WHAT MAKES A GOOD MOTHER?: COMPONENTS AND COMPARATIVE ASPECTS OF MATERNAL BEHAVIOUR IN UNGULATES

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SUMMARY

This review examines the components of maternal and offspring behaviour in ungulates. The large literature on non domestic species is drawn to the attention of scientists who work with domestic animals. The review identifies behavioural traits of demonstrated or putative value for Survival of Offspring, especially in sheep, The mechanisms of control of maternal behaviour and of mutual recognition between mother and young are also briefly reviewed. The possible use of behavioural traits in selection programs for improving lamb survival, and in designing systems of husbandry for lambing is considered.

INTRODUCTION

There are few, if any species of mammal, and certainly no species of ungulate, in which the young can survive in the absence of maternal care, or a substitute that provides sustenance and protection. A knowledge of maternal behaviour is therefore essential in any program aimed at reducing mortality of infant animals, although factors other than behaviour may be major causes of mortality (Alexander 1984).

The large literature on maternal behaviour in mammals covers quantitative and qualitative descriptions of behaviour in a wide variety of species representing many mammalian families. It deals with the growing body of experimental evidence about factors governing the onset and maintenance of maternal behaviour, and about the senses and sensory cues involved in mutual recognition between mother and offspring. The literature includes books and reviews that deal with mammals generally (Hediger 1955; Lehrman 1961; Rheingold 1963; Harper 1970; Shillito-Walser 1977; Rosenblatt 1980; Gubernick and Klopfer 1981), with ungulates (Fraser 1968; Lent 1974) and with sheep specifically (Alexander 1960, 1980; Hersher et al. 1963; Squires 1975; Gonyou 1983/4; Poindron et al. 1984).

The primary objects of the present review were to draw the large literature on non-domestic species to the attention' of people who work with domestic animals, and to search for and identify behavioural traits that might be correlated with superior mothering ability, especially in sheep. These traits could be used in selection programs or in the design of husbandry procedures aimed at reducing infant mortality. The review examines maternal behaviour in the "ungulate" families which have an evolutionary relationship with sheep and where members. mostly produce a single offspring each' year. Offspring behaviour and the role of the male are also considered briefly. The ungulates represent about 200 species of quadrupeds, that are predominantly horned and herbivorous and include most of 'the animals farmed by humans; The Suidae (pig family) whose members, mostly produce several large litters of immature young each year are largely excluded from the review. It is recognized that some of the behavioural traits might be only indirectly relevant to modern livestock and farming conditions, yet their presence might reflect a superior,

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innate mothering ability.

It was not practicable to cite more than a fraction of the hundreds of papers describing maternal behaviour; recent papers are given precedence, and the reader is referred to Lent (1974) for a comprehensive review of earlier papers dealing with ungulates. In contrast with the extensive, detailed literature on domestic ungulates, the copious literature on maternal behaviour in wild ungulates is sparse on detail of peri-partum events, for the obvious reason that these are difficult to observe in the wild. Even with zoo animals, few observers seem prepared to mount the necessary surveillance.

FACTORS SHAPING MATERNAL BEHAVIOUR IN UNGULATES

Consideration of the major influences likely to have shaped mother and young behaviour ungulates during their evolution should facilitate identification of significant behavioural traits.

Ungulates are generally mobile, social animals, and since their young are entirely dependent on maternal milk supply initially, there is a need for the mother to develop a bond with her offspring, and to recognize, maintain contact with, and suckle her own offspring to the exclusion of alien young, which could monopolize the limited milk supply.

The ungulate mother needs to graze or browse throughout most of the daylight hours, to meet her nutritional requirements, which are about 50% higher during lactation than in advanced pregnancy (Weston and Hogan 1986). Behaviour patterns that allow grazing, as well as any watering, without the mother losing track of the offspring, are therefore necessary.

The position of ungulates in the food chain means that they are subject to predation. The young are of an attractive size for the mammalian and avian predators that usually share their habitat (Rowley 1970; Ryan 1972; Nowasad 1975; Estes and Estes 1979; Gluesing et al. 1980). Predator avoidance would therefore be expected to be a feature of maternal behaviour.

