ASPECTS OF BEHAVIOURAL

ECOLOGY OF CAPTIVE FERAL GOATS

(CAPRA HIRCUS L.) WITH EMPHASIS

ON THE MOTHER-OFFSPRING RELATIONSHIP

A thesis presented in partial fulfilment
of the requirements for the degree of
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ABSTRACT

A 10-month study of the behaviour of a herd of 60 captive feral goats (*Capra hircus*) was carried out at the Ballantrae D.S.I.R. hill country research station in the lower North Island of New Zealand from April 1990 to February 1991. The primary aim of the study was to describe the mother-offspring relationship over the first three months of the kid's life and to investigate sex differences in maternal investment.

There was no significant sex difference in the mother-offspring spatial relationship, however, it was found that twins remained closer to their mothers during the first three months. There were small sex differences in the frequency of suckling in single kids only, but other variables of suckling behaviour including total time spent suckling, and the duration, initiation and termination of suckling were not significantly different between the sexes. Total suckling time, suckling duration and frequency, mother initiation and kid termination all decreased with kid maturation. There were significant differences in all suckling variables between single and twin kids.Sexual differences in kid birth weight, and growth rate, were also highly significant. Discrepancy in the proximate measures of parental investment made it difficult to conclude whether sex-biased maternal investment occurs in feral goats. Further investigation is required to determine the accuracy of suckling behaviour as a measure of maternal investment.

The second part of the study involved the construction of diurnal activity budgets for adults and for kids over the period 0830 to 1630 hours. The percentage of time spent grazing was greatest during the mating season whereas in the

gestation and kidding season a larger portion of time was devoted to rest. Female kids spent more time grazing and less time playing and resting than male kids up to the age of three month. Time spent grazing was greater in single than in twin kids. The time allocated to different activities changed significantly over the first three months of age.

In the third part of the study, the social events following the introduction of a new entrant to the herd was investigated. Exploration was the most common action of herd members toward the new entrant. A peak of agonism occurred within the first hour following the introduction of each new entrant then decreased rapidly. The response of the herd was influenced by the dominance status of the new entrant, and the season of the introduction.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF PLATES

GENERAL INTRODUCTION

BACKGROUND

Since Captain Cook first introduced goats to New Zealand more than 200 years ago there have been some marked changes in attitude towards these animals (Yerex, 1986). Although they were brought to New Zealand as a desirable companion and food source for early settlers, by 1937 feral goats were officially recognised as noxious pests. The extensive damage they caused to indigenous forest, and soil stability was acknowledged, and control measures were carried out to reduce their numbers (Rudge, 1976).

In 1979, however, during an era of diversification in New Zealand farming, the status of goats switched from that of a noxious pest to a highly valued commercial asset (Batten, 1985). Fueled by high international demand for both mohair and cashmere fibre, wild populations of feral goats were captured from back country areas of New Zealand and auctioned nation wide. The price of pure bred angoras rose steeply and, to meet the demand, they were imported or intensively bred using artificial insemination and embryo transfer techniques. This caused a boom in the number of farmed goats in New Zealand. Coupled with the development of the goat fibre export market was research indicating that goats could provide a viable alternative to chemical weed control (Clark et al, 1981, 1983; Batten, 1983; Radcliffe, 1984).

In 1990, just ten years after it was established, the goat fibre industry crashed and a poorly developed goat meat industry left frustrated farmers stranded with worthless stock (Anon., 1990). While some farmers currently maintain feral goat herds for weed control there is little monetary incentive to upgrade fences, and the number of goats escaping back to the wild is presumed to be high. For this reason the control and eradication of feral goats has never been more important.

The mixed status of goats in New Zealand has led to research with ecological and farming perspectives. Work on aspects of the control and eradication of goats has been in progress for twenty years and includes reports on the reproductive biology (Rudge, 1969; Williams & Rudge, 1969; Parkes, 1989), diet (Atkinson, 1963, 1964; Mitchell et al, 1987), distribution and density (Parkes, 1984), population dynamics (Rudge & Smit, 1970), home ranges (Rudge, 1970) and control methodology (Parkes, 1983, 1989, 1990). Research aimed at improving the management of farmed feral goats includes: disease and parasites (Daniel, 1967; Heath et al, 1983; Brassington, 1987) meat and fibre productivity (Kirton, 1970; Kirton et al, 1977), and weed control (Clark et al, 1981, 1982, 1983).

In New Zealand, only broad scale behavioural studies on feral goats have been carried out. Kilgour (1983) and Holmes (1985) dealt with the behaviour of goats as livestock and how this could be applied to their management, while Riney & Caughley (1959) briefly described herd structure in a wild feral population and the discussed the affiliation of its members. Rudge (1970) described the mother-kid relationship in wild feral goats.

Studies of the social behaviour of feral goats in New Zealand, have been largely descriptive (Rudge 1970; Kilgour, 1980, 1984; Holmes, 1985). Contemporary models of parental investment developed by Trivers (1972) have not been applied to feral goat social behaviour, and quantitative comparisons with other ungulates are limited. There is therefore a need for studies that adopt the quantitative approach used in recent research on ungulate social behaviour overseas (Gauthier & Barrette, 1985; Wolff, 1988; Byers & Moodie, 1990). Such studies would enable better use of the pool of knowledge on closely related ungulates to help explain the apparent variation in aspects of social behaviour of different feral goat populations in New Zealand (O'Brien, 1988).

Behavioural studies of feral goats are important from ecological, agricultural and ethological standpoints. An understanding of the social behaviour underlying the success of the feral goat in indigenous New Zealand habitats is an important step in the search for an effective control or eradication programme. In view of the optimistic long term commercial prospects for goat farming, a knowledge of the social organisation of feral goats is important for developing alternative farm management programmes which recognise species-specific patterns of behaviour. Finally, empirical studies of the social behaviour of feral goats provide an opportunity to test theoretical models of social behaviour.

GENERAL AIMS

The general aims of this study were to :-

(1) Examine the mother-offspring relationship in feral goats and to test hypotheses generated by contemporary theories of parental investment and parent-offspring conflict.

(2) Quantitatively describe the diurnal behaviour of a feral goat herd, and construct activity budgets to determine seasonal variation in the behaviour of the female herd, and behavioural differences between the sexes in kids.

(3) Describe the social climate following the introduction of a new entrant.

THE STUDY SITE AND HERD

The 10-month observational study from April 1990 to February 1991 was carried out on a feral goat (*Capra hircus*) herd at Ballantrae, a D.S.I.R. Hill Country Research Station 4 km NW of Woodville. The study herd consisted of 60 feral does of mixed ages (ranging from 2-8 years) selected from a larger herd of approximately 200 animals. The criteria used to select animals for the study herd were the presence of distinctive coat markings to aid identification, and a good standard of health. Juveniles had been weaned and removed from the herd at 4-5 months of age as part of a low intensity farm management programme. Although the original source of the herd could not be established with certainty it is likely that does older than 5 years were some of the original feral stock captured in the lower North Island hill country between 1983 and 1985. The majority of does, however, were born and reared in captivity. Some members of the study herd appeared to be closely related because they shared identical coat markings. Once selected, the animals were left undisturbed for a month to allow the group to establish as a herd. Colour coded leather collars and ear tags were used to ensure that all animals could be recognised individually.

In April, 1990 a young (2 tooth) free-ranging feral buck was caught in the Northern Tararua foothills. Before he was introduced to the herd the buck underwent a fertility test at Massey University Veterinary Clinic. This showed that he was fertile, and accordingly he was fitted with a harness so that his mating performance could be monitored. The failure of this young buck to inseminate the majority of does necessitated the release of another two feral bucks into the study herd during the last week of May.

Throughout the study, the herd was rotated on a monthly basis around four paddocks of variable size, terrain and vegetation:

i)   'Front-face paddock' was of approximately 1.06 hectares and consisted of a steep east-facing slope. Restricted flat areas were located along the ridge and at the foot of the slope. Shelter was provided by several isolated trees but particularly by a large eroded depression in the hill side surrounded by a few trees. Some fallen trees were also present along with a water trough. Ragwort was prominent in late spring-summer. (See Plate 1)

Plate 1

ii)   'Office paddock' was a small flat paddock of approximately 0.5 hectares. This paddock was in the immediate vicinity
        of the D.S.I.R. research laboratory. Shelter was provided by buildings   bordering the paddock, two water tanks and
        large clumps of rushes. Vegetation consisted largely of   pasture. (See Plate 1) .

iii)   'Grant's paddock' was approximately 1 hectare and had a gentle west facing slope. A small valley provided the only shelter. There was no tall vegetation in the paddock. The only forage available was pasture. (See Plate 2)

Plate 2

iv) 'Terrace paddock' was a relatively large paddock (approximately 1.74
hectares) divided by a small stream. The terrain was variable, consisting of
steep to moderately-steep east-facing slopes and a flat river terrace. A row
of macrocarpa (*Cupressus macrocarpa*), willow trees (*Salix* sp.), wattles
(*Acacia* sp.) and a large pine tree (*Pinus radiata*) provided plenty of natural
shelter. Manuka and rushes were also present, but there was no scrub. (See
Plate 3)

Observations of the study herd while it was confined in the 'Front-face' and the
'Office' paddocks were made from inside the research laboratory. Two observation
hides were set up 10-200m from the other two paddocks. A map of the paddocks
and their respective observation hides is given in Figure 1.
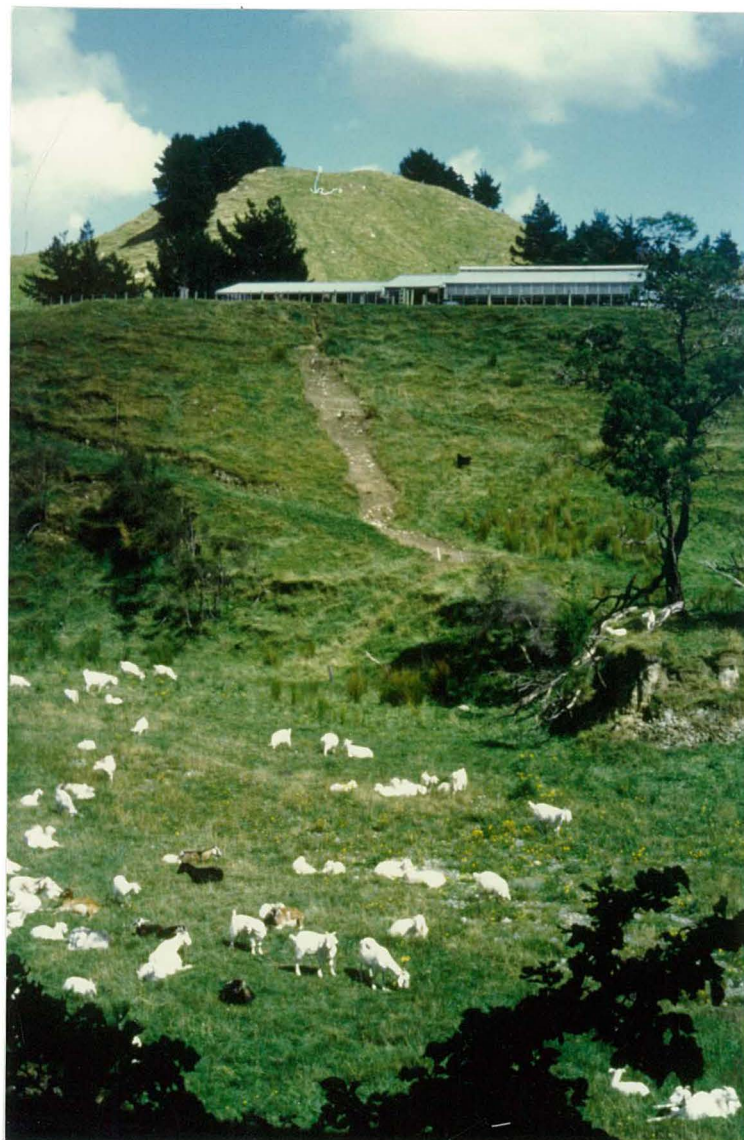
Plate 3

EASTERN SECTION OF THE BALLANTRAE D.S.I.R.
HILL COUNTRY RESEARCH STATION

North

Grants

Front-face

Office

Terrace

Hopes Road

Woodville 3 km

LEGEND

Vehicle track

Observation hide ●

Fences

Building

Stream

Scale 0 ⊢————⊣ 100m
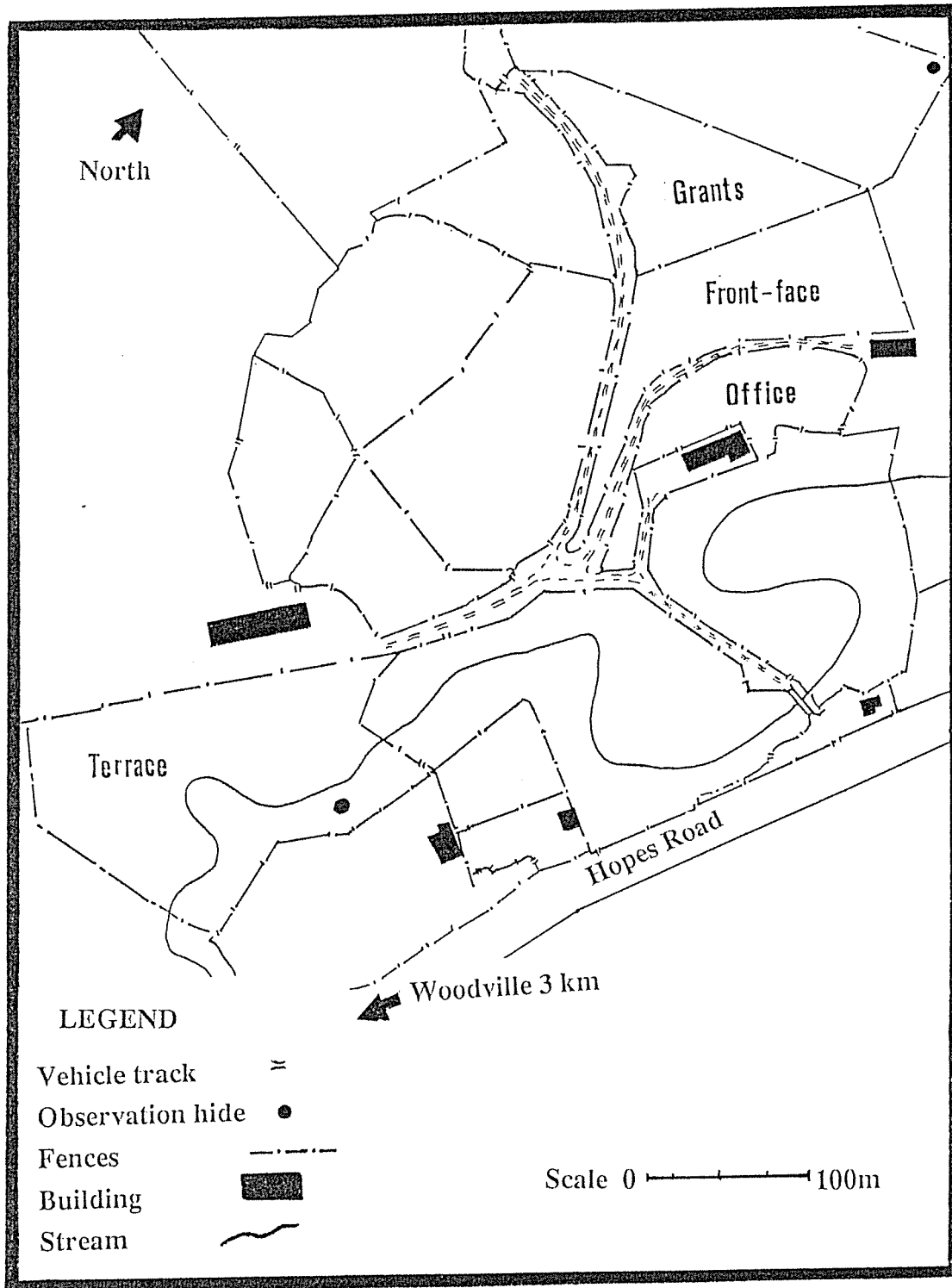
CHAPTER 1

THE MOTHER-OFFSPRING SPATIAL RELATIONSHIP

INTRODUCTION

Many studies on feral goats have described the mother-offspring spatial relationship (Lickliter, 1984, 1987; O'Brien, 1984; Allan et al, 1991), however, they have been centred entirely on the hider/follower model which was developed by Walther (1964) and applied by Lent (1974) to all ungulates. "Hiders" are defined as species in which the mother and her offspring are separated for long intervals immediately post-partum, and interaction between the two is relatively infrequent during this phase. "Followers", on the other hand, are species in which mother and offspring maintain close proximity during post-partum, and interact frequently (Walther, 1964).

Most researchers consider that there is a clear-cut dichotomy of the mother-offspring relationship in ungulates in regard to spatial behaviour (Leuthold, 1977). However, there is confusion over the classification of goats, because in this species the hiding phase varies considerably between populations. Some studies have found the hiding phase to be either completely absent (Gilbert, 1968; Tennessen & Hudson, 1981), or to last for only a few days after parturition (Rudge, 1970; Lent, 1974; Lickliter, 1987). Other studies have reported hiding behaviour extending well into the second week (Lickliter, 1984).

In an attempt to resolve this confusion Walther (1984) claimed that goats should be grouped next to sheep as intermediates on a continuum with "true" hiders (Elk) at one extreme and "true" followers (Chamois) at the other. The argument advanced by Walther was that these intermediate species do not demonstrate completely the hiding behaviour complex. O'Brien (1984), however, concluded that goats deploy both strategies.

From the confusion over differences in the expression of hiding behaviour between domestic goats and their feral counterparts (Licklitter, 1984) and between different populations of feral goats (O'Brien, 1988) has come support for Lent's (1974) suggestion that a combination of factors, including genetic differences, variation in habitat, and tradition, may be responsible for the considerable plasticity of hiding behaviour in goats. However, there have been few investigations of the factors contributing to individual variation in the mother-infant spatial relationship found within a goat population. O'Brien (1984) found maternal age to be an important factor, and mentioned that mothers of twins had significantly different mother-offspring relationships to those of mothers with single kids.

The following study was undertaken to investigate the source of variation within a feral goat population and determine whether there is any significant difference in the mother-offspring spatial relationship between sexes, and between singles and twins.

OBSERVATIONAL METHOD

The animals studied were part of a larger herd of 60 feral goats. The composition of the herd and the location of the study site have been described previously (see General Introduction). Data were recorded from observations of 26 single kids (14 females and 12 males), 11 pairs of twins, and their respective does. All twin pairs consisted of a male and a female kid. Most observations were carried out between 0830 hrs and 1500 hrs. Sample-scans lasting 10 mins were taken at 30 min intervals. The distance between the mother and her kid(s) was estimated in increments of the mother's body length (approximately one metre). Mother-kid distances exceeding

10 mother lengths were grouped into a category referred to as >10 mother lengths. Observation of each mother and her offspring began at parturition during the September to December 1990 period and ended when the majority of kids reached three months of age.

STATISTICAL ANALYSIS

Median distances were calculated for all mother-offspring pairs, using 1-week data blocks. Two single females (those contributing the least number of data points) were omitted from the analysis in order to equalize the sample sizes, thus simplifying the statistical procedure. Data on singles and twins were treated separately, and a Splitplot analysis of variance was done on a computer using Genstat5 Release1.3 software. Sex effect, age effect and the sex and age interaction were determined.

RESULTS

AGE RELATED CHANGES IN THE MOTHER-OFFSPRING SPATIAL RELATIONSHIP

The mother-offspring spatial relationship observed for 26 single kids and 11 twin pairs over the first three months of life is shown in Figures 1.1 & 1.2 ANOVA of mean mother-offspring distance in relation to kid age revealed a significant age effect for twins ($F_{10,160}=5.68$, $P <0.01$) but not single kids ($F_{10,202}=1.99$, NS.). Mother and offspring were relatively close together in the first week. In the second and third week, the mother-offspring distance reached a maximum.
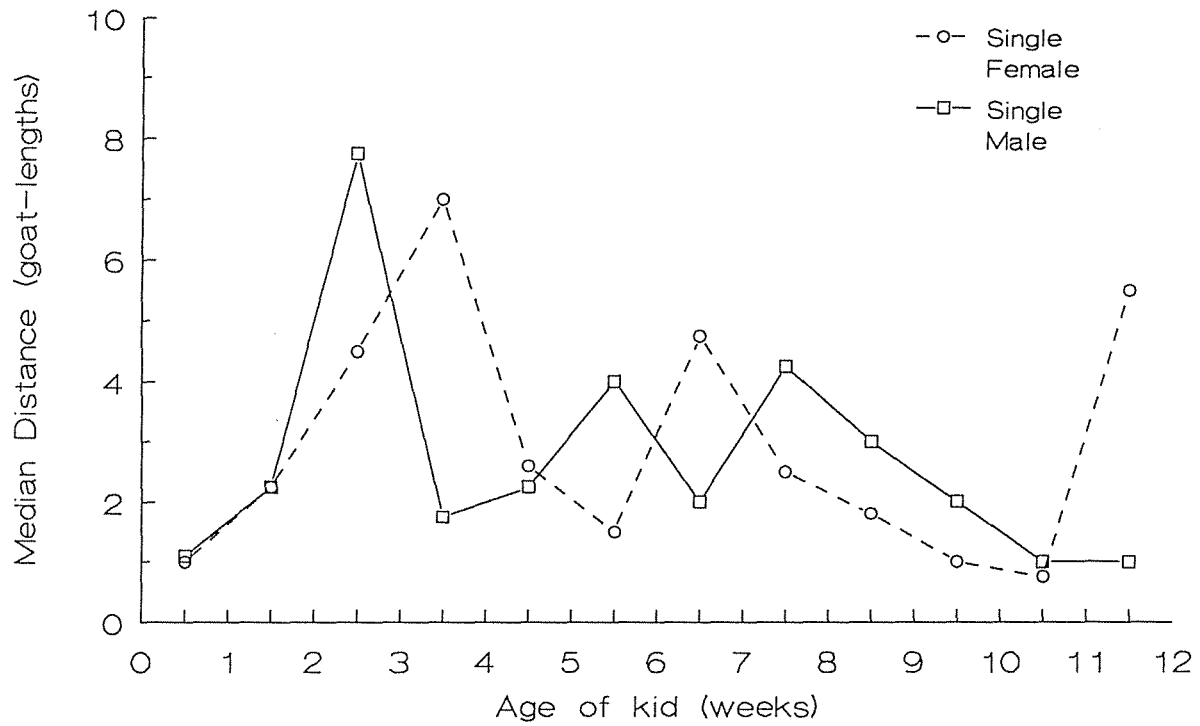
Figure 1.1 Mother—Offspring Distance For Single Feral Goat Kids At Ballantrae, September 1990 — February 1991. One Goat-length = c1.5m.
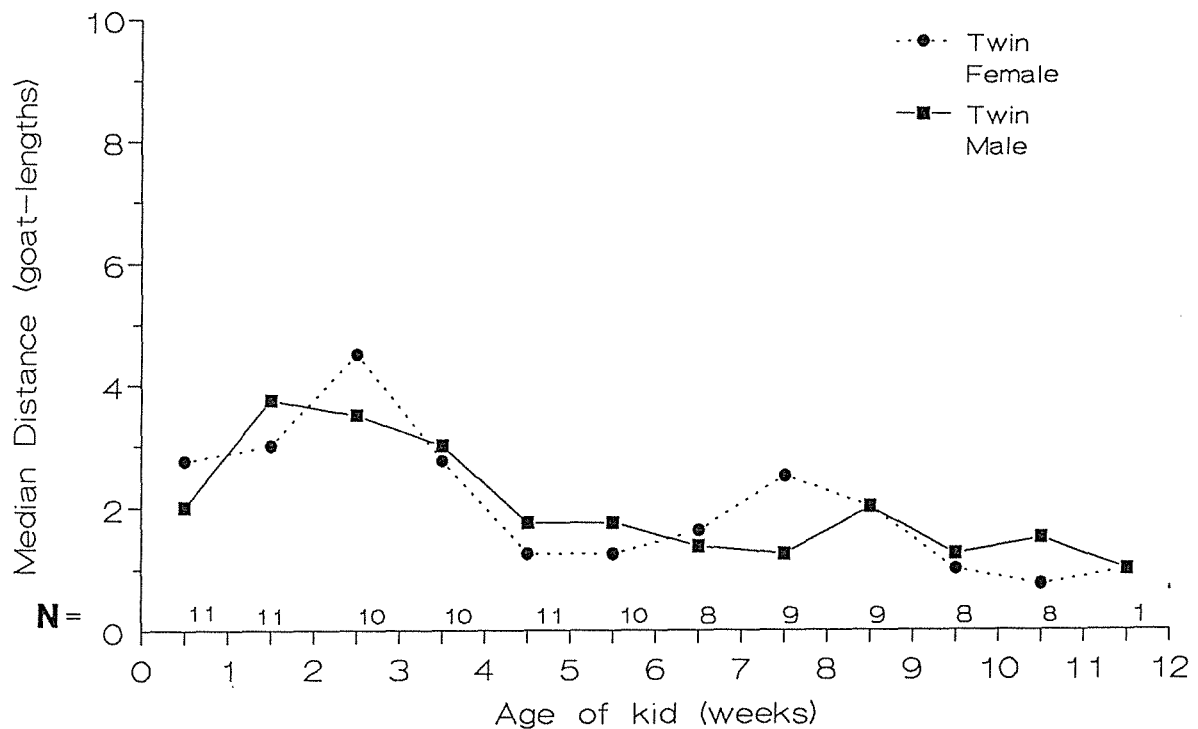
Figure 1.2 Mother—Offspring Distance For Mixed—Twin Feral Goat Kids At Ballantrae, September 1990—February 1991. One Goat-length = c1.5m.

Month 1:
Immediate Post-Partum Period

Immediately after parturition all the does remained in close physical contact with their kid(s). During this time the doe frequently licked the kid and nudged it towards her udder. After attempting to suckle, the neonate eventually lay down. At this point some does remained sitting along side their kids although they occasionally stood to lick and nuzzle them encouraging suckling. Other does stood beside their kids until they lay down to rest. They then slowly moved away, often grazing as they did so, to join the rest of the herd (See Plate 1.1). While some does grazed with the herd others grazed on the outskirts of the herd. These animals were highly vigilant, frequently returning to the kid when conspecifics or humans approached the recumbent kid too closely.

Lying-out Period

During the first three weeks after parturition, does spent on average 35% of their time at a distance > 10 mother lengths from their kid(s). There was considerable variation between does (range 0-76%), but the variation of each doe over the three week period was relatively small. During the period of mother-offspring separation kids were most often observed lying (95% in the first week). In the second and third weeks groups of kids were often left lying-out together, and spent increasing time playing. It was in this early stage of development that kids were first observed nibbling dirt and vegetation. The actual quantity of vegetation consumed was not measured, however, it was unlikely to significantly supplement their milk intake.

Month 2:
Exploratory Period

Over the first month the kids followed their mothers more frequently away from the lying-out site as the doe returned to the herd after suckling. By the fifth week the proportion of time the kids spent > 10 mother lengths from their mother decreased by an average of 25% (P <0.001). While the does grazed, the kids often wandered

Plate 1.1   Following a suckling bout a pair of two-week old twins settle down to rest, their mother grazes close by but slowly moves off to join the rest of the herd (December 1990, 'Office' paddock).

