GENETICS OF MATERNAL ABILITY IN CATTLE AND SHEEP

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SUMMARY
Maternal behaviour is a highly integrated mechanism essential for the survival of young and the growth of the offspring, especially in extensive husbandry systems. At least two essential components can be differentiated in the maternal behaviour of cattle and sheep; the care the females give to the young and their selectivity which limits that care to specific young. In addition, maternal behaviour is one of the major expressions of the interactions of the individual with its social environment. Relationships between those different traits are elaborated in this paper. We report results on one experiment on cattle and of two others on sheep. Friesian cows differed substantially in their selectivity from cows of a more primitive breed, the Salers, but also in the amount of social interaction with the other cows as well as with their own calves. Social behaviour of sheep from two breeds and their crossbreds were observed. Differences in maternal and social behaviours and in reaction to humans were found between those different breeds it seems that these traits are not genetically linked. Moderate heritability estimates of social traits were found in a third experiment on sheep. These may have important consequences in terms of genetic selection.
Keywords: Maternal behaviour, cattle, sheep, temperament, selectivity.

INTRODUCTION
Maternal behaviour is a highly integrated mechanism essential for the young to survive and for the growth of the offspring, especially in extensive husbandry systems. Factors such as milk production and ease of parturition have been shown for a very long time to be important for survival of young and on their growth. However, maternal behaviour is one of the components of maternal ability which has received much less attention. We will in this paper analyse more specifically the genetic variability of maternal behaviour. Other aspects such as the behaviour of the young and other factors related to the mother's behaviour such as parity, environmental conditions and nutrition are not considered here (Lindsay *et al.* 1990).

A major element specific to sheep and cattle is their sociality. They live in groups and are very attracted to other animals in the group. Maternal behaviour is one of the many items associated with the social life of the animals. Moreover, because they are farm animals, sheep and cattle also have to deal with humans. Thus, in this paper we will analyse the relationships between maternal behaviour and the other social traits in these two species. We will present results obtained both independently and in collaboration by the authors in Australia and in France

which for most part are still unpublished. Only preliminary results will be presented for some experiments that are still in progress..

A Maternal behaviour of sheep and cattle and productivity traits. Cows and ewes usually try to isolate themselves before parturition. At this time they are less attracted than normal by other females. They stay on a birth site for some time after parturition and the young elicits a specific behaviour described typically by Levy and Poindron (1987) in sheep and by Le Neindre (1987) in cattle. The dam licks her young, facilitates access by the young to the udder and protects it against predators (eg. Rankin and Donaldson 1968). After this, the females will accept suckling from only their own young or young that they have adopted; that is, they are "selective". After some time on the birth site females rejoin the group. Offspring interact quite soon with the other young and they are slowly integrated into the group. The behaviour of cattle differs from that of sheep in several ways. Calves will *hide* when not with their mothers during few days after birth. Lambs, on the other hand, *follow* their mothers after the few hours spent together on the birth site. Cows lick their young during the whole of the suckling period at least until weaning but ewes lick their young only during few hours after birth. Weaning occurs after some 3 to 4 months in sheep and is provoked by the dam. It is very much later in cattle and sucklings can be observed till the birth of the next calf if they are left together (Veissier *et al.* 1990).

After parturition, cows and ewes are more upset by the presence of humans than in other physiological states. The exact position of humans in the social network of the lactating female is difficult to define (Estep and Hetts 1992) and depends on the previous experience of the animals. Humans can be perceived by the mother to be a predator, a source of food or a social partner. For example in sheep, O'Connor *et al.* (1985) and Putu *et al.* (1988) found significant correlations between lamb mortality and the temperament of ewes which they defined as reaction to the presence of a human on the lambing site or as reactivity in an "open-field".

The interactions of the dam with its young therefore vary not only because of the interest of the dam in taking care of her young but because of the way she resolves different conflicts. The first of these conflicts is the relative importance of the young and of the other females of the group. Animals can try to join the group without their young or will react strongly when isolated. The second is the animal's reaction towards humans. Dams can try to avoid human proximity. In the extreme, ewes can leave their young leading to the death of the lambs by starvation (Putu 1988). Cows, on the other hand, may react by attacking humans (Buddenberg *et al.* 1986).