Small ungulate young such as lambs (Alexander and McCance 1958), caribou (Hart et al. 1961) and piglets (Curtis 1970) are prone to hypothermia during the post-partum drying of the coat, or longer in Suidae; and newborn young are also inexperienced in coping with environmental hazards such as steep slopes, streams and bogs. Behaviour 'of the mother might therefore be expected to provide environmental protection for the newborn.,

COMPONENTS OF MOTHER AND YOUNG BEHAVIOUR

Pre-partum isolation

The' females of many species tend to leave the social group during the days or hours prior to birth. These species include giraffe (Lang-man 1977), horse (Tyler 1972-3), zebra (Klingel 1969), antelope (Sekulic 1976), impala (Jarman 1979), feral goat (Rudge 1970), Barbary sheep (Haas 1959), Big horn sheep (Shackleton and Haywood 1985), feral Soay sheep (Grubb 1974; Shillito and Hoyland 1971) and domestic sheep (Fraser 1926; Sharafeldin et al. 1971; Kilgour 1972; Whitelaw and Watchorn 1975; Gonyou 1983/4). However, isolation for parturition is by no means the rule for domestic sheep (Stevens, et al. 1981) or cattle (Edwards and Broom 1982), and appears subordinate to selection of a birth site in feral goats (O'Brien 1983). The tendency to seek isolation is less marked in primiparas than in multiparas, for. example in domestic goats (Lickliter 1984/5a). With sheep, the tendency for isolation 'can be exploited for for the purpose of identification of lambs during indoor lambing, by

providing cubicles for sheep to enter, but with a high step which prevents lambs from leaving (Gonyou and Stookey 1981).

At the pre-partum stage the previous season's offspring may be driven off, as observed for example, in hog deer (Miller 1975) or reedbuck (Jungius 1970), but this behaviour was not observed in feral Soay sheep (Grubb 1974).

Birth in isolation should facilitate formation of an exclusive bond between mother and newborn; where birth takes place in the presence of other parturient females aberrations in bond formation are common (Welch and Kilgour 1970; Alexander et al. 1983a). In many species, parturient females are attracted by a recent or imminent birth, and in some species, such as moose, isolation is maintained by vigorous aggression towards encroachment by others of the same species (Bogomolova and Kurochkin 1984).

Selection of a birth site

There is little objective evidence about factors that determine the precise site of birth and features that might be attractive to the parturient female of any ungulate species, except feral goats (O'Brien 1983) which are likely to choose birth sites that are protected either by overhead cover or by proximity to vertical surfaces that reduce wind velocity. Subjectively, mountain sheep (Ovis dalli) are said to be attracted by the security of high cliffs (Pitzman 1970; Geist 1971) and domestic sheep are said to favour depressions and slopes, and proximity to hedges or walls (Smith 1965; Whitelaw and Watchorn 1975) and Soay sheep to seek a sheltered site (Shillito and Hoyland 1971). Domestic sheep show a consistent preference to lamb at the highest end of a paddock (Alexander, unpublished data 1982). Other species such as moose (Stringham 1974) and a variety of deer and antelopes (Lent 1969; Kok 1975; Jarman 1979) are said to seek the seclusion of thick vegetation for parturition.

There would be survival advantages in selecting a birth site that provided protection from weather, and safety from misadventure, but the limited literature indicates that neither wild nor domestic ungulates display wisdom here. Goats may be exceptional (O'Brien 1983), but studies with other species in an environment as varied as O'Brien's study area would be revealing. Sheep have been reported to seek shelter more often as parturition approaches (Hunter 1954), but generally, when sheep lamb in shelter they are themselves cold; such as soon after being shorn (Hunter 1954; Miller 1968; Winfield et al. 1969; Lynch and Alexander 1977). In addition, newborn lambs and the young of other species, such as red deer and lechwe, have been observed mired, drowned or abandoned after tumbling down a steep incline, when born in close proximity to natural hazards (Lent 1969; Pitzman 1970; Arman et al. 1978; Kilgour 'et al, 1983).

In many species, including domestic' and mountain sheep, the exact birth site frequently appears to be at the location where the foetal fluids are spilt (Fraser' 1965; Smith 1965; Pitzman 19.70; Kilgour 1972; Arnold and Morgan 1975). The female appears to be 'strongly attracted to this spot; however, if the birth process is prolonged the animal may wander away and give birth elsewhere.

Pre-partum attraction to foetal fluids

Although there are few data for wild species generally, most ungulates, with the apparent exception of members of Suidae and Camelidae, are strongly attracted to their own spilt foetal fluids or to the fluids of other parturient females; examples are documented for sheep (Fraser 1926; Alexander 1960; Shillito and Hoyland 1971), cattle (Brownlee 1950; Selman et al. 1970a), horse (Tyler 1972-3) and red deer (Arman 1974). This attraction probably represents

an essential 'first stage in the bonding process discussed below (Levy and Poindron 1984; Alexander et al. 1986), but it can lead to neglect if the newborn rolls from the birth site immediately after birth. As reported for domestic sheep (Kilgour et al. 1982), horses (Tyler 1972-3) and red deer (Arman et al. 1978), the mother concentrates on the spilt fluids and fails 'to attend to her offspring.