Plate 1.2   A twenty five day old male kid approaches his mother (M) who rests alongside other female herd members. The kid's responsibility for maintaining the mother-offspring spatial relationship increases as the kid matures. This photo was taken early in the kidding season October 1990), 'Office' paddock.

away exploring unfamiliar objects and conspecifics, nibbling vegetation and playing with siblings. During the excitement of a playing bout, or after being frightened by a conspecific, the kids often ran back to their mothers and attempted to suckle. The awareness and movement of mother and kid in relation to one another indicated that both were responsible for maintaining the mother-offspring distance (See Plate 1.2). The proportion of time the kid spent > 1 mother length but < 10 mother lengths from its mother reached a maximum during this period.

Month 3:
The Initial Phase of the Weaning Period

The median mother-offspring distance fell to a minimum during the third month post-partum (Figure 1.1 & 1.2). The kids spent more time grazing next to their mothers and attempting to suckle. The proportion of time spent > 10 mother lengths was not significantly different from month two.

SEX DIFFERENCES

As illustrated in Figure 1.1 the median mother-offspring distance for single females was not significantly different from that for single males (ANOVA: two-way interaction Sex, Age; $F_{10, 202}=0.83$, P >0.05).

Twins were often seen moving together as a pair. Individual twins were observed at equal distance from their mother 84% of the time (n=6) over the first three months. Comparison of the mother-offspring distance of male and female twin pairs is shown in Figure 1.2 . The overall mean for the 11 week period did not differ between the sexes and analysis of variance in relation to age also showed no sex differences (ANOVA: two-way interaction Sex, Age; $F_{10,160}=0.15$, NS.).

COMPARISON BETWEEN SINGLES AND TWINS

Figures 1.1 and 1.2 show that the median mother-offspring distance for twins was less than for singles throughout the first three months except for the first week after birth. The difference between singles and twins was very slight during the first month but reached a maximum in the third week.

DISCUSSION

Application of the hider/follower model to goats

Applying the follower/hider dichotomy to goats is problematic, as has been pointed out by several researchers (Lent, 1974; O'Brien, 1984; Lickliter, 1984; Ralls et al, 1987; Allan et al, 1991). The classical topology of hider and follower species proposed by Walther (1968) is confined to the mother-offspring spatial relationships in the very early stages of ontogeny. In the present study a high degree of variability was observed in post-partum behaviour between does, consequently no credible conclusion can be drawn as to whether goats are hiders or followers.

Lent (1974) further distinguished between hider and follower species by proposing a schema which typifies the spatial relationship occurring from birth to weaning. In spite of the large variation between individuals, the general ontogenetic trend in the mother-offspring spatial relationship observed in this study appears roughly fit the schema for hider type species proposed by Lent (1974) ie. there is a short phase early in kid development during which the mother and kid spend prolonged periods separated. O'Brien (1983) reported a similar divergence of post-partum behaviour within a feral goat population and considered that the classification of goats as a hider type failed to recognise the extent of variability in the species.

The use of median distance between mother and offspring to measure the spatial relationship provides only a broad description of this complex inter-relationship. It is difficult to assess the extent to which lying-out occurs in a goat herd because mothers and kids also separate during the exploratory phase of ontogeny.

Factors contributing to variation in the mother-offspring relationship

Conventionally, researchers have regarded the mother in hiding species to be largely responsible for maintaining mother-offspring distance during the initial lying-out phase (Lent, 1974). Hence, previous investigations of the variability in spatial relationships during early ontogeny have focused exclusively on the plasticity of maternal behaviour (O'Brien, 1984). More recent research (Allan et al, 1991), however, indicates that the potential role of the kid during the hiding phase has been over-looked. Therefore, factors which influence both mother and offspring behavioural processes may contribute to the variability of spatial relations. Some of these factors include: (1) the sex of the offspring, (2) the number of siblings, (3) maternal characteristics and, (4) environmental features.

1) Sex Effect

Differences between male and female kids in their spatial relationship with the mother may arise from either sex-biased maternal investment of the mother, or sexual dimorphism in the behavioural development of the neonate (ie. a more advanced stage of development at birth of either sex could correspond to greater tendency to follow the mother at an earlier age). The present study shows that if the sex of kid affects the mother-offspring spatial relationship it plays a very minor role, and other sources of variation mask any effects. It is likely, however, that sex differences would become apparent after the fourth month when males reach sexual maturity.

2) Effect of Litter size

Earlier studies have shown that throughout lactation mothers of twins remain closer to their offspring than mothers of singles (Morgan and Arnold, 1974; O'Brien 1983). In the present study, this trend was also observed, except during the first two weeks. Competition between individual twins for access to the mother's milk was proposed by Morgan and Arnold (1974) as a biological explanation for the difference between twins and singles observed in sheep. Although highly variable, the delayed following response of kids in the very early stages of development is a fundamental behavioural difference between sheep and goats. In later stages of ontogeny, when the kid's following response is fully developed, competition between individual twins seems a plausible explanation for their closer relationship. During the first week, however, when the neonate is relatively feeble and the maintenance of the parent-offspring relationship is primarily the does responsibility, nutritional intake required to sustain lactation may vary between does. Possibly mothers of twins may need to forage more intensely immediately after parturition than mothers of singles to obtain sufficient nutrients to sustain lactation (Moen, 1978; Mendl, 1988).

3) Maternal Factors

The does nutritional requirements immediately after parturition may be influenced by a number of factors other than litter size. Genetic variation within the feral goat herd may cause individual differences in metabolic rate and fat reserves. Maternal-age may also affect nutritional requirements, as postulated by O'Brien (1983). He suggests that older does tend to be larger and have larger fat reserves than younger does, and therefore are better able to sustain lactation on a restricted diet.

The nutritional condition of a doe and her subsequent ability to lactate governs the supply of nutrients to the neonate. Allan et al (1991) proposed that goat kids are able to adapt their hiding behaviour in accordance with energy availability. Undernourished kids readily adapt to the 'follower' behaviour pattern.

4) Environmental Features

As a consequence of experimental design and temporal distribution of parturition it must be assumed that not all does were exposed to identical environmental conditions. Because no attempt was made to measure variation in environmental conditions the relative effect of environmental factors on maternal behaviour is speculative. Variation in weather conditions, and corresponding fluctuation in grass growth over the season as well as between paddocks, may have been sufficient to affect the foraging efficiency of lactating does. Topography of the paddocks may also have been a source of variation of maternal behaviour. Lickliter's (1984) study on domestic goats illustrated the importance of appropriate hiding sites in inducing lying-out behaviour. During the peak of kidding, when on average three does gave birth each day, lying-out was restricted to one small valley. Occasionally a doe was seen displacing another doe's kid from its lying place, and coaxing its own kid to lie there. This behaviour indicates that favoured hiding sites may have been limited.

Recommendations

Lying-out behaviour can be viewed as troublesome in present farming management systems if only because moving stock to fresh pasture during the early stages of kidding can be hazardous for young kids. Similarly, lying-out makes it difficult to achieve a full muster at docking time. On the other hand lying-out may be regarded as an asset by reducing the incidence of mismothering when the herd is disturbed during kidding. What ever assessment the farmer makes, recognising the variation which exists in post-partum behaviour of feral goats is a step towards improved farm management. By identifying key stimuli which trigger hiding behaviour it may be possible to manipulate environmental conditions to induce or inhibit lying-out. The degree to which the variation in maternal and neonate behaviour is genetic needs also to be assessed so that the preferred post natal behaviour can be selected for.

Conclusion

The inadequacies of the hider/follower model is becoming increasingly apparent. Although the model provides a rough generalisation of mother-offspring relations in ungulates it fails to describe variation between ungulate species or between individual of a particular species. Results from this study indicates that a better understanding of the mother-offspring relationship of feral goats will come from investigation of the source of variation in hiding behaviour rather than attempting to generalise the spatial relationship according to the hider/follower model.

CHAPTER 2

MATERNAL INVESTMENT

INTRODUCTION

The evolutionary perspective of maternal investment proposed by Trivers (1972) has been applied to numerous polygynous species. Trivers' definition of parental investment has been widely cited as "anything done by the parent that increases its offspring's chance of survival and reproduction while decreasing the parent's ability to invest in other offspring" (Braza & San Jose, 1988; Babbitt & Parkard, 1990; Clark et al, 1990). According to Trivers' theory, natural selection favours parents which invest more in offspring of the sex with the greater variance in reproductive success. In polygynous species it is generally the male which has the largest variance in reproductive success. Therefore the theory implies that a mother should invest more heavily in male offspring to the extent that fitness is related to competitive ability. Byers & Moodie (1990) provide a comparative review of sex-biased parental investment in polygynous mammals.

Previous research indicates that feral goats fulfil the assumptions of the parental investment model. Feral goats are polygynous and sexually dimorphic with males weighing 1.2 times as much as females (Kirton, 1970). Sexual segregation of the herd occurs after kidding, but during the mating season males converge around limited oestrous females, and intense competition occurs between males (Dunbar et al, 1990). Access to oestrous females is correlated with large body and horn size (Shank, 1972).

The aim of the present study was to determine whether there is any sex-specific difference in maternal investment in feral goats. The proximate measures of maternal investment investigated were:

(1)   birth weight
(2)   growth rate from birth to three months of age
(3)   maternal weight change
(4)   milk intake based on measures of suckling.

METHODS

The animals studied were part of a larger herd of 60 does. The composition of the herd and location of study site have been described in the General Introduction. Kidding began on 18 September and extended through to 16 December 1990, however, 60% of kids were born between 3-14 November. The kidding season was prolonged because the original buck introduced into the herd in April successfully fertilised only seven of the 60 does (11%) over a one month period. Accordingly two further bucks were introduced and serviced most of the remaining females.

Birth Weight and Kid Growth Rate

Newly born kids were weighed as soon after birth as possible. All birth weights were recorded within 24 hours of parturition. The weighing procedure involved removing the neonate from its mother at the birth site. An electronic scale was used to measure the weight of the kid to the nearest 0.01 Kg (See Plate 2.1). After marking the kids with aerosol paint for identification, the kids were returned immediately to their birth site (See Plate 2.2). No mismothering resulted from this weighing procedure even when, in some cases, kids were removed for weighing within 10 minutes of parturition.

Plate 2.1   A new born kid is weighed on an electronic scale.

Plate 2.2   After the weighing procedure the neonate is marked with aerosol
             paint for identification and returned to its birth site.

During the first three months following kidding the herd was mustered once a week, and the kids were weighed .

Plate 2.3   The study herd is being mustered to the wool shed where the kids will be weighed. A weekly event during the kidding season (September 1990 - February 1991.

Maternal Weight

Over the course of the reproductive cycle two measurements of doe weight were made on electronic scales to the nearest 0.1 Kg.

Pre-gestation Weight: all does were weighed on 22 May 1990, the week prior to the release of the bucks.

Post-partum Weight: does were weighed during the first week following parturition

Two-sample t-tests were performed to test for differences in weight changes of does which bore singles and twins of each sex.

Suckling Data

Suckling data and relevant information included: kid and mother identity, suckling event initiator and terminator, suckling duration. These aspects of suckling behaviour were obtained by *ad lib* sampling. Most observations were made between 0830 and 1600 hours.

Suckling Behaviour Terminology and Definition

Suckling Event: A suckling event begins when the kid first puts its head in the udder region, often accompanied by tail-wagging and nudging the udder (bunting), and ends when the kid withdraws its head or the mother terminates the suckle by stepping forward and lifting her hind leg over the suckling kid. Suckling episodes less than 5 secs apart were recorded as a single suckling event. A suckling event as defined here is equivalent to the 'suckling bout' of Hinch (1989).

Suckling Duration: The length, in seconds, of a single suckling event.

Suckling Frequency: The number of suckling events occurring in a 12-hour period.

Suckling Bout: This was defined by Gauthier & Barrette (1985) as one or more suckling events separated by an interval of less than 10 minutes.

Unsuccessful Suckling Attempt: Any unsuccessful attempt by the kid to reach the udder, or any suckling event in which contact with the teat lasted less than 1 second before termination by the mother.

Total Suckling Time: The total time in seconds, spent suckling in a 12-hour period. This is calculated by multiplying the mean suckling duration by the mean suckling frequency for each individual.

Initiation and Termination of suckling

Initiation of a suckling event by the mother frequently involved calling to her young prior to the kid running to her and suckling. The mother sometimes walked towards the kid, stood a few metres away and looked towards it. In the early phase of kid development the mother often licked, pawed, and muzzled her young prior to suckling. These actions were included as incidents when suckling was initiated by the mother. Initiation of a suckling event by the kid involved any vocalisation by the kid to which the mother responded either by calling, or walking toward the kid. Suckling was also preceded immediately by tactile behaviour such as the kid climbing on its mothers back.

Termination of a suckling event by the mother usually involved lifting her hind leg(s) over the suckling kid(s) and walking a couple of paces forward (See Plate 2.4). Suckling was also terminated when the kid voluntarily withdrew its head from the udder region.

Plate 2.4   A 1.5 month old kid stands on his mother's back. Often this causes the mother to stand, providing the kid with access to the udder.

Plate 2.5   A doe terminates the suckling of her 1.5 month old male kid by lifting her hind leg over the kid and walking forward a few paces.

STATISTICAL ANALYSIS

Birth Weight and Growth Rate

0-3 month, 0-1 month, and 1-2 month growth rates: Kid weight was plotted against kid age (in weeks) during the first three months. For each kid, the gradient of the regression line over the entire three months, the first month, and the second month (respectively) was calculated. The mean growth rate was determined for singles and twins of both sexes. Two sample t-tests were used to test for sex differences in birth weights and growth rates between single kids and to compare twins and singles of the same sex. Paired t-tests were used to test for a sex difference between kids of mixed-twins.

Suckling Duration, Frequency and Total Suckling Time

Weekly means for each of the suckling variables were calculated for each kid. Data on singles and twins were treated separately and a Splitplot analysis of variance was done on a computer using Genstat5 Release 1.3 software. Sex effect, age effect and the sex and age interaction were determined.

Initiation and Termination of Suckling

The mean age (in days) when kids no longer terminated suckling events was calculated for singles and twins of both sexes. Mann Whitney U tests were used to compare sexes and birth types.

RESULTS

Kidding Rate and Sex Ratio

The herd was in good condition with 90% of does kidding. Out of a total of 52 pregnant does 23 gave birth to twins or triplets (44%), resulting in a kidding rate of 140%. Triplets were not included in the quantitative analysis because there were too few of these birth types.

The sex ratio of all kids born, 46 females:31 males, was not significantly different from unity (X^2=2.92, NS.), but the sex ratio of twins was biased towards females, 33 female :17 male (X^2=5.12, P <0.05).

Mortality

Of the seven kids which died during kidding only one was male. This male died of starvation following the death of his mother three days after parturition. Postmortem diagnoses at Massey University Veterinary School revealed that two of the six doe kids died of white muscle disease (a single and twin female); two died of goitre (a twin pair); and one set of twins died after birth one week prematurely. Kid mortality therefore appeared to be biased towards kids of multiple births. In 11 incidents of multiple births (23 kids) five kids died. In 29 single births only 1 kid died (X^2=4.21, P <0.05).

Kid mortality also occurred in later stages of kid development. A female of a mixed twin died at 46 days old and a female from a set of triplets died aged 25 days. Inability to compete with siblings for limited milk supply appeared to be the cause of death.

Length of Gestation

There was no significant difference (t=0.75, df=29, NS.) in the length of gestation between singles and twins, and between males and females (mean 149 days, range 130-168 days, t=0.85, df=16, NS.).

Maternal Weight Changes

The pre-gestation weight, post-partum weight and seasonal weight change of does which bore singles did not differ significantly from that of does which had twins (Pre-gestation t=0.57, df=41 ; Kidding t= -1.71, df=37 ; Weight change t=1.84, df=28 ; P >0.05). Similarly there was no significant difference in the three maternal weight variables of does with male kids compared to those with female kids (Pre-gestation t=0.09, df=21 ; Kidding t= -0.35, df=22 ; Weight change t= -1.34, df=18 ; P >0.05).

Birth Weight

The average birth weight for each sex and birth type is given in Table 2.1. Single males were significantly heavier at birth than individual male twins, and single females P <0.05). Single females were born heavier than individual female twins (t=2.29, df=21, P <0.05). The birth weight of male twins was on average 8% greater than female twins (t=2.48, df=12, P <0.05).

Growth Rate

Table 2.1 gives the average growth rate of kids during the first three months after parturition. Differences between sexes are shown in Figure 2.1. Singles grew faster than twins (Single male vs twin male t=4.47, df=20 ; Single female vs twin female t=4.86, df=22 ; P <0.0001) and males grew faster than females (Singles; t=3.42 , df=23, P <0.005 ; Mixed-twins t=3.32, df=10, P <0.01). Single females and

females in twin births grew faster during the first month than the second month of life (Single females t=2.97, df=6 ; Twin females t=3.24, df=5 ; P <0.05). Although twin males tended to grow more rapidly in the first month, the growth rate of single males remained constant over the first two months (Single males t=1.94, df=10, NS. ; Twin males t=3.29, df=5, P <0.05). The growth rate of females from single sexed twins was not significantly different from the growth rate of females from mixed twins (t=1.83, df=20, NS.).

Table 2.1   Feral Goat Kid Birth Weight and Growth Rate to Three Months of Age. Ballantrae, September 1990-February 1991.

Type of Birth		Kid No.	Birth Weight kg (σ)	Growth Rate (Kg/Day) (σ)
Single	Male	12	2.91 (0.35)	0.149 (0.019)
	Female	13	2.62 (0.28)	0.123 (0.019)
Twins	Male	11	2.53 (0.24)	0.110 (0.020)
	Female	11	2.34 (0.34)	0.089 (0.016)

Correlations between kid birth weight, kid growth rate over the first month, and maternal weight were calculated for singles and twins of each sex and the coefficients of correlation are shown in Table 2.2. There was significant positive correlation between kid birth weight and growth rate for single males only. This correlation is illustrated in Figure 2.2. Although there was no significant correlation between maternal weight and kid birth weight, the tendency for birth weight of single kids to be positively correlated to maternal weight was stronger than for twin kids. Growth rate of single female kids over the first month was positively correlated to maternal weight.

Figure 2.1 Mean Weights Of Single And Twin Kids In Relation To Age. Feral Goats at Ballantrae. September 1990 — February 1991.

	0	1	2	3	4	5	6	7	8	9	10	11	12
Single M	10	10	12	10	10	9	9	8	9	1	6	4	1
Single F	10	10	12	10	10	9	9	8	9	1	6	4	1
Twin M & F	10	10	12	10	10	9	9	8	—	1	6	4	1
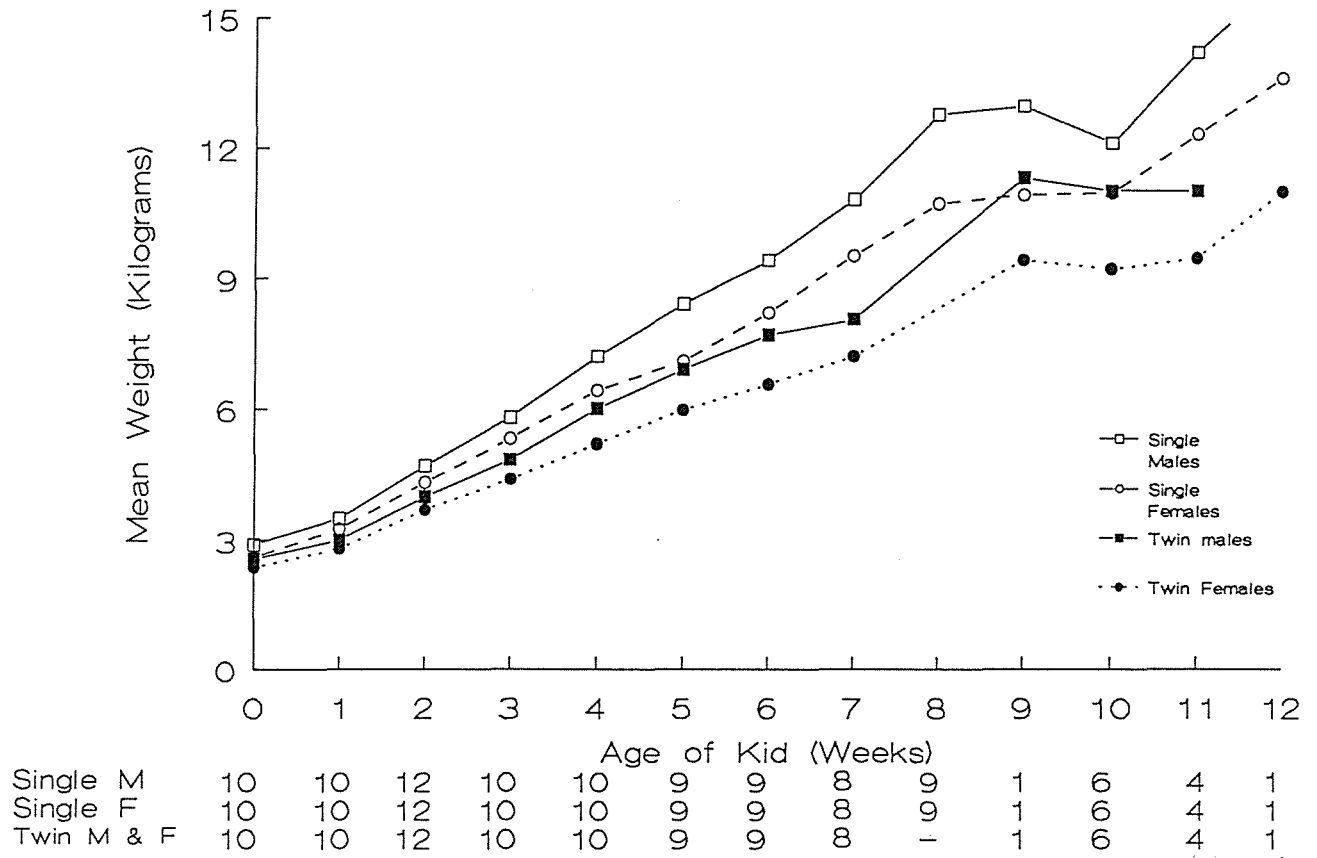
Table 2.2   Coefficients of Correlation Between Kid Birth Weight, Kid Growth
Rate and Maternal Pre-gestation Weight for Feral Goats at Ballantrae
September 1990-February 1991

| | Type of Birth | | | |
| | Singles | | Twins | |
Factors Correlated	Male	Female	Male	Female
Maternal wt. and kid birth wt.	0.41	0.33	-0.07	-0.07
Maternal wt. and kid growth rate				
0-1 month	0.22	0.36	0.02	0.24
0-3 months	0.26	0.74**	0.13	0.18
Kid birth wt. and kid growth rate	0.66*	0.12	-0.08	0.46

Significance: *P <0.05 **P <0.01
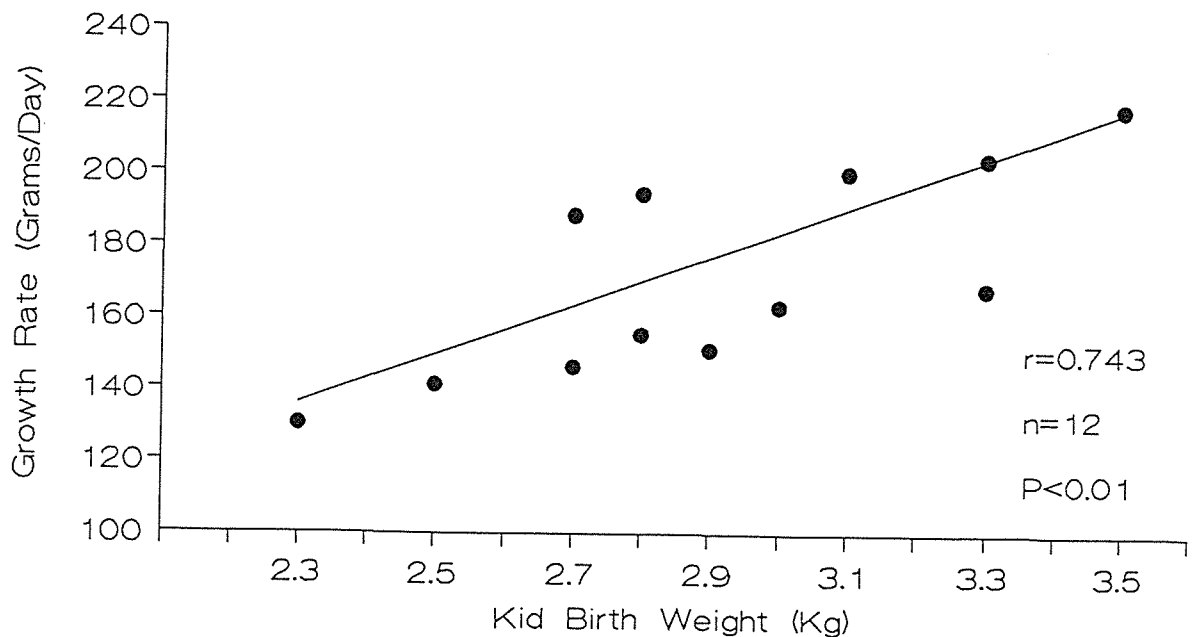
Figure 2.2 Correlation Between Birth Weight And Growth Rate In The First Month For Single
Male Kids. Feral Goats At Ballantrae September 1990 — February 1991.

Suckling Duration

Figures 2.3 & 2.4 show that the sex of a kid did not significantly influence the duration of suckling for twins (ANOVA: two-factor Sex, Age $F_{7,180}=0.27$, NS.) or singles (ANOVA: two-factor Sex, Age $F_{8,143}=0.82$, NS.). It was also noted that mothers of twins allowed their kids to suckle for longer when both were present, however, there is no quantitative data presented in this study to support this. The mean length of suckling events decreased during the first two months of life in both single kids ($F_{8,143}=20.56$, P <0.0001) and twins ($F_{7,108}=12.54$, P <0.01).

Figure 2.5 shows that single kids tended to suckle longer than twins. Suckling duration was highly variable in the first three weeks (ranging from 5 secs to over 3 mins) but then stabilized at 25 seconds during the second month. In the third month suckling duration fell to a mean of 20 seconds (S.E$^{\pm}$ 0.87) for singles and 18 seconds (S.E$^{\pm}$1.7) for twins.

Suckling duration depended on the interval between suckles. When suckling events occurred close together the duration of suckling also depended on the length of the previous suckling events thus relatively short suckles (<10 secs) mostly occurred most soon after a relatively long suckle >100 secs).

Figure 2.3 Suckling Duration For Single Kids During The First Three Months. Feral Goats At Ballantae. September 1990–February 1991.

