

How has the risk of predation shaped the behavioural responses of sheep to fear and distress?

CM Dwyer

Animal Behaviour and Welfare, Sustainable Livestock Systems, Scottish Agricultural College, West Mains Road, Edinburgh EH9 3JG, UK; c.dwyer@ed.sac.ac.uk

Abstract

To use behaviours as indicators of stress it is important to understand their underlying causation. For a prey animal in the wild, such as a sheep, behavioural responses have evolved to evade detection and capture by predators. The behavioural responses of the wild ancestors of domestic sheep to the threat of predation are characterised predominantly by vigilance, flocking, flight to cover and behavioural inhibition once refuge has been reached. Some limited defensive behaviours are seen, mainly in females with young against small predators. Vigilance and flight distance are affected by the animal's assessment of risk and are influenced by the environment, social group size, age, sex and reproductive condition, as well as by previous experience with potential predators. Under conditions of stress, domestic sheep show similar behavioural reactions to wild sheep, although the threshold at which they are elicited may be elevated. This is particularly evident when comparing less selected hill breeds with more highly selected lowland breeds, and suggests that a continuum of responsiveness exists between wild and feral sheep, through hill breeds to the lowland sheep breeds. However, this may be confounded by the previous experience of the breeds, particularly their familiarity with humans. Behavioural and neurobiological evidence suggests that, although the behavioural response to predators (vigilance, flight) is innate, the stimuli that elicit this behavioural pattern may have a learned component. Since vigilance and flight distances are affected by the animal's perception of threat, they may be useful indices of stress in sheep and, as graded responses, give some indication of the level of threat experienced by the sheep. Thus they may indicate the amount of fear or distress experienced by the sheep and hence have the potential to be used in the assessment of welfare states.

Keywords: animal welfare, behaviour, domestication, predation, sheep, stress

Introduction

Behavioural measures are frequently used to assess animal stress states upon exposure to a threat (either real or artificially imposed by the experimenter) or as tools for welfare assessment. However, in common with many measures of animal welfare, interpretation of behaviour can be difficult and misleading (Mason & Mendl 1993; Rushen 2000). Rushen (2000) therefore argues that to interpret behaviours and use them as indicators of stress or welfare compromise, we must first understand the underlying causes of the behaviour. Behavioural responses to stress are thought to derive from the evolved anti-predator responses of a species (Blanchard *et al* 1998; Boissy 1998). Recent arguments suggest that prey have evolved anti-predator responses both to actual encounters with predators and to generalised threatening stimuli, such as loud noises or sudden events (Frid & Dill 2002), which supports the concept of stress responses being anti-predator behaviours in prey species. Thus, understanding the functional significance of anti-predator behaviours may help in the interpretation of behavioural responses to stress. Animals may, however, experience stress through, for example, interactions with

conspecifics or physical stressors such as under-nutrition or exposure. This review will therefore be limited to those stress responses that relate to threatening or fearful stimuli (eg sudden events, fear of humans, etc) that are analogous to anti-predator behaviours in wild sheep. The review will consider how the evolved anti-predator behavioural responses of the wild animal relate to the behavioural stress responses of the domestic animal; focusing on the sheep as a model. The sheep was chosen for two main reasons: firstly, the behavioural responses of sheep are considered to be 'cryptic' and difficult to interpret, and, secondly, the literature on the behaviour of wild sheep is particularly rich as a source of information on anti-predator responses. The review will consider firstly the social organisation and anti-predator behaviours of wild sheep. The impact of domestication on the expression of these behaviours in domestic sheep will be reviewed. Predictions regarding the behavioural responses of domestic sheep under stress conditions based on the anti-predator behaviours of wild sheep will then be tested from examples in the literature. Finally, the implications of understanding the anti-predator behaviour of wild sheep in terms of interpreting behavioural stress

responses and assessing the welfare of domestic sheep will be considered.

Vestigial populations of seven species of wild sheep still exist (Ryder 1984; Clutton-Brock 1987; Hemmer 1990): the Mouflon (*Ovis musimon*) in Europe, Asiatic Mouflon (*O. orientalis*), Urial (*O. vignei*), Argali (*O. ammon*), and Snow sheep (*O. nivicola*) in Asia, and Dall's (*O. dalli*) and Bighorn sheep (*O. canadensis*) in North America. The most likely progenitor of domestic sheep is thought to be the Mouflon (Hemmer 1990; Hiendleder *et al* 1998), although the Argali may be the origin of some non-European breeds (Melinkova *et al* 1995; Jugo & Vicario 2000). Ungulates have co-evolved with their predators for millions of years, and this association has directed the evolution of their morphology, habitat choice and behaviour (Wilson 1975). Wild sheep occupy mountain ranges in North America and lower mountain slopes and hill country in Asia and Europe (Clutton-Brock 1987). However, they are highly adaptive and have successfully colonised a variety of terrains, including desert (Berger 1979) and island habitats (Grubb & Jewell 1966). Behaviourally, all species of wild sheep share common characteristics in their use of habitat, and in their social organisation, reproductive and other behaviours, which appear to be retained in domestic sheep (Hafez & Scott 1962; Lynch & Alexander 1973; Shackleton & Shank 1984). Group size is moderate, comprising matrifocal groups of females (approximately 8–12 ewes per group [Woolf *et al* 1970; Shannon *et al* 1975; Shackleton & Shank 1984]) and offspring that remain within the home range. Smaller groups of male sheep (average 5–6 individuals [Woolf *et al* 1970]) are segregated from the female and juvenile flocks, but share an overlapping home range (Geist 1971; Bon *et al* 1993). The most studied populations of wild sheep are mountain Bighorns (Geist 1971), European Mouflon (eg Bon *et al* 1993, 1995; Langbein *et al* 1997, 1998; Reale *et al* 1999) and Himalayan Argali (Schaller 1977). The primitive feral Soay sheep of St Kilda, although once domesticated, have remained almost unchanged since the Bronze age and continue to be the subject of extensive study (eg Grubb & Jewell 1966; Clutton-Brock *et al* 1996; Conradt 1999).

Social behaviours and predatory pressures

Predators of wild and free-ranging domestic sheep include lynx, mountain lions, coyotes, dingoes, wolves, foxes, eagles and other predatory birds. Predators preferentially kill lambs, juveniles, females and individuals with reduced locomotor capabilities in wild and domestic sheep populations (Gluesing *et al* 1980; Palmqvist *et al* 1996; Ross *et al* 1997; Stahl *et al* 2001). Coyotes prey preferentially on lambs that behave abnormally (eg limping, hunched, lethargic), but also on lambs from ewes that are not healthy, and on single rather than twin lambs (Gluesing *et al* 1980). Healthy lambs that are killed are generally more active in investigatory and play behaviours than are lambs that survive. In general, predators appear to prey most heavily on animals that are most likely to be on the periphery of the social group. Thus, the social group is important in

minimising individual predation risk, and it seems likely that there will be strong selection pressure on prey species to appear behaviourally similar to the other members of the group (since abnormal animals are preferential prey). Smaller and younger animals also appear to be more vulnerable to predation (Gluesing *et al* 1980).

Defence against predation is a strong factor determining the behaviour of sheep, and interacting with their need to feed and reproduce. The anti-predator behaviours of sheep can be broadly divided into those responses that are elicited by the immediate presence of a predator and those that have evolved to minimise the chances of detection and capture. In some cases the same behaviour may be involved in both responses.

Responses to the presence of a predator

Since wild sheep are generally too small to mount a successful defence against predators, their main anti-predator defence is flight to cover (Geist 1971; Bleich 1999). This behaviour is termed 'refuging' by Lima (1998), and a heightened threat of predation, for example, an increase in predator activity, is accompanied by increased refuging and decreased movement once the refuge has been reached. Many prey animals will permit a predator to approach to a certain point before responding (the flight distance). In Himalayan sheep, danger is tolerated at a 'safe' distance based on the experience of the sheep (Schaller 1977). Similarly, Mouflon modify their flight distance in the presence of different types of intruders (hikers alone or accompanied by dogs [Martinetto & Cugnasse 2001]). The presence of escape terrain (mountain slopes) influences the propensity to flight of Bighorns: ewes are more likely to run when threatened with predation in the open than when near slopes or cover (Berger 1991; Bleich 1999). In Dall's sheep, vigilance is also influenced by the openness of the habitat and the distance to escape terrain, but this interacts with group size (Frid 1997). Bighorn sheep are more alert after dark and flee more rapidly when approached at night (Woolf *et al* 1970). This is supported by studies of other species (eg woodchucks, deer, moose, elk) where flight distances and vigilance increase in riskier situations (reviewed by Lima & Dill 1990; Altendorf *et al* 2001; White *et al* 2001; Wolff & van Horn 2003). The frequent behavioural response both of wild and domestic sheep to the presence of a predator is to bunch together and run (Hafez & Scott 1962; Geist 1971; Schaller 1977). Formation of a dense, tightly packed flock in the presence of a predator may occur as each animal attempts to move towards the central position in the flock (as animals on the outside are at greater risk [Gluesing *et al* 1980]); the net effect of all animals behaving in this way is a circling aggregation (Vine 1971). This 'centripetal' movement reduces the predation risk of animals in the centre of the herd if the predator is likely to kill only the first encountered animal in the group (Triesman 1975b), and may reduce predator capture efficiency by a confusion effect.