The attraction to the fluids can also lead to interference in births by other parturient females (Lent 1974), and to attraction or permanent attachment of females to alien newborn young. This is well documented for sheep (Fraser 1926). Inexperienced ewes are particularly prone to having their newborn lambs stolen by experienced ewes (Alexander et al. 1984).

Nesting

Obvious thermal protection for the young is provided by Suidae only, whose members build nests about 2 m across and 1 m high of grass and shrubs (Atwell 1976; Stolba and Wood-Gush 1981; Martys 1982; Jensen 1986). Among Bovidae (sheep and cattle family) pawing the ground and scraping out a shallow depression where the fluids have been spilt is frequently observed just before or during birth; this behaviour could be regarded as vestigial nest-building (Fraser 1926; Pitzman 1970; Sharafeldin et al. 1971; Arnold and Morgan 1975; Whitelaw and Watchorn 1975). These "birth beds" remain the focus of activity during birth and for several hours thereafter (Pitzman 1970; Kilgour 1982), and the animals may return to them during the next few days.

Parturition

Normal delivery in most ungulates follows a regular pattern (Lent 1974) and rarely lasts more than 1-2 h. The female usually lies during labour, but birth is often completed by the female standing, and the cord breaks when stretched, without maternal intervention. However, mares usually remain recumbent for 10 min or more, allowing a significant transfer of blood from the placenta to the foal (Rossdale 1967). Primiparous cattle (Edwards and Broom 1982) and sheep (Alexander 1960) tend to remain recumbent for many minutes after delivery whereas multiparas are usually on their feet almost immediately. The delay in standing usually delays the start of grooming.

The offspring are usually born in the anterior position (nose and forefeet foremost).Some ungulates, such as horses and zebra (Klingel 1969) and perhaps cattle (Duffy 1972) appear to suspend parturition when disturbed by humans or predators, but sometimes to the detriment of the foetus.

Because of environmental control of the breeding season, mediated by photoperiod and perhaps by other factors, such as forage supply (Bunnell 1982), females of most ungulate species tend to mate synchronously, and give birth in spring and summer when forage is plentiful (Rutberg 1984). The concentration of 80 per cent of births in the space of an oestrous cycle (2-3 weeks), typical of the wildebeest for example, has been labelled a predator defence by Estes '(1976). The predators may be deterred by large aggregations of calving females; and the presence of predation-prone young for a limited period only, may restrict the numbers killed. This interpretation of the value of synchronous births has been disputed by Rutberg (1984) on the grounds that the American bison,, which calve synchronously, do not aggregate for calving.

The distribution of births throughout the 24 h of the day varies widely between species. In wildebeest there is a peak between 6 a.m. and 12 noon, regarded by Estes (1976) as a mechanism for avoidance of nocturnal predators. In'horses most births' occur during the hours of darkness (Rossdale 1968a; Tyler 1972a), whereas there appears to be no consistent peak of births in sheep

(George 1969; Sharafeldin et al. 1971; Tomar 1979) or cattle (Edwards 1979) despite individual reports of peak lambing or calving at certain hours (George 1969; George and Barger 1974). While the endocrine events that lead to birth in ungulates have been well researched (Nathanielsz 1976), it is clear that the environmental factors that influence the hour of birth are poorly understood. The hour of feeding is, however, known to influence the hour of birth in domestic sheep (Gonyou et al. 1981).

It is well documented that prolonged or difficult birth (dystokia) inhibits maternal behaviour in sheep (Wallace 1949; Alexander 1960; Shelley 1970; Winfield et al. 1972) and cattle (Neumann et al. 1974; Edwards and Broom 1982), probably through pain and shock. Dystokia appears to be prevalent in certain breeds (George 1975, 1976; Whitelaw and Watchorn 1975; Elving et al. 1986). Birth problems also occur in other species including musk ox (Norment 1973), whitetailed deer (Townsend and Bailey 1975) and wildebeest (Estes and Estes 1979), no doubt with similar results. Birth difficulty also affects behaviour of the newborn, and may delay or prevent successful sucking (Haughey 1980).

Grooming of the newborn

Grooming has been described for a variety of species including red deer (Arman 1974), bontebok (David 1975), zebra (Wüst 1976), cattle (Brownlee 1950; Selman et al. 1970a; Edwards and Broom 1982) and sheep (Alexander 1960; Morgan and Arnold 1975; Bareham 1976). Grooming appears to be an extension of the attraction to the spilt foetal fluids, and usually begins by consumption of the remnants of the foetal membranes. It grades into a thorough licking of the newborn, usually beginning with the head, the first part of the offspring to move, and continues onto the body after the newborn has stood, with particular attention being paid to the anogenital region. The direction of the licking appears to be against the lie of the hair (Meier 1973). Fluids on the ground and soiled vegetation are also sometimes consumed, as by mule deer for example (Goldberg and Haas 1978).