Figure 2.4 Suckling Duration For Mixed—Twin Kids During The First Two Months. Feral Goats At Ballantrae. September 1990 — February 1991.
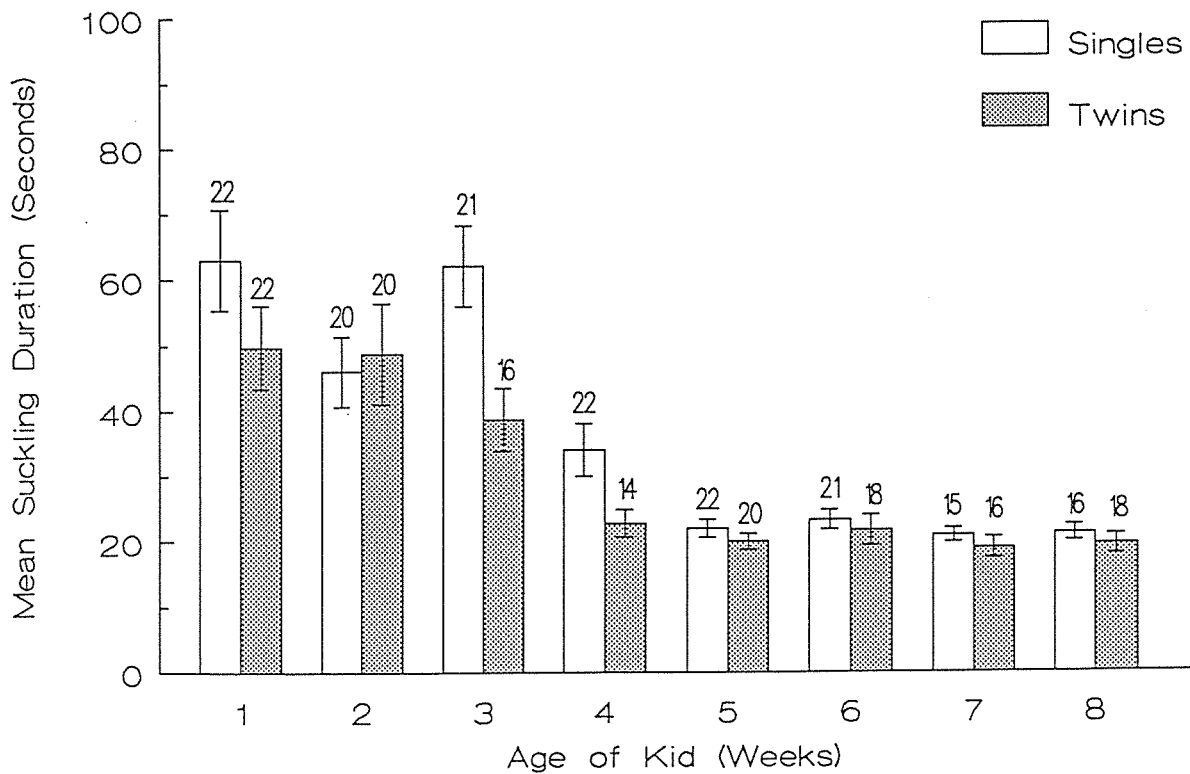
Figure 2.5 Suckling Duration For Single And Twin Kids During The First Two Months. Feral Goats At Ballantrae. September 1990 — February 1991.

Suckling Frequency

Figure 2.6 shows the mean number of individual suckling events that occurred in a 12 hour period for twins and singles in the two months following parturition. The frequency of suckling was high during the first week (11 events in 12 hours) for both singles and twins. There was, however, considerable variation between individuals (range 1-33 events in 12 hrs.). The suckling frequency for twins steadily declined during the first month then stabilized at 3 events in 12 hours over the second and third month ($F_{5,80}$=27.79 ; P <0.001). Singles exhibited a more abrupt decrease in suckling frequency during the first three weeks than did twins, and the frequency levelled off at 5 events in 12 hours ($F_{4,76}$=5.55 ; P <0.001)

ANOVA showed single males suckled more frequently than single females during the first two months ($F_{4,76}$=4.86 ; P <0.05). However, as shown in Figure 2.7, sex differences occurred mostly in the first two weeks of life (ANOVA: Two-way interaction Sex, Age ; $F_{1,76}$=4.06 ; P <0.05).

Figure 2.8 shows that differences in suckling frequency between males and females of mixed-twins occurred in the first month. During this period, only one twin suckled 40% of the time. During the second and third month, individual twins seldom suckled without their sibling. Throughout the three month study period there was no significant difference in the suckling frequency between males and females of mixed-twins (ANOVA: Two-way interaction Sex, Age, $F_{5,80}$=0.59, NS.).

The pattern of suckling changed as the kids grew older. Initially, the mother and kid spent a large portion of their time apart and suckling bouts were separated by relatively long intervals. During these intervals the mother grazed, while the kid rested. However, each suckling bout consisted of a series of suckling events of variable duration. The kid was allowed to suckle until satiated; suckling bouts lasting for 5-15 minutes. For triplets suckling bouts lasted longer because they competed vigorously for access to the mother's teats. On one occasion a female suckled her triplets for over an hour with intervals between suckles less than 10 minutes long. As the kids, matured suckling bouts became more evenly distributed over the day, and the number of suckling events per suckling bout decreased. By the second month suckling bouts seldom occurred less than 10 minutes apart.
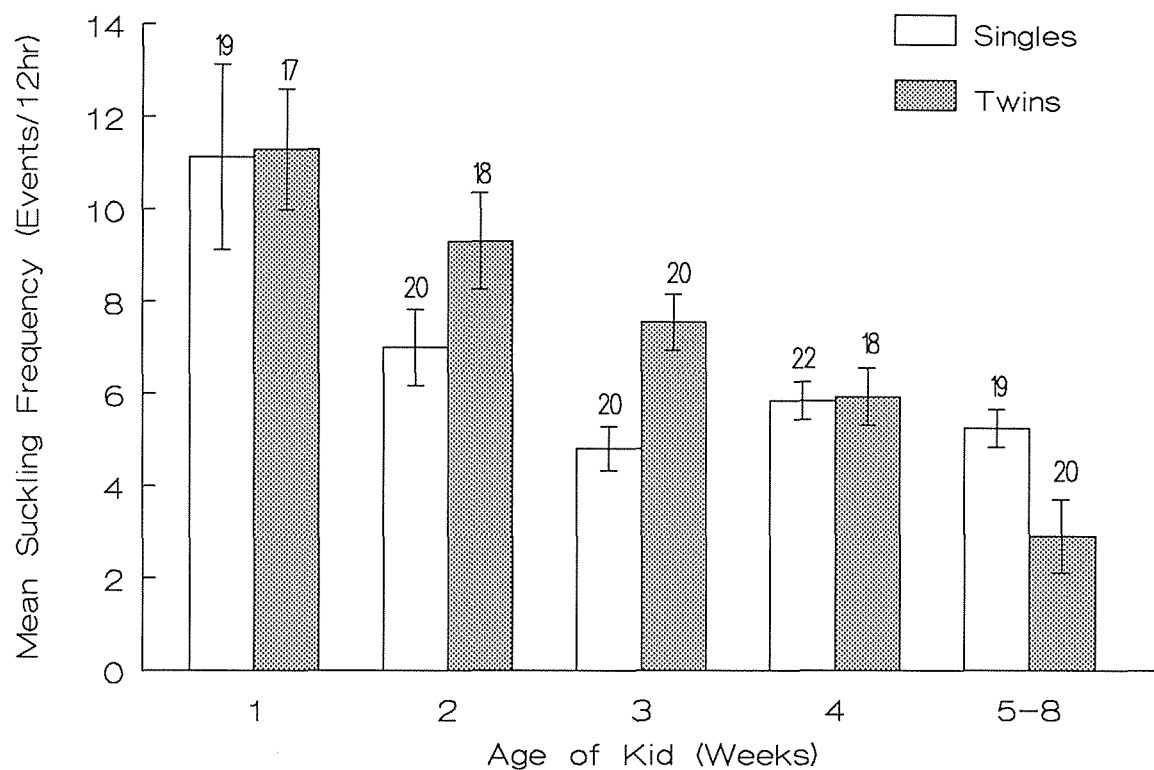
Figure 2.6 Suckling Frequency of Single And Twin Kids During The First Two Months Feral Goats At Ballantrae September 1990–February 1991.
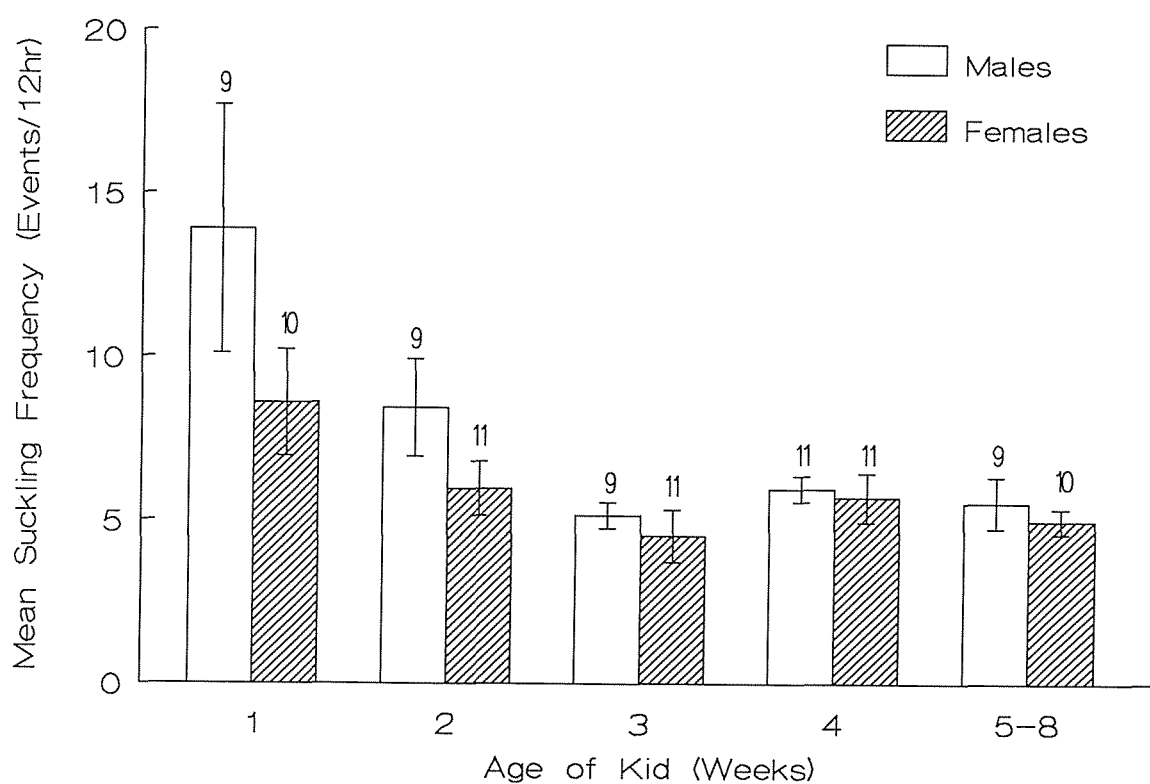
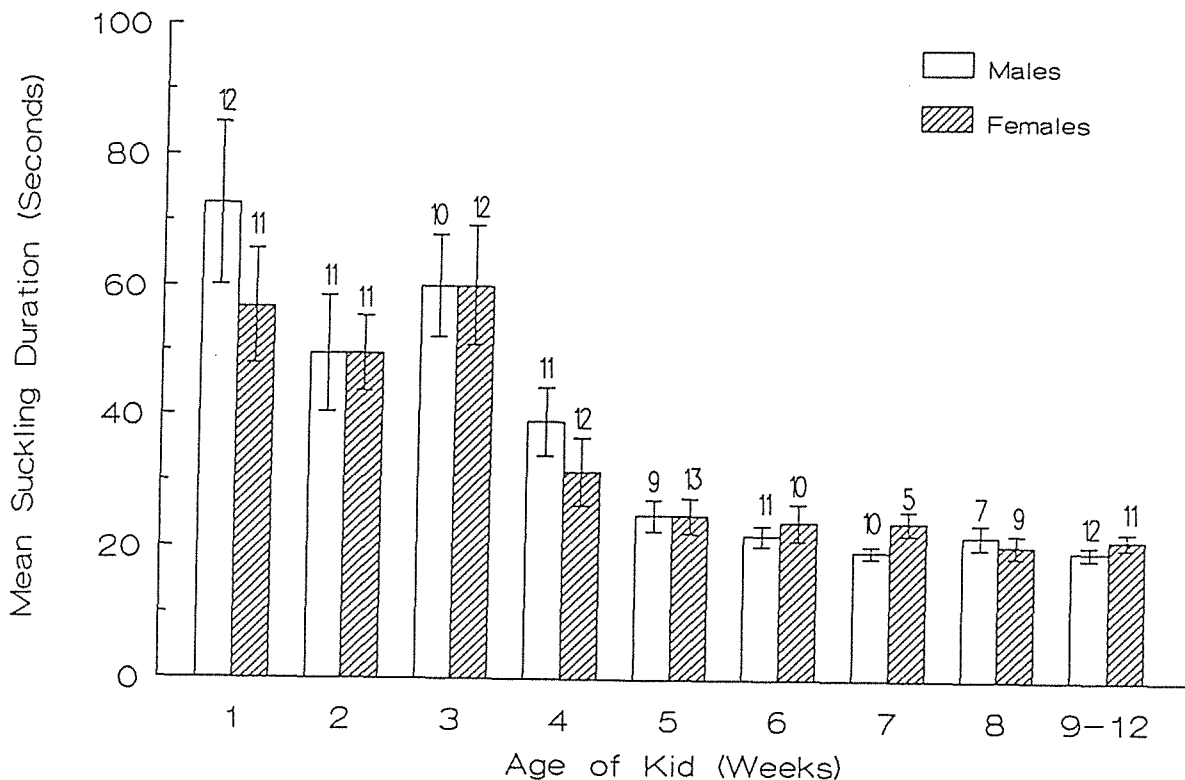Figure 2.7 Suckling Frequency For Single Kids During The First Two Months. Feral Goats At Ballantrae September 1990–February 1991.
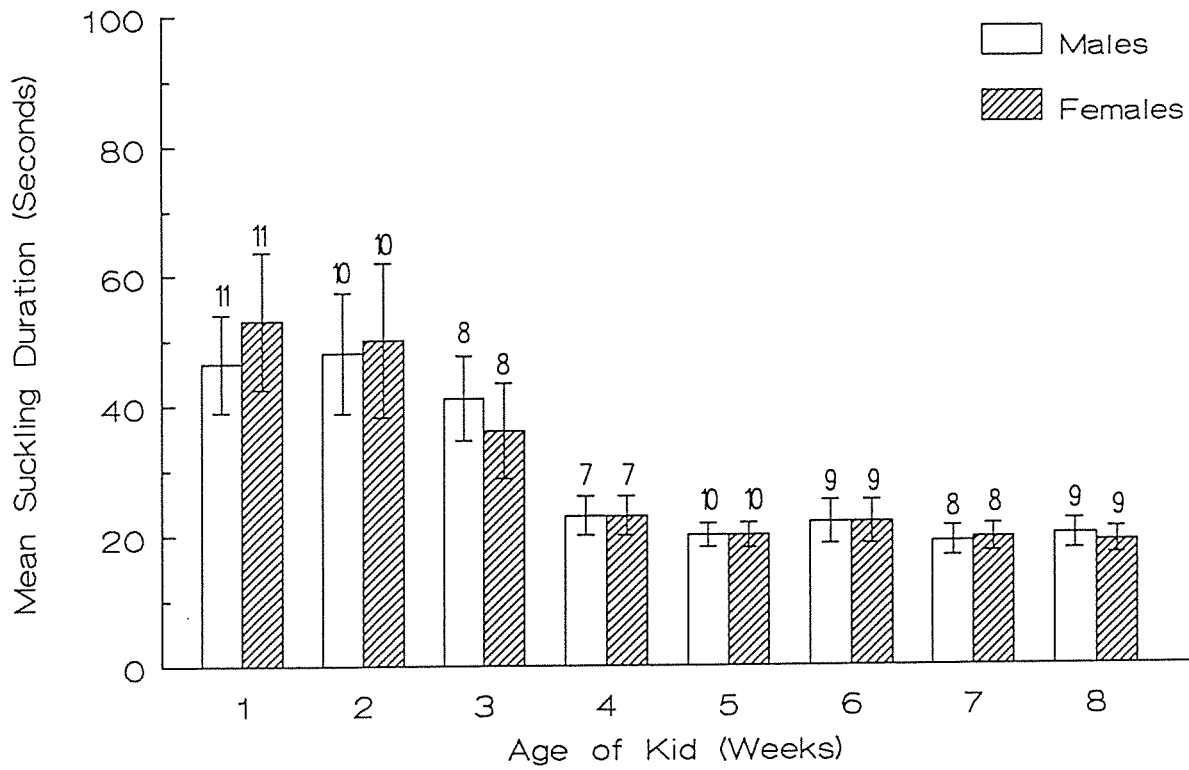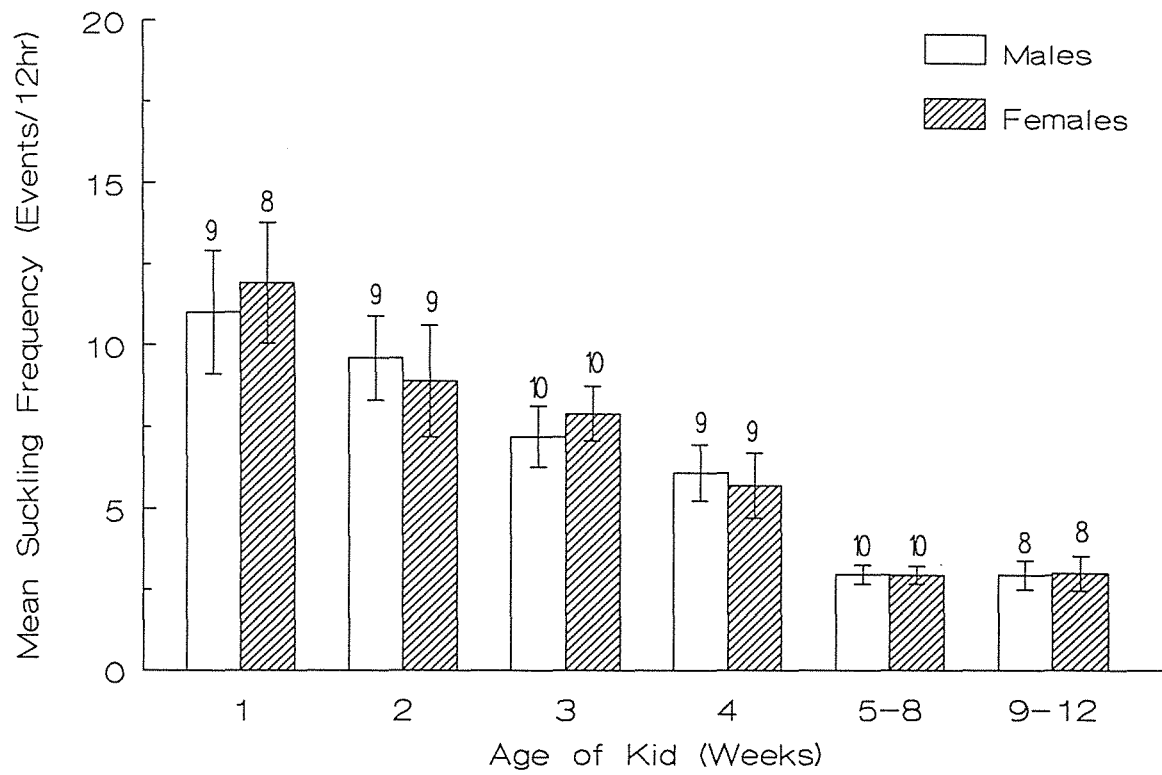
Figure 2.8 Suckling Frequency For Mixed-Twin Kids During The First Three Months. Feral Goats At Ballantrae September 1990-February 1991.

Total Suckling Time

The total time spent suckling steadily decreased during the first two months as seen in Figures 2.9, 2.10 & 2.11. Figure 2.9 shows that throughout the two months following parturition the total suckling time for single males was greater than for females, however, statistical tests revealed the difference to be insignificant. As seen in Figure 2.10 there was no significant sex difference between individuals of mixed-twins (ANOVA: Two-way interaction Sex, Age ; $F_{5,62}$=0.15 ; NS.).
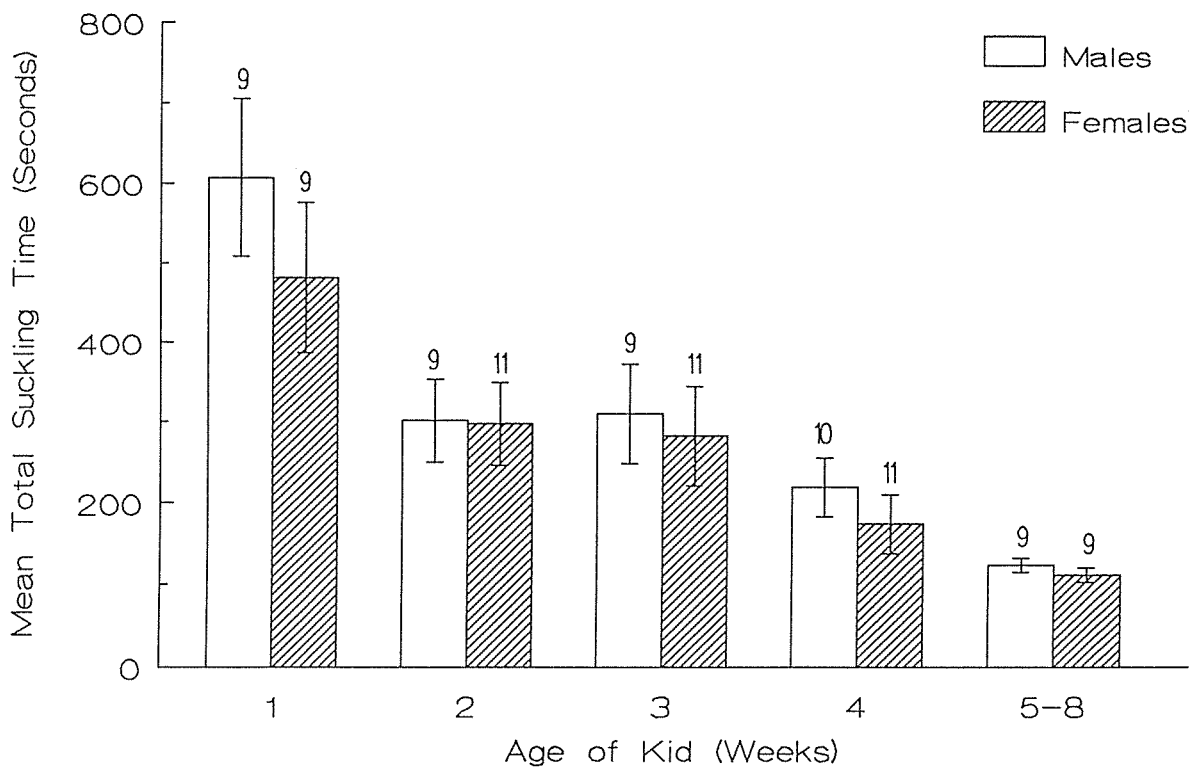
Figure 2.9 Total Suckling Time For Single Kids During The First Two Months. Feral Goats At Ballantrae. September 1990–February 1991.
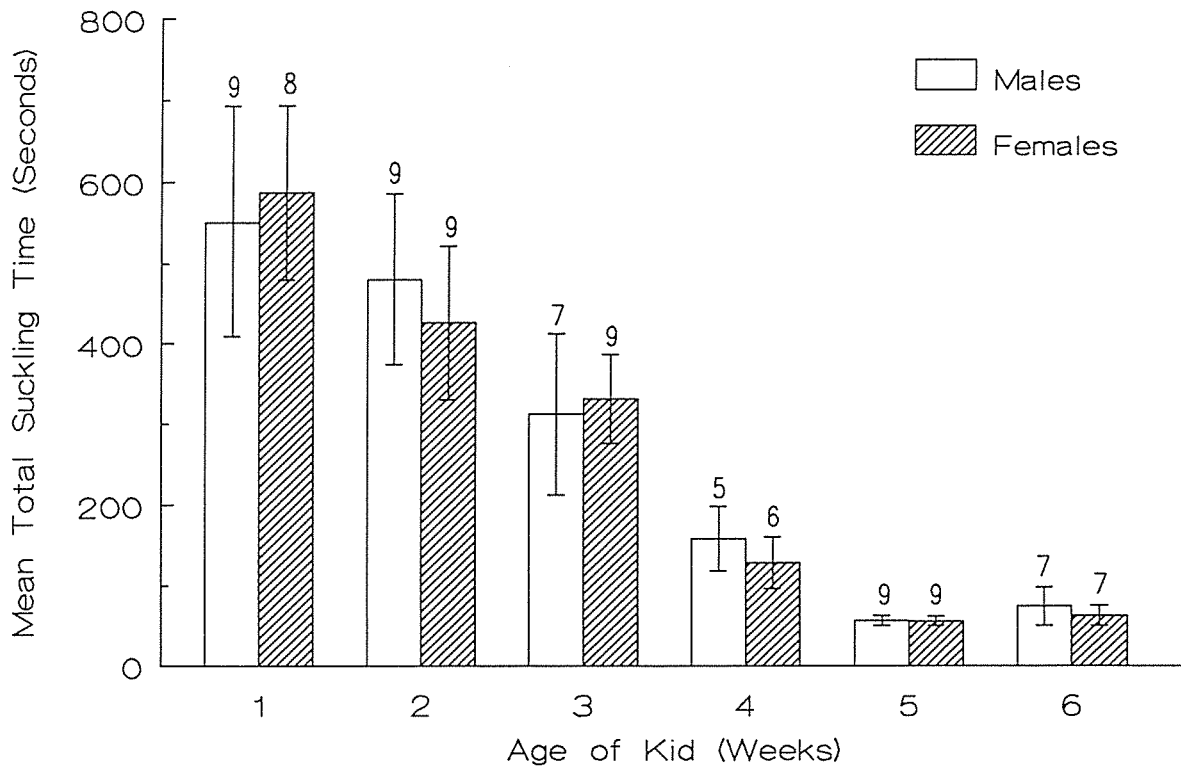
Figure 2.10 Total Suckling Time For Mixed–Twin Kids During The First Six Weeks. Feral Goats At Ballantrae September 1990–December 1990.
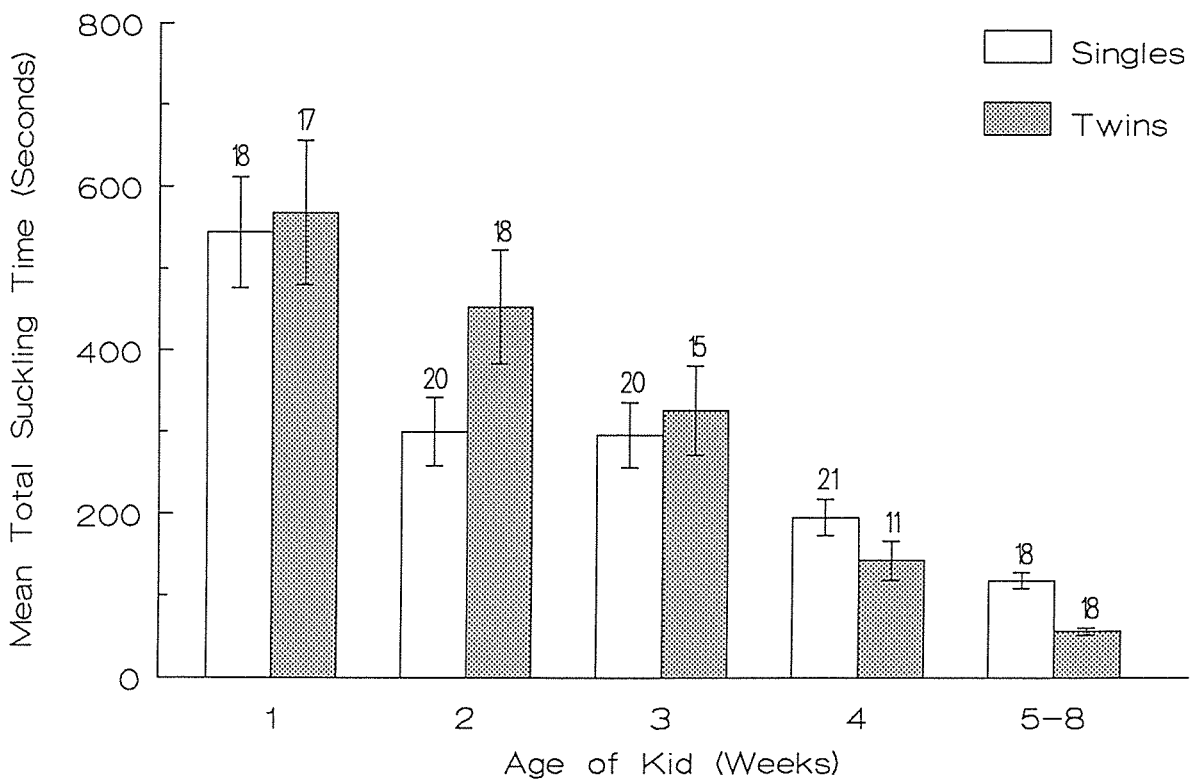
Figure 2.11 Total Suckling Time For Singles And Twins During The First Two Months. Feral Goats At Ballantrae. September 1990–February 1991.