B. The influence of breed on the maternal behaviour of cattle (Le Neindre, 1989). In domestication, calves are reared after birth by a variety of systems. Isolation of calves from the time of birth is a normal practise in dairy farms. On the other hand, beef calves stay with their mothers for several months. Experiments were designed to study the mother-young relationships of cows from Friesian (dairy) and Salers (beef) breeds reared under these very different conditions.

The cows suckled their own calves during the first lactation. In the second lactation they had two calves, their own and a fostered one assigned to the cow as soon as possible after calving. They were 30 months old at this time and were observed closely at pasture during the first 4 hours *postpartum*. Social behaviour was observed for several days at pasture during both the first and second lactations.

Table 1 shows that just after calving cows from the two breeds were all maternal. Later, when suckling one calf, Friesian cows were sucked more often than Salers by alien calves. When in the double suckling system, Friesian cows accepted the fostered calf more readily than the Salers and licked their own calf and other cows less often (Table 1).

Table 1. Maternal behaviour of Friesian and Salers cows

	Friesian	Salers	Significance *
4h period after birth			
Number of cows	6	7	
Interval from birth to first suckling (min)	69.5	75.3	NS
Total licking time (min)	41.9	44.3	NS
First lactation (single suckling, mean calf age : 28 days)			
Number of cows	21	18	
Suckling time of their own calves (min/day)	23.3	27.0	P<.05
Cows suckled by alien calves (%)	50	10	P<.05
Second lactation (double suckling, mean calf age : 172 days)			
Number of cows	19	17	
Suckling time (own calf minus fostered calf, min/day)	11	27	P<.001
Growth (own calf-fostered calf, g/day)	169	399	P<.01
Licking time of the own calf (min/day)	2.3	7.2	P<.001
Licking time of cows (min/day)	.8	4.1	P<.001

* (variance analysis or Chi squared test)

Compared to Friesians, Salers cows interact more with the other members of the group, yet they are more selective in taking care of and suckling only their own calf. This difference is probably the result of different selection pressures that have been applied to these two breeds. Dairy cows have been selected for a high milking ability and an ability to become easily detached from their calves. On the contrary, it is still important for beef cows, and probably for the wild ancestors of dairy cows, to give milk to and care only for their own to ensure better fitness. This is attained by a very strong attachment to the young. The comparison between Salers and Friesians suggests that attachment is related to the high social motivation to interact with the other members of the group.

C. The maternal behaviour of different genotypes of sheep and the social reactivity of their lambs. Breed differences in maternal behaviour of sheep have been

described by several authors. For example, O'Connor *et al.* (1992) found differences in maternal behaviour between ewes from different breeds and concluded that those differences could be due to the litter size. Putu *et al.* (1988) found that Merino crosses with a Trangie strain selected for high fertility spent more time on the birth site than crosses with Booroola and AMS (Australian Merino Society) sheep. Poindron *et al.* (1984) observed ewes from different breeds indoors. They found that 60% of Romanov ewes had 'normal' maternal behaviour but only 34% of the ewes from two other breeds (Ile de France et Préalpes) had 'normal' behavioural patterns.

The experiment described here was designed to understand better the importance of the genetic variability on different components of the social behaviour of sheep, particularly on maternal traits. The experiment was located in the South of France. Four genotypes of ewes were observed in an extensive area: two purebreds, Romanov and Lacaune, and crosses between them. the Romanov is a highly prolific breed widely used to improve prolificacy in the French sheep population. When reared indoors those ewes have very good maternal behaviour compared to other French breeds (Poindron *et al.* 1984). The Lacaune is a breed from a dry region of the South of France mainly used for milking.

The ewes were observed just after lambing in their usual environment and during a specific test 24 hours later. At lambing, licking behaviour of the ewes was recorded for 15 minutes before any human interference. Then a human came close to the litter and the flight reaction of the ewe was recorded. The test was performed in a corridor (12.5m x 1.75m) about 24 hours after lambing. During that test, the lambs of the ewe were at one end of the corridor behind a grid and a human stood in front of the grid. We recorded the time spent close to the lambs and to the human, during a 4 minute period. The lambs were then removed and the number of high pitched bleats from the ewe were counted during a 4 minute period.