If attacked by small predators such as crows and foxes, mountain and domestic sheep will defend their young by

standing over the lamb (Geist 1971; Lynch & Alexander 1973). Geist (1971) reports that Bighorn ewes have successfully driven off or killed eagles with their horns when protecting their lambs. Stamping and stotting (bounding with all four feet leaving the ground simultaneously) by ewes with lambs have also been reported in threatened Urials (Schaller 1977). In other ungulate species, maternal aggression towards predators improves neonate survival chances (Sarno *et al* 1999), suggesting that maternal aggression may be a successful strategy with smaller predators where the risk of maternal death is not too great. Prey species also perform a number of postural and vocal signals at the sight of a predator: stamping, snorting and tail-flagging in deer for example (Woolf *et al* 1970; Caro 1994; Caro *et al* 1995). Although these were previously believed to be warning signals directed towards conspecifics, more recent analysis of predator behaviour suggests that some may function as 'pursuit-deterrence' signals to inform the predator that it has been detected (Caro *et al* 1995; Lima 1998). Snorts, orienting towards the disturbance, stotting and stiff-legged bouncing (Hafez & Scott 1962; Geist 1971; Schaller 1977) may serve this function in sheep.

Recovery from predation threat

The cues used by sheep to signal that it is safe to resume activity following flight from a predator have received little attention, although clearly animals must assess whether the danger has passed before continuing previous activity. Research in other species suggests that animals will remain inactive for longer in riskier situations and that animals in poorer condition may resume feeding earlier than well-fed animals (Lima 1998).

Flocking responses

Flocking is a well-described response of sheep to the presence of a predator. Flocking or gregariousness is thought to serve functions such as assisting mating, finding food, care of the young and detection and evasion of predators, in addition to its defensive use against predators (Triesman 1975a; Wilson 1975). Predation on solitary moose is greater than for animals in social groups (White *et al* 2001). Studies of kill rates in coyotes suggest that more kills are made in areas of low prey density than where prey abundance is high (Patterson & Messier 2000), thus demonstrating the importance of sociality as an anti-predator behaviour. An increase in group size also allows animals to reduce individual vigilance behaviours, leaving the animal free to devote more time to other behaviours such as feeding and social interaction (reviewed by Roberts 1996; Frid 1997). Whether the reduction in vigilance behaviours per animal is due to the increased group vigilance (Pulliam 1973) or because an increase in group size reduces predation risk and therefore the need for vigilance, or a combination of the two, is not known (Roberts 1996).

Within different populations of wild sheep, social group size varies with environment and with the age and sex composition of the population. Desert-living Bighorn sheep live in smaller groups than do mountain Bighorn, are less behaviourally diverse and exhibit fewer social behaviours and less

play (Berger 1979). Age and sex affects the strength of flocking behaviour and preferred flock mates in Bighorn (Geist 1971; Bon & Campan 1989; Berger 1991), Mouflon (Le Pendu *et al* 1995, 1996; Cransac & Hewison 1997) and Himalayan sheep (Schaller 1977). In all species, ewes, lambs and juveniles remain together whilst males become segregated, particularly by age class. This preference for animals of a similar age and sex appears to be an anti-predator strategy since being a smaller or larger individual than the surrounding animals may be conspicuous to predators (Lima 1998). Weaned ram lambs and older males show a marked social preference to associate with peers (Woolf *et al* 1970; Geist 1971; Le Pendu *et al* 1995). However, as males become more mature they show increasing independence from the social group (Geist 1971; Schaller 1977). Geist (1971) reported that 7% of fully mature adult male Bighorns were observed alone compared to 3.6% of younger males and 1.3% of male yearlings and ewes. This may reflect the lower predation risks experienced by mature males in comparison with younger males and with female sheep (as described above), thus reducing their dependence on the social group.

Following behaviours and behavioural synchrony

Food distribution is patchy within the range of wild sheep, with food sites being linked by migratory routes (Geist 1971). Within sheep ranges there would be no unused habitat, and juveniles do not migrate into new habitat. Dispersion is a dangerous and non-productive strategy, hence selection favours juveniles that remain within the flock and follow adult animals (Geist 1971). Ewes form close bonds to their young lambs that encourage following behaviour from the lamb at the earliest stage (Lent 1974) and allow stable mother–young bonds to exist within a mobile flock (Hersher *et al* 1963). However, after weaning it is more appropriate for lambs to follow adult animals other than their mothers (Geist 1971) because of social disruption during the rut, and changes in the nutrient requirements and foraging behaviour of pregnant ewes in comparison to other adults. The rut period in Mouflon results in high social instability and accelerates dissociation of mother–young bonds (Bon *et al* 1993). It is therefore important for juveniles to transfer their social attachments from their mothers to other adults. By following older sheep, the juveniles learn about the home range and the habits that have successfully led to the longevity of the adult (Grubb & Jewell 1966; Geist 1971).

Synchronous or 'allomimetic' behaviour of sheep may function as an anti-predator strategy by ensuring that individual animals are inconspicuous from the rest of the flock. Following behaviour is a particular example of allomimetic behaviour, but sheep are also synchronised in their grazing and resting behaviours (Hafez & Scott 1962). In Mouflon, nearest neighbours were closest together when carrying out the same activity (Le Pendu *et al* 1996). The drive to maintain behavioural synchrony with the rest of the flock is responsible for other behavioural patterns seen in sheep. When moving around the home range, Bighorn and Soay

are known to move in single file following a leader, which is generally an older and more independent sheep (Grubb & Jewell 1966; Geist 1971). The segregation of the flock by age and sex may also be a consequence of allomimetic social behaviours. Sheep aggregate with animals showing similar behaviour patterns or requirements to themselves (Cransac *et al* 1998; Conradt 1999; Ruckstuhl & Neuhaus 2000), and are more synchronised in same than mixed age groups (Ruckstuhl & Neuhaus 2001). The diurnal rhythm of sheep movements — moving down the hill to graze during the day and back up to camp grounds at night (Grubb & Jewell 1966; Woolf *et al* 1970) — are enhanced by each animal's desire to remain synchronised with others.

Risk assessment and habitat usage

The behavioural responses of sheep and their use of habitat are not constant throughout their life cycle. Ewes and juveniles are more likely to flee from a predator threat than are male sheep (Bleich 1999), and ewes are also more vigilant than males (Schaller 1977; Laundre *et al* 2001). Since females and juveniles are preferentially preyed upon, these behavioural responses suggest that the sheep are responding to the relative risk of predation. Likewise, male Bighorn sheep, with a lower risk of predation, graze further from the slopes and spend more time in the open than do ewes (Woolf *et al* 1970; Berger 1991; Bleich *et al* 1997). However, ewes do not maintain the same pattern of habitat use throughout their reproductive cycle. Ewes are more likely to forage on better grazing during pregnancy to meet their increased nutritional demands (Geist 1971; Schaller 1977; Bon *et al* 1995; Langbein *et al* 1998), even if this means incurring greater risk of predation (Berger 1991). By contrast, at the onset of birth, ewes withdraw to secluded parts of their home range where predation risks are minimal (Grubb & Jewell 1966; Geist 1971; Schaller 1977; Bon *et al* 1995). Ewes and their lambs return to the matriarchal group some days after the birth but remain closer to escape terrain (Berger 1991; Bon *et al* 1995; Bleich *et al* 1997; White & Berger 2001) and are more vigilant than non-lactating ewes. Female vigilance is also increased when their offspring are active (White & Berger 2001) and when predator density is high (Laundre *et al* 2001). The behaviour of wild ewes during lactation presumably acts to minimise the predation risks of their young, even though this means utilising areas of poorer forage and reducing feeding times.