Initiation of Suckling

On average, kids initiated most (63%) suckling events and the proportion increased steadily between birth and 10 weeks of age (Table 2.3).

Table 2.3   The Mean Percentage of Suckling Events Initiated by Feral Goat Kids as a Function of Kid Age. Ballantrae, September 1990-February 1991.

Birth Type		Kid Age (Days)				
		0-14	15-28	29-42	43-56	57-70
Singles	Mean	32	44	62	80	79
	SE	7.6	8.1	6.6	6.1	5.4
	n	25	24	22	21	15
Twins	Mean	28	61	73	86	77
	SE	7.1	9.3	8.7	9.0	8.0
	n	8	9	11	6	9

There was no significant sex difference in the percentage of suckling events initiated by the kid for both singles and mixed-twins (Singles $z=1.30$, $df=21$; twins $z=1.21$ $df=10$; NS.). Figure 2.12 shows there was a tendency for twins to initiate suckling events more often during the first two months of life. However, only during the second period (15-28 days of age) was this difference significant. Twin kids initiated suckling events sooner than single kids but this difference was not significant ($z=1.94$, $df=32$; NS.). There was no difference between the sexes in the average age at which initiation of suckling events became the responsibility of the kid. ($z=0.76$, $df=11$, NS.).
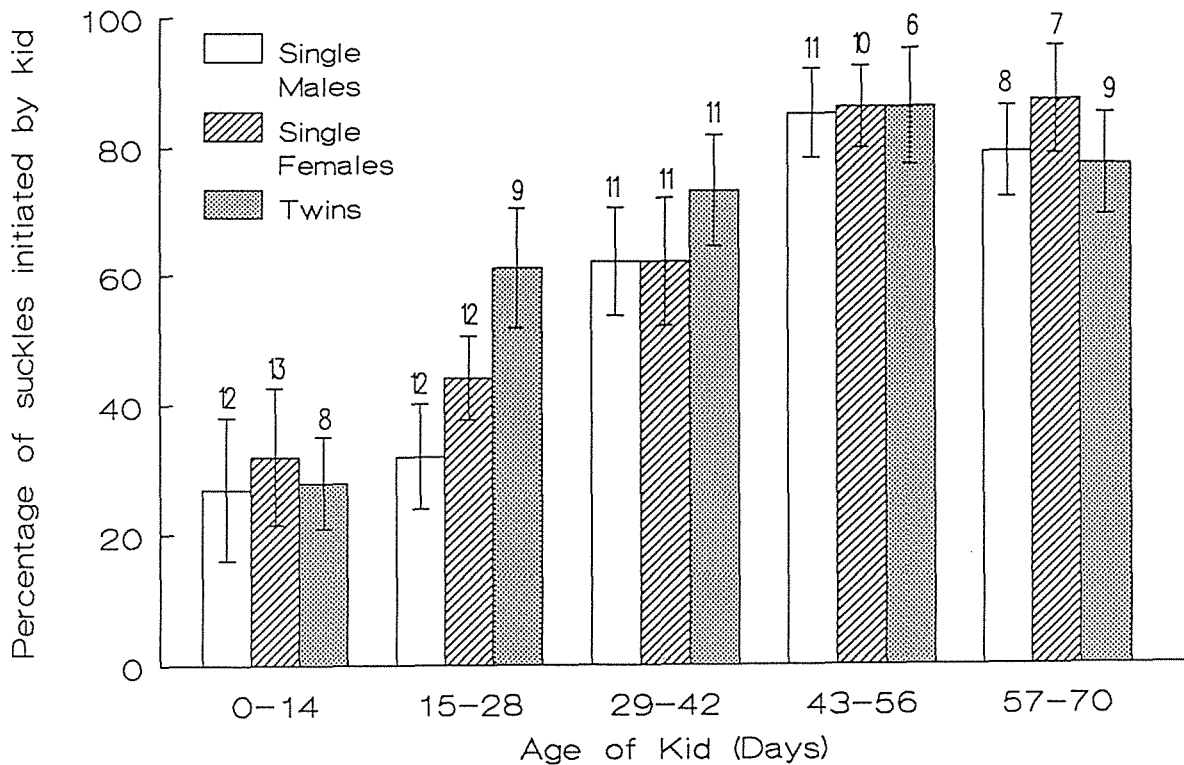
Figure 2.12 Proportion Of Suckling Events Initiated By Single And Twin Kids In Relation To Age. Feral Goats At Ballantrae. September 1990—February 1991.

During the first week when the kid was relatively inactive and the mother determined the mother-offspring distance, virtually all suckling bouts were initiated by the mother. However, on occasions when the mother grazed in the near vicinity of the kid she returned to it in response to its calls. After the second or third suckling bout when suckling motor patterns had fully developed the kid frequently initiated suckling events within a suckling bout. During this early period does were generous with their milk and often tried to stimulate recumbent kids to suckle by licking and nuzzling them, or less frequently, scraping them with a foreleg. By the second week the kid responded to its mother's call by running toward her as she approached. In the third week, the kid would attempt to locate its mother, calling frequently as it wandered through the herd. A kid's ability to recognise its mother from a distance appeared to be limited, and it was not unusual for a kid to fail to find her if she did

not respond to its call. During this period there were occasions when a kid identified the wrong doe as its mother. The kid would run toward the doe, stop within approximately two metres of her and not attempt to suckle.

Initially mothers allowed kids to feed until satiated, but as the kids grew they became more demanding on milk supplies. Tactile behaviour by the kid towards its mother, such as rubbing its head against the mother's neck, or playfully leaping on and off the her back often induced the mother to stand, providing the kid with access to the udder, and therefore served in initiating suckling. When the mother was walking the kid often initiated suckling by first cutting across its mother's path and causing her to stop. It then attempted to suckle on the opposite side to which it approached her. When the mother was grazing the kid followed closely, grazing very close to the mother's head. The success of the kid's attempt to suckle depended on the mother's response.

Plate 2.6   Seven day old twin kids respond to their mother's call by running toward her as she approaches.

Termination of Suckling

The increase in the proportion of successful suckles terminated by the mother is shown in Figure 2.13. For singles, all suckling events during the first 6 days were terminated by the kid. During the second and third week progressively more suckling events were terminated by the mother. By the fourth week the mother terminated the majority (90%) of suckles. In twins, termination of suckling by the mother occurred even on the kids first day of life as the mother tried to nurse both kids simultaneously. By the third week all suckling events were terminated by the mother. Vigorous competition between triplets for access to the mother's udder meant suckling was normally terminated by the mother at all stages during the first three months.

The initial period during which the kid took part in terminating suckling lasted significantly (z=1.76, df=32, P <0.001) longer for singles (mean 23 days, SE 1.8) than for twins (mean 11 days, SE 1.6), however there was no significant difference between the sexes (z=1.76, df=18, NS.).
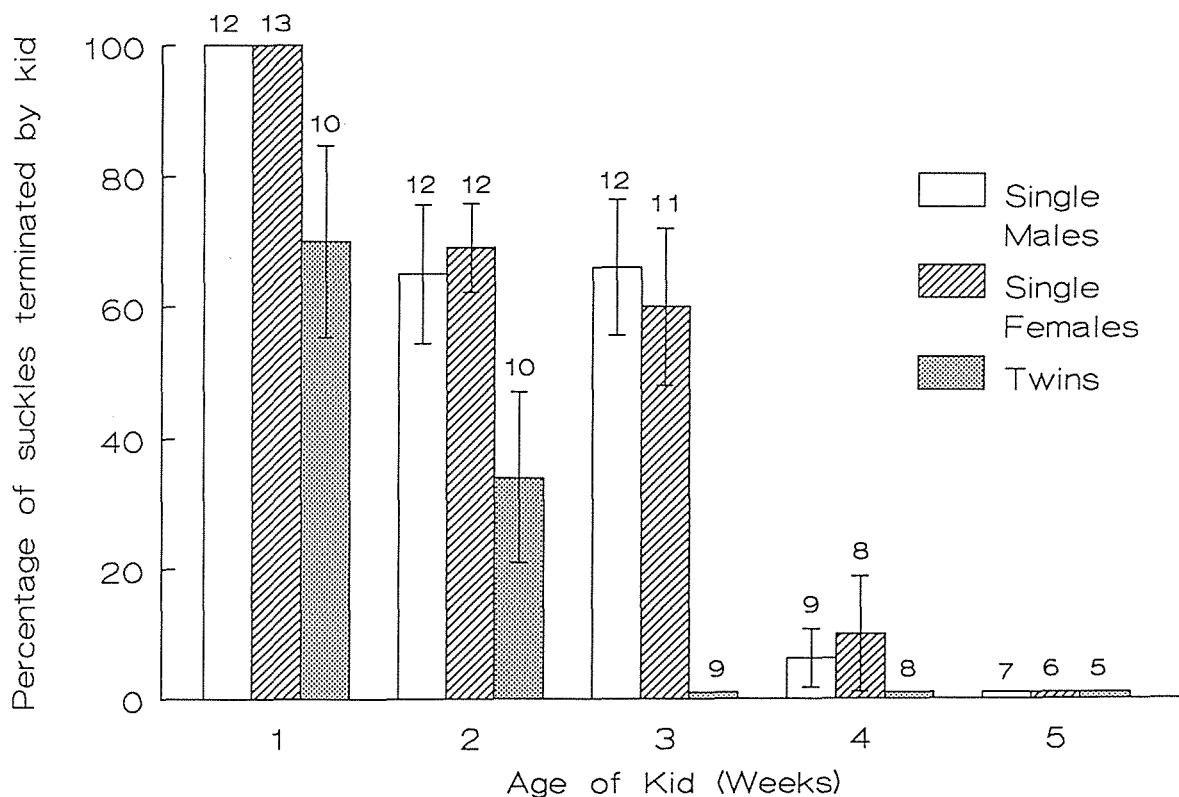
Figure 2.13 Proportion Of Suckling Events Terminated By Single And Twin Kids During The First Five Weeks. Feral Goats At Ballantrae, September 1990 — February 1991.

Unsuccessful Attempts at Suckling

Figure 2.14 shows an increase in the proportion of suckling attempts which were unsuccessful for each week during the first two months of the kids life.
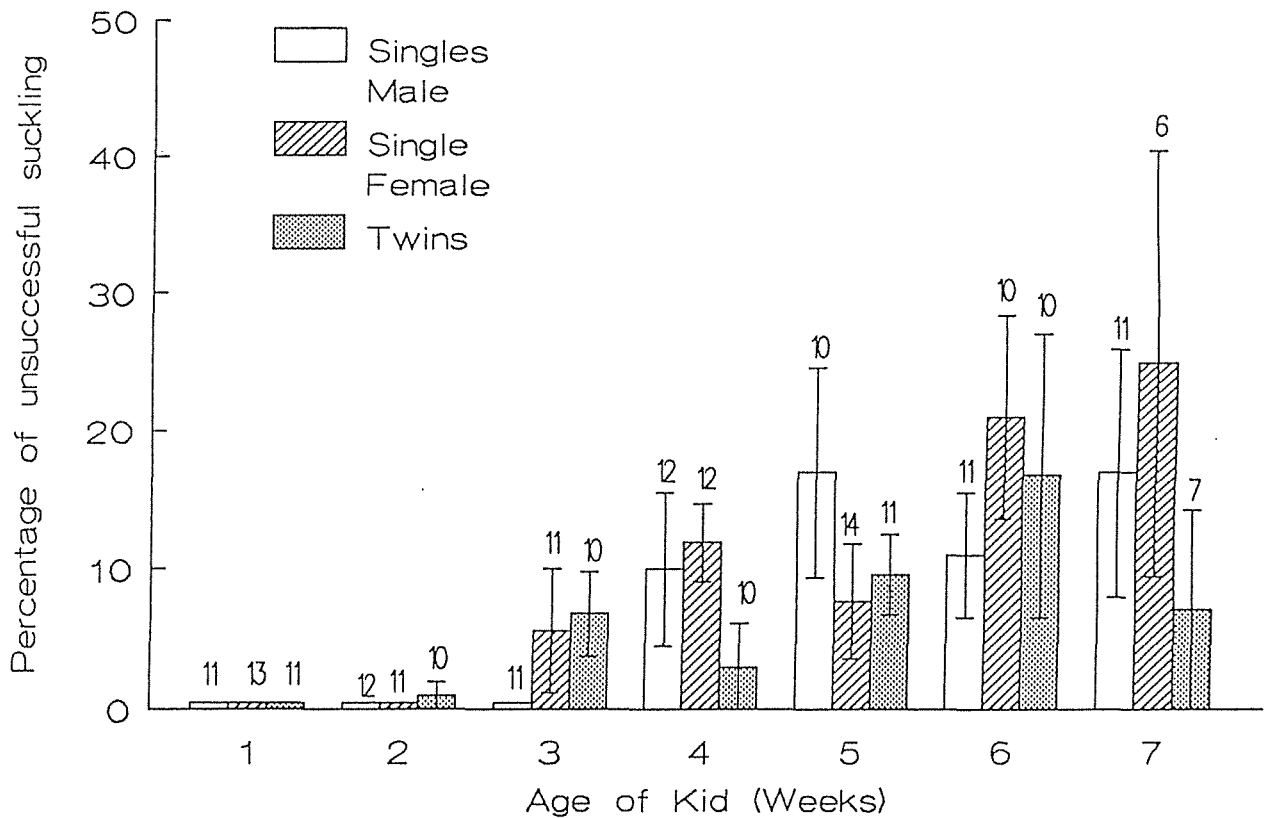
Figure 2.14 Mean Percentage Of Suckling Events That Were Unsuccessful For Single And Twin Kids In Relation To Age. Feral Goats At Ballantrae. September 1990– February 199

Plates 2.7, 2.8, and 2.9 are a sequence of photos showing a two month old male kid attempting to suckle.

Plate 2.7   The kid attempts to reach his mother's udder while she is resting.

Plate 2.8   The kid suckles even before it's mother stands.

Plate 2.9   The mother is reluctant to let her kid suckle and terminates the
                 suckling event by lifting her hind leg over the kid.

DISCUSSION

Birth Weight and Growth Rate

The birth weights recorded for a wide variety of goat breeds range from 2.32 Kg for the Negev goat to 4.0 Kg for the Appenzeller (Epstein et al, 1964). Birth weights observed in the feral goats in the present study fall near the lighter end of this range. Despite the variation in birth weights between breeds, the tendencies for males to be heavier at birth than females, and for birth weight to decrease with litter size, are a common pattern among goat breeds and are reflected in the present study.

Birth weights were recorded as close to the time of parturition as practical. Although all weights were taken within 24 hours of birth there was some variation in the time lapse between parturition and measurement of birth weight. Milk intake during the first few suckling bouts is likely to be a function of the kid birth weight; the larger, stronger kids being able to suckle sooner and extract milk at a faster rate. Consequently it is possible that the recorded differences in birth weight may be over estimates. Following parturition the weight of the kid decreases through rapid heat loss and evaporation of uterine fluids on the kid's body. Body size affects metabolic rate and therefore weight loss over the first 24 hours may be related to birth weight (McCutcheon et al, 1983).

The assumption that greater birth weights indicate more energy expenditure on the part of the mother is questionable. Past research has reported significant sex differences in body composition of feral goats. For instance Kirton (1970) reports that in feral goats the males contain less fat, and more protein and water. Therefore sex differences in birth weight may reflect difference in relative proportions of body constituents and not represent differential acquisition of maternal resources.

In agreement with other studies (Carl & Robbins, 1988; Byers & Moodie, 1990), it was found here that twins grew more slowly than singles. Competition between siblings for a limited nutrient supply has been accepted as the explanation for the

difference between birth types. However, sex differences in growth rate also apparent in this study may not necessarily correspond to differential acquisition of nutrients. Several researchers have suggested that in mammals, males are more efficient at converting dietary protein into biomass (Nordan, 1970; Glucksmann, 1981). Testosterone has been identified as the hormone enhancing anabolic processes in males (Booth & McDonald, 1988). Verme (1989) found a significant sex difference between individual mixed-twins and postulated that the same amount of energy results in faster rate of growth for males than females.

In the current study birth weights were positively correlated with kid growth rate in single male kids, but not in twins or single females. Bajhau & Kennedy (1990) reported that in feral goats birth weight played a central role in determining growth. These findings are consistent with the parental investment theory. However, a fundamental assumption of the parental investment theory is that differences in maternal investment during gestation and lactation correspond with differences at and beyond sexual maturity. The validity of this assumption is questionable. It is commonly agreed that availability of nutrients early in an animal's life can affect its growth and subsequently its final body size (Clutton-Brock, 1982). According to Dickinson (1960), however, environmental conditions must be "subminimal" before the expression of a growing animal's genotype for body size is precluded permanently. Growth studies have shown that in some ungulate species young can compensate for inadequate milk supply by increased foraging (Verme, 1989). Therefore, the crux of the argument is, to what extent can maternal investment be restricted before it is severe enough to permanently stunt growth. Maternal investment also affects the rate of growth and thus the age at which mature size is reached. For polygynous males, which may fertilize up to 100 females in one breeding season, it isn't difficult to see the genetic advantage of rapid maturity.

Suckling Behaviour

The high degree of variability in suckling frequency which occurred during the first two weeks of this study has also been reported by Rudge (1970) in his description of the hiding phase of a population of free ranging feral goats. According to Gauthier & Barrette (1985) infrequent suckling with corresponding long suckling bouts is characteristic of hider-species. In the early stages of ontogeny, the mother-offspring relationship changes from hider to follower type in a wide range of ungulates (Ewer, 1968). The speed of this process varies between individuals as well as between species and consequently the changing suckling pattern associated with the transition is not well defined.

Measurement of frequency of suckling in feral goats is difficult. The underlying problem lies in finding a sampling technique which can encompass a range of suckling patterns. Initially, a suckling session consists of a series of suckles of variable length with a relatively long period separating each suckling session. As the kid matures suckling is distributed more evenly throughout the day. At three months of age suckling occurs very rarely at intervals less than 10 minutes apart. During this later stage of ontogeny suckling tends to last 15-20 seconds but the duration may be very brief (< 5 secs).

Estimates of suckling frequency may be achieved by carrying out a focal study on a small, randomly selected sub-group. The major pitfall of this technique is that all individuals in the subgroup must be visible throughout the observation period. For the feral goats in this study it was common for kids to suckle in a secluded lying-out site early in their life. Another draw back in employing such a technique is that all the observer's attention is focused on recording all instances of suckling carried out by the individuals in the sub-group and, as a consequence, little or no additional information can be gathered during the observation period. Scan-sampling is another option for estimating suckling frequency, however the variability in suckling duration in feral goats presents some difficulties. Suckles of very short duration (< 10 secs) are very rarely recorded when intervals between scans are too long while on the other hand, long suckles (> 2 mins) will overlap from one scan to the next if the interval between scans is too short.

Synchrony of behaviour amongst the herd members also presents a problem for estimating suckling frequency. The diurnal pattern of behaviour means that observations made in a restricted portion of the day may not represent the true frequency of suckling. In this study few dawn and dusk observations were made and there were no night observations. Studies of other ungulates indicate that suckling peaks in early morning and late afternoon (Leuthold,1977). When analysing the results from this study it was assumed that there were no sex differences or differences between singles or twins in the daily pattern of suckling. However, further research is needed to justify this assumption.

The frequency of suckling is partly influenced by the environment. Many ungulate young when disturbed seek their mothers and attempt to suckle (Lent, 1974). Adler et al (1958) considers the behaviour to be an instinctive motor pattern similar to the 'grasping' reflex observed in human infants.

The activity pattern of the herd can determine the frequency of suckling, particularly during the lying-out phase. This is most evident when kids are born temporally and spatially close together. In these circumstances the does would return to their kids *en mass*. It appeared as if mothers "distrusted" fellow herd members particularly during the first couple of days following parturition. Schloeth (1961) describes how feral cattle frequently nurse at the time of a change of activities. Therefore synchrony of suckling may simply be a product of herd activity.

Plate 2.10   Two does suckle their young simultaneously

Suckling behaviour is a proximate measure of milk intake. According to Adler et al (1958) not all suckling involves the transfer of milk. In bighorn sheep, non-nutritive suckling occurs most often during periods when the lamb is active (Shackleton et al, 1985). Shackleton et al suggest that the function of these short suckles is to strengthen the mother-offspring bond.

Milk intake depends on frequency, duration, and rate of milk withdrawal at each suckling period (Fletcher, 1971). In this study the frequency and duration of suckling was measured. The rate of milk withdrawal which depends both on milk let down and the suckling ability of the kid was not taken into account. Milk consumed during a suckling bout can be measured by weighing the kid prior to suckling and immediately after. Such a technique would have been of limited value in the present study as both mother and kid were subject to stress during the weighing procedure which in turn would have affected suckling behaviour.

Except on rare occasions when spatial and temporal close proximity of parturition resulted in the adoption of a kid by another female during the immediate post-partum period, no kid in this study was observed suckling successfully from females other than its own mother. However, successful suckling from alien mothers has been reported to occur in a number of other ungulates (Reindeer: Espmark, 1971; Bighorn sheep: Hass, 1990). In the present study mothers tended to be aggressive towards alien kids, frequently interrupting the suckling of their own kid in order to butt an alien kid away. One kid was observed suckling from two females throughout the three months after parturition. The genetic relationship of the two females was unknown.

As the kids grew, communication between mother and kid became more subtle. With increasing age the kid's eagerness to suckle grew, vocalisation by mother became less common, and postural signals sufficed to invite suckling. Walther (1984) suggests that ' a stiffening of the legs and a more or less erect posture' assumed by the mother during suckling acts as a visual stimulus for initiating suckling in some ungulates. This posture resembles the alert stance and thus may explain attempts made by kids to suckle during disturbances. In the current study kids sometimes attempted to suckle when the mother squatted to urinate. Again, the kids may confuse this behaviour with a postural invitation to suckle.

More detailed study of sex differences in maternal investment would need to include measures of milk quality during lactation. A difficulty with this could be that frequent sampling of milk would interfere with the nutritional regime of kids and thus affect their suckling behaviour.

The present study found that as kids grew older there was an increase in the frequency of active termination of suckling by the mother, an increase in the proportion of suckling initiated by the kid, and an increase in unsuccessful suckling attempts. This transition in the responsibility of initiating and terminating suckling during kid development has been reported in several species of ungulates (Gauthier & Barrette, 1985), and is a measure of conflict between mother and offspring proposed by Trivers (1974). As has been reported in other ungulate species (Espmark, 1969; Shackleton et al, 1985; Hinch, 1989) termination of suckling was primarily the mother's responsibility by the third week.

Conclusion

Apart from a small difference in suckling frequency, data on suckling behaviour showed no sex differences. This is in contrast to the observed sexual dimorphism observed in birth weights and growth rates. Before any valid conclusion can be drawn as to whether sex-biased parental investment occurs in feral goats the discrepancy between the two proximate measures of parental investment needs to be further investigated. Firstly, nursing behaviour alone may not estimate milk intake with sufficient accuracy. The absence of measures of the rate of milk flow leads to ambiguity in the interpretation of suckling duration and suckling frequency. Suckling that lasts for short spells may represent less milk consumption, or on the other hand it may reflect increased suckling efficiency. Secondly, sex differences in birth weight and growth rate may not be a reliable indication of differential allocation of maternal resources because it may arise from differences in the efficiency in which each sex utilises nutrients.

PART TWO

ACTIVITY BUDGETS OF THE

FERAL GOAT HERD

SEASONAL VARIATION IN THE DIURNAL ACTIVITY
OF THE ADULT HERD

INTRODUCTION

The proportion of time an animal spends each day engaged in different activities is a measurement common to many behavioural ecology studies. Activity budgets are also used to determine the energy expenditure of a species and are, therefore, a prerequisite for the investigation of contemporary theories of optimal foraging (McFarland 1977). Methodological difficulties associated with data collection have, however, restricted most studies to the behaviour of captive animals during the diurnal period. Activity patterns of a species are a fundamental aspect of its interaction with its environment and therefore are important from both a farming and ecological perspective.

It is generally agreed that the daily pattern of activity of ruminants consists of periods of grazing alternating with rest and that the timing and number of alternations between rest and grazing occurring over 24 hours is under the influence of a complex of factors which include species, season, weather and photoperiod (Halfez et al, 1969). Several authors (Halfez et al, 1969; Kilgour, 1980, 1984; Van Soest, 1982; Scheurman, 1990) refer to the daily pattern of activity of sheep and goats as an oscillation between grazing and resting. However, there is little quantitative data to support this view, and other important activities (agonism, courtship, bodily care etc.) are ignored.

The aim of this study was to quantitatively describe the diurnal behaviour of a feral goat herd, and construct activity budgets to determine seasonal variation in the behaviour of the herd. The activity budgets are based primarily on the activity of does because the doe/buck ratio in the study herd was very high, as it is in wild feral goat herds (O'Brien, 1988; Dunbar, 1990). and furthermore, the central aim of this thesis is maternal investment and mother-kid relationships.

METHODS

The composition and location of the study herd has been described previously in the General Introduction. During the observation period the study herd was scanned once every 10 mins, using 10x50 binoculars. As each animal was encountered, its behaviour was categorised and recorded. Not all individuals were visible during a scan. A scan could take several minutes to complete, but none exceeded 10 mins. A tape recorder was used to record the observations and help to reduce the length of each scan.

The behaviour was classified as follows:-

Grazing   (stationary and moving).
Browsing.
Resting   (included lying and sitting).
Standing.
Walking   (not associated with foraging).
Nursing   (suckling, muzzling, licking, pawing and playing with offspring).
Sexual behaviour   (standing, tail-wagging in near vicinity of buck, mounting, or standing to be mounted).
Agonism   (clash, butt, bite, threat displays -see Chapter 5 for a full description).
Maintenance behaviour   (mutual grooming, self grooming or grooming against an inanimate object. Urination not associated with sexual activity).

Most observations were made between 0830 hours and 1530 hours, although occasional observations were also made from sunrise to 0830 and from 1530 to sunset. Two nocturnal observations were made during May and June (mating season) with the aid of a night scope. Graphs and activity budgets were constructed by combining data from the same number of hours after sunset collected on different days. Data from six scans per hour were pooled.

The data were divided into three seasonal blocks:

Mating season:-   30 April 1990 - 31 July 1990
Gestation season:-   1 August 1990 - 31 October 1990
Kidding season:-   1 November 1990 - 30 January 1991

The variation in photoperiod between seasons was taken into account by correcting times to the number of hours after the local time of sunrise. Within season variation in photoperiod was not accounted for (maximum error of 30 mins).

Results were based on a total of 31,975 observations (Mating season: 17,896 observations, Gestation: 12,639, Kidding: 1,440). The number of observations made during kidding season was substantially less than the other two seasons because during the peak kidding period, observation sample scans were made every 30 mins as data on suckling behaviour was being collected simultaneously.

RESULTS

Over the 9 month study period grazing was the predominant activity of adults between 0800 and 1600 hours, occurring 55% of the time. The second most common activity was resting. Time devoted to resting was also considerably greater (35%) than the other behavioural states . (See Figures 3.1, 3.2 & 3.3)

Grazing

In all three seasons, time spent grazing increased throughout the day with most intense grazing between 1400 hours and sunset. No consistent daily grazing fluctuations were apparent. The percentage of time spent grazing during the 3-8 hours after sunrise, was greater during mating than in the gestation and kidding seasons.