Before any disturbance the Romanovs licked their lambs more often than the Lacaunes (Table 2). They were also very disturbed after removal of the lamb. That confirmed the results of Poindron *et al.* (1985) that Romanov ewes take excellent care of their young. Despite this, these animals fled more often than the Lacaune when a human approached and stood further from their lambs when in the presence of a human than the Lacaune. The crossbreds were as maternal as the Romanov but did not appear to be as perturbed by humans.

Table 2. Behaviour of ewes from different genotypes after lambing

Genotype	Number of animals	Outside behaviour		Behaviour during test	
		Ewes licking their lambs (%)	Flight reaction to approach of a human (%)	Time spent close to human (sec)	high pitch bleats after removal of the lamb (n)
Romanov (RO)	21	96^{ac}	89^{a}	30^{a}	48^{a}
Lacaune (LA)	40	75^{b}	45^{b}	98^{bc}	33^{b}
LA x RO	11	100^{c}	70^{ab}	120^{b}	52^{a}
RO x LA	23	88^{ac}	68^{ab}	80^{c}	44^{ab}

^{abcd} Values in the same column with different superscripts are significantly different ($P<0.05$)

Lambs were also observed in this experiment. There was 8 genotypes, the four mother genotypes and the crossbred ewes from ewes from those four genotypes with Berrichon du Cher (BC) rams. The Berrichon du Cher is a French meat breed often used for terminal crossings. The experimental schedule was designed to estimate the direct effects of the breed, the maternal effect and the direct and maternal heterosis. Lambs were observed about two weeks after weaning in three different tests. In the first, they were isolated in a pen (4m x 6m) for four minutes. In the second, they were in the same room but could see 3 cohorts behind a grid with a human standing in front of the grid. Those two types of tests had been previously used to compare different genotypes of ewe lambs (Le Neindre et *al.* 1993). In the third test, they were in a continuous, rectangular corridor (8.5 long, 4.5 wide) with a human walking around the corridor for 2 minutes observing the time that the lambs remained in the same straight part of the corridor as the human. Table 3 shows the number of squares crossed during the isolation test, the time spent in the zone close to the human and the number of contacts with the grid during the second test and the distance between the observer and the lamb in the third test. Genetic parameters have been estimated by variance analyses.

Romanov lambs moved less when isolated in a pen and spent less time close to the cohorts in the presence of a human than the Lacaune lambs. They tried to avoid human contact when in the corridor. They seems to be no less social than the Lacaune but very distressed in the presence of a human. In contrast, Berrichon du Cher crossbred lambs were very disturbed by social isolation but did not bother too much about humans.

Table 3. Behaviour of weaned lambs during different tests: estimates and significance levels (variance analyses)

Genotype	Number of animals	Isolation test	Test with cohorts and human		Corridor test
		Number of squares crossed (n)	Time spend in the human zone (s)	Contacts with the grid (n)	Time when the observer was close enough to see the lamb (s)
Romanov (RO)	117	31.4	24.6	1.0	10.8
Lacaune (LA)	140	36.7	38.8	1.2	16.0
LA x RO	137	33.0	31.1	0.9	14.4
RO x LA	89	38.5	29.9	1.2	13.5
BC x RO	77	39.9	36.8	3.6	12.4
BC x LA	129	39.6	53.0	3.8	17.6
BC x (LAxRO and ROxLA)	395	37.7	37.7	2.9	14.0
Standard error		14.2	25.9	3.8	7.2

Direct ROLA effects	-12.9 *p=.0001*	-12.9 *p=.0008*	NS	-4.2 *p=.0001*
BCRO	13.3 *p=.0004*	43.7 *p=.0001*	.6 *p=.0001*	6.3 *p=.0008*
BCLA	NS	NS	.5 p=.001	NS
Maternal effect	5.5 *p=.0004*	NS	NS	NS
Heterosis (i) direct	NS	NS	NS	NS
(ii) maternal	NS	-7.2 *p=.02*	-.4 *p=.007*	NS

A significant maternal effect was observed. Crossbred lambs reared by Romanovs behaved differently from those reared by Lacaunes. This is an important factor which has been reviewed by Avital and Jablonka (1994) and observed on other traits in sheep. Dwyers and Lawrence (1997) found a maternal effect on the general and grazing activities of lambs. We found no significant direct heterosis in these variables but there was a maternal heterosis in the variables in the second test.