Communication

Many group living animals have signals that facilitate maintenance of group cohesion. Sheep appear to rely predominantly on visual cues to recognise one another, although they can also make use of olfactory and auditory information. Sheep use graded communication signals (Wilson 1975; Berger 1979), largely based on behavioural and postural signalling. The survival costs of using vocal communication mean that wild sheep rarely use vocalisation as a signal. Bleating is most common between ewes and lambs, using low-intensity contact calls. Geist (1971) identified 17 social behaviour patterns used by Bighorn sheep in communication, whereas 22 have been recorded for the

Urial (Schaller 1977). These are signals, postures and actions performed in stereotyped, distinct manners to conspecifics, occasionally accompanied by sounds or odours, characterised by unusual body conformations, and that may be faster, slower, jerkier or stiffer than normal movements and may accompany non-random orientations. For example, the vigilance posture (or 'head-up') is characterised by the head and neck being held rigid, ears alert and forward, a frozen posture and staring in the direction of the disturbance (Geist 1971; Schaller 1977). The posture is rigid for fearful or threatening stimuli, and repeated and less rigid if indicating imminent direction of travel.

Vocal communication is elicited only at high threshold (Kiley 1972) and may be added to postural signalling to give a graded, composite system of communication (Hafez & Scott 1962). Vocal communication in sheep consists of various contact calls, usually of low intensity, distress calls when separated from companions, and alarm snorts, which may function either to warn conspecifics of approaching danger or as pursuit-deterrence signals (Caro *et al* 1995). Sheep do not have greeting vocalisations. Vocalisations in wild sheep appear to be inhibited in fear situations (Kiley 1972), in which sheep instead rely on visual forms of communication.

Domestication and husbandry

Domestication, and the husbandry practices connected with it, are associated with a number of morphological and physiological changes in the animal that may result from unconscious selection. Changes may result from relaxation of certain selection pressures, in particular from a reduction in the threat of predation (eg leading to diversity in coat colour, polling), from the culling of certain types of animals and from alterations in the diet (Zohary *et al* 1998). For example, a reduction in body size, which is a feature of domestication in many species, may have occurred through the killing of larger males for meat before they had bred, or because smaller animals were originally chosen to form the 'founder' flocks because they were easier to handle (Clutton-Brock 1992). Reduction in body size may also have been an evolutionary response to human protection from predation (Zohary *et al* 1998).

Despite some restrictions on their movements and behaviour, hill and range sheep still retain considerable control over how they use resources to feed, survive and reproduce (Deag 1996). A limited amount of predation of these animals may still occur. Natural selection is therefore supplemented rather than replaced by artificial selection and management. This is particularly the case where animals remain on the hillside for the entire year and are usually free to move over large areas. These animals form home ranges, within which ewes of the same social group restrict themselves to particular areas and become familiar with the location of resources such as food, water and shelter (Hunter & Milner 1963; Hewson & Wilson 1979; Lawrence & Wood-Gush 1988). If natural weaning is allowed to occur in these animals it takes place at about six months, with ewe lambs ranging independently of their mothers but having

similar home ranges (Hunter & Milner 1963; Lawrence 1990, 1991). This allows transmission of cultural information about the home range to be passed from older to younger animals. Hill sheep also have the same diurnal patterns of behaviour reported for wild sheep — moving up the hill and maintaining a closer inter-individual distance at night than during the day when they move down to graze (Hewson & Wilson 1979). Traditional husbandry practices therefore allow a large number of the evolved behaviour patterns of sheep to persist in domestication.

In more intensive systems of sheep husbandry, although still falling within a definition of extensive farming in that the animal will get most or all of its food from the environment (Appleby 1996), animals are kept in fenced paddocks. These animals will be more constrained in their freedom of movement, and true home ranges probably cannot exist, although ewes do form sub-groups (Arnold & Pahl 1967; Winfield & Mullaney 1973; Shillito-Walser & Hague 1981). Cultural transmission of information from animal to animal is less likely to occur because lambs are weaned early and are generally removed from the social group. Under even more intensive systems, sheep are kept confined, are maintained in large groups and at high stocking densities, are given little choice in feed type and are routinely and frequently subjected to handling procedures. In more intensive systems, artificial selection for particular traits (such as growth rate, wool quality, lean tissue content) plays a larger role in determining sheep characteristics than in more extensive systems where natural selection also plays a role.

In comparison to wild species, domesticated species show a reduced alertness and attentiveness to the environment and attenuated flight distances (Price 1984; Hemmer 1990), but increased sexual and social behaviours (Künzl & Sachser 1999). These behavioural differences are, however, considered to be due to changes in the frequency of expression of behaviour patterns via a shift in threshold (Ratner & Boice 1975; Price 1984). Loss of behavioural elements or addition of novel behaviour patterns is not believed to occur during the normal process of domestication (Künzl & Sachser 1999). Changes in behavioural frequency are accompanied by functional alterations in the adrenal glands (Hemmer 1990) and reduced reactivity both of the hypothalamic–pituitary–adrenal (HPA) axis and the sympathetic–adrenomedullary system (Künzl & Sachser 1999). These physiological data suggest that thresholds for eliciting stress responses and fear-associated behaviours, such as flight, may be elevated in domestic species. This may be due to artificial selection by man for docility and ease of handling in domestic species, or an adaptation of species being domesticated to cope with the environments under which they are kept. Although the threshold for these types of behaviour (eg fear responses) may be elevated in domestic sheep, there is no evidence that these behaviours are not expressed once that threshold has been reached. Fear and anxiety-related behaviours have adaptive value in promoting survival both in domestic and wild sheep (Boissy 1998), and are considered components of the anti-predator response

(Frid & Dill 2002). Thus, the anti-predator strategies that evolved in wild sheep will persist in domestic animals, even in the absence of natural predators (Byers 1997).

Domestic animals are often kept either in larger groups or in more crowded conditions than they would experience in the wild. It would therefore be adaptive for them to perform more sociopositive and less aggressive behaviours under these conditions. For example, the vocal behaviour of domestic sheep is increased in frequency in comparison to wild sheep (Kiley 1972). This may have arisen because of the need for more complex social signals in larger groups (as suggested by Berger 1979) and because the selection pressure against vocalisation — the risk of predation — is reduced in domestic sheep (Price 1984). More intensively managed breeds of domestic sheep are vocal when socially isolated and at feeding time (Shillito-Walser *et al* 1982), but tend to have inhibited vocalisations in other situations, for example in the presence of a tethered dog (Torres-Hernandez & Hohenboken 1979). This mirrors the behaviour of wild sheep in the presence of a predator (Kiley 1972).

Some of the behaviour patterns of wild sheep, for example their diurnal pattern of movements, may not be observed in domestic sheep if they are restricted by their habitat. However, if provided with an appropriate physical or social environment in which to perform their full behavioural repertoire, domestic sheep express the same social and movement behaviours as wild sheep (Scott 1945, cited in Hafez & Scott 1962; Arnold & Pahl 1967; Stolba *et al* 1990). These data suggest that the ethogram of the domestic sheep resembles that of wild sheep, differing only in the threshold for the initiation of some behaviours.

Breed and genetic influences on stress responses

Domestication, or selection for production characteristics, alters the threshold for the expression of some behaviours (Hemmer 1990; Lankin 1997; Hansen *et al* 2001). There does, however, appear to be a continuum of behavioural response from wild and feral sheep to highly selected sheep via the more extensively managed hill and upland sheep (eg see Table 1).

Social behaviours

Although flocking remains an integral part of the behavioural response of sheep, the formation of home ranges and subgroups is variable amongst sheep breeds. Hill sheep form subgroups within home ranges (Hunter & Milner 1963; Hewson & Wilson 1979), whereas Merinos form single flocks with close associations to other sheep. Subgrouping is seen in Merinos only in times of food shortage. The preferred size of the social group is affected by breed: lowland, highly selected breeds aggregate into larger subgroups than do hill breeds, even when kept under the same conditions (Winfield & Mullaney 1973; Shillito-Walser & Hague 1981; Dwyer & Lawrence 1999; Table 1). This is accompanied by tolerance for greater crowding because shorter nearest neighbour distances are maintained in lowland breeds.

Table 1 Changes in anti-predator behaviours with increasing domestication in sheep.