Figure 3.1 Daily Activity Budget For Ballantrae Adult Feral Goat Herd During Mating Season (30 April — 31 July 1990), n=17,896 Individual Obsevations
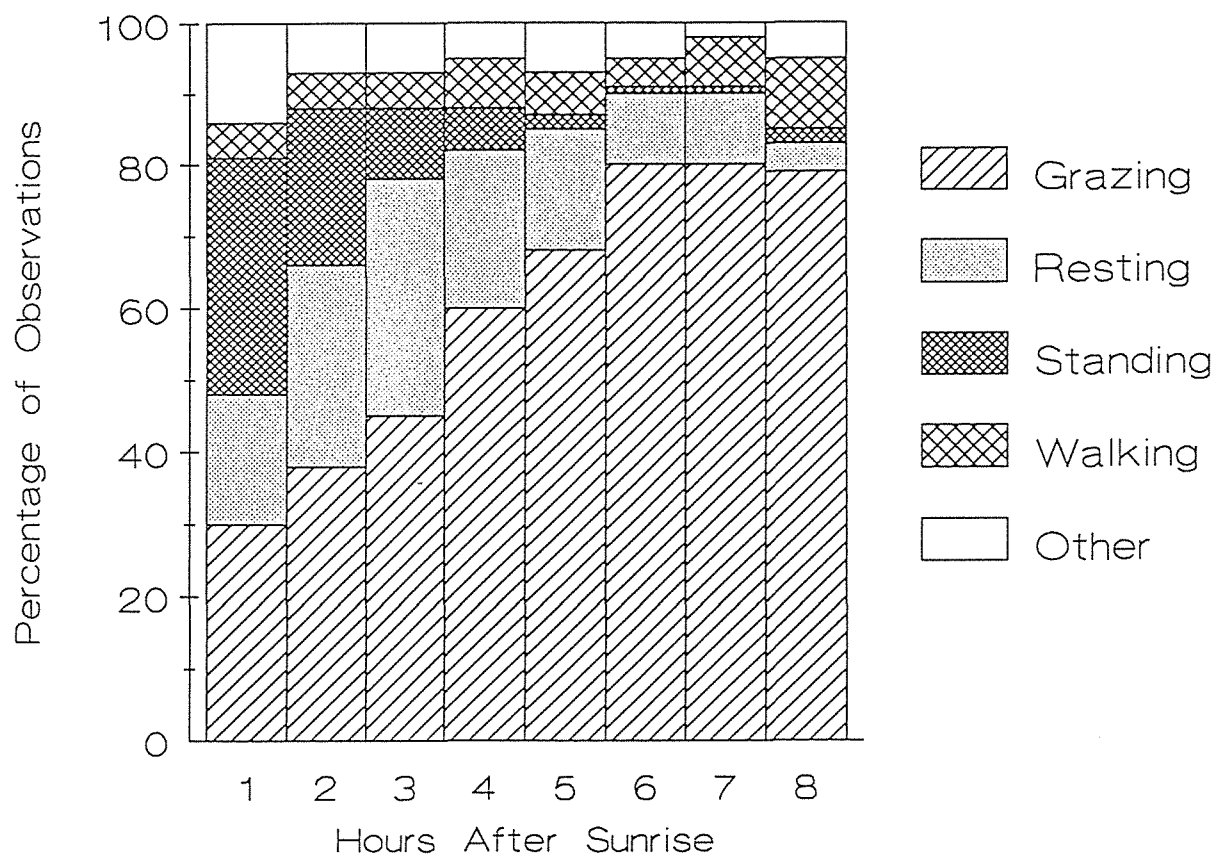
Figure 3.2 Daily Activity Budget For Ballantrae Adult Feral Goat Herd During Gestation Season (August – 31 October 1990), n=12,639 Individual Observations.
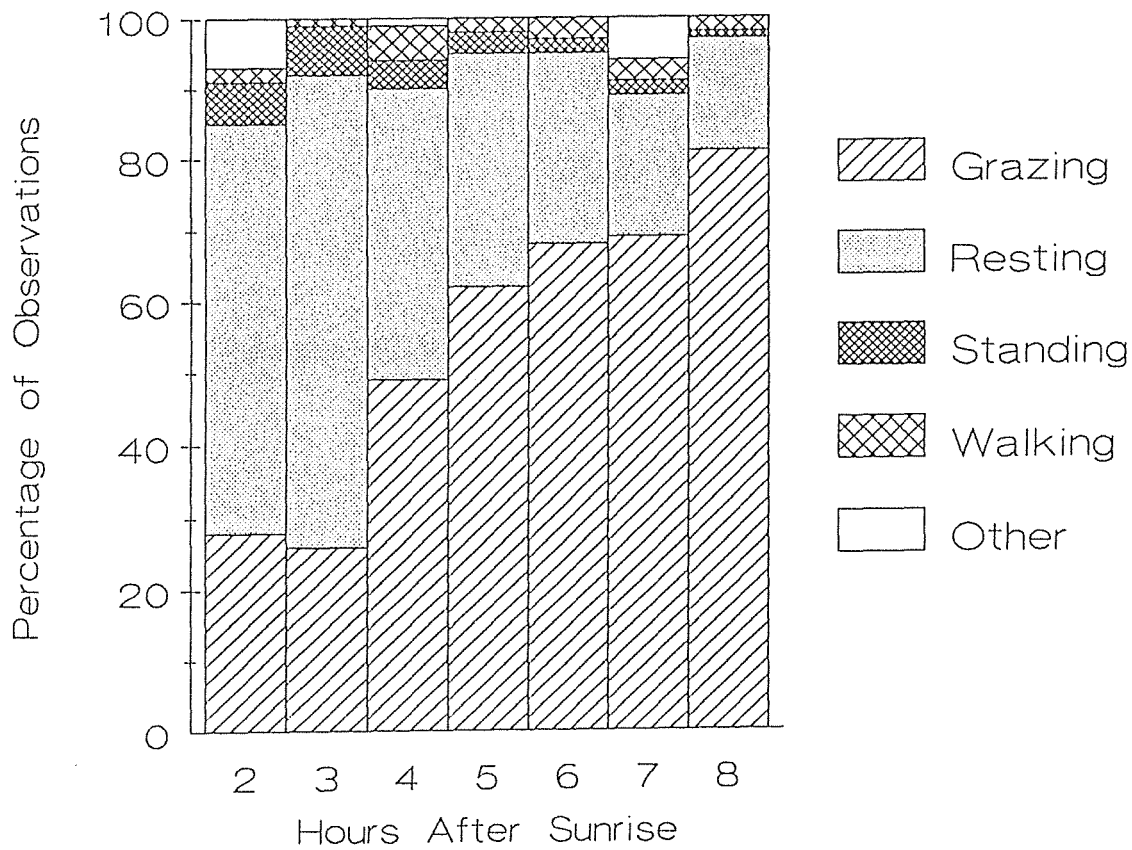
Figure 3.3 Daily Activity Budget For Ballantrae Adult Feral Goat Herd During Kiddir Season (1 November 1990 — 30 January 1991). n=1,440 Individual Observations
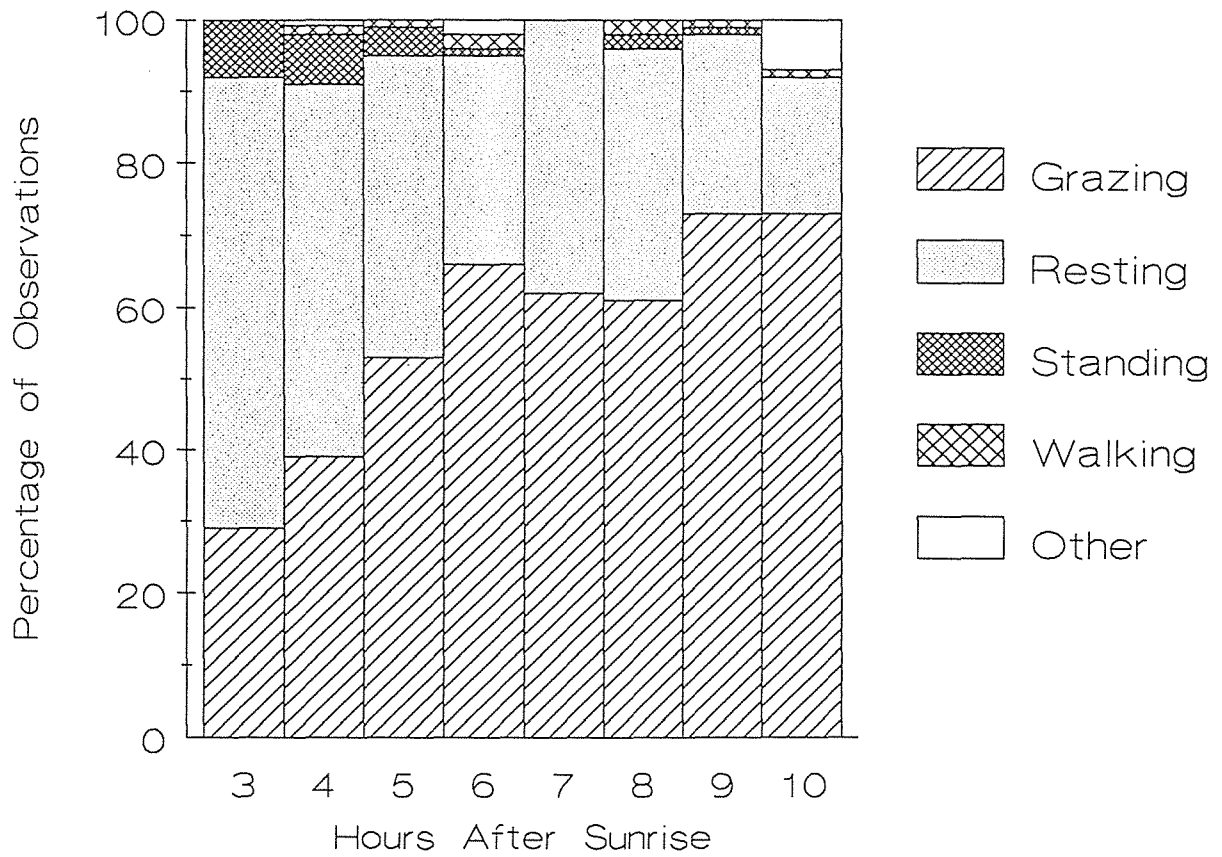
Resting

During the diurnal period studied (2-10 hrs after sunrise) the mean percentage of time spent resting was 35%. Of this, the majority (94%) was spent in a sternal position. Seldom was the whole herd observed resting at the same time. All three seasons showed a decline in the time spent resting during the course of the day. Resting in a recumbent position (sternally and laterally) was greater during gestation and kidding than in the mating season.

Lying (lateral recumbency) occurred more often during the gestation period than during either mating season or kidding season. On average 3.4 goats (range 1-14) were observed lying at the same time during gestation, whereas on average 1.8 goats (range 1-8) were observed lying simultaneously during the other two seasons. During the mating season and gestation period, lying occurred more often between 0900 and 1100 hours. However, in the kidding season lying was spread more widely over the day.

Standing

Adult feral goats spent more time standing during the mating season than during gestation or kidding. In the morning, time spent standing represented a large portion of the total percentage of resting time. The proportion of time spent standing declined throughout the day, so that by afternoon an insignificant amount of time was spent engaged in this activity.

Browsing

Relatively little time was spent feeding on roughage such as leaves, young shoots, woody shrubs, and weeds (< 5%). The availability of these food sources determined the extent of browsing. When the goats were introduced to a new paddock with diverse vegetation they browsed extensively. Social facilitation appeared to be a factor contributing to the erratic occurrence of browsing. For

instance, during windy conditions a branch of a tree occasionally snapped and fell to the ground, whereupon several goats would cluster around and rapidly defoliate it. Agonism between herd members occurred frequently in such situations.

Agonism

Agonism was relatively rare, occupying < 3% of time on average. Aggression was closely associated with oestrus and parturition; clashes being the most common form of agonism between oestrous does. Immediately prior to parturition does showed intolerance towards herd members by threatening and butting them. During kidding season most overt aggressive actions were by lactating does directed towards foreign kids and later their own kids. Casual observations revealed that agonism occurred frequently during intense periods of grazing.

During the mating season agonism between bucks was greatest. The largest most dominant buck attempted to prevent the other two bucks from mating by chasing them.

Sexual Activity

Intense sexual activity was observed the day following the introduction of the bucks into the herd (See General Introduction) but no clear diurnal pattern emerged. Sexual activity was observed at all hours of day and night, except between 1200 and 0100 hours (observations for this period were derived from one day only). Sexual activity continued even while the majority of the herd rested. It was also observed in all weather conditions. During periods of heavy rain the herd clustered together in a sheltered area (ie. under a pine tree) and intense sexual interactions were observed. Topography appeared to influence sexual behaviour. Agonistic chases occurred on the steep terrain, while mounting was restricted largely to the flat regions of the paddock. Seventy percent of sexual activity was recorded in the first month after the bucks were introduced and on only one day during this period was no sexual behaviour recorded. Sexual activity ceased after 23 July 1990 but commenced again 7 January 1991.

Social segregation of the bucks from the herd occurred after the mating season ended in August. Plates 3.1 and 3.2 show the close proximity of bucks while grazing and while at rest.

Plate 3.1
Three bucks graze together isolated from the rest of the herd. 'Office'paddock (27 December 1990).

Plate 3.2
The bucks rest together, 'Office' paddock (27 December 1990).

DISCUSSION

Diurnal Grazing Pattern

A bimodal circadian rhythm of feeding is the most common pattern in ruminants (Aschoff, 1966). In this study no clear pattern of oscillation in feeding activity was observed.

As pointed out by Ballance (1985) in her work on Campbell Island sheep, the general pattern obtained by pooling data from several days shows the daily pattern poorly. The onset of the "mid-day" rest in sheep, varied on any particular day between 1100 and 1300 hours so that when data was pooled grazing appeared to continue throughout the day. In the present study it was found that on any one day there would generally be a decrease in grazing activity, of at least 50% in the middle portion of the day.

Seasonal Variation in Grazing

The time spent foraging was greater in the current study in autumn-early winter during mating than during spring and summer gestation and kidding. This is not in agreement with conventional theories of female reproductive physiology. In ungulate species, the nutritional demands of pregnancy (particularly the last third of gestation) and lactation are large (Moen, 1973; Widdowson, 1981). Additional energy and proteins are obtained both by mobilisation of body reserves and increased ingestion of forage by the mother. The importance of increased feeding to meet the extra nutritional demands of reproduction has been demonstrated in studies which compare food uptake in barren, pregnant and lactating females. (Hadjpleris & Holmes, 1966; Boyd, 1988). The extent to which a female draws on body fat reserves depends on the food availability, so that when food supply is marginal or nutritionally inadequate, loss of body condition is greatest (Widdowson, 1981).

Seasonal variation in climate also influences the energetic requirements of animals. In cold weather, the metabolic rate necessary for maintaining body temperature is energetically demanding. Appleman and DeLouche (1958) have

shown that in Nubian goats, feeding time and mastication rate increase when ambient temperatures decrease, but below 10°C feeding is reduced. Gates and Hudson's (1979) investigation of thermoregulation in white-tailed deer suggested that restricted activity in animals exposed to adverse winter conditions is energetically advantageous. Winter temperatures in the lower North Island of New Zealand are not severe; ambient temperatures below 10°C are largely restricted to early morning, therefore winter conditions overall are likely to enhance rather than inhibit feeding as found in the present study. But because goats are short-day breeders, decreased energy requirements associated with rising temperatures of spring and summer compared to winter are confounded by the increasing nutritional demands of the developing offspring.In New Zealand, however, the temperate climate is unlikely to generate nutritional demands which exceed the large energetic costs associated with female reproduction.

Seasonal climate may indirectly affect the time an animal spends feeding by determining the quality and quantity of forage available. For species such as goats, in which rumination is an important digestive process, a sizable portion of the day is spent ruminating, therefore seasonal changes in the palatability of vegetation may affect the time available for feeding. Palatability may in turn, be influenced by seasonal changes in plant morphology (Leuthold, 1977) because younger, less fibrous plants are more easily digested. Consequently, time spent ruminating may be reduced during spring when new growth is abundant and thus more time is available for foraging. However, a more complete picture would also consider the relative palatability of plant species and the seasonal variation in their abundancy. In winter, pasture is less diverse, consisting largely of grass leaf. The herbaceous biomass of thistles, ragwort and other common pastoral weeds rapidly increases in late spring and summer along with the development of grass seed heads (Clark et al, 1981, 1982, 1983).

Seasonal changes in diet may also be more pronounced in opportunistic browsers, such as goats than in grazing species like sheep and cattle. Goats show a preference for browse (Devendra & Burns, 1983) and when scarce may spend longer searching.

The relationship between time spent feeding and nutritional uptake is not clear. Work done on cattle has shown that food availability (ie. grass length) is an

important factor in the relationship because it determines bite size (Mckenzie, pers. comm.). More research is needed to clarify this relationship for browsing species.

Photoperiod is another seasonal variable which is likely to affect time spent feeding. Pachlatko and Nievergelt (1985) observed that chamois spend a greater percentage of time feeding in autumn than in spring. They concluded that since chamois were only active during the day, shorter days in autumn would mean less time available for feeding. Nocturnal observations in the present study showed that very little feeding occurred after dark, however observations were restricted to the mating season. Although few nocturnal observations have been made of goats it seem likely that goats follow the feeding pattern of chamois more closely than that of cattle.

Browsing

Although goats are referred to as browsing animals (Hafez, 1969; Kilgour, 1984; Radcliffe, 1984), labelling the goat a browser underemphasizes the versatility of its foraging behaviour, which has enabled it to survive in widely differing habitats. The feeding habit of goats depends on the relative availability and palatability of the bush and tree constituents as well as the herbaceous ground vegetation (Campbell, 1962). Goats readily adopt a grazing type of feeding strategy when confined to pasture.

The opportunistic feeding habits of goats, observed in this study have been highlighted by several researchers (Devendra and Burns, 1983; Mitchell et al, 1985). In this study browsing occurred too infrequently to reveal any daily pattern.

Standing

In the current study there was a marked difference in the percentage of time spent standing during the mating season compared to the gestation and kidding seasons. The association between increased time spent standing and oestrus has been reported in cows by Kiley-Worthington and de La Plain (1983). Although does were not always in close vicinity to the buck whilst standing, it is possible that this

behaviour is a component of female courtship display.

Goats dislike of wet conditions contributes to variation in the time they spend standing, as seen by their tendency to stand in sheltered areas to avoid adverse weather, as well as by their preference to ruminate while standing when the ground is wet from rain, frost or heavy morning dew.

Agonism

Many researchers have reported intrasexual competition occurring between males for access to females and stress its importance in polygynous ungulates (Wolff, 1988; Dunbar, 1990). However, female-female competition was also apparent in this study. During oestrus, dominant does often butted subordinate does and this was particularly pronounced when only one buck tended the herd. Agonism also occurred during the kidding season, does were observed displacing other does kids from their lying-out site (see Chapter 1). This may be a display of dominance similar to competition among does for parturition sites previously reported by O'Brien, 1983)

Sexual Activity

Studies describing the reproductive biology of wild feral goats in New Zealand have reported that breeding is continuous throughout the year (Rudge, 1969; Mitchell, 1985). In the current study, however, six barren does present in the study herd did not exhibit oestrous behaviour during gestation or during the early kidding season.

Kilgour and Winfield (1974) in their investigation of mating behaviour in sheep report the influence of terrain on sexual behaviour and their findings are similar to those observed in goats in the present study.

In wild feral goats, bucks dissociate from the female herd at the end of kidding season and form bachelor herds (Dunbar et al, 1990). Social seperation of the bucks

was observed in this study eventhough the animals' home range was restricted by fences. This suggests that the modification of behaviour of wild goats due to domestication may be over estimated.

CHAPTER 4

ACTIVITY BUDGETS OF FERAL GOAT KIDS

INTRODUCTION

The behaviour of juvenile ungulates has been studied mainly in association with the mother-offspring relationship. The behavioural synchrony of mother and offspring has been discussed by Morgan & Arnold (1974), Shackleton & Haywood (1985), and Lickliter (1987), and the early ontogeny of behaviour has been described in relation to developmental changes in the spatial relationship between mother and offspring (Crowell-Davis,1986; Hinch et al, 1987). That suckling behaviour has received special attention by investigators of ungulate behaviour is hardly surprising because it is central to the bonding of mother and infant in these species. However, the evolutionary perspective of the mother-offspring relationship advanced by Trivers (1972) has stimulated more detailed examination of suckling behaviour, and attempts at testing Trivers' parental investment theory have led to investigation of sex differences in suckling behaviour in numerous ungulate species (Clutton-Brock et al, 1981; Lee & Moss, 1986; Wolff, 1988; Byers & Moodie, 1990).

Play behaviour, on the other hand, has always been of interest to ethologists; its evolutionary function being the primary focus. Recently, researchers have been concerned with sex differences in the play behaviour of sexually dimorphic species of polygynous ungulates. It has been suggested, in relation to the sexual selection theory, that sex differences in play may throw light on the adaptive function of play (Berger,1980). In sexually dimorphic polygynous ungulates intrasexual competition is more intense among males than among females, therefore the ability to fight is considerably more advantageous to males than females (Crowell-Davis, 1987).

It has been acknowledged that behaviour is established and refined during ontogeny and therefore sex differences in adult behaviour must correspond with sex differences in juvenile behaviour (Berger, 1980; Clutton-Brock et al, 1982). However, the study of sexual differences has been confined to a selection of juvenile activities considered to be closely associated with adult reproductive strategies.

This study has endeavored to take a holistic approach to the investigation of juvenile behaviour of a polygynous ungulate. A quantitative investigation of the entire behaviour repertoire of feral goat kids has been carried out in order to determine age and sex differences in their diurnal activity budget.

METHODS

Observations were made on 24 single kids (12 male, 12 female) and 12 pairs of mixed twins belonging to the larger study herd described in the General Introduction. The observations began at the start of kidding on 18 September 1990 and ended on 16 January 1990 when the majority of kids were three months of age. Only observations taken between 0830 and 1600 hours were used to construct the activity budget of kids.

The behaviour of four single kids was omitted; two female kids born late in the season (at least 2-4 weeks after the peak kidding period), a male kid orphaned in its second week of life and another male kid born with shortened tendons.Triplets and single-sexed twins were also omitted from the study because there were too few of these birth types.

Instantaneous sample scans of the herd were taken at 30 minute intervals. The identity, sex and activity of the kids were recorded during each scan. The kid's activity was categorized as follows:

a) Resting:-   Including recumbency, standing or ruminating.

b) Grazing:-   All non-suckling forms of feeding including browsing, nibbling dirt and vegetation.

c) Suckling:- Suckling bouts and unsuccessful suckling attempts. Behaviour closely associated with suckling was also included in this category. This included standing or recumbent while receiving maternal care in the form of licking, nuzzling and other grooming actions.

d) Playing:- Running, leaping, mounting, rubbing against each other and pawing each other, kicking, mock battles, jumping on and off things (including the mother's back). A full description of each of these behaviour patterns is given by Chepko (1971) and Byers (1977).

e) Exploring:- Including sniffing or mouthing inanimate objects as well as approaching and looking or sniffing conspecifics.

f) Other:- Mainly including grooming activities such as licking, scratching or rubbing any part of the body with or without the aid of an inanimate object. Also including elimination, and standing or wandering through the herd while calling for its mother.

STATISTICAL ANALYSIS

A total of 8123 scans were recorded (4404 of single kids, 3719 of twins). The median number of scans per kid was 145. See table 4.1 (pp.70) for the number of scans recorded for single and twin kids during morning, mid-day and afternoon for each age group. Data points were not independent of each other therefore the proportion of time spent by each kid in each category of behaviour was calculated then the mean of these proportions was used for statistical analysis. The arcsin transformation was applied to proportional data from the scans to improve the equality of variance (Snedecor & Cochran, 1967).

Data were grouped in to three time periods:

Morning   0830 - 1100 h
Mid-day   1100 - 1330 h
Afternoon   1330 - 1600 h

Data from singles and twins was analysed separately and were treated in monthly blocks to test for age differences in activity budgets. ANOVA of sex and activity interaction; age and activity interaction; time and activity interaction; litter and activity interaction, was carried out using SAS computer software package.

Table 4.1   Number of scans for single and twin kids during morning, midday and afternoon time periods for each age group.

Age (months)	Time of Day	Singles	Twins
	Morning	743	734
Month 1	Mid-day	580	466
	Afternoon	489	438
	Morning	514	430
Month 2	Mid-day	231	300
	Afternoon	241	340
	Morning	475	428
Month 3	Mid-day	357	304
	Afternoon	427	256

RESULTS

During their first three months of life kids spent on average more than half their time resting (53%). Grazing occurred 20% of the time, while nursing accounted for only 10% of observation time. Kids spent the remaining 20% of the time playing, grooming, and exploring their surroundings.

During the lying-out phase of development little exploration occurred. In many cases physical separation from other herd members may have been responsible for this, however, even when several kids were lying-out together, surprisingly little exploration occurred. Initially, investigation of conspecifics formed a major part of exploratory behaviour; the neonate approached and sniffed both adults and juveniles. Rejection was sometimes vigorous, and caused foreign kids to refrain from exploring adult herd members. Exploration of other kids, however, developed into play behaviour. Casual observation showed that by the second week of life most exploratory behaviour involved investigation of potential food.

Overt sexual behaviour was not observed until the fourth month when the low stretch (Kilgour, 1984) was exhibited by a male kid towards an adult female. The courted female responded aggressively to his actions, frequently threatening and butting him away, however the kid persistently followed and attempted to court her.

Effect of Sex

The activity budget constructed for the first three months of life for single male kids was significantly different from that of single females (ANOVA: sex effect, $F_{5,420}=2.28$, $P < 0.05$). Figure 4.1 shows that females spent more time grazing, and less time playing than their male peers. Further analysis of data showed that when activity budgets were calculated separately for the morning, noon, and afternoon periods, sex differences were found to be significant between afternoon activity budgets only (ANOVA: sex effect ; Morning, $F_{5,132}=0.63$, NS. ; Mid-day, $F_{5,132}=1.94$, NS. ; Afternoon, $_{5,132}=2.98$, $P < 0.05$).