If we consider the ewe and lamb results together, the breeds have very different social patterns. In particular, Romanovs are very maternal, are disturbed by proximity to humans but are not affected greatly by social contact with cohorts whereas Lacaunes are less maternal and social but do not attempt actively to avoid the presence of humans.

D. Selection on social traits in sheep and the influence on maternal abilities. Existing information shows that maternal traits and in other behavioural traits vary genetically. To analyse this variability further, a selection experiment was set up in Western Australia to develop divergent flocks based on their temperament and response to humans. As a first step, male and female lambs from a commercial flock were tested two weeks after weaning in two standardised environments. The first was an enclosed box (1.5m x 1.5m) in which the animal spent one minute. The number of general movements and loud vocalisations of the box was recorded as indicator of the animal's discomfort (Putu, 1990). In the second test, each animal was placed for 4 minutes in a pen, 7m long x 3m wide, with 6 unrelated lambs at one end behind a grid with an immobile human observer in front of the grid. Six zones were defined in the pen. The number of zones crossed during the test (TOTC), the total time spent in the zones and the mean distance from the human (TOTI), the box movements (BOX), and a subjective score of reaction (SCORE) were recorded. The repeatabilities of the measures were estimated by testing 264 of these animals when they were 2 years old. Repeatabilities were highly significant and ranged from 0.62 (SCORE and TOTC) to 0.72 (BOX).

In the second step, an index was calculated INDEX = 10 + (BOX(i) - BOX(x))/BOX(sd) + (TOTC(i) - TOTC(x))/TOTC(sd) to select the animals. 652 ewes were tested and divided in two groups of high and low indexes. Of about 400 male lambs 30 with high and low indices were selected and mated with ewes of the same extreme indices. The behaviour of the two groups of ewes was observed at lambing and the 822 lambs born from those animals were also tested after weaning, in the same way as their parents .

Table 4. Multivariate estimates of genetic parameters of the reactivity of sheep during two tests. Heritability estimates and their standard errors are on the diagonal with phenotypic variances above, and genotypic variances below

	TOTI	TOTC	BOX	SCORE
Time in zone and distance to human (TOTI)	*0.24±.07*	0.01	-0.08	0.40
Number of crossings of zones of arena (TOTC)	-0.47	*0.11±.06*	0.19	0.32
Measure of agitation (BOX)	-0.09	0.56	*0.22±.07*	0.10
Subjective score (SCORE)	0.57	0.40	0.38	*0.17±.07*
Phenotypic coefficient of variation (%)	22	53	62	38

The heritability estimates were moderate to low but as the phenotypic variations were moderate to high, efficient selection on those traits could be expected (Table 4). The phenotypic correlations between the variables were generally low but some of the genetic ones were moderate to high. The correlations between the variables suggest that TOTI and SCORE on one hand and TOTC and BOX on the other are probably under different genetic control.

The maternal behaviour of the two groups of selected ewes were observed at lambing. Excluding the mortality due to difficult lambings and stillborn lambs, the mortality of lambs that might have been influenced by behaviour was significantly higher for the highly temperamental animals (18% of 426 ewes) than for the calmer animals (6% of 405 ewes).

CONCLUSION

At least two components should be differentiated in maternal behaviour: the ability to take care of an offspring and selectivity. Maternal behaviour cannot be isolated from the other components of the social life of animals. Sociality is very strong in both cattle and sheep and both species have to interact with humans. Experience is important in the expression of these behaviours, but genetic variability is essential. As they are probably all linked, selection for one of these traits can have consequences for the other traits. For example, selecting for docility (Le Neindre *et al.* 1994), or low reactivity to handling, could decrease the expression of maternal behaviour traits. Such an hypothesis is currently being tested on Limousine cattle.

To understand animals better and to have more powerful selection tools, it is important to identify general components that can be selected independently. The tendency to react to novel changes in the environment, or emotional reactivity, (Boissy, 1995) is probably one of these components and sociality is another. For example, Mills and Faure (1992) selected quails for or against sociality and found that it can be selected independently of tonic immobility which is a measure of emotionality. There are undoubtedly other behavioural traits for which one could select and it will always be important when selecting for such behavioural traits to be sure that they do not have a negative impact on other traits. Identification of such traits could then make it possible to determine their genetic background as has already been done with "social cognition" in humans (Skuse *et al.* 1997).

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