Behaviour	Wild sheep	Primitive breeds	Hill/range sheep	Lowland/intensive	Source
Flight distance (m)	30 (Mouflon)	12 (Soay) 14 (Old Norwegian)	7 (Norwegian fur sheep)	4–7 (Texel) 4–5 (Suffolk, Steigar)	Hemmer 1990; Hansen <i>et al</i> 2001
Social group size	6–10 (Bighorn) 3–12 (Urial)	4–13 (Soay)	3–7 (Scottish Blackface)	45 (Merino) 10–15 (Dorset Horn cross) 8–11 (Suffolk)	Grubb & Jewell 1966; Arnold & Pahl 1967; Woolf <i>et al</i> 1970; Shannon <i>et al</i> 1975; Schaller 1977; Dwyer & Lawrence 1999
Nearest neighbour distance (m)			8–11 (Scottish Blackface) 7 (Welsh Mountain)	2–3 (Merino) 3–5 (Suffolk)	Arnold 1985; Dwyer & Lawrence 1999
% vocalise in presence of predator		1.8 (Old Norwegian)	10.6 (Norwegian Fur)	12.5 (Suffolk, Steigar)	Hansen <i>et al</i> 2001
Length of isolation at parturition	5–7 days (Bighorn, Urial, Mouflon)	2–4 days (Soay)	1–2 days (Scottish Blackface) 12–36 h (Romneys)	2–5 h (Merinos)	Geist 1971; Hewson & Wilson 1979; Alexander <i>et al</i> 1983; Lynch <i>et al</i> 1992

Recognition and vocalisations

When placed in the same enclosure, sheep of the same breed but unfamiliar to one another become integrated into a single flock after a period of time (Lynch & Alexander 1973; Arnold & Pahl 1974). However, sheep of different breeds, even after being maintained in the same environment for a number of months, do not integrate (Winfield & Mullaney 1973; Arnold & Pahl 1974; Shillito-Walser & Hague 1981; Dwyer & Lawrence 1999). There are a number of reasons why this may occur: (a) Breed identity may be maintained by visual cues, perhaps learnt by lambs recognising the appearance of their own mothers (Shillito-Walser 1980), whereas social group recognition occurs by olfaction (Arnold 1985). (b) Different breeds are known to differ in activity pattern (Cresswell 1960; Key & McIver 1980; Dwyer & Lawrence 2000), thus the desire for animals to remain synchronised with one another may lead indirectly to breed segregation. This is a similar argument to that proposed above for the preference of wild sheep for peers of a similar age and size as themselves. (c) Isolated sheep respond with greater fear responses to photographs of ewes of a different breed than to same-breed images (Bouissou *et al* 1996), and preferentially choose images of ewes of the same breed as themselves (Kendrick *et al* 1996); thus individuals of a breed may actively avoid individuals of other breeds.

At parturition, less selected breeds of ewe make more low-pitched and less high-pitched bleats than do highly selected, lowland ewes (Le Neindre *et al* 1993; Dwyer *et al* 1998), and both ewes and lambs are more responsive to the bleats of the other (Shillito-Walser *et al* 1984). Lowland lambs are also more vocal than hill lambs (Dwyer *et al* 1998), however, feral and hill breeds are better at vocal recognition than are lowland breeds (Shillito-Walser 1978, 1980). In tests with predator-like stimuli, lightweight primitive breeds were less

vocal than heavier ewes (Hansen *et al* 2001), and, apart from ewe–lamb contact calls, more highly domesticated breeds are more vocal than feral or hill breeds in all situations (Shillito-Walser *et al* 1982, 1984; Dwyer *et al* 1998). This may have arisen due to a relaxation of selection pressure against bleating as a result of reduced predation, and because bleating strengthens social bonds (Nowak 1990).

Fear responses

Tests measuring sheep responses to surprise effects, to the presence of a human or novel object, or to exposure to an open field or unfamiliar environment, have been used to assess genetic or breed differences in fear responses (Romeyer & Bouissou 1992). Other tests have looked at an animal's feeding behaviour in the presence of a human intruder (Le Neindre *et al* 1993; Lankin 1997), and responses to stuffed predators (Hansen *et al* 2001). These studies show consistent behavioural differences between breeds in their fear behaviour (eg see Table 1). Less highly selected breeds are more fearful than are highly selected breeds — they make more low-pitched but less high-pitched bleats in the test arena, feed less often in the presence of an observer, are more immobile and urinate or defecate more frequently (Romeyer & Bouissou 1992; Le Neindre *et al* 1993; Lankin 1997). In the presence of stuffed predators, more primitive lightweight breeds of sheep have greater flight distances, tighter flocking behaviour and take longer to recover than do more highly selected heavier breeds (Hansen *et al* 2001). The less selected hill and upland breeds or more primitive breeds appear to have a greater reactivity to the same stressor and take longer to recover. Although some of these studies might be explained by the effects of experience on fearfulness in the presence of humans, the responses of sheep to predators (Hansen *et al*

2001) or to photographic images (Bouissou *et al* 1996) suggest that these are genuine differences between breeds.

However, the impact of genotype is confounded with the normal husbandry practice of that breed. The physical environment can influence sheep behaviour: for example, the frequency of alarm behaviours in Merinos decreases in more complex physical environments (Stolba *et al* 1990), presumably because the sheep perceive an open, barren paddock as more threatening. Some of the apparent breed effects could therefore be due to the rearing environment usually experienced by these animals, rather than to a genetic effect *per se*. Studies of the effects of dam rearing versus artificial rearing on lambs' responses to fearful stimuli (eg Romeyer & Bouissou 1992), or of the effects of keeping different breeds in different environments (Goddard *et al* 2000), suggest that there is a genetic component to fear that may be potentiated by rearing environment, particularly in more reactive breeds. It is unclear, however, to what extent maternal responses and the physical environment are responsible for shaping the behavioural responses of lambs to fear-eliciting stimuli. For example, in the anti-predator responses of the sheep in the experiments described by Hansen *et al* (2001), to what extent is the greater fearfulness of the primitive sheep a function of their small body size and reduced ability to defend themselves against predators; a function of rearing environment, in which they may have been exposed to more fearful stimuli leading to sensitisation to predators; or a function of their relative domestication and genetic make-up? Thus, sheep may have an underlying 'blueprint' for behavioural fear responses that relates to their evolutionary history, but the factors that elicit this behaviour may be a function of experience (as also suggested for wild sheep [Schaller 1977]), environment and domestication.

Individual differences in stress responses

Understanding what factors influence an animal's responses to a stressor are important because they help to explain not only why an animal may find particular stimuli more or less stressful than another animal, but also what might be stressful to some animals and not to others. The behaviour and predation risks of wild sheep (described previously), should predict how animals will behave in stress conditions if stress responses have developed from anti-predator behaviours.

Effects of age

Young animals have differing requirements from adults in terms of social behaviours, and have differing time budgets, metabolic rates, disease susceptibility and predation risks. Lambs maintain closer spatial relationships than do older sheep. The early behaviours of the lamb are generally directed towards its mother and suckling; this period coincides with an extremely close mother–young relationship (Le Pendu *et al* 1996) and, in wild sheep, a period of isolation from the social group (Obregon *et al* 1992). This connection is particularly strong in ewe lambs, which are generally closer to their dams than are ram lambs

(Shillito-Walser & Williams 1986). From two weeks of age onwards, lambs make increasingly frequent contact with peers and show a peak in play behaviour at approximately three weeks of age (Sachs & Harris 1978). Play behaviour in young animals is very susceptible to environmental perturbations, and the chances of injury and predation are increased in playing animals (Gluesing *et al* 1980; Fagen 1981; Byers 1987). Play is reduced in Mouflon lambs in years associated with poor diet quality (Reale *et al* 1999), and in Bighorn lambs living in a more risky desert environment compared to mountain living Bighorn lambs (Berger 1979). Thus, play behaviour is likely to be a sensitive indicator of stress in young lambs.

Juvenile Bighorns are more likely to flee in the presence of predators than are older sheep (Bleich 1999). This suggests that young sheep are probably more fearful than older animals of stimuli associated with predation (eg the presence of human observers). Experimental data from domestic sheep support this since older ewes have lower 'panic' reactions to humans than do younger ewes (Vandenhede *et al* 1998), are less likely to flee when their lambs are handled by an observer (Lambe *et al* 2001), and are less reactive to humans in tests (Viérin & Bouissou 2002).

In addition to closer spatial relationships and associations, lambs have a stronger following response than older animals (Geist 1971). In wild sheep, lambs and juveniles are never seen alone, although older sheep have greater independence. Lambs and juveniles face greater predation risks in the open and when isolated than older animals. Lambs are therefore likely to find social isolation and open-field tests more stressful than would older sheep, and they may be more likely to use vocalisation and immobility in these situations since this would be the appropriate behaviour pattern to attract their dam. Social partners can reduce stress in some situations and the presence of the dam is effective for very young animals (Veissier *et al* 1998), as is the presence of a twin sibling for older lambs (Porter *et al* 1995).