Grooming is initially intense but becomes spasmodic within half an hour or so of birth in sheep and after several hours in horses (Rossdale 1968b); bouts of grooming can be interspersed by episodes of grazing or eating hay at least in sheep and cattle (Edwards and Broom 1982). In sheep the amount of grooming of individual lambs is less for multiples than for singles, and is reduced for the lambs born later in a litter (Holmes 1976; Atroski and Osterberg 1979). Beyond this immediate post partum period, grooming of the young in most species is confined to brief occasional episodes.

Several functions of grooming have been postulated, mostly with little' or no experimental evidence (Lent 1966, 1974; Bareham 1976) Edwards and Groom 1982). They include stimulation of respiration, muscle tone, circulation and excretion, drying to reduce heat loss, removal of birth odour-to avoid attracting predators, hair-care to increase thermal insulation and finally the bonding and learning of offspring odour by the mother (Poindron et al. 1984).

Grooming. is minimal or absent in some ungulate families (Suidae, Camelidae, Hippapotamidae).

Placentaphaqia

The placenta, or "afterbirth"; in most ungulates is voided within 'about 6 h of birth; but there appears to be wide variation between species, even within the same family. The median period appears to be about 1 h in Equidae as in horses, (Rossdale 1967) and zebras(Wüst 1976) and in Cervidae such as caribou (Lent 1966). It is frequently longer in Bovidae; for example,. about 3 h .

in sheep (Arnold and Morgan 1975), about 4 h in cattle (Edwards and Broom 1982) though only about 1 h in hartebeest (Gosling 1969). In discussing the possible attraction of afterbirth to predators, David (1975) and Estes and Estes (1979) claim that there is a survival advantage in delaying the dropping of the placenta until the newborn is strong enough to run from any predator.

Complete placentaphagia is common in some ungulate families such as Cervidae, for example in mule deer (Goldberg and Haas 1978), and Bovidae, including domestic cattle (Brownlee 1950; Edwards and Broom 1982). Partial consumption of the placenta is sometimes seen in sheep (Arnold and Morgan 1975) and many other species such as giraffe (Kristal and Noonan 1978). Placentaphagia is not seen in Equidae (Klingel 1969; Tyler 1972-3), Camelidae, or Suidae (Frädrich 1974). Placentaphagia is postulated to minimize the risk of predation in species that remain near the birth site for several days or longer (Gosling 1969; Townsend and Bailey 1975). Female elephants appear to eat little or none of the foetal membranes or placenta, but are reported to disperse the birth detritus or to stamp it into the ground and cover it (Leuthold and Leuthold 1975); with such a large animal as a newborn elephant, this disposal can scarcely be regarded as a predator defence. Also, "afterbirths" are a substantial, readily available source of food for potential predators such as foxes (Alexander et al. 1967), and it can be argued that not to eat the placenta would be a better defence than consuming it. Nutrition and endocrine functions have also been suggested for placentaphagia (Townsend and Bailey 1975; Edwards and Groom 1982), but experimental evidence is lacking.

Maternal behaviour and offspring's excretions

Maternal licking of the ano-genital region appears to facilitate defaecation and urination in some, species including domestic cattle (Kovalcik et al. 1980; Metz and Metz 1986) and zebra (Wüst 1976), but it is not essential for excretion, at least in sheep (Grubb 1974). Many ungulates, including domestic cattle (Selman et al. 1970a), Barbary sheep (Haas 1959), red deer (Arman 1974), white tailed deer (Faatz 1977) and hartebeest (Gosling 1969) consume the faeces and/or urine of their young. Consumption of offspring's excretions does not appear to have been recorded in domestic sheep. Like placentaphagia, removal of the odour of the excretions is said to minimize the risk of predation (Gosling 1969; Stringham 1974).

Reactions of group members to newborn

In most species, non-parturient females appear to pay only desultory attention to the newborn. However, female elephants show excitement and interest in birth by another female and assist in the dispersal of birth' detritus (Leuthold and Leuthold 1975). Pony mares are reported to gather around a parturient mare and may interupt the progress of labour (Rossdale 1968b), and non-parturient mountain sheep may also display interest in newborn lambs (Geist 1971).

Suckling behaviour

A variety of maternal cues appear to aid the ungulate newborn in 'its initial search for the udder. These include warmth and softness of bare skin (goats, Stevens and Linzell 1974; sheep, Vince 1986; swine, Welch and Baxter 1986) and maternal orientation and geometry (sheep, Smith 1971; Alexander et al. 1964). A hunched stance appears to facilitate suckling in most species, whereas some suckle initially in the lying position (red deer, Ax-man 1974; moose, Stringham 1974; white tailed deer, Langenau and Lerg 1976; steenbok, Robinson 1977). It is important at this time that the mother remains still (Alexander 1960).