Figure 4.1 Activity Budgets of Male and Female Single Kids. Obsevations were taken betwee 0830h and 1600h During the First Three Months of Life. Ballantrae September – January 1991, n=12 For Each Sex.
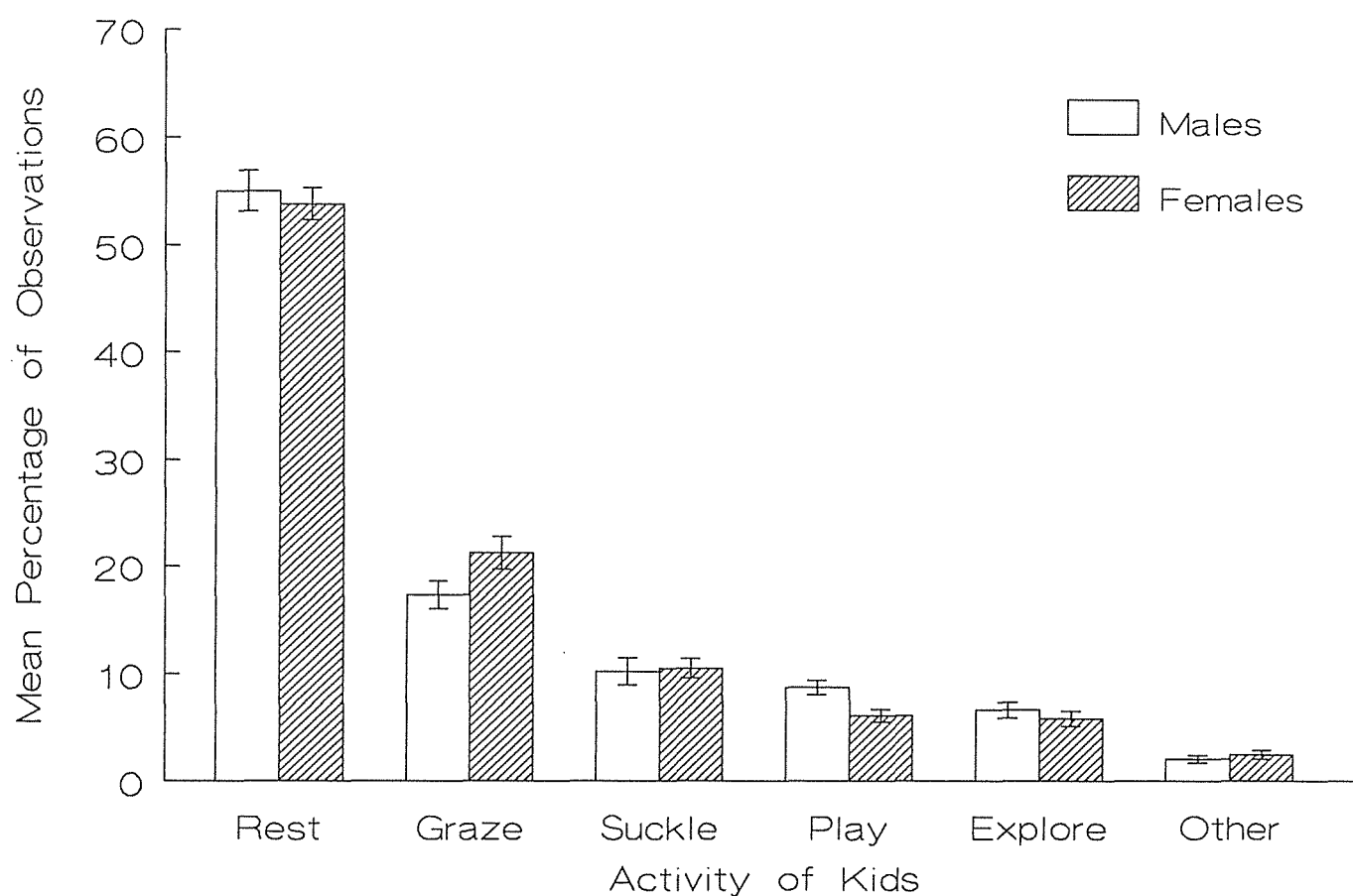
Analysis of data in monthly blocks showed no significant sex differences in daily activity pattern as the kids matured. No sex differences occurred between the activity budgets of mixed twins, and casual observation revealed that most of the time twin peers were engaged in the same activity at the same time.

Effects of Age

As single kids matured the amount of time they spent in various activities changed (ANOVA: age effect, $F_{10,1260}$=57.13, P <0.0001). Figures 4.2, 4.3 & 4.4 shows that kids spent less time resting, playing, and exploring, but more time grazing as they increased in age. The proportion of time spent in grooming and nursing activities remained relatively constant for the three age categories.

Age dependent variation of kid activity was exhibited by both sexes and was discernible at each of the three time periods analysed.

Diurnal Effects

The time kids spent engaged in various activities at different times of the day varied significantly (ANOVA diurnal effect, $F_{10,414}$=3.87, P <0.0001). Figures 4.2-4.4 shows that kids spent more time resting and less time grazing in the morning compared to noon and afternoon. These diurnal changes in grazing and resting were observed for each of the three age groups. However, there was no clear diurnal variation in the time spent nursing, playing, grooming, and exploring.

Comparison Between Twins and Singles

ANOVA of the effect of age and time on the activity of twins was not carried out, however, a comparison of Figures 4.5-4.7 shows that diurnal and age related changes in activity of twins was similar to that of singles.

The activity budget of twins constructed for the first three months of life was significantly different from singles ($F_{5,420}$=2.28 P <0.0001).

Figure 4.2 Activity Budgets During the Morning (0830–1100 hrs.) For Three Age Groups of Single Kids. Ballantrae September (1990) – January (1991). n=12 for each sex.

Figure 4.3 Activity Budgets During Mid–day (1100–1330 hrs.) For Three Age Groups of Single Kids. Ballantrae September (1990) – January (1991). n=12 for each sex.

Figure 4.4 Activity Budgets During The Afternoon (1330–1600 hrs.) For Three Age Groups of Single Kids. Ballantrae September (1990) – January (1991). n=12 For Each Sex.

Figure 4.5 Activity Budgets During the Morning (0830–1100 hrs.) For Three Age Groups of Twin Kids. Ballantrae September (1990) – January (1991). n=12 For Each Sex.

Figure 4.6 Activity Budgets During Mid-day (1100-1330 hrs.) For Three Age Groups of Twin Kids. Ballantrae September (1990) - January (1991). n=12 for each sex.
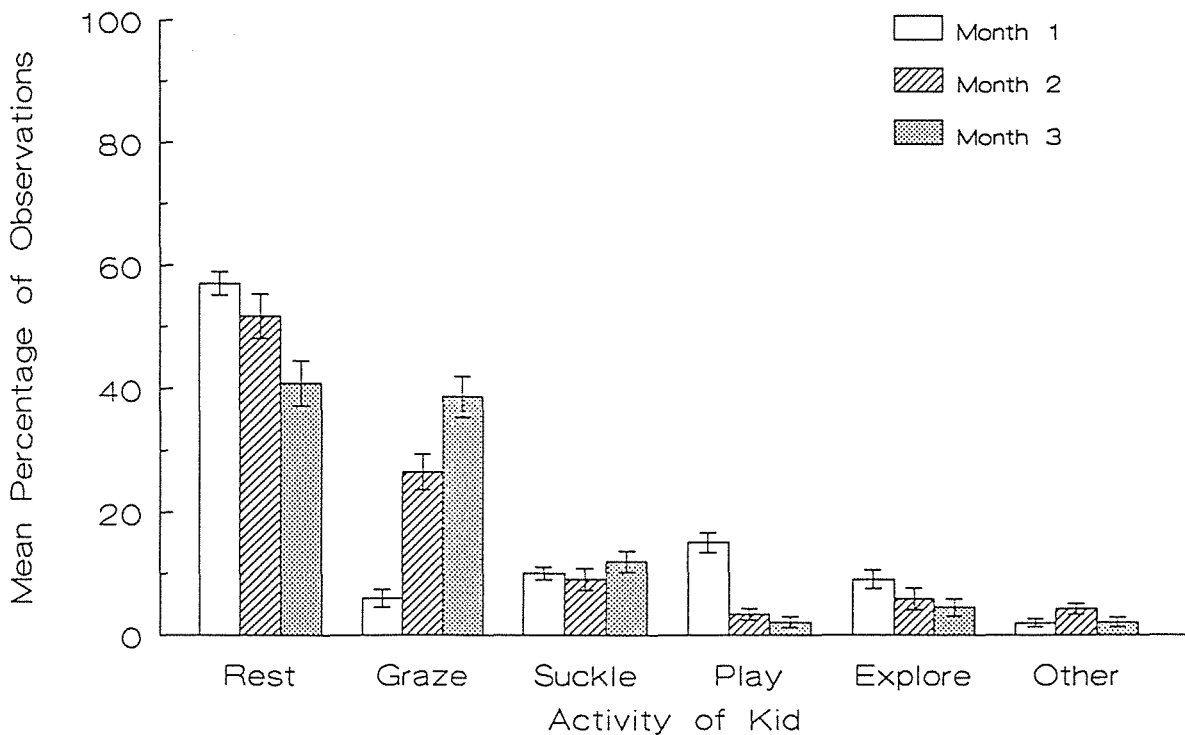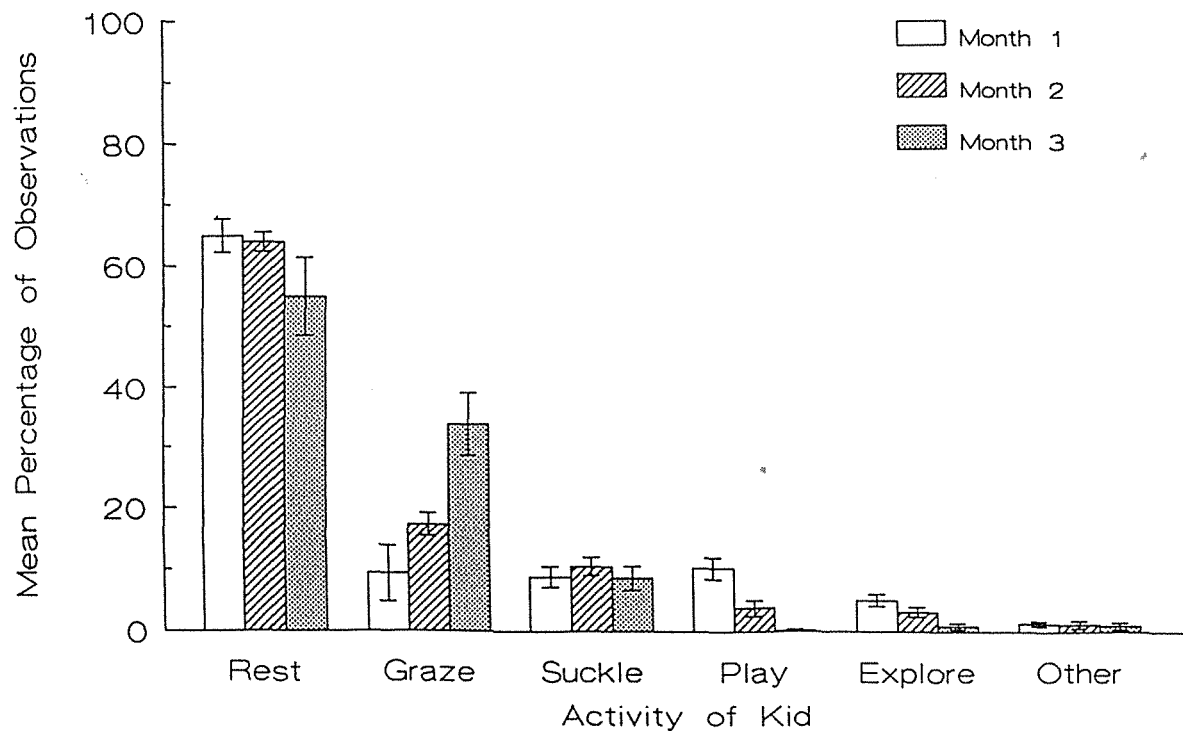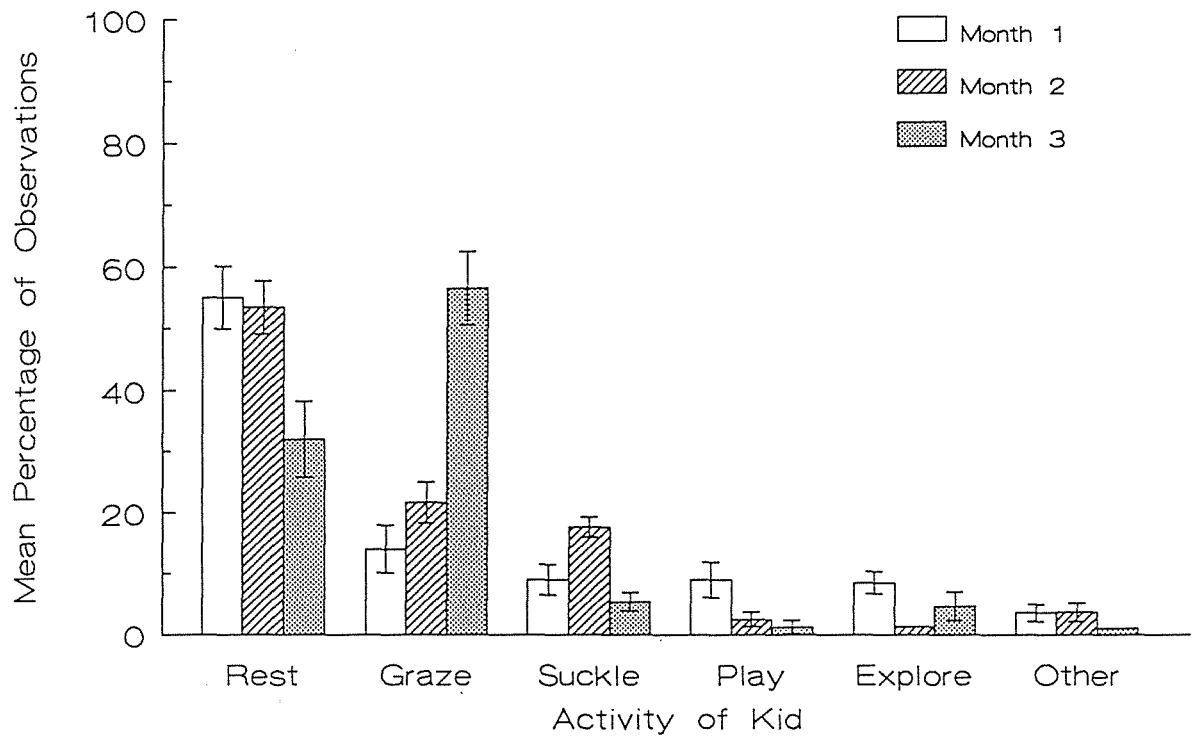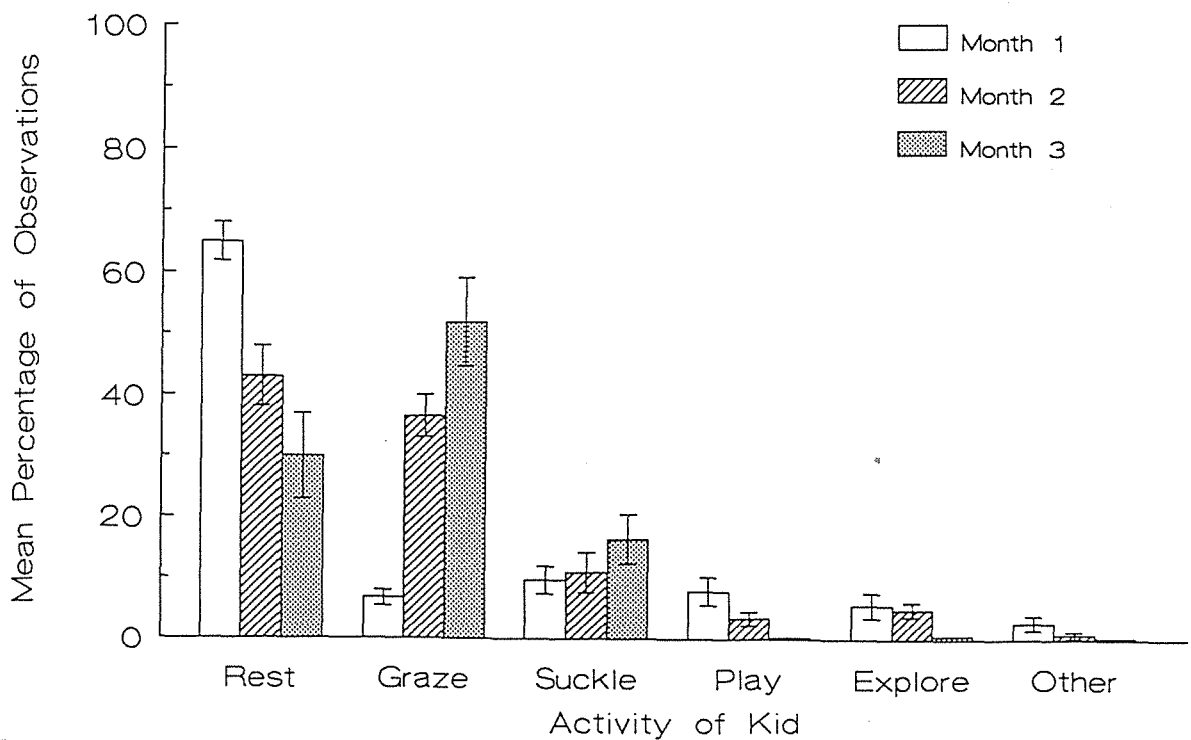

Figure 4.7 Activity Budget During the Afternoon (1330-1600 hrs.) For Three Age Groups of Twin Kids. Ballantrae September (1990) - January (1991). n=12 for each sex.

DISCUSSION

Sex Diffences In Play Behaviour

In this study males spent a larger portion of time engaged in play than females, particularly during the afternoon. Previous studies investigating sex differences in the play behaviour of juveniles have been primarily concerned with the relative frequency of different types of play for each sex (Lumia, 1972; Byers, 1977; Sachs & Harris, 1978; Berger, 1980).

Of the few studies which have examined sex differences in the proportion of the activity budget devoted to play there appears to be variation among species of sexually dimorphic polygynous mammals. There were no sex differences in time spent playing in horses (Crowell-Davis 1987) or grey seals (Kovacs 1987), but significant differences have been reported for elephants (Lee, 1986).

Age differences in play

A peak in the time kids spent playing occurred during the first month after birth. Studies of other precocial mammals have reported similar findings (Bighorn sheep: Berger, 1980; Horses: Crowell-Davis, 1987; Gazelles: Gomendio, 1988). In New Zealand, Rudge (1970) suggested that play formed a large part of early life in feral goats, although no quantitative data was available to verify his observation. These findings agree with Fagen's (1977) immediate cost-delayed benefit hypothesis which states that the "optimal period" of play for precocious mammals is during the earliest stage of development. Although immediate costs, which include energetic, time and survivorship costs are found to be large (Harcourt,1991) the model assumes delayed benefits are greatest for relatively feeble and poorly coordinated neonates. A large number of researchers have recently criticised this hypothesis by arguing that natural selection acts at all stages of the life cycle. These researchers have concentrated on the immediate benefits of play. Gomendio (1988) stated that 'behaviour at each stage must be concerned not only with assuring adequate performance during the following stage, but also with the particular needs and problems encountered at each point'. He has further postulated that species which

are subject to high predation pressures have not only been selected for highly precocious young but also young which maximise the rate at which they acquire the endurance and strength necessary for the flight response.

While most studies investigating age-specificity of play behaviour have reported a gradual decline in play after the initial peak,a second peak in the frequency of play has been observed later in the ontogeny of the young of some ungulate species (Sach & Harris, 1978). Fagen (1977) explains that the optimal age schedule of play is dependent on several aspects of development, and that at certain periods during ontogeny play is deleterious. In some species young are subject to temporary but intense periods of parent-offspring conflict and during this stressful period juveniles rarely play, however they resume their original level of play once the critical phase has past. The present study involved the analysis of data in monthly blocks and therefore a bimodal developmental trend in play behaviour would probably not be detected. Further research is therefore needed to investigate the age specificity of different types of play behaviour in feral goats.

In the current study, as in many previous studies on play behaviour, several behaviour patterns have been lumped together as play and treated as a homogeneous behavioural category. Recently, however, researchers have argued that play is not a monolithic category and that different types of play behaviour occur at different stages of ontogeny (Gomendio, 1988; Pellis, 1991). Developmental differences between types of play could mean that the underlying motivation factors, and possibly evolutionary adaptive functions of play, may differ.

Although other authors have stated that play behaviour is largely confined to juveniles, casual observations in this study showed that barren does were frequently involved in social play with kids. This is contradicts Lickliter's (1987) finding that in domestic goats, kids avoided non-maternal adult females. Play between parent and young in several ungulate species (Fagen, 1981) complies with the parental investment theory because the potential benefits to the kids' reproductive success, acquired from play, corresponds with greater fitness of the parent. Functionalists, however, have difficulty explaining the occurrence of play between genetically unrelated adults and young.

Temporal Pattern in Play Behaviour

Although observations in the current study were made over a seven hour period, a major weakness in its design was the lack of information obtained on behaviour occurring at dawn and dusk. Although interspecies differences in the temporal distribution of play are known to occur (Chepko, 1971) the high frequency of play occurring in the early morning and evening has been widely reported in ungulates (Lumia, 1972; Walther 1973; Byers 1977). Consequently the proportion of time devoted to these activities will be under estimated by the activity budget obtained in this study. Lack of a definite temporal pattern in play of the feral goat kids of this study is in agreement with Chepko's (1971) study of domestic goats. Chepko found that between dawn and dusk play bouts varied in length and number in accordance with age, weather and temperature.

Social facilitation (alleomimetic: behaviour Walther, 1973) is characteristic of many ungulate species and underlies the coordination of the herd. The unpredictable nature of the occurrence of play behaviour may partially be attributed to its "contagious" effect. The extent to which it spreads through the herd may depend on the spatial distribution of the herd thus play may be more pronounced in the early morning and evening when the herd members congregate at the camp site.

As pointed out by Leuthold (1977) play in the neonate differs from that in more mature kids in being orientated toward suckling. The frequency of suckling is largely determined by the mother during the lying-out phase and is highly variable (see Chapter 2). Therefore it is expected that play would be equally variable during this early stage of development.

Age differences in grazing

Some investigators of goat behaviour claim that grazing first occurs in the third week of life (Yerex, 1986; Lickliter, 1987). In the current study a more vague time frame of 2-3 weeks was obtained for the onset of grazing. Kids were observed mouthing soil and grass in the first week after birth. Development of this

exploratory behaviour during the second and third week made it difficult to determine whether or not food was actually being ingested. Initially grazing was sporadic, but with maturity more and more time was spent on this activity. It appears that juvenile ungulates learn to forage independently very early in life, some as early as the 2-3 days (Espmark, 1971). Although it is generally accepted all ungulates spend more time grazing as they mature what is more interesting is the rate at which grazing increases. Recent research in this area has found that ecological conditions may determine how rapidly the weaning process occurs (Berger, 1979).

Exploratory Behaviour

Little has been reported on exploratory behaviour of ungulates (Leuthold, 1977). Several different types of exploratory behaviour were observed in the present study, and it therefore appears that it is not a homogeneous behavioural category as is thought to be the case with play behaviour.

Age differences in resting

During the three months of the present study, resting was the main activity of feral goat kids, however, resting declined as the kids matured. These findings agree with Lickliter's (1987) study of domestic goats kids. The age-dependent changes in resting correspond with Triver's parent-offspring conflict model. This model predicts that early in ontogeny mothers should be generous in attention to offspring. However, as the young develop the benefits received by the mother from her investment diminish to a point where she gives less than the kid demands. Thus, early in development when the kid suckles until satiated; indicated by a large number of suckling bouts initiated by mother and terminated by the kid (see chapter 2) the kid can afford to spend most of its time resting. But as maternal investment decreases and the kid's nutritional requirements increase, the kid must allocate more time to foraging. In ungulates there is a trade-off between the time young need for rest to conserve energy required to support rapid growth, and time spent active and thus enhancing their endurance and strength.

Sex differences in grazing

Significantly more time was spent grazing by single females than single males. This is in agreement with Festa-Bianchet's (1988) study on bighorn sheep, but is contrary to the sex differences recently found in pronghorns by Byer and Moodie (1990).

The development of sexual behaviour

In the present study sexual behaviour was not included as part of the repertoire of kid behaviour. However, a four month old male kid was seen courting an adult female with incomplete sexual displays. According to Kilgour (1984) "puberty" in feral goats occurs at four months for males and six months for females, and Rudge (1970) reported that in feral goats males first attempted to sniff the perineal area of females and mount them at six months. Further activity budgets of the later stages of kid development are therefore likely to reveal some important sex differences.

Differential allocation of parental investment would result in differences in the time apportioned to various activities. Study of sex differences in the activity budgets of young goats does not by itself provide evidence of sex-biased parental investment. However, it is necessary for a fuller understanding of the ecological and evolutionary basis of the mother-infant relationship.

PART THREE

INTRODUCTION OF A NEW ENTRANT

CHAPTER 5

SOCIAL EVENTS FOLLOWING THE
INTRODUCTION OF A NEW ENTRANT TO THE HERD

INTRODUCTION

The social organisation of feral goats has been described by numerous authors
(Riney & Caughley, 1959; Hafez et al, 1969; Shank, 1972; O'Brien, 1988). During
the kidding season segregation of the sexes leads to the formation of bachelor herds,
but during mating bucks temporarily unite with herds of does. Although interchange
of males between established female herds is considered an essential part of the
breeding system of feral goats only a brief account of the phenomenon is given in
the literature (McDougall, 1975). Movement of females between herds is apparently
rare (Riney & Caughley, 1959) but is likely to be a common event where shooting
repeatedly dislocates and shifts the herds. For both sexes information on the
behavioural interactions between unfamiliar conspecifics in the wild is scant.

Farm management, however, frequently involves grouping unfamiliar animals
together. Several studies involving farmed goats describe the agonistic interactions
underlying the maintenance of a social dominance hierarchy (Hafez et al, 1969;
Pretorius, 1970; Shank, 1972; Crowley & Grace, 1988) but there are no detailed
reports describing the social events which occur when an unfamiliar goat enters this
hierarchy.

The aim of this study was to quantitatively measure the behavioural response of
the members of a captive feral goat herd to the introduction of unfamiliar does.

METHODS

Two experimental situations were used to assess the response of the goat herd to the introduction of an unfamiliar animal.

Experiment 1:

Over a 10-month period unfamiliar goats were introduced to the herd on five occasions and the response to each new entrant was described. The composition of the study herd and the location of the study site were the same as that described previously (General Introduction). Each new entrant became the focal animal for observations and all interactions with herd members were recorded. Observations were made between 0830 and 1600 hours. A video camera was used to record periods of intense interaction.

First New Entrant (NE 1)

A barren feral doe approximately three years old, and weighing 23 Kg was introduced into the study herd on 31 July 1990. At this time the majority of does in the herd were six weeks pregnant. NE 1 was released into the paddock at 0930 hours and observed continuously for the following six hours. The next day she was observed for another six hours. Observations on the study herd were also made on the third and fifth day, focal study of NE 1 was terminated due to the low frequency of encounters.

Second New Entrant (NE 2)

A feral doe (3-4 months pregnant) approximately six years old and weighing 26 Kg was introduced into the study herd on 18 August 1990. At this time the majority of does in the herd were eight weeks pregnant. NE 2 was released into the paddock at 1530 hours and observed for two hours. Observations were terminated at this time because the intensity of social interaction was too high for accurate recording of behaviour by a single observer. The next day she was observed for six hours.

Third New Entrant (NE 3)

A barren feral doe aged approximately three years old and weighing 20 Kg was introduced into the study herd on 3 September 1990. At this time the majority of does were 10 weeks pregnant. NE 3 was released into the paddock at 1240 hours and observed for the following four hours. Observations were terminated at 1640 hours after NE 3 became isolated from the herd in a distant region of the paddock and was not visible from the observation hide. NE 3 was mistakenly removed by farm staff on the second day.

Fourth New Entrant (NE 4)

A lactating feral doe aged approximately five years old and weighing 38 Kg was introduced into the herd on 19 January 1991 together with her four month old wether kid (Angora half-cross). This was the post-kidding season and most kids in the herd were two months old. NE 4 and her kid were released into the paddock at 1200 hours and observed for five hours. On the following day the pair were observed for five hours. Observations also were made on the third, sixth, tenth and eleventh day.

Fifth New Entrant (NE 5)

A feral doe (reproductive status unknown) approximately four years old and weighing 30 Kg was introduced to the herd on 4 February 1991. At this time the majority of kids were three months old. NE 5 was released into the herd at 0830 and observed for the following five hours. On the second day she was observed for three hours.