Effects of sex

In wild sheep, rams forage further from cover and for longer than do ewes (Woolf *et al* 1970; Berger 1991; Bleich *et al* 1997), are less vigilant (Schaller 1977) and are more likely to be seen alone (Geist 1971). Rams are less likely to be predated than ewes or juveniles and this is apparently reflected in their perception of risk. Similarly, in domestic sheep, in standard tests of the fear responses of ewes and rams, ewes had higher levels of locomotion, made more frequent escape attempts and had higher rates of high-pitched vocalisation than did rams (Vandenhede & Bouissou 1993). These tests suggest that ewes are more fearful than rams under the same conditions, as might be predicted from the behaviour of wild sheep. Ewes have larger adrenal glands than rams and show heightened activity of the HPA axis (Canny *et al* 1999). Thus, the behaviour of domestic ewes and rams to stress or fear-eliciting situations is reflective of their behaviour in the wild: ewes are more fearful of situations in which there

would be a greater risk of predation in the wild (social isolation, presence of a predator).

Effects of pregnancy and lactation

The behaviour of wild sheep suggests that sheep vary in the risks that they take at various stages in their life cycle. Bighorn ewes adjust their assessment of risk and their use of habitat with reproductive status (Berger 1991; Bon *et al* 1995; Bleich *et al* 1997). Pregnant domestic ewes have a decreased response to social isolation compared to non-pregnant control ewes (Poindron *et al* 1997), and a reduced response to surprise tests (Viérin & Bouissou 2001). Decreased fearfulness may facilitate isolation of the ewes from the flock at parturition and allow pregnant ewes to forage in more risky areas in the wild. However, Viérin and Bouissou (2001) showed that pregnant ewes retain their fearfulness to the presence of humans, suggesting that pregnant ewes may show greater risk behaviours, as is true of wild sheep, but still retain responsiveness to the presence of potential predators. Lactating ewes are also non-responsive to isolation from the flock as long as they are with their lamb (Poindron *et al* 1994). This does not appear to be due to the lamb functioning as a social companion, as it is specific to the presence of the ewe's own lamb, and the presence of a lamb does not diminish agitation in non-lactating ewes (Porter *et al* 1991; Poindron *et al* 1994). Maternal ewes will remain near their lambs when a human approaches (O'Connor *et al* 1985), and, when accompanied by their lambs, may display aggressive behaviours towards handlers and dogs. These responses may stem either from a reduction in fearfulness or an increase in aggression (Lawrence *et al* 1998), and demonstrate a profound change in the behaviour of lactating ewes to stressful stimuli.

Effects of early life experiences

Prenatal stress can cause permanent alterations in the functioning of the HPA axis (Weinstock 1997), and hence has far-reaching effects by increasing stress responsiveness in adulthood (Braastad 1998; Lay 2000). In sheep, treatment of pregnant ewes with glucocorticoids, to mimic elevations caused by stressful events, causes a reduction in birth weight and increased plasma adrenocorticotrophic hormone (ACTH) and cortisol in the offspring (Sloboda *et al* 2000). This prenatal stress effect could be adaptive in wild sheep where an increased risk of predation or environmental stress is transmitted by the ewe to her unborn lamb to programme increased stress responsiveness after birth. In domestic sheep, an unfortunate consequence of this mechanism is that stress experienced by pregnant ewes can be detrimental to the welfare of their offspring by making them more stress responsive to unavoidable events in the captive environment. In neonatal rats, maternal deprivation paradigms make pups less reactive to challenges experienced in later life (reviewed by Mason 2000), apparently through enhanced maternal care when the pups are returned at the end of a deprivation period (reviewed by Lay 2000). In open-field and novel object tests and in the presence of a human, lambs reared without their dams or peers respond with behavioural

inhibition, in comparison to the active responses of dam-reared lambs (Moberg & Wood 1982; Romeyer & Bouissou 1992). The data suggest different styles of responding to stress (active versus inhibition), rather than changes in stress responsiveness as a result of maternal deprivation. In these studies, however, lambs were totally deprived of their mothers, thus preventing both the opportunity of the lambs to learn from their mothers, and for differences in maternal care to affect lamb responsiveness. Separation of neonatal lambs from their dams for two days, during which they were handled by humans, caused a decrease in lamb timidity in the presence of humans that persisted for three months (Markowitz *et al* 1998). Whether this response would generalise to decreased stress responses in other tests, and whether maternal care of the separated lamb increased upon reunion of ewe and lamb, were not reported. This response was effective only when the lambs were very young, suggesting that the potential for lambs' stress responses to be affected may exist only in the first few days of life. This coincides with the period during which wild sheep would be isolated from their flocks with their lambs, and raises the intriguing possibility that ewes may be able to influence their lamb's development by their behaviour at this time.

Learned fears

Several studies have shown that sheep readily learn to associate unpleasant experiences with places, people or auditory stimuli (Fell & Shutt 1989; Rushen 1996; Mears *et al* 1999), and that they show long-term avoidance of these stimuli (Hutson 1985), which is not seen in naïve animals. The ability to rapidly learn about unpleasant stimuli is highly adaptive for a predated animal and might aid survival through avoidance of places where predators have been encountered.

Studies of wild sheep suggest that experience may alter responsiveness to perceived predator stimuli (Schaller 1977). Griffin (2001) suggests that prey animals on the African plains are able to assess the likelihood of imminent attack by monitoring predator behaviour. It is clearly adaptive for a prey animal to respond only to perceived threats rather than wasting energy and foraging opportunities in unnecessary flight. In domestic sheep, lambs, unlike ewes, did not respond with aversion to images of dogs (Porter & Bouissou 1999), suggesting that the lambs had not yet learned to attach an appropriate significance to these images. Studies of facial recognition in sheep have shown that populations of cells in the temporal cortex respond to faces of a common social significance (Kendrick & Baldwin 1987; Kendrick 1991). Thus, there are cells that respond to faces of sheep of the same breed, and particularly to familiar animals, and cells that respond to human and dog faces. Although human and dog faces do not have many similar physical characteristics, they apparently represent a similar threat to the sheep and so are coded similarly. However, Peirce *et al* (2001) showed that cells that respond to socially familiar sheep were also responsive to images of particularly familiar stockpersons but not to images of other humans. Behavioural studies have also demonstrated that

sheep can distinguish between different handlers on the basis of their previous experience of them (Fell & Shutt 1989; Boivin *et al* 1997; Davis *et al* 1998). Furthermore, the effective use of guard dogs that live within the sheep flock (eg Green & Woodruff 1980; Andelt & Hopper 2000), suggests that sheep might also classify some dogs differently depending on their experience of them. Thus, predator recognition appears not to be innate, but instead dependent on the previous experience of the sheep.

Conclusions

Many aspects of the behavioural organisation of wild sheep have evolved as a means to avoid detection and capture by predators. The behavioural responses of flocking, flight and behavioural inhibition in cover are the dominant behaviours expressed in the presence of threat, and domestic sheep also express these behaviours. In wild sheep, flight responses and vigilance behaviours are influenced by the animal's assessment of risk, and are thus modified by age, experience, reproductive status and social group size. Play behaviour in young lambs, both wild and domestic, is also modified by risk. These behaviours may therefore reflect the underlying level of distress that the sheep is experiencing, and may be useful indicators for welfare assessment.

Different breeds of sheep differ in their stress responses, although there appears to be a behavioural continuum from the wild sheep via the more primitive feral breeds and the hill and upland breeds to lowland sheep. The decreased behavioural responses of lowland sheep may result from their experience of more intensive husbandry conditions than hill and upland sheep. Thus, their increased tolerance of crowding may reflect an adaptive response to the stress of close confinement with other sheep in intensive husbandry systems. However, there does appear to be a real genetic difference between breeds in their responsiveness to stressors, which may be potentiated or modified by experience. An increase in vocal behaviour, particularly of high-pitched bleats, in all contexts (eg lamb vocalisations, bleats in anticipation of food, distress vocalisations in isolation) is a feature of increased domestication. The use of vocalisations as indicators of distress is often considered attractive, as vocalisations are easily measured; however, this may be confounded with the normal vocal behaviour of the breed. Furthermore, in sheep, the inhibition of vocalisation that occurs in the presence of perceived predators may confuse assessments of distress based on vocalisation.

Studies of the neurobiological and behavioural responses of sheep to images of dogs and humans (Kendrick 1991; Porter & Bouissou 1999; Hansen *et al* 2001) suggest that the emotional significance to the sheep of a particular stimulus may be a learned response. Thus, animals with differing exposure to environmental stimuli, as will occur in extensive and intensive husbandry conditions, may form different emotional connections between the same stimuli, resulting in different behavioural responses on later exposure.