Maternal facilitation of early post-partum sucking appears to be important

for the intake of colostrum and the development of effective blood levels of maternal antibodies by the offspring (Selman et al. 1971; Kim et al. 1983). Many calves of dairy cattle appear slow to suck for the first time because of the large dairy type udder and the positioning of the teats low to the ground (Selman et al. 1970b; Kovalcik et al. 1980; Edwards 1981a). Similar problems have been observed with Dorset Horn sheep with pendulous udders and Merino sheep with greatly enlarged "bottle" teats (Alexander, unpublished; Hayman et al. 1955). On the other hand, calves of some beef breeds such as the Saler show little aptitude for bottle feeding, compared with dairy breeds. The maternal presence is necessary for these beef breeds to survive (Le Neindre et al. 1979).

Many reports show real species differences in the frequency and duration of suckling bouts (Lent 1974), but these do not appear to be significant survival factors.

Ungulate mothers do not normally permit sucking by offspring other than their own, although a high incidence of cross-suckling has been reported in domestic cattle (Edwards 1981b; Lewandrowski and Hurnik 1981) and a lower incidence in groups of sheep with large litters (Hess et al. 1974). Occasional cross suckling has also been reported for white-tailed deer (Faatz 1977).

Spatial association of mother and offspring

The degree of association between mother and offspring during the post-partum period is commonly used to divide ungulate species into two major classes (Lent 1974), described as "hiders", with young that lie concealed, and "followers", with young that remain with the mother. However, types with intermediate behaviour patterns such as moose (Stringham 1974) are common and both types of behaviour have been described for the same species, for example in giraffe (Langmann 1977; Pratt and Anderson 1982). The concept has been modified several times to accommodate problems in classification (Ralls et al. 1986). It has been suggested that isolation for birth by followers represents a vestigial hiding phase (Langman 1977).

Most species of ungulate are hiders; the offspring remain concealed near the birth site while the mother feeds, sometimes several kilometers away.' 'O'Brien (1984) drew attention to individual variability and to, environmental effects on the distance the mother moves from the hidden. offspring; those remaining close were termed "stayers" and those moving away were termed "leavers".. The young of hider species are suckled as infrequently as 2-3 times daily, and appear to lack the endurance to: travel. The process of concealment. usually 'appears to be initiated by the offspring themselves, as seen in a variety of species-:', (Harper 1970) including water buck. (Spinage 1969), red deer (Clutton-Brock and Guinness 1975), mule deer (Truett 1977), and goats (Lickliter 3984). The characteristics of-the. sites of concealment of goat kids have been closely examined '(O'Brien 1983.) and feature putative protection from predators. arid weather. The choice of sheltered sites by red deer calves more than a day old has also been 'recorded (Kelly and Drew 1976). The hiding strategy is not without hazards. In hot climates the screen of vegetation may reduce4 air movement without providing shade, and calf mortality under such conditions has been documented (Smith and Alexander 1966). The duration of 'the hiding phase is a characteristic of the species; it may persist for a few days only, as in cattle and goats (Rudge 1970; Lent 1974; O'Brien 1984; Lickliter 1984/5b), for a month as in giraffe (Langman 1977) and white-tailed deer (Hirth 1985) or even 2 months as with reedbuck (Jungius 1970) and Uganda kob (Leuthold 1967). Hiding is replaced by following behaviour and of-ten by aggregation of the young into nurserygroups (Lent 1974).

With a minority of ungulate species, the "followers", the young normally leave the birth site and follow the mother closely within hours of birth while she grazes or travels to water. The follower species inhabit open grassland (Lent 1974) and include the horse (Fraser 1980a), caribou (Miller and Broughton 1973), bontebok (David 1975), bison (McHugh 1958), wildebeest (Estes 1976) and mountain and domestic sheep (Pitzman 1970; Morgan and Arnold 1974). In this class, mother and offspring remain within earshot of each other for days or weeks; suckling is frequent, and initially may occur several times hourly (Lent [illegible]). **Travelling** in hot weather can, however, lead to mortality of lambs due to heat exhaustion (Smith 1961; Morgan et al. 1972).

Hiding and following are considered by many observers to represent different **strategies** in predator defence. With hiders, concealment and immobility coupled with placentaphagia and consumption of offsprings' excretions are believed to be the main defences. With followers, predators could be deterred or repelled by the mother, or avoided by flight.