Experiment 2:

A barren doe (NE 6) aged approximately six years old weighing 38 Kg was removed from the study herd and introduced to a new herd (ca.150 animals) on 31 January 1991. The goats in this large herd were not identified individually, but comprised feral and angora goats of varying ages and reproductive status (ie. wethers, lactating does, barren does, yearlings, and pre-weaned kids). This herd was also located at Ballantrae Hill Country Research Station and at the time of

observation was confined in a paddock normally grazed by the study herd. NE 6 was released into the herd at 1050 hours and observed for the next four hours. On the second day NE 6 was observed for two and a half hours, on the third day one and a half hours, on the fourth day one hour and on the fifth day a further one and a half hours.

Ethogram For Interactions Between Herd Members and New Entrant

Investigative Behaviour

\A. Look-   an individual approaches another animal but stops further than two metres from the opponent and stands looking at it. (See Plate 5.1)

\B. Sniff-   an individual approaches another animal, usually from behind, and sniffs any part of its body (usually its rear), its urine, or an object with which the animal has had recent contact (Leuthold, 1977; Walther, 1984). (See Plate 5.2 & 5.3)

Plate 5.1
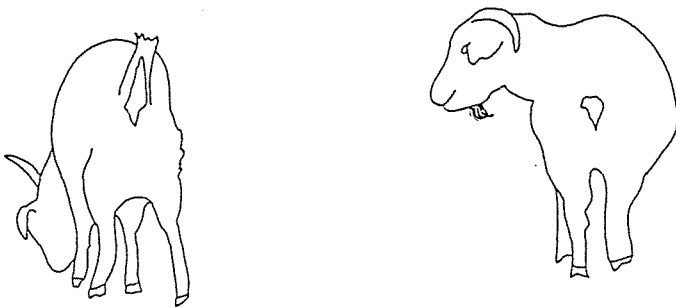
Investigative behaviour (looking). An adult female stands and looks at a new entrant (NE 2) from a distance of 1-2 goat lengths. The tracing was drawn from a video recording of the Ballantrae herd (1990).

Plate 5.2
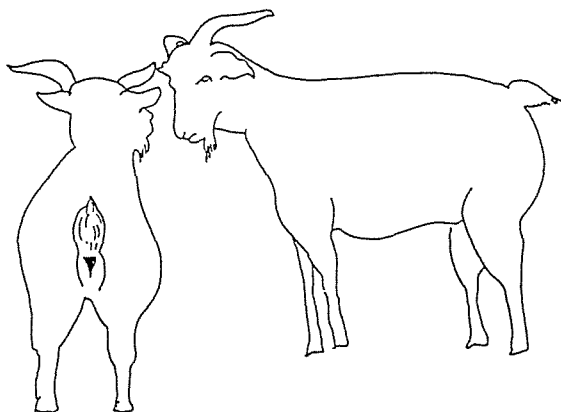
Investigative behaviour (mutual sniffing). Both the new entrant (NE 2) and a herd member explore each other simultaneously. The tracing was drawn from a video recording of the Ballantrae herd (1990).

Plate 5.3   Investigative behaviour (sniffing). Two does investigate a new entrant (NE 3) by following and sniffing her hind quarters. A buck stands and looks from 2-3 goat lengths. NE 3 displays a submissive posture (ie. tail down). The tracing was drawn from a video recording of the Ballantrae herd (1990).

Threat Displays

\A. Dominance-
Approach

two types of approach have been classified as displays of dominance.

Type 1: an animal approaches its opponent from the front. This frequently involves walking past the opponent then circling around in order to face the opponent head on. Type 2: an animal approaches briskly exhibiting a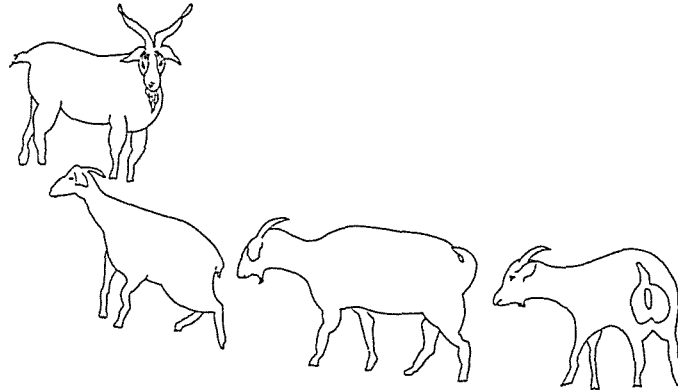 dominance posture, that is, it possesses a very stiff stance, pilo-erection, and its tail is held vertically or bent forward over its back. (See 5.4)

\B. Stare Threat -

an animal extends its neck and stares intensely towards its opponent (Shank, 1972).

\C. Horn Threat -

described by Geist (1971) as when 'an animal lowers or 'jerks' its head downward or sideways directing its horns toward the opponent'.

\D. Rear Threat -

defined by Shank (1972) as when 'the antagonist rears up on to hind legs. One hind leg is placed behind the other, and the head and torso are twisted so the face is toward the receiver'. The rear threat is also referred to as the "jump" or "threat jump" (Geist, 1971; Schaller, 1977).

\E. Rush Threat -

this is a rapid run towards an opponent with the head tucked into chest as if to butt the opponent (Shank, 1972).

Plate 5.4   Dominance approach (Type 2). Two does approach the new entrant (NE 2). No.12 displays her dominance by approaching briskly, holding her head high and tail erect. The tracing was taken from a video recording of the Ballantrae study herd (1990).
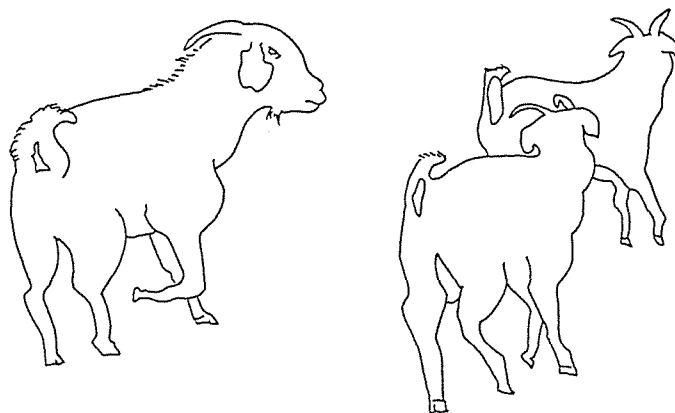
Overt Aggression

\A. Bite -   grabbing and pulling hair on the opponent's back with the teeth.

\B. Butt -   delivery of a swift blow, usually to an opponent's flank or side of its neck, by an individual with its head lowered and its chin tucked in.

\C. Clash -   also referred to in the literature as the 'ritual fight'. Defined by Shank (1972) as 'forceful contact of the adversaries heads where one, both or neither opponent rear up onto the hind legs'. (See Plate 5.5)

\D. Horn hook -   an individual hooks its horn under an opponent's front or back leg. Upward motion of the head results in the opponent being partially lifted off the ground. (See 5.6)

\E. Head Swipe-   lateral and upward movement of the head towards the opponents neck. (See Plate 5.7)

Plate 5.5   Sequence of tracings showing a herd member exhibiting overt aggression (clash) toward a new entrant (NE 2). The tracings was drawn from a video recording of the Ballantrae herd (1990).
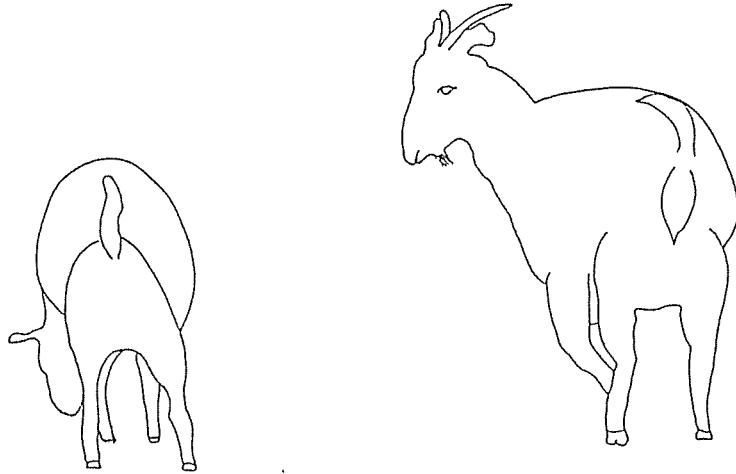
i) Herd member threatens NE 2 as she approaches.
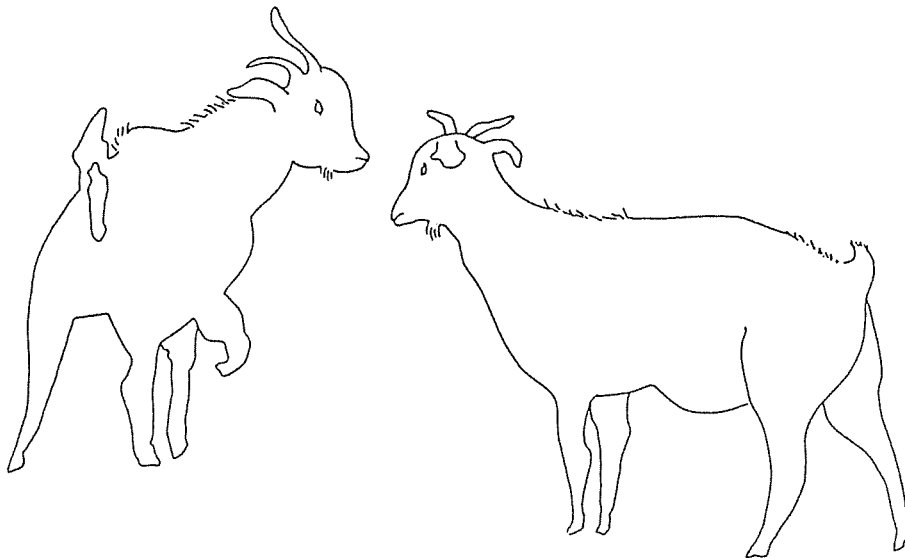
ii) NE 2 responds by lifting her head from grazing.
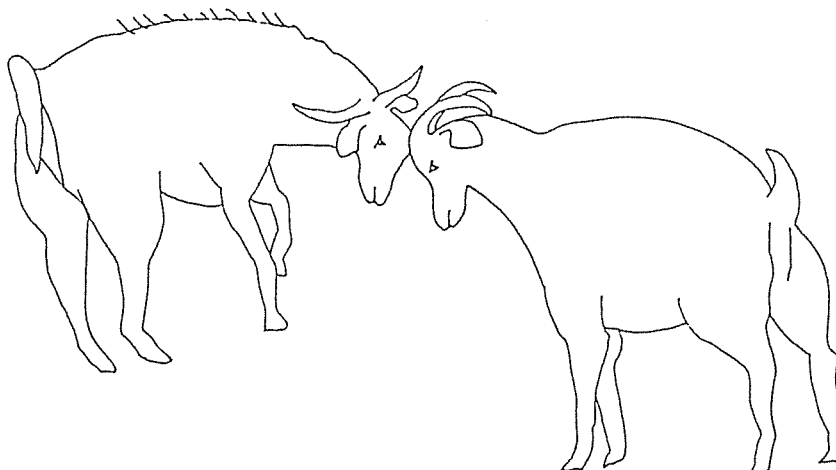
iii) The two does clash their heads together.

Plate 5.6   Overt aggression (horn hook) is shown in this sequence. Sequence
The tracings was drawn from a video recording of the Ballantrae
herd (1990).
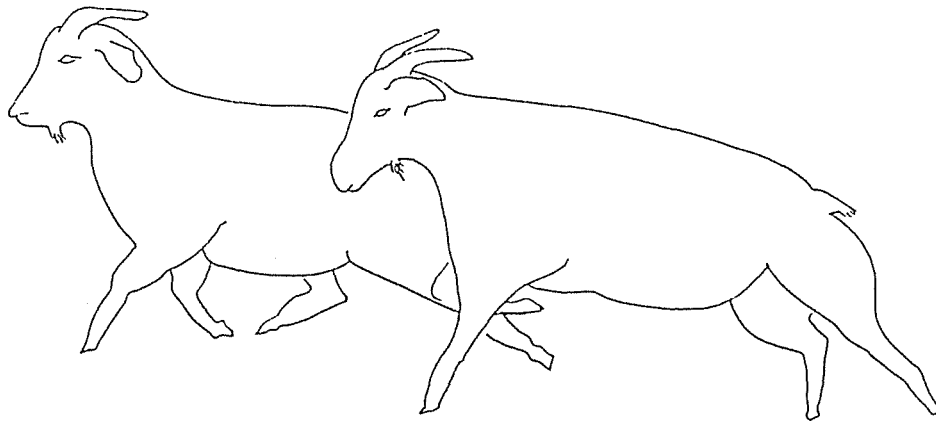
i) A dominant doe rapidly approaches NE (2).
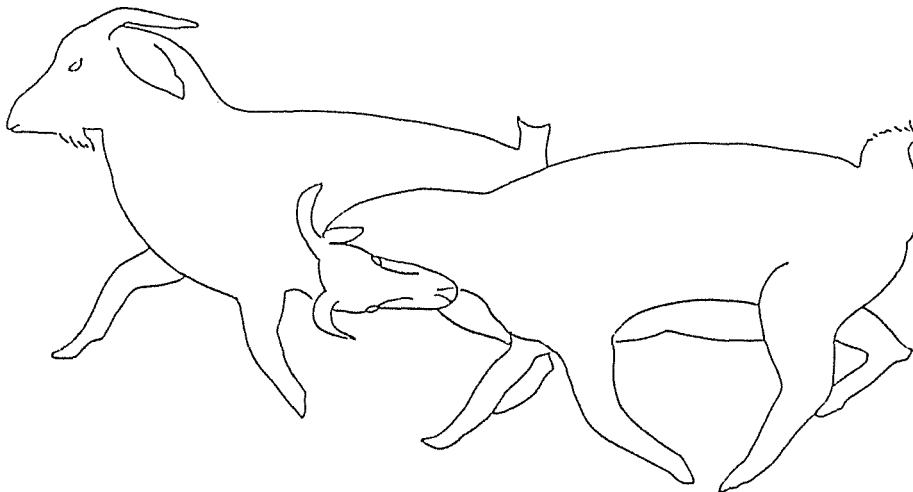
ii)   The doe lowers her head and places her horns under NE 2's abdomen.
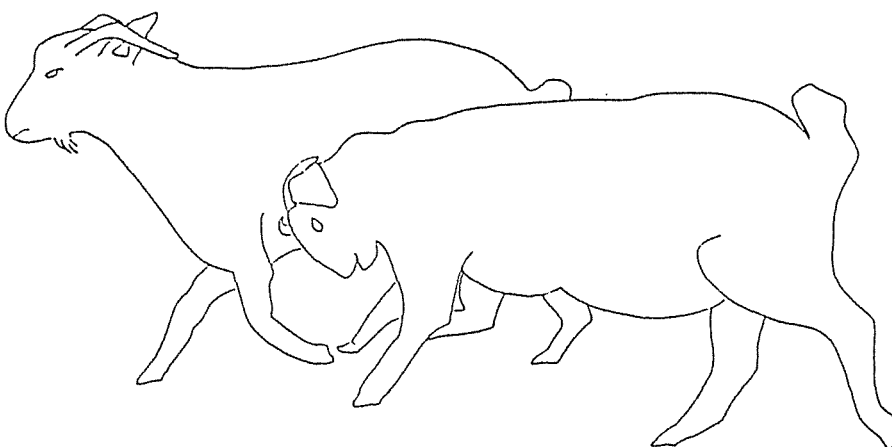
iii)   NE 2's left hind leg is lifted of the ground by the aggressive herd member.

Plate 5.7   Overt aggression (horn swipe). A new entrant (NE 6) rises from a resting position (sternal recumbency) and directs it's horns in an upward jerk towards a kid. The kid retreats rapidly to avoid physical contact. The tracing was drawn from a video recording of the Ballantrae study herd (1990).
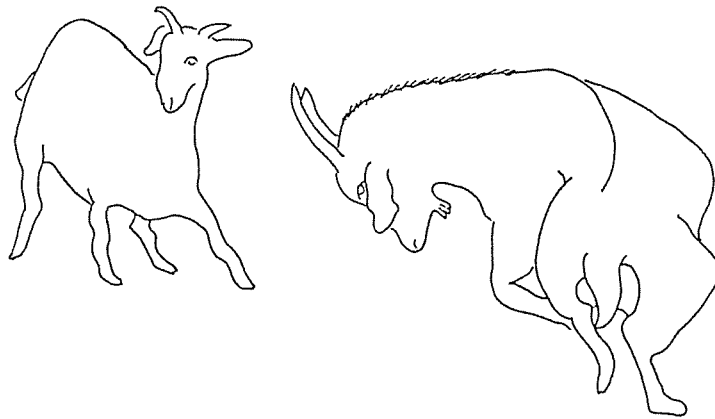
Submissive Behaviour

\A. Avoidance of-
Eye-Eye
Contact

an animal holds its head low to the of ground, and often grazes frequently (Schaller, 1977).

\B. Turn Away -

an animal attempts to avoid conflict by facing away from its opponent either by turning its head or changing the orientation of its body (Schaller,1977).

\C. Walk Off -

an animal walks away from its opponent. The distance travelled is usually relatively short (< 5 metres).

\D. Run Away-

the animal moves rapidly to escape its opponent. The distance travelled is often > 5 metres.

RESULTS

A) Experiment 1

First New Entrant

Initial Response of the Herd

Immediately after its release in to the paddock, NE 1 ran directly towards the herd. The herd members were alarmed by the rapid approach of the new entrant and clustered together. NE 1 slowed as she approached the herd and stood at the edge. Several herd members approached the new entrant simultaneously; sniffing and following her. Throughout the first half hour NE 1 moved about the paddock almost continuously. Although there were several occasions in which NE 1 passed through the centre of the herd, she tended to remain near the periphery. About 35 minutes after her introduction NE 1 moved away from the herd (>20 metres), and it was during this period of isolation that she was first observed grazing sporadically.

Frequency of Encounters

Figure 5.1 gives the number of encounters between NE 1 and herd members for each hour of observation during the first two days. There were more than 50 encounters recorded during the first hour after the introduction of NE 1 into the herd but the frequency of encounters fell substantially in the next five hours of observation. During the second day there were never more than 15 encounters per hour. On the fifth day no encounters were observed during a five hour observation period. Herd members were responsible for initiating all encounters with NE 1.

Table 5.1 shows the frequency with which herd members and NE 1 exhibited exploratory and agonistic behaviour.

Figure 5.1 The number of encounters between NE 1 and herd members for each hour of observation during the first two days after the introduction of NE 1 into the herd. Ballantrae 31 July 1990.
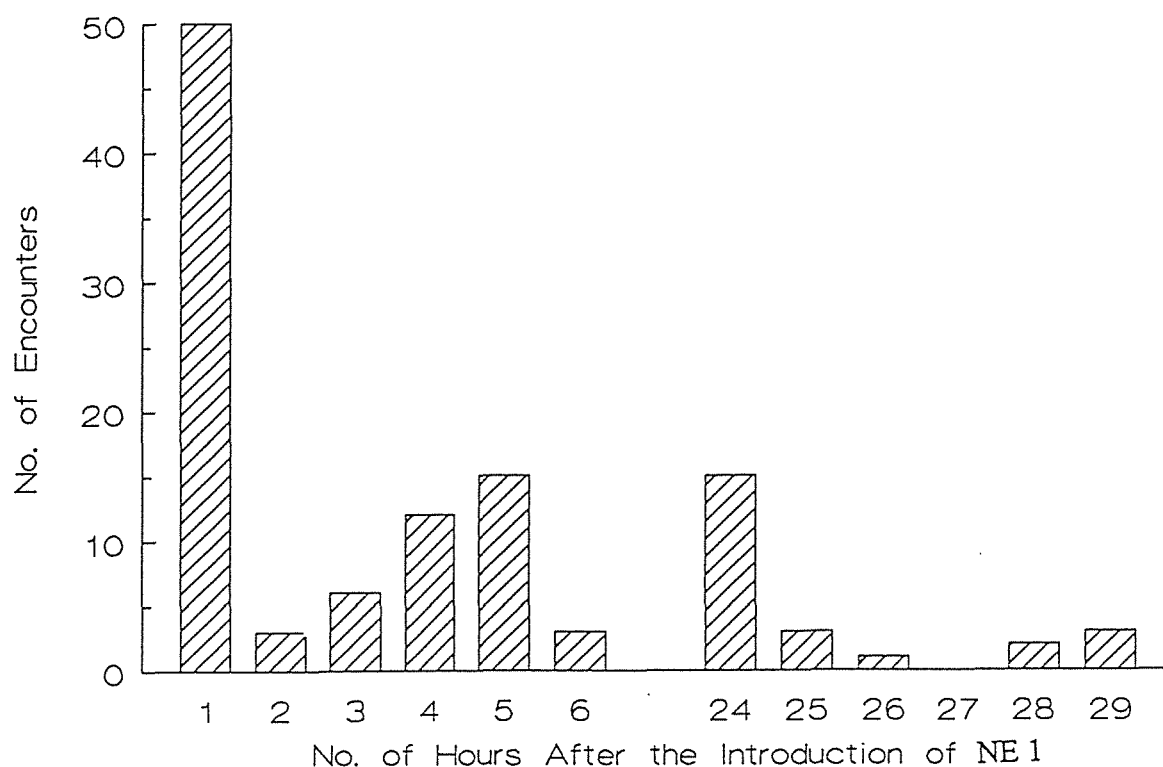
Action of Herd Members Toward NE 1

Over half (58%) of the encounters involved investigation of NE 1 by herd members. Herd members exhibited threatening behaviour toward NE 1 39% of the time. In 25% of cases threats were in the form of dominance approaches, while more specific threat displays occurred 14% of the time. Overt aggression occurred rarely (<3%).

Outcome of Encounters

More than 85% of observed encounters resulted in the displacement of NE 1. At no time during the period of observation did herd members show any submissive behaviour toward NE 1.

Second New Entrant

Initial Response of the Herd

The herd was scattered throughout the paddock at the time of the introduction and the majority of animals were grazing. NE 2 held her head low and grazed as she moved through the herd. Initially only herd members in the immediate vicinity of NE 2 showed any interest in her, lifting their head from grazing and looking at her. While some herd members approached NE 2 the majority walked away or continued to graze immediately after NE 2 was displaced. Seven minutes after NE 2 was introduced a couple of herd members followed her in an aggressive pursuit. The effect appeared to be contagious, for during the following two hours interactions between NE 2 and herd members were intense.

Frequency of Encounters

Figure 5.2 gives the number of encounters between NE 2 and herd members for each hour of observation during the first two days. NE 2 interacted with herd members at maximal frequency of 80 encounters per hour during the first day. By the second day encounters reduced substantially to an average rate of 6.5 per hour. Herd members initiated 97% of interactions.

Action of Herd Members Toward NE 2

Herd members explored NE 2 on 33% of occasions, especially sniffing and walking behind her. Overt aggression was the second most common action exhibited by herd members, butting being the predominant form of physical combat (14%). Herd members exhibited specific threat displays in 14% of the encounters, however they exerted their dominance in 24% of encounters by frontal approaches and aggressive pursuit.

Figure 5.2 The number of encounters between NE 2 and herd members for each hour of observation during the first two days after the introduction of NE 2 into the herd. Ballantrae 18 August July 1990.
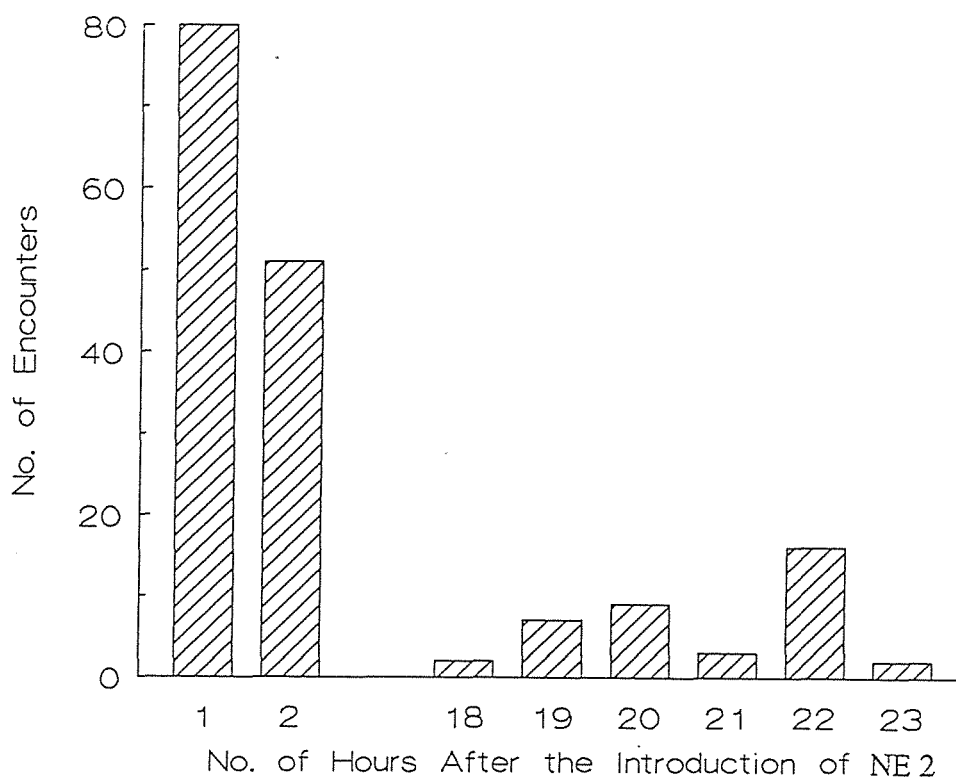
Outcome of Encounters

NE 2 lost 140 of 167 (84%) observed encounters and won only 2%. In the remaining 14% of encounters no clear physical displacement of either opponent occurred.

Proportion of Herd Members Involved
in Encounters with NE 2

During the first hour 56% of the herd interacted with NE 2. By the end of the second hour 69% of the herd had encountered NE 2 at least once. Two does interacted more frequently than all other herd members. In the first hour these two animals were involved in 28% of encounters with NE 2, and both bit the new entrant (a form of aggression rarely observed in this study herd).

Third New Entrant

Initial Response of the Herd

After introduction NE 3 ran directly towards the herd. Herd members on the periphery nearest to NE 3 stopped grazing and stood watching her approach. Several herd members gathered around NE 3 and followed her as she ran energetically through the herd. Some goats (up to 14) followed NE 3 at the same time, and within the first 10 minutes 22 herd members attempted to approach her. Four animals were particularly interested in NE 3, following her almost continuously during the first 10 minutes. However, NE 3 moved away, remaining distant (>20m) from the herd for the next 25 minutes (NE 3 behaviour was not recorded during this period of isolation because she was out of view). When NE 3 returned to the herd again, exploration was the predominant action of herd members, however, threats became more frequent.

Frequency of Encounters

Figure 5.3 gives the number of encounters between NE 3 and herd members for the first four hours following the introduction of NE 3. The maximum number of encounters occurred in the first hour. The frequency of encounters was still relatively high during the second hour, but by the third and fourth hour NE 3 interacted with herd members < 5 times per hour. All interactions were initiated by herd members.

Action of Herd Members Toward NE 3

The most common action of herd members was exploratory, occurring in 71% of cases. Herd members threatened NE 3 27% of the time. While 9% of threats were in the form of specific threat displays, 18% of encounters involved threat towards NE 3 via a dominance approach. Overt aggression occurred in only 2% of encounters.

Figure 5.3 The number of encounters between NE 3 and herd members for each hour of observation during the first two days after the introduction of NE 3 into the herd. Ballantrae 3 September 1990.