Animal welfare implications

An understanding of the causal mechanisms underlying behavioural expression, and the link between behaviours and emotional states, are crucial if behavioural indices are to be used as indicators of welfare. Judging by the behaviour of wild sheep, changes in vigilance behaviour and flight distances, and play in young animals, may have potential as welfare indicators in domestic sheep since they appear to be related to the animal's perception of threat. This suggests that these responses are graded by the amount of fear or distress the animal is experiencing and thus act as indicators of the animal's emotional state. As such they have the potential to contribute to assessment of the animal's welfare state. These behaviours may have relevance both to acute and chronically stressful events because in the wild the animal may experience both short-term acute exposure to a predator and live under conditions of chronic exposure and harassment by predators. The previous experiences of sheep appear to be important in determining whether a stimulus elicits the evolved anti-predator behavioural repertoire. The extent to which these behaviours can be modified by, for example rearing experience, and whether such factors account for the breed and husbandry influences on stress responses requires further investigation.

Acknowledgements

This paper was written from a chapter that formed part of a literature review funded by the Ministry of Agriculture, Fisheries and Food (AW0909) on 'The Welfare of Sheep: A Review of Behavioural Indicators of Pain, Suffering and Distress'. The author also received support from the Scottish Executive Environment and Rural Affairs Department. Particular thanks to Alistair Lawrence for his helpful comments on draft versions of the manuscript.

References

- Alexander G, Stevens D, Kilgour R, de Langen H, Mottershead BE and Lynch JJ** 1983 Separation of ewes from twin lambs: incidence in several sheep breeds. *Applied Animal Ethology* 10: 301-317
- Altendorf KB, Laundre JW, Gonzalez CAL and Brown JS** 2001 Assessing effects of predation risk on foraging behaviour of mule deer. *Journal of Mammalogy* 82: 430-439
- Andelt WF and Hopper SN** 2000 Livestock guard dogs reduce predation on domestic sheep in Colorado. *Journal of Range Management* 53: 259-267
- Appleby MC** 1996 Can we extrapolate from intensive to extensive conditions? *Applied Animal Behaviour Science* 49: 23-28
- Arnold GW** 1985 Associations and social behaviour. In: Fraser AF (ed) *Ethology of Farm Animals* pp 246-248. Elsevier: Amsterdam, The Netherlands
- Arnold GW and Pahl PJ** 1967 Sub-grouping in sheep flocks. *Proceedings of the Ecological Society of Australia* 2: 183-189
- Arnold GW and Pahl PJ** 1974 Some aspects of the social behaviour of domestic sheep. *Animal Behaviour* 22: 592-600
- Berger J** 1979 Social ontogeny and behavioural diversity: consequences for Bighorn sheep *Ovis canadensis* inhabiting desert and mountain environments. *Journal of Zoology, London* 188: 251-266
- Berger J** 1991 Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild Bighorn sheep. *Animal Behaviour* 41: 61-77

- Blanchard RJ, Nikulina JN, Sakai RR, McKittrick C, McEwen B and Blandchard DC** 1998 Behavioural and endocrine change following chronic predatory stress. *Physiology and Behavior* 63: 561-569
- Bleich VC** 1999 Mountain sheep and coyotes: patterns of predator evasion in a mountain ungulate. *Journal of Mammalogy* 80: 283-289
- Bleich VC, Bowyer RT and Wehausen JD** 1997 Sexual segregation in mountain sheep: resources or predation? *Wildlife Monographs* 134: 3-50
- Boissy A** 1998 Fear and fearfulness in determining behaviour. In: Grandin T (ed) *Genetics and the Behaviour of Domestic Animals* pp 67-111. Academic Press: London, UK
- Boivin X, Nowak R, Desprès G, Tournadre H and Le Neindre P** 1997 Discrimination between shepherds by lambs reared under artificial conditions. *Journal of Animal Science* 75: 2892-2898
- Bon R, Badia J, Maublanc ML and Recarte JM** 1993 Social grouping dynamics of Mouflon (*Ovis ammon*) during rut. *International Journal of Mammalian Biology* 58: 294-301
- Bon R and Campan R** 1989 Social tendencies of the Corsican Mouflon (*Ovis ammon musimon*) in the Caroux-Espinouse Massif (South of France). *Behavioural Processes* 19: 57-78
- Bon R, Joachim J and Maublanc ML** 1995 Do lambs affect feeding habitat use by lactating female Mouflons in spring in areas free of predators? *Journal of Zoology* 235: 43-51
- Bouissou M-F, Porter RH, Boyle L and Ferreira G** 1996 Influence of a conspecific image of own vs. different breed on fear reactions of ewes. *Behavioural Processes* 38: 37-44
- Braastad BO** 1998 Effects of prenatal stress on behaviour of offspring of laboratory and farmed mammals. *Applied Animal Behaviour Science* 61: 159-180
- Byers JA** 1987 Why the deer and the antelope play. *Natural History (May)*: 54-61
- Byers JA** 1997 *American Pronghorn, Social Adaptations and the Ghosts of Predators Past*. University of Chicago Press: Chicago, USA
- Canny BJ, O'Farrell KA, Clarke IJ and Tilbrook AJ** 1999 The influence of sex and gonadectomy on the hypothalamo-pituitary-adrenal axis of the sheep. *Journal of Endocrinology* 162: 215-225
- Caro TM** 1994 Ungulate anti-predator behaviour — preliminary and comparative data from African bovids. *Behaviour* 128: 189-228
- Caro TM, Lombardo L, Goldizen AW and Kelly M** 1995 Tail-flagging and other anti-predator signals in white-tailed deer: new data and synthesis. *Behavioural Ecology* 6: 442-450
- Clutton-Brock J** 1987 *The Natural History of Domesticated Mammals*. Cambridge University Press and the British Museum (Natural History): Cambridge, UK
- Clutton-Brock J** 1992 The process of domestication. *Mammal Review* 22: 79-85
- Clutton-Brock TH, Stevenson IR, Marrow P, MacColl AD, Houston AI and McNamara JM** 1996 Population fluctuations, reproductive costs and life-history tactics in female Soay sheep. *Journal of Animal Ecology* 65: 675-689
- Conradt L** 1999 Social segregation is not a consequence of habitat segregation in red deer and feral Soay sheep. *Animal Behaviour* 57: 1151-1157
- Cransac N, Gerard J-F, Maublanc M-L and Pepin D** 1998 An example of segregation between age and sex classes only weakly related to habitat use in Mouflon sheep (*Ovis gmelini*). *Journal of Zoology* 244: 371-378
- Cransac N and Hewison AJM** 1997 Seasonal use and selection of habitat by Mouflon (*Ovis gmelini*): comparison of the sexes. *Behavioural Processes* 41: 57-67
- Cresswell E** 1960. Ranging behaviour studies with Romney Marsh and Cheviot sheep in New Zealand. *Animal Behaviour* 8: 32-38
- Davis H, Norris C and Taylor A** 1998 Wether ewe know me or not: the discrimination of individual humans by sheep. *Behavioural Processes* 43: 27-32
- Deag JM** 1996 Behavioural ecology and the welfare of extensively farmed animals. *Applied Animal Behaviour Science* 49: 9-22
- Dwyer CM and Lawrence AB** 1999 Ewe-ewe and ewe-lamb behaviour in a hill and a lowland breed of sheep: a study using embryo transfer. *Applied Animal Behaviour Science* 61: 319-334
- Dwyer CM and Lawrence AB** 2000 Effects of maternal genotype and behaviour on the behavioural development of their offspring in sheep. *Behaviour* 137: 1629-1654
- Dwyer CM, McLean KA, Deans LA, Chirnside J, Calvert SK and Lawrence AB** 1998 Vocalisations between mother and young in the sheep: effects of breed and maternal experience. *Applied Animal Behaviour Science* 58: 105-119
- Fagen R** 1981 *Animal Play Behaviour*. Oxford University Press: Oxford, UK
- Fell LR and Shutt DA** 1989 Behavioural and hormonal responses to acute surgical stress in sheep. *Applied Animal Behaviour Science* 22: 283-294
- Frid A** 1997 Vigilance by female Dall's sheep: interactions between predation risk factors. *Animal Behaviour* 53: 799-808
- Frid A and Dill L** 2002 Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6: article 11
- Geist V** 1971 *Mountain Sheep: A Study in Behaviour and Evolution*. University of Chicago Press: Chicago, USA
- Gluesing EA, Balph DF and Knowlton FF** 1980 Behavioural patterns of domestic sheep and their relationship to coyote predation. *Applied Animal Ethology* 6: 315-330
- Goddard PJ, Fawcett AR, Macdonald AJ and Reid HW** 2000 The behavioural, physiological and immunological responses of lambs from two rearing systems and two genotypes to exposure to humans. *Applied Animal Behaviour Science* 66: 305-321
- Green JS and Woodruff RA** 1980 Is predator control going to the dogs? *Rangelands* 2: 187-189
- Griffin DR** 2001 *Animal Minds: Beyond Cognition to Consciousness*. University of Chicago Press: Chicago, USA
- Grubb P and Jewell PA** 1966 Social grouping and home range in feral Soay sheep. *Symposia of the Zoological Society of London* 18: 179-210
- Hafez ESE and Scott JP** 1962 The behaviour of sheep and goats. In: Hafez ESE (ed) *The Behaviour of Domestic Animals*. Balliere Tindall: London, UK
- Hansen I, Christiansen F, Hansen HS, Braastad B and Bakken M** 2001 Variation in behavioural responses of ewes towards predator-related stimuli. *Applied Animal Behaviour Science* 70: 227-237
- Hemmer H** 1990 *Domestication: The Decline in Environmental Appreciation*. Cambridge University Press: Cambridge, UK
- Hersher L, Richmond JB and Moore AU** 1963 Maternal behaviour in sheep and goats. In: Rheingold HL (ed) *Maternal Behaviour in Mammals* pp 203-232. John Wiley and Sons: New York, USA
- Hewson R and Wilson CJ** 1979 Home range and movements of Scottish Blackface sheep in Lochaber, north-west Scotland. *Journal of Applied Ecology* 16: 743-751
- Hiendleder S, Mainz K, Plante Y and Lewalski H** 1998 Analysis of mitochondrial DNA indicates that domestic sheep are derived from two different ancestral maternal sources: no evidence for contributions from Urial and Argali sheep. *Journal of Heredity* 89: 113-120