In an evolutionary sense hiding may represent a remnant of an ancient nesting phase; it seems reasonable to suggest that followers with their precocious young represent an **advanced stage in. the evolution of behaviour of ungulate mothers and young.**

Maternal defence against predators

Flight is the common strategy with followers (Harper 1970; Valdez **and Alamia 1977) but vigorous** defence of the offspring has been reported for a variety of species (Lent 1974; Berger 1978; Tyler **1972-3).** Such species **include elk, musk ox, moose, zebra,** Dall **sheep,** bighorn sheep and horses. However, **domestic sheep have been observed to remain undisturbed by the presence of foxes, a potential predator of sheep (Alexander et al. 1967), and Geist** (1971) reported **that mountain ewes were much less protective than the large** mountain **goats with their lethal** horns. **Giving birth in the presence of many other parturient females, as in caribou for example, is also regarded as a predator defence (Bergerud 1974).**

Care of multiples

The few references to maternal behaviour of ungulate females, other than Suidae, producing litters of more than one offspring deal largely with pen situations (Holmes 1975, 1976; Atroshi and Österberg 1979; Owens et al. 1980). **While** problems **with** grooming **and suckling of 'litters have been identified, the problems of maintaining contact with all members of a litter under field conditions are much greater than for a single offspring. This is indicated, for example, by the high lamb mortality due to accidental separation of** twin **lambs from their mothers during the first day of life (Stevens et al.** 1982). **Events at birth can lead to separation at that, time,. or to uneven grooming of litter mates and hence to uneven maternal bonding of ewes to lambs: this can lead to. later separation (Kilgour et** al. 1983). **Such events include litter mates being born several metres apart, straying of one of the litter during the grooming of the other(s), interference by other parturient females, separation due to physical characteristics of the birth site, such as slope and vegetation, different susceptibilities of lambs to 'chilling in inclement weather, and** interference by **humans. Ewes of some sheep breeds appear to.** leave **their lambs more readily than others** in **response to human interference (Morgan et al. 1974).**

Separation frequently occurs when ewes move from the birth site to water or graze. Even when all members of a litter appear to have been groomed normally, many ewes appear satisfied if accompanied by one lamb only, especially if the movement from the birth site occurs within 4 **h'of birth (Alexander et al.**

1983; Alexander 1984). It appears that the strength of bonding, or the ewe's awareness of her litter size depends on the time spent on the birth site (Kilgour et al. 1983). The importance of the birth site or "birth beds" in bonding of mountain sheep has been stressed by Pitzman (1970). The ability to care for twins appears to vary between breeds, and improves with experience rather than with age (Alexander et al. 1984). Permanent separation beyond the first day after birth is rare.

Offspring behaviour

Species vary widely in the rate of progress of their young but the newborn of most species suck within an hour of birth. The wildebeest appears to be the species with the most precocious young, which stand within 10 min of birth and suck within 20 min (Estes 1976). The young of some other species take several hours to suck for the first time (Lent 1974). The rate of progress within a species such as sheep also varies widely, possibly associated with differing susceptibilities to hypothermia (Slee and Springbett 1986).

Estes and Estes (1979) distinguished three stages in the development of young ungulates. A short "immobile" stage, when the young cannot stand or run, is followed by a "feeble" stage when they lack the speed and endurance of adults. This is followed by a "vigorous" stage when the young are as able as adults in avoiding predators. The feeble stage in hiders corresponds with the hiding phase, but probably lasts no more than 2-3 days in followers.

Very young offspring of some species such as nyala (Anderson 1980) contribute to predator defence by adapting a prone immobile posture when disturbed, for example, by handling. Lent (1974) indicated that this response was not limited to hiders but had not been observed in Bovidae, the sheep and cattle family. However, the prone response is common in young lambs after handling during the feeble stage (Alexander unpublished).

From an early age the offspring also play a significant role in the maintenance of contact between mother and young, as was shown by a study in which crossbred lambs were less frequently separated from their Merino mothers than purebred Merino lambs during the first day of life (Stevens et al. 1984). Also, in a recent study (Nowak et al. 1987) young crossbred lambs were shown to be more efficient in recognizing their dams than were Merino lambs. The role of the mother in maintaining contact with the offspring may have been overemphasized (Stevens et al. 1982).

Role of the male

The male has a general role in the care of offspring through defence of harems and territories (Lent 1974), in klipspringer, for example (Dunbar and Dunbar 1974); but the male is usually repelled by the female if he approaches the offspring (Spencer-Booth 1970). The male is usually excluded from parturient females in the husbandry of domestic species.

