therefore be advisable to avoid the culling of older females that have offspring and regularly participate in group fusion events such as J, K, L and FF. Similarly population management strategies should concentrate on decreasing the numbers of socially isolated males such as X and Y. Although this may, over time, lead to decreased genetic variability these measures are expected to have the smallest influence on group cohesion and the welfare of the feral goats on Lundy.

Feral goat identification key

A full key for feral goat identification is available at www.lundy.org.uk/resources, which was created and accurate during the study, April 2010. The key contains a series of pictures supplemented with descriptions of the individual's prominent features. The key also contains information on the individual's sex, approximate age (juvenile, small adult and adult), maternal relationships if apparent, formal identification code from A-LL and the 'nick-name' of each of the 38 feral goats on Lundy. Although it is not suitable to state that all the feral goats on Lundy were sampled we are confident that the vast majority were.

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