- Hunter RF and Milner C** 1963 The behaviour of individual, related and groups of South Country Cheviot hill sheep. *Animal Behaviour* 11: 507-513
- Hutson GD** 1985 The influence of barley food rewards on sheep movement through a handling system. *Applied Animal Behaviour Science* 14: 263-273
- Jugo BM and Vicario A** 2000 Single-strand conformational polymorphism and sequence polymorphism of Mhc-DRB in Latxa and Karrantzar sheep: implications for Caprinae phylogeny. *Immunogenetics* 51: 887-897
- Kendrick KM** 1991 How the sheep's brain controls the visual recognition of sheep and humans. *Journal of Animal Science* 69: 5008-5016
- Kendrick KM, Atkins K, Hinton MR, Heavens P and Keverne EB** 1996 Are faces special for sheep? Evidence from facial and object discrimination learning tests showing effects of inversion and social familiarity. *Behavioural Processes* 38: 19-35
- Kendrick KM and Baldwin BA** 1987 Cells in the temporal cortex of conscious sheep can respond preferentially to the sight of faces. *Science* 236: 448-450
- Key C and MacIver RM** 1980 The effects of maternal influences on sheep: breed differences in grazing, resting and courtship behaviour. *Applied Animal Ethology* 6: 33-48
- Kiley M** 1972 The vocalisations of ungulates, their causation and function. *Zeitschrift für Tierpsychologie* 31: 171-222
- Künzl C and Sachser N** 1999 The behavioural endocrinology of domestication: a comparison between the domestic guinea pig (*Cavia aperea f. porcellus*) and its wild ancestor, the Cavy (*Cavia aperea*). *Hormones and Behavior* 35: 28-37
- Lambe NR, Conington J, Bishop SC, Waterhouse A and Simm G** 2001 A genetic analysis of maternal behaviour score in Scottish Blackface sheep. *Animal Science* 72: 415-425
- Langbein J, Scheibe KM and Eichhorn K** 1997 Seasonal changes in the circadian patterns of European Mouflons (*Ovis ammon musimon* Pallas 1811). *International Journal of Mammalian Biology* 62: 117-123
- Langbein J, Streich J and Scheibe KM** 1998 Characteristic activity patterns of female mouflons (*Ovis orientalis musimon*) in the lambing period. *Applied Animal Behaviour Science* 58: 281-292
- Lankin V** 1997 Factors of diversity of domestic behaviour in sheep. *Genetics, Selection, Evolution* 29: 73-92
- Laundre JW, Hernandez L and Altendorf KB** 2001 Wolves, elk, and bison: re-establishing the "landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology* 79: 1401-1409
- Lawrence AB** 1990 Mother-daughter and peer relationships of Scottish hill sheep. *Animal Behaviour* 39: 481-486
- Lawrence AB** 1991 Mother-daughter bonds in sheep. *Animal Behaviour* 42: 683-685
- Lawrence A, Dwyer C and Jarvis S** 1998 An interactive model of behavioural change in parturient and lactating farm animals. In: Veissier I and Boissy A (eds) *Proceedings of the 32nd Congress of the International Society for Applied Ethology* pp 38 (Abstract). Clermont-Ferrant: France
- Lawrence AB and Wood-Gush DGM** 1988 Home-range behaviour and social organization of Scottish Blackface sheep. *Journal of Applied Ecology* 25: 25-40
- Lay DC** 2000 Consequences of stress during development. In: Moberg GP and Mench JA (eds) *The Biology of Animal Stress* pp 249-267. CAB International: Wallingford, UK
- Le Neindre P, Poindron P, Trillat G and Orgeur P** 1993 Influence of breed on reactivity of sheep to humans. *Genetics, Selection, Evolution* 25: 447-458
- Lent PC** 1974 Mother-infant relationships in ungulates. In: Geist V and Walther F (eds) *The Behaviour of Ungulates and its Relationship to Management* pp 14-55. International Union for the Conservation of Nature and Natural Resources (IUCN): Morges, Switzerland
- Le Pendu Y, Briedermann L, Gerard J-F and Maublanc M-L** 1995 Interindividual associations and social structure of a Mouflon population (*Ovis orientalis musimon*). *Behavioural Processes* 34: 67-80
- Le Pendu Y, Maublanc M-L, Briedermann L and Dubois M** 1996 Spatial structure and activity in groups of Mediterranean Mouflon (*Ovis gmelini*): a comparative study. *Applied Animal Behaviour Science* 46: 201-216
- Lima SL** 1998 Stress and decision making under the risk of predation: recent developments from behavioural, reproductive and ecological perspectives. *Advances in the Study of Behaviour* 27: 215-290
- Lima SL and Dill LM** 1990 Behavioural decision making under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68: 619-640
- Lynch JJ and Alexander G** 1973 Animal behaviour and the pastoral industries. In: Alexander G and Williams OB (eds) *Pastoral Industries of Australia* pp 371-400. Sydney University Press: Sydney, Australia
- Lynch JJ, Hinch GN and Adams DB** 1992 *The Behaviour of Sheep: Biological Principles and Implications for Production*. CAB International: Wallingford, UK and the Commonwealth Scientific and Industrial Research Organisation (CSIRO): Victoria, Australia
- Martinetto K and Cugnasse JM** 2001 Reaction distance in Mediterranean Mouflon (*Ovis gmelini musimon* × *Ovis* sp) in the presence of hikers with a dog on the Caroux plateau (Herault, France). *Revue de Ecologie — La Terre et la Vie* 56: 231-242
- Markowitz TM, Dally MR, Gursky K and Price EO** 1998 Early handling increases lamb affinity for humans. *Animal Behaviour* 55: 573-587
- Mason G and Mendl M** 1993 Why is there no simple way of measuring animal welfare? *Animal Welfare* 2: 301-319
- Mason WA** 2000 Early developmental influences of experience on behaviour, temperament and stress. In: Moberg GP and Mench JA (eds) *The Biology of Animal Stress* pp 269-290. CAB International: Wallingford, UK
- Mears GJ, Brown FA and Redmond LR** 1999 Effects of handling, shearing and previous exposure to shearing on cortisol and β -endorphin responses in ewes. *Canadian Journal of Animal Science* 79: 35-38
- Melinkova MN, Grechko VV and Mednikov BM** 1995 Investigation of genetic divergence and polymorphism of nuclear DNA in species and populations of domestic and wild sheep. *Genetika* 31: 1120-1131
- Moberg GP and Wood VA** 1982 Effect of differential rearing on the behavioural and adrenocortical response of lambs to a novel environment. *Applied Animal Ethology* 8: 269-279
- Nowak R** 1990 Lamb's bleats: important for the establishment of the mother-young bond? *Behaviour* 115: 14-29
- Obregon F, Dereyna LA and Recuerda P** 1992 Nursing and suckling behaviour in the Mouflon. *Ethology, Ecology and Evolution* 4: 285-291
- O'Connor CE, Jay NP, Nicol AM and Beatson PR** 1985 Ewe maternal behaviour score and lamb survival. *Proceedings of the New Zealand Society for Animal Production* 45: 159-162
- Palmqvist P, Martinez-Navarro B and Arribas A** 1996 Prey selection by terrestrial carnivores in a lower Pleistocene paleo-community. *Paleobiology* 22: 514-534