Abnormal behaviour

Abnormal behaviour patterns prejudicial to survival of offspring have been documented for a wide variety of wild and domestic species including members of Suidae, Equidae, Cervidae and Bovidae. Some of these behaviours have already been mentioned. They include abandonment of offspring, delays in the first suckling through slowness of the mother to stand or failure to stand still, failure to groom the offspring or eat the placenta in placentophagic species, and behaviour that leads to weakened bonds that are susceptible to disruption. Predisposing factors reported for sheep include inexperience (primiparity) (Sharefeldin and Kandeel 1971), birth of large litters (Holmes 1976), difficult birth, cold windy weather (Obst and Ellis 1977) and undernutrition (Thomson and

Thomson 1949). The effects of undernutrition in white tailed deer have also been documented (Langenau and Lerg 1976).

Maternal aggression towards the offspring has also been reported, especially in primiparous sheep (Alexander 1960) and in deer (Langenau and Lerg 1976); cannibolism in swine is not uncommon (Fraser 1980b). In sheep the aggression occurs when the newborn moves, but is gradually replaced by normal care-giving behaviour: similarly maternal reluctance to stand still during the offspring's initial attempts to reach the udder is usually short lived.

Premature resumption of grazing by ewes at the expense of grooming has also been observed recently (Alexander, unpublished data); the ewe acts as if appetite has been stimulated by delivery.

MECHANISMS

Control of maternal behaviour

Maternal behaviour in ungulates is initiated shortly before parturition, but maternal interest, at least in sheep, is sometimes apparent at other stages of the reproductive cycle. The available evidence indicates that steroid hormones, particularly oestrogen, play an important role, while in ungulates studied so far (Rosenblatt 1980; Poindron et al. 1984) no role in the onset of maternal behaviour has yet been found for the so called "mothering hormone" prolactin.

Oestrogen given to non-pregnant ewes primed with progesterone induces maternal behaviour in only about 50% of multiparous ewes. This proportion is increased to about 80% by mechanical stimulation of the vagina to simulate passage of the foetus down the birth canal, which has therefore been regarded as a necessary adjunct to hormonal status (Keverne et al. 1983). However, with multiparous ewes subjected to Caesarian section, all exhibited . maternal behaviour (Alexander et al. 1987), suggesting that stimulation of the birth canal is not essential. This result, together with the 50% response with oestrogen, indicates that other 'hormones may be involved in the normal control of maternal behaviour. The role of prostaglandins, which induce nest building behaviour in swine (Blackshaw and Blackshaw 1982) requires investigation in other ungulates. Previous experience also plays a role because primiparous ewes subjected to Caesarian section showlittle or no maternal behaviour (Alexander et al. 1987).

Bonding and mutual recognition of mother and young

If female sheep and goats are separated from their offspring at birth', their maternal behavioural responses to newborn young decline with time, and few remain maternal after 12 h, or after 24 h if parturition has 'been induced with oestrogen (Poindron et al. 1984). The period of maternal responsiveness is known as the sensitive period. The effects of separation are much less if the mother is given contact with the newborn for a few minutes immediately post-partum; and if the contact is extended to half an hour or more most females show signs of exclusive attachment to their own offspring (Poindron and Le Neindre 1980).

The importance of olfaction in the process of exclusive attachment has been demonstrated in females made anosmic by surgical removal of the olfactory bulbs before parturition; this leads to indiscriminate suckling (Bouissou 1968; Baldwin and Shillito 1974; Poindron 1976). Experiments with intact ewes prevented from licking or touching their lambs also show that dams need to be very close to their young in order to perceive their specific odour (Poindron and Le Neindre 1980). Similar experiments showed that it is particularly

important for exclusive attachment that the ungulate mother be exposed to the odour of the foetal fluids immediately after birth, as demonstrated with sheep (Alexander et al. 1986), although this is less important for multiparas than for inexperienced primiparas, as shown for goats (Lickliter 1982). These experiments in which ewes made no contact with lambs demonstrate that the origin of the specific odour by which ewes recognize their lambs in the early post-partum period derives from the lamb and not from maternal labelling, via the milk or saliva, as suggested by Gubernick (1980) for goats. Further experiments are required to show whether maternal labelling plays a significant role in ungulates.

The senses and sensory cues used for mutual recognition beyond the post partum period have been widely studied, using observational techniques, especially in domestic sheep (Grubb 1974; Lent 1974; Alexander 1980; Shillito-Walser and Alexander 1980; Walser et al. 1984), but also in Mouflon (Tschanz 1962), horses (Wolski et al. 1980; LeBlanc and Bouissou 1981), zebra (Klingel 1974) and reindeer (Kallquist and Mossing 1982).

Olfactory, visual and auditory cues, all appear to play some role but the importance of visual and auditory cues varies even between breeds of sheep (Walser et al. 1984). Visual and auditory cues probably serve to bring mother and young together, but olfaction clearly provides the most specific and final information for recognition of offspring by mothers; 'the presence of the correct odour on the offspring is essential for most mothers to suckle. However, olfaction appears to be less important for some species such as cattle than for others such as sheep (Poindron and Le Neindre 1875). The role of olfaction in the recognition of mother by offspring is less certain (Müller-Schwarze and Müller-Schwarze 1971) and many offspring appear less discriminating in their approach to the dam than the dam appears in its approach to the offspring (Lickliter and Heron 1984; Alexander 1977).