No. of Hours After the Introduction of NE 3.
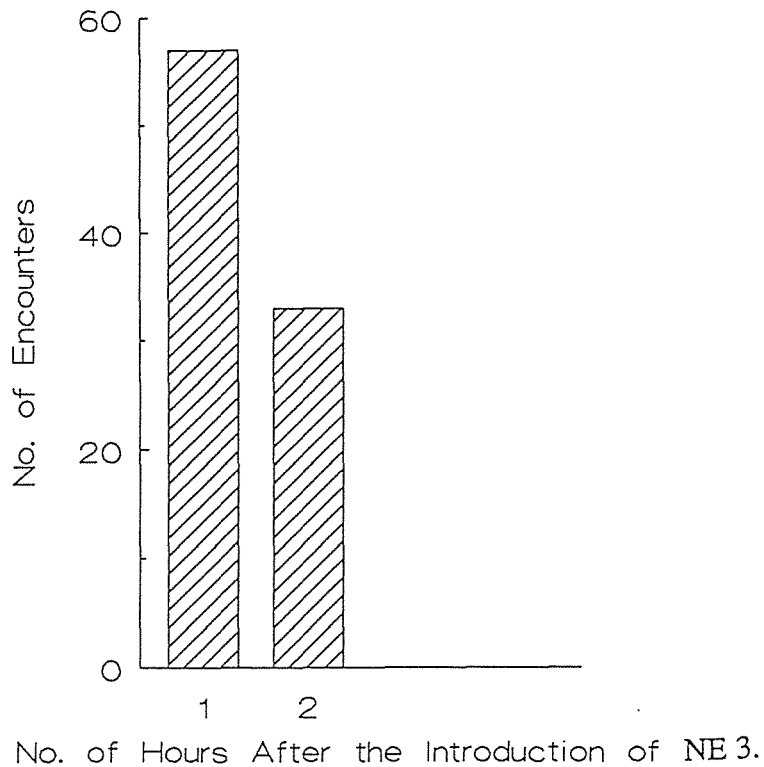
Outcome of Encounters

All observed interactions involved the displacement of NE 3. No herd member behaved submissively.

Proportion of the Herd Involved in Encounters with NE 3

During the first hour following the introduction of NE 3 48% of the herd interacted with NE 3. Four herd members were involved in over half (55%) these

Fourth New Entrant

Initial Response of the Herd

Prior to the introduction of NE 4 the herd was dispersed throughout the paddock and the majority (82%) of animals were grazing. NE 4 and her kid moved away from the site at which they had been released. The herd member nearest them urinated as the pair approached. Neither doe came within 1 metre of the other, there was no clear outcome to the encounter, and NE 4 and her kid moved off. The herd did not react as a single group to NE 4, but goats in the near vicinity of NE 4 reacted individually. Herd members showed interest in NE 4 and their grazing was interrupted as they lifted their heads to look or approach.

Frequency of Encounters

The frequency with which NE 4 encountered herd members during the first two days is shown in Figure 5.4. Overall relatively few interactions took place between NE 4 and herd members, and most occurred in the first hour. Herd members initiated encounters 76% of the time.

Action of Herd Members Toward NE 4

Nearly half (48%) of the encounters initiated by herd members were exploratory. In the majority of cases herd members approached and looked from a distance. Although herd members exhibited very few threat displays, they challenged NE 4 by approaching from a frontal orientation. Overt aggression accounted for 12% of herd members actions.

Figure 5.4 The number of encounters between NE 4 and herd members for each hour of observation during the first two days after the introduction of NE 4 into the herd. Ballantrae 19 January 1991
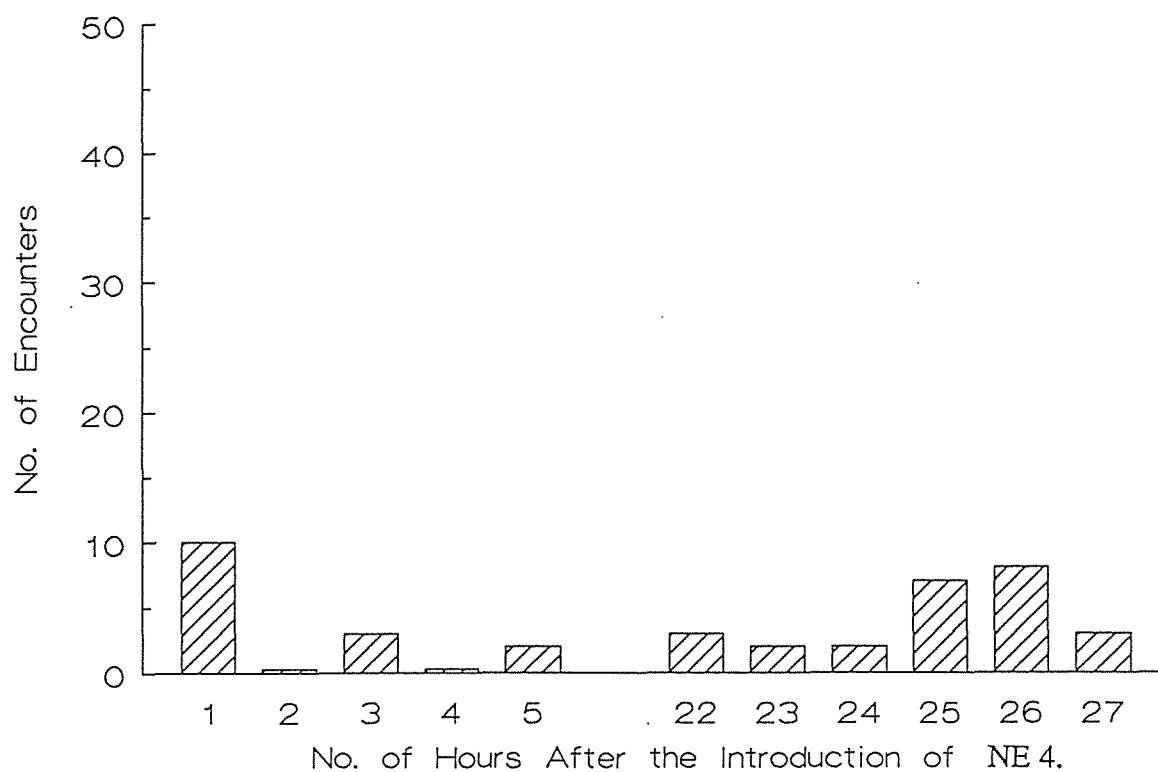
Outcome of Encounters

In the 33 observed encounters NE 4 lost (ie. was displaced) eight (24%) and NE 4 won nine encounters (27%). In 16 encounters (48%) neither opponent was displaced. In these instances an interchange of behaviour often occurred between antagonists (ie. grooming or horn thrashing), however these actions were too subtle to use in gauging dominance status.

Proportion of the Herd Interacting with NE 4

During the first two days only 30% of the herd were observed interacting with NE 4. No single goat was prominently involved in agonistic encounters with the new entrant.

Fifth New Entrant

Initial Response of the Herd

Half the herd were resting together in the camp site at the time of the introduction. Approximately 25% were grazing below NE 5 on a flat portion of the paddock, and the rest of the herd moved or stood between the two groups. These animals were in transition from resting to grazing. A buck was the first herd member to interact with NE 5.

Frequency of Encounters

Figure 5.5 gives the number of encounters occurring in the first two days. The maximum frequency occurred in the first hour. Nearly all encounters (97%) were initiated by herd members.

Figure 5.5 The number of encounters between NE 5 and herd members for each hour of observation during the first two days after the introduction of NE 5 into the herd. Ballantrae 4 February 1991.
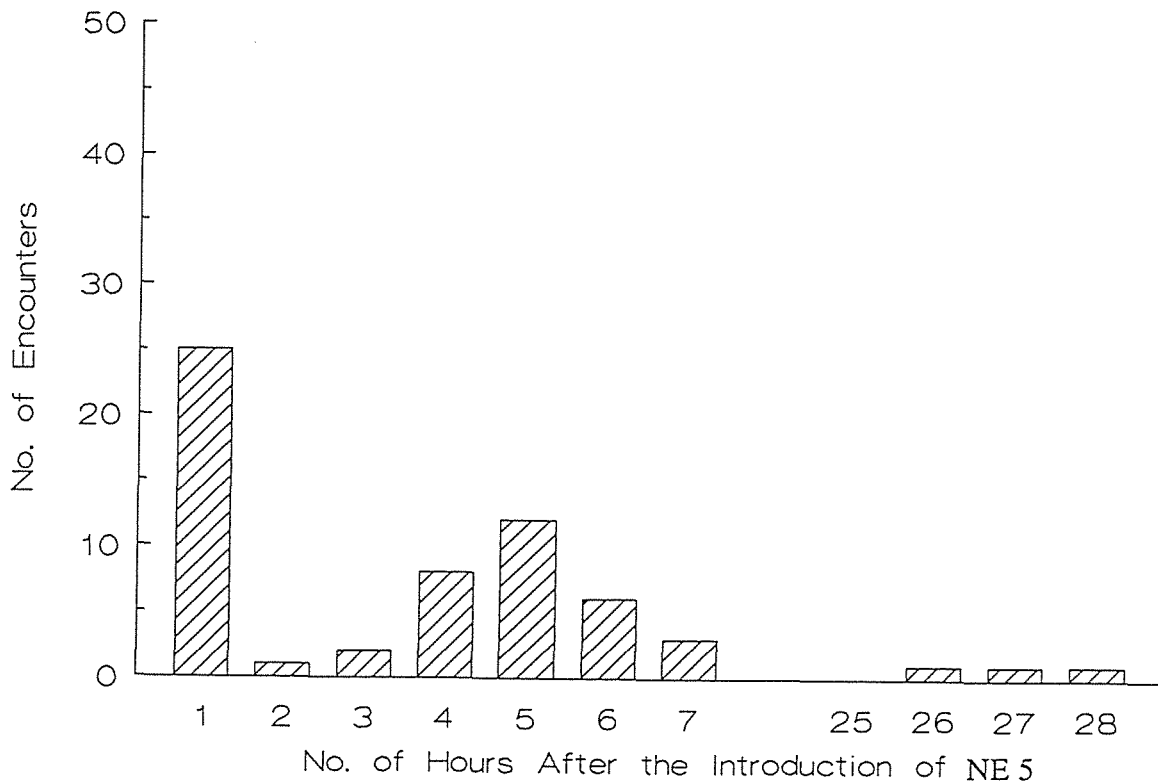
Action of Herd Members Toward NE 5

Over half the actions of the herd members (51%) were exploratory. In 15% of encounters they exhibited specific threat displays and on 29% of occasions they challenged NE 6 by a dominance approach. Physical combat occurred 5% of the time.

Outcome of Encounters

During the first two days NE 5 lost 50 of the 60 encounters observed and won two. However, in both of these instances the opponent was only a kid. No clear outcome occurred in eight encounters.

B) Experiment 2

Sixth New Entrant

Initial Response of the Herd

For the first two hours following her release into the paddock NE 6 remained isolated (>20 metres) from the herd. During this period she moved with energetic, jerky actions. The animal appeared to be "excited", wagging her tail and breaking into short runs. She also grazed in short bouts, often lowering her head to the ground without actually grazing. NE 6 was highly watchful but frequently groomed herself by scratching her stomach with a hind leg and rubbing her muzzle against her flank. On one occasion she was observed sliding down the hill on her stomach (a behaviour rarely seen in goats). At the time of introduction the herd grazed in a fairly confined area of the paddock. Some herd members appeared to show some interest in NE 6 by occasionally glancing at her. As the herd expanded its grazing

range two does approached NE 6 in turn but neither came within 1 metre of her.
Two and a half hours passed before NE 6 approached the herd, but she then behaved
in an overtly dominant manner. She walked straight through the herd frequently
butting aside kids which came too close and adult members of the herd did not
approach her. During this initial period of association with the herd NE 6 exhibited
several 'horn thrashing' displays. Fifteen minutes after approaching the herd NE 6
sat down, and spent the following hour undisturbed and grooming herself.

Frequency of Encounters

Figure 5.6 gives the number of encounters between NE 6 and herd members for
each hour of observation during the first three days following NE 6's introduction
into the herd. A maximum of 34 encounters occurred in the third hour. Most (79%)
interactions were initiated by herd members.

Figure 5.6 The number of encounters between NE 6 and herd members for each hour of
observation during the first three days after the introduction of NE 6 into the herd.
Ballantrae 31 January 1991.
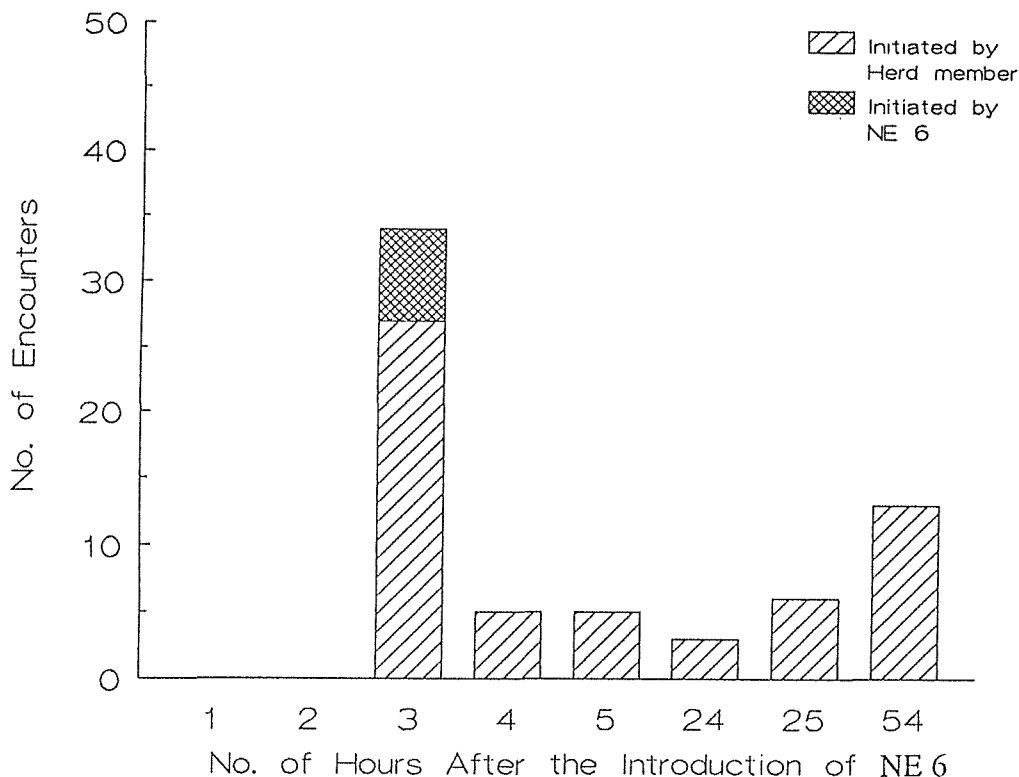
Action of Herd Members Toward NE 6

Table 5.1 shows that exploration was the predominant (73%) action of herd members. Although threat displays and overt aggression were rare, herd members did intrude on NE 6's personal space by means of frontal orientation.

Outcome of Encounters

There were no occasions when NE 6 was displaced from a site. When confronted by a herd member NE 6 turned (either her whole body or just her head) away from her opponent, avoiding eye-eye contact on 16% of occasions. 16% of the time she threatened the intruding herd member. In 6% of incidents she resorted to overt aggression. Over half the time (61%), however, an approach by a herd member did not elicite an obvious response; NE 6 either continued grazing, groomed or showed a similar low intensity response.

Table 5.1   The Number of Exploratory and Agonistic Actions by New Entrants and Herd Members During the First Day or First Two Days (*) Following the Introduction of the New Entrant into the Herd. See Text for Dates and Details of Each Introduction.

New Entrant	Submission		Exploration		Threat		Overt Aggression	
	NE	HERD	NE	HERD	NE	HERD	NE	HERD
1	74	0	0	48	31	3	0	5
*2	140	0	3	55	0	64	7	48
3	95	0	0	48	0	45	0	4
*4	8	6	4	12	3	11	4	3
5	46	0	2	29	4	24	0	3
*6	8	8	2	31	15	16	3	2

DISCUSSION

Categorization of Exploratory and Agonistic Behaviour

The categories used to classify agonistic behaviour in this study mainly followed Shanks (1972). But after analysing initial video recordings of behavioural interactions these categories were modified by adding a category for dominance approach behaviour. An approach by an animal exhibiting an aggressive posture, or an approach from a frontal orientation, as described by Walther (1984) often precedes a threat display, however, it may, on its own, be sufficient to challenge an opponent. Although dominance approach behaviour was classed as a threat in the current study, it occurs along a continuum between exploratory behaviour and threatening behaviour. Shanks (1972) did not include investigative behaviour in his otherwise comprehensive descriptive account of feral goat behaviour. Other researchers have recognised this type of behaviour in ungulate species as being neither purely sexual nor agonistic (Hafez et al, 1969).

The ethogram developed for use in this study did not include all behaviour which occurs during social encounters between herd members and the new entrants. There were a number of behaviours and displays which appeared to have no clear relevance to the situation in which they occurred. Such behaviour is well known to ethologists and some refer to them as "displacement" activities. Comfort behaviours (ie.grooming and urination), horn thrashing, and agonistic grazing which occurred frequently during social encounters in this study could not adequately be classified as exploratory, dominance or submissive behaviour and were ignored. Future research may clarify their intermediate position between the categories.

The Response of the Herd

The introduction of each new entrant into the two herds studied resulted in a sudden upsurge in exploratory and agonistic behaviour. This peak in social interaction occurred immediately after the new entrant joined the herd and lasted up to two hours. Several other studies have reported similar initial high levels of agonism in response to the introduction of an unfamiliar animal (Non-human primates: Beinstein & Gordon, 1974; Domestic pigs: Tan & Shackleton, 1990; Domestic goats: Addison & Baker, 1982). Exploratory behaviour, however, was not described in these reports. On the other hand, the brief descriptive account of the natural introduction of unfamiliar animals into a wild feral goat herd by Riney & Caughley (1959) reported extreme investigative behaviour towards the new entrants but no aggressive behaviour.

A rapid decline in the number of social interactions during the first 24 hours was common to all the introductions in this study. During the second day, however, the frequency of interactions tended to fluctuate considerably. This variation is likely to be a function of the daily activity pattern of the herd since social interactions are most frequent during the active periods of the diurnal behaviour cycle (see Activity Budget of a Female Feral Goat Herd, Chapter 3). The rate at which agonism declines and the incorporation of the new entrant into an established group is not covered well in the literature. Beinstein & Gordon's (1974) study on non-human primates reported a substantial decrease in the initial intense agonism in the first hour following the introduction of an unfamiliar conspecific. Addison & Baker (1982) found the decrease in agonism to occur slowly over 3-4 weeks in domestic goats.

Here exploratory behaviour was the most common action exhibited by herd members toward a new entrant; overt aggression the least common. This finding therefore supports Maynard-Smith & Parker's (1976) theory of conflict behaviour which states that contestants should use minimal acts of aggression to win dominance.

Differences between New Entrants

The behaviour of NE 1 and NE 3 were very similar, and so were the responses of the study herd to them. Within only a few minutes of being introduced both NE 1 and NE 3 attempted to join the herd. An intense episode of exploratory behaviour by herd members then followed and groups of curious goats followed the new entrants. Both NE 1 and NE 3 behaved submissively by retreating and avoiding confrontations with herd members. Thus in the early post-introductory phase both these new entrants had attained a subordinate position in the herd's dominance hierarchy and almost all (>85%) actions by herd members resulted in their displacement. Apart from the occasional clash with herd members, both NE 1 and NE 3 showed no overt aggression. Any threat displays from them occurred in a defensive context. Within half an hour of their introduction NE 1 and NE 3 were isolated from the herd. This behaviour was in sharp contrast to that of NE 4 and NE 6, both of which were slow to join the herd and were seldom displaced by herd members. Unlike NE 1 and NE 3 there were occasions in which NE 4 and NE 6 initiated encounters.

Horn thrashing was common in the encounters of herd members with the dominant does NE 4 and NE 6, but did not occur in the interactions with other, more subordinate, new entrants. Thrashing the horns against small bushes, bunches of long grass, or the ground, has been described by several investigators of bovid agonistic behaviour, consequently a number of names such as "horn thrashing" (Shank, 1972), "horning" (Geist, 1971), "weaving" (Estes, 1967), "bodenhornen" (Schloeth, 1961), and "bodenforkeln" (Walther, 1964) refer to similar behavioural displays of several bovid species. Neither the motivation nor social function of this behaviour is clear. Some researchers consider it serves a communicative function in agonistic interactions. The behaviour can be interpreted as a display of strength, in which the actor demonstrates to its opponent its ability to fight (Leuthold, 1977). Other researchers (eg. Walther, 1974; Geist, 1979), however, question this view point because unlike other threat displays it very rarely elicits a response by the opponent. A common view among these researchers is that horn thrashing has no adaptive function and instead they search for a proximate cause for the behaviour. Walther (1974) suggests that horn thrashing is simply an outlet for surplus energy.

Leuthold (1977), however, interprets the behaviour as a sign of ambivalence, resulting from the simultaneous arousal of attack and escape tendencies. More research is therefore needed to clarify the causation and social function of horn thrashing.

The introduction of NE 1, NE 2 and NE 3 into the study herd resulted in double the level of social interaction to that observed after NE 4 and NE 6 joined the herd. This variation in response may result from several factors, especially the dominance status of the new entrant, and seasonal changes in socio-sexual behaviour.

A) Seasonal Variation

In experiment 1, the five unfamiliar animals were introduced into the herd at various times over a 10 month period. The first three new entrants were introduced during the early stages of the gestation period where as NE 4 and NE 5 were introduced during the post-kidding period.

Changes in hormone levels over the course of reproduction and their effect have been described by many researchers (Goodman & Karsch, 1980; Broom, 1981). According to Huntingford and Turner (1987) prolactin increases aggression and thus explains the maternal defence exhibited by lactating females. It therefore seems possible that seasonal physiological changes contributed to the variation in herd members response to the unfamiliar animals.

Seasonal changes in the composition of the herd are also likely to be partly responsible for the different outcomes of the introductions. For instance the presence of kids may affect the interaction between the mother and the new entrant and generate a new set of interactions which occur between kids and the new entrant. Because does are usually protective of their offspring, and kids are often inquisitive, the likelihood of agonistic encounters is increased. Age is also known to be an important determinant of dominance (Hafez et al, 1969), therefore an adult goat introduced to a herd during kidding season will not occupy the lowest position in the social hierarchy.

B) Dominance of New Entrants

Previous studies on social hierarchies have revealed a spectrum of agonistic interactions which occur between animals of various dominance stature (Hafez et al, 1969; Shank, 1972). The type of interaction occurring between individuals depends on the degree by which the individuals differ with respect to their dominance rank. Overt aggression seldom occurs between animals in which there is a large disparity in dominance. It follows ,therefore, that the type of reception an animal receives when it enters an unfamiliar herd is likely to depend on the position of that animal in the herds dominance hierarchy. In this study the new entrants varied in age, size and weight and these characteristics are known to correlate closely with dominance in feral goats (Hafez et al, 1969). Although the social status of each new entrant was unknown, similarities in the response of the herd to new entrants equal in age, size and weight implies that dominance contributed to variation in the response of the herd to the new entrant.

Introduction of the new entrants took place over a 10 month period, which allowed the herd ample time to settle between introductions. However, changing seasonal effects in goat social behaviour may have masked any effects of each new entrants' dominance status upon the herd.

Recommendations

Because the study herd was large, the dominance hierarchy could not be determined before the introduction of each entrant. This prevented detailed analysis of any changes resulting from the presence of a new animal in the herd. Future studies should therefore use herds near in size to natural groupings (Riney and Caughley, 1959) in which the dominance patterns are well established.

It is clear that new entrants low in social rank can suffer severe stress when introduced to a large herd of goats. Accordingly, space is required so that the new entrant can isolate itself from herd members during the first few days and avoid repeated aggression. The introduction of pregnant females to a large herd is not

recommended as the present study indicates they may experience a large amount of stress which is likely to cause abortion (Merrall, 1985).

The work suggests that in the wild new immigrant goats could be accepted by a feral herd and participate in relatively infrequent agonistic encounters within 24 hours. The longer term effects upon the physical wellbeing, social status, and later reproduction of a new entrant, all of which could in turn influence herd demography, need further study.

GENERAL DISCUSSION

Several authorities on ethology (eg. Slater, 1978; Martin & Bateson, 1986) have given theoretical guidelines for the categorization of animal behaviour according to its form. The practical difficulties of dividing behaviour into discrete homogeneous categories, however, are formidable and seriously undermine the value of strict classification systems. Not all behaviour patterns fit easily into the discrete categories because behaviour is a continuum of movements and events.

During the course of the study the non-distinct nature of the boundaries between behaviour was evident. For instance, in Chapter 4 (Activity Budgets of Feral Goat Kids) it was apparent that as kids became older exploratory behaviour developed into grazing behaviour. No standard criterion is available to distinguish behaviour when these two behavioural categories overlap. Similarly, in Chapter 2 (Maternal Investment) difficulties arose when ascribing the initiation of suckling events to mother or offspring. The transition from mother-initiation of suckling events to kid-initiation was not sudden, but rather a gradual change in the behavioural complex between mother and kid. Currently in ethology, the classification of intermediate forms of behaviour is subjective and consequently comparisons between studies are difficult to interpret. Recent research indicates that determining the homogeneity of behavioural categories appears to be more difficult than previously assumed. Play, long recognised as a single behavioural category (Fagen, 1981), is more recently divided into several types of play behaviour (Gomendio, 1988; Pellis, 1991).

In the current study, apart from a small sex difference in the suckling frequency of single kids, measures of suckling behaviour gave no evidence of sex-biased maternal investment in feral goats. Comparison of activity budgets for male and female kids showed that females spent more time grazing than males. According to Byers and Moodie (1990), the sex which receives the least maternal care is expected to spend more time foraging. Data on kid growth (ie. male kids had larger birth

weights and grew faster than female kids) was also in agreement with Triver's (1972) parental investment theory. The discrepancy in proximate measures of parental investment stress the need for a detailed analysis of the relationship between measures of suckling behaviour and actual milk intake throughout development of the offspring. It also appears that sex differences in birth weight and growth rate may not be a reliable indication of differential allocation of maternal resources.

Several limitations in the quantitative comparison of parental investment of ungulate species have been highlighted in the present study. Ambiguity of terminology in the literature on parental investment presently restricts the value of comparative studies. In particular, terms used to describe suckling behaviour, such as "suckling bout", are used inconsistently by researchers. For example, Hinch's 1989 definition of "suckling bout" is equivalent to the "successful suckle" of Shackleton (1985).

The lack of standard observational and statistical methods in quantitative studies of parental investment have also hindered the interpretation of comparative studies. For instance, suckling frequency (number of bouts per hour) is not strictly comparable with suckling rate (time spend suckling per hour).

Throughout this study reference has been made to environmental factors and their influence on the behaviour of feral goats. Although captive feral goats are genetically similar to their wild counterparts, it is clear that their behaviour is greatly modified by the nature of the surroundings in their enclosure. For instance, feeding behaviour depends on the type and diversity of forage available while lying-out only occurs when sufficient lying-out sites are available and when nutritional requirements of the mother and neonate are fulfilled.

In spite of the obvious limitations, behavioural studies of semi-captive feral animals are relevant to the behaviour of animals in their wild state and should not be

discounted. There are numerous methodological difficulties associated with the study of wild feral animals, particularly the goat, which has evolved under high selection pressures from predation, and thus has well developed sense organs which enable it to readily detect and respond to humans. Some of these difficulties are obviated in captive situations.

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