- Patterson BR and Messier F** 2000 Factors influencing the killing rates of white-tailed deer by coyotes in eastern Canada. *Journal of Wildlife Management* 64: 721-732
- Peirce JW, Leigh AE, DaCosta APC and Kendrick KM** 2001 Human face recognition in sheep: lack of configurational coding and right hemisphere advantage. *Behavioural Processes* 55: 13-26
- Poindron P, Caba M, Gomora Arrati P, Krehbiel D and Beyer C** 1994 Responses of maternal and non-maternal ewes to social and mother-young separation. *Behavioural Processes* 31: 97-110
- Poindron P, Soto R and Romeyer A** 1997 Decrease of response to social separation in preparturient ewes. *Behavioural Processes* 40: 45-51
- Porter RH and Bouissou MF** 1999 Discriminative responsiveness by lambs to visual images of conspecifics. *Behavioural Processes* 48: 101-110
- Porter RH, Levy F, Poindron P, Litterio M, Schaal B and Beyer C** 1991 Individual olfactory signatures as major determinants of early maternal discrimination in sheep. *Developmental Psychobiology* 24: 151-158
- Porter RH, Nowak R and Orgeur P** 1995 Influence of a conspecific agemate on distress bleating by lambs. *Applied Animal Behaviour Science* 45: 239-244
- Price EO** 1984 Behavioural aspects of animal domestication. *The Quarterly Review of Biology* 59: 1-32
- Pulliam HR** 1973 On the advantages of flocking. *Journal of Theoretical Biology* 38: 419
- Ratner SC and Boice R** 1975 Effects of domestication on behaviour. In: Hafez ESE (ed) *The Behaviour of Domestic Animals* pp 3-19. Williams and Wilkins: Baltimore, USA
- Reale D, Bousses P and Chapuis JL** 1999 Nursing behaviour and mother-lamb relationships in Mouflon under fluctuating population densities. *Behavioural Processes* 47: 81-94
- Roberts G** 1996 Why individual vigilance declines as group size increases. *Animal Behaviour* 51: 1077-1086
- Romeyer A and Bouissou M-F** 1992 Assessment of fear reactions in domestic sheep, and influence of breed and rearing conditions. *Applied Animal Behaviour Science* 34: 93-119
- Ross PI, Jalkotzy MG and FestaBianchet M** 1997 Cougar predation on Bighorn sheep in southwestern Alberta during winter. *Canadian Journal of Zoology* 75: 771-775
- Ruckstuhl KE and Neuhaus P** 2000 Sexual segregation in ungulates: a new approach. *Behaviour* 137: 361-377
- Ruckstuhl KE and Neuhaus P** 2001 Behavioural synchrony in ibex groups: effects of age, sex and habitat. *Behaviour* 138: 1033-1046
- Rushen J** 1996 Using aversion learning techniques to assess the mental state, suffering and welfare of farm animals. *Journal of Animal Science* 74: 1990-1995
- Rushen J** 2000 Some issues in the interpretation of behavioural responses to stress. In: Moberg GP and Mench JA (eds) *The Biology of Animal Stress* pp 23-42. CAB International: Wallingford, UK
- Ryder ML** 1984 Sheep. In: Mason IL (ed) *Evolution of Domesticated Animals*. Longman: London, UK
- Sachs BD and Harris VS** 1978 Sex differences and developmental changes in selected juvenile activities (play) of domestic lambs. *Animal Behaviour* 26: 678-684
- Sarno RJ, Clark WR, Bank MS, Prexl WS, Behl MJ, Johnson WE and Franklin WL** 1999 Juvenile guanaco survival: management and conservation implications. *Journal of Applied Ecology* 36: 937-945
- Schaller GB** 1977 *Mountain Monarchs*. University of Chicago Press: Chicago, USA
- Shackleton DM and Shank CC** 1984 A review of the social behaviour of feral and wild sheep and goats. *Journal of Animal Science* 58: 500-509
- Shannon NH, Hudson RJ, Brink VC and Kitts WD** 1975 Determinants of spatial distribution of Rocky Mountain Bighorn sheep. *Journal of Wildlife Management* 39: 387-401
- Shillito-Walser EE** 1978 A comparison of the role of vision and hearing in ewes finding their own lambs. *Applied Animal Ethology* 4: 71-79
- Shillito-Walser EE** 1980 Maternal recognition and breed identity in lambs living in a mixed flock of Jacob, Clun Forest and Dalesbred sheep. *Applied Animal Ethology* 6: 221-231
- Shillito-Walser E and Hague P** 1981 Field observations on a flock of ewes and lambs made up of Clun Forest, Dalesbred and Jacob sheep. *Applied Animal Ethology* 7: 175-178
- Shillito-Walser E, Walters E and Ellison J** 1984 Observations on vocalisation of ewes and lambs in the field. *Behaviour* 91: 190-203
- Shillito-Walser E, Walters E and Hague P** 1982 Vocal communication between ewes and their own and alien lambs. *Behaviour* 81: 140-151
- Shillito-Walser E and Williams T** 1986 Pair-associations in twin lambs before and after weaning. *Applied Animal Behaviour Science* 15: 241-245
- Sloboda DM, Newnham JP and Challis JRG** 2000 Effects of repeated maternal betamethasone administration on growth and hypothalamic-pituitary-adrenal function of the ovine fetus at term. *Journal of Endocrinology* 165: 79-91
- Stahl P, Vandel JM, Herrenscheidt V and Migot P** 2001 Predation on livestock by an expanding reintroduced lynx population: long-term trend and spatial variability. *Journal of Applied Ecology* 38: 674-687
- Stolba A, Hinch GN, Lynch JJ, Adams DB, Munro RK and Davies HI** 1990 Social organisation of Merino sheep of different ages, sex and family structure. *Applied Animal Behaviour Science* 27: 337-349
- Torres-Hernandez G and Hohenboken W** 1979 An attempt to assess traits of emotionality in crossbred ewes. *Applied Animal Ethology* 5: 71-83
- Triesman M** 1975a Predation and the evolution of gregariousness. I. Models for concealment and evasion. *Animal Behaviour* 23: 779-800
- Triesman M** 1975b Predation and the evolution of gregariousness. II. An economic model for predator-prey interaction. *Animal Behaviour* 23: 801-825
- Vandenheede M and Bouissou MF** 1993 Sex differences in fear reactions in sheep. *Applied Animal Behaviour Science* 37: 39-55
- Vandenheede M, Bouissou MF and Picard M** 1998 Interpretation of behavioural reactions of sheep towards fear-eliciting situations. *Applied Animal Behaviour Science* 58: 293-310
- Veissier I, Boissy A, Nowak R, Orgeur P and Poindron P** 1998 Ontogeny of social awareness in domestic herbivores. *Applied Animal Behaviour Science* 57: 233-245
- Viérin M and Bouissou M-F** 2001 Pregnancy is associated with low fear reactions in ewes. *Physiology and Behavior* 72: 579-587
- Viérin M and Bouissou M-F** 2002 Influence of maternal experience on fear reactions in ewes. *Applied Animal Behaviour Science* 75: 307-315
- Vine I** 1971 Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. *Journal of Theoretical Biology* 30: 405-422

White KS and Berger J 2001 Anti-predator strategies of Alaskan moose: are maternal trade-offs influenced by offspring activity? *Canadian Journal of Zoology* 79: 2055-2062

White KS, Testa JW and Berger J 2001 Behavioral and ecologic effects of differential predation pressure on moose in Alaska. *Journal of Mammalogy* 82: 422-429

Wienstock M 1997 Does prenatal stress impair coping and regulation of hypothalamic-pituitary-adrenal axis? *Neuroscience and Biobehavioural Reviews* 21: 1-10

Wilson EO 1975 *Sociobiology: The New Synthesis*. Belknap Press of Harvard University Press: Cambridge, Massachusetts, USA

Winfield CG and Mullaney PD 1973 A note on the social behaviour of a flock of Merino and Wiltshire Horn sheep. *Animal Production* 17: 93-95

Wolff JO and van Horn T 2003 Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. *Canadian Journal of Zoology* 81: 266-271

Woolf A, O'Shea T and Gilbert DL 1970 Movements and behavior of Bighorn sheep on summer ranges in Yellowstone National Park. *Journal of Wildlife Management* 34: 446-450

Zohary D, Tchernov E and Horwitz LK 1998 The role of unconscious selection in the domestication of sheep and goats. *Journal of Zoology* 245: 129-135