The relative importance of visual and auditory cues may vary with species and could depend on coat coloration. Visual cues, especially from the head, are important for recognition of their offspring by ewes (Alexander 1980), and auditory cues appear to be particularly important for goat kids to recognize their dams (Lickliter 1984) during the first few days, after which visual cues are involved. However, mother goats do not appear to rely on the kid's voice initially because the kid's voice does not acquire individuality for 'at least four days (Lenhardt 1977).

BEHAVIOUR WITH SURVIVAL VALUE

This review provides a basis for enumerating a list of observable maternal traits the presence of which should, on known or hypothetical grounds, maximize survival of lambs.

- 'the seeking of isolation for birth
- the selection of a safe, sheltered birth site
- birth of short or average duration
- absence of interference with or by other parturient ewes
- intense persistent grooming of all members of a litter
- absence of aggression towards the newborn
- co-operation with the lamb's first attempts to suck
- placentaphagia (a trait of uncertain significance)
- remaining on the birth site for at least 5 h
- concern at the'absence of a lamb
- an ability to keep the litter together after leaving the birth site

- active defence of the lamb in the presence of a predator or predator substitute such as a dog.

A shorter list can be developed of desirable behavioural traits of recently born lambs:

- standing soon after birth
- sucking soon after standing
- a well defined "prone" response to handling
- an ability to follow the mother closely and to move to the mother if separated
- absence of separation from the mother.

PRACTICAL IMPLICATIONS

These traits provide a reasonable basis for selection programs aimed at improving lamb survival, and they highlight areas requiring research into husbandry procedures at lambing.

Selection programs

The use of these traits in a selection program has the disadvantage of requiring intensive observations at lambing. Nevertheless, an attempt to use this approach is in progress at CSIRO Armidale (NSW) where data are being collected for the estimation of repeatability and heritability of parameters, and for correlation of the various traits with lamb survival.

Breed comparisons already provide evidence of genetic diversity in some of the traits such as ease of birth (George 1975, 1976), time spent on the birth site and ability to care for twins (Alexander et al. 1983) and also in the competition between flocking behaviour and maternal behaviour with its tendency towards isolation (Walser et al. 1983). Less direct evidence indicatives possible breed differences in maternal qualities. For example, there are breed differences in the behaviour of ewes with young lambs in the presence of disturbance by humans (Morgan et al. 1974; Alexander et al. 1983), and in the ease of fostering strange lambs onto ewes (Alexander et al. 1985).

Husbandry at lambing

Practical implications of ewe behaviour at lambing have been discussed elsewhere (Kilgour 1982). However, investigations are required on the characteristics of lambing paddocks, such as size, topography and aspect, shelter, pasture availability, disposition of watering points and stocking rate. These may be particularly important for survival of multiples.

The concentration of lambing sites along fence lines (Welch and Kilgour 1970) indicates that the tendency 'to seek isolation may often be frustrated, and that large paddocks and low stocking rates may be desirable to minimize interference between ewes. On the other hand, the probability of separated multiples being retrieved by their dam is likely to be lower in large than in small paddocks. The characteristics of favoured lambing sites require definition, together with the effects of placing shelter on the favoured areas. It seems likely that in previous studies, such as those of Welch and Kilgour (1972) and Stevens et al. (1981), the paddock environment has not been sufficiently varied to allow full expression of behavioural traits.

Investigation is needed into means of inducing ewes to remain near the birth site to facilitate the formation of strong bonds; the provision of abundant pasture may be critical here, as well as judicial assessment of the need for supervision of lambing or for drifting, if the sheep are not trained to

accept the presence of a shepherd, in which case disturbance can lead to desertion of lambs (Whateley et al. 1974).

Now that prenatal scanning for litter size is a practical option using ultrasound techniques (Fowler and Wilkins 1982), investigations are required into the desirability of lambing single- and twin-bearing ewes separately. The susceptibility of multiples to separation could be counteracted by lambing twin-bearers at low stocking rates (Winfield 1970) in small sheltered paddocks with plentiful pasture and several watering points, to reduce the need for the ewe to travel. Requirements are likely to be less critical for lambing ewes with singles, because the demands on maternal care are lower for singles than for multiples (Holmes 1975). Supervision to provide assistance with difficult lambings by single bearing ewes may be necessary, with fewer risks of separation than for twin bearers, but training ewes, before lambing, to accept a shepherd% presence would be desirable.

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