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Original article

Factors of diversity of domestic behaviour in sheep

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Summary – An ethological test situation with stimuli that induce fear-motivated withdrawal reactions, such as isolation from the herd, presence of man, and change of feeding and locomotion routine, was used to measure domestic behaviour. The reactions of withdrawal from man in sheep of various breeds were reduced by increasing food motivation and vice versa. Withdrawal reactions decreased with ageing and the rate of decrease was higher with increasing food motivation. Interbreed comparisons involving 11 breeds have detected a breed specificity of behavioural variation in sheep. Lowly-specialized breeds are characterized by a large number (77.0–94.7%) of animals of the 'wild' class, with a high prevalence of man-withdrawal reaction and a low incidence of feeding reactions in the behavioural test. In highly-specialized commercial breeds, the range of behavioural diversity is wider and the number of animals in domesticated classes is larger, reaching, eg, 86.0% in the East-Friesian breed. It is hypothesized that the polymorphism of domestication-related behaviour in commercial breeds has developed under the influence of natural selection for adaption under stressful conditions of breeding under the control of man and selection for productivity.

sheep / behaviour / breed / domestication

Résumé – Facteurs de variation du comportement domestique chez le mouton. *Le comportement des animaux domestiqués se caractérise par une absence de réaction de retrait vis-à-vis de l'homme. Ce comportement est mesuré dans un test faisant appel à un conflit de motivation entre la réaction de peur induite par l'isolement du troupeau et la présence de l'homme, et la réaction d'approche vers une auge contenant de la nourriture. L'influence des facteurs d'environnement et la variabilité du comportement ont été étudiées chez 467 béliers et plus de 4 000 brebis appartenant à 11 races ovines. L'augmentation de la motivation alimentaire, soit par un jeûne de durée variable (12–14 h vs 2 h), soit en modifiant la valeur nutritionnelle de la nourriture présentée lors du test (avoine écrasée vs pellets d'herbe), réduit les réactions de retrait. Avec l'âge augmente également le nombre des animaux qui approchent de l'auge pour se nourrir en dépit de la présence de l'homme. Cette diminution des réponses d'évitement avec l'âge, étudiée chez la race Altaï entre 12 et 26 mois, est plus marquée lorsque la motivation alimentaire est plus grande. La comparaison de 11 races ovines montre de grandes variations dans le polymorphisme de ce comportement. Les races peu spécialisées se caractérisent par une*

grande proportion d'animaux « sauvages » qui ne s'approchent pas de la nourriture en présence de l'homme (77,0% pour la race de Mongolie à 94,7% pour la race Awassi). Chez les races commerciales spécialisées, la gamme de variation est plus importante et la proportion des animaux « domestiqués » atteint 86,0% dans la race de Frise orientale. Il est probable que ce polymorphisme du comportement caractéristique de la domestication s'est développé historiquement sous l'influence conjointe de la sélection pour l'adaptation aux stress liés aux conditions d'élevage imposées par l'homme et de la sélection pour la productivité.

ovin / comportement / race / domestication

INTRODUCTION

One of the principal results of domestication in animals is the hereditary alteration of fear-motivated defensive reactions towards man (Belyaev, 1969), which is considered as the main characteristic of domestic behaviour (Belyaev and Trut, 1964; Hale, 1969), together with the reorganization of regulatory neuroendocrine systems such as the hypothalamic–pituitary–adrenal system (Naumenko and Belyaev, 1981; Naumenko et al, 1987). These aspects of domestication were studied in breeding experiments of silver foxes (Belyaev and Trut, 1964; Belyaev, 1972, 1979; Trut, 1981, 1987), minks (Trapezov, 1987) and wild rats (Dygalo et al, 1986). Unlike these and other comparative investigations of wild and domesticated animals as well as those on domestication (Bogolyubsky, 1959; Boice, 1973; Baskin, 1976; Price, 1984), intraspecific studies of domestic behaviour diversity in species of productive animals, such as sheep, are practically absent.

An impulse to the development of this type of research has been the discovery of polymorphism in the domestic behaviour of sheep of the Altaian breed (Belyaev and Martynova, 1973). This has led to a number of studies on the phenotypic and genetic relationships between this behaviour and some characteristics of production in sheep of various breeds (Martynova et al, 1975; Kutz and Hazratculov, 1977; Toshchev, 1980; Liev, 1983; Yashunin and Svinchenko, 1984). However, in spite of the demonstrated polygenic inheritance of domestic behaviour in sheep (Stakan et al, 1976), the task of studying the motivational nature of this behaviour and the influence of environmental factors on its diversity has not been tackled in this work.

The heterogeneous motivation of domestic behaviour was clearly demonstrated in domesticated foxes, in that it includes not only the absence of man-withdrawal reactions, but also the appearance of a new trait of 'attachment and sociability' towards man (Belyaev and Trut, 1982; Vasilyeva, 1991). It also involves feeding reactions, including motor feeding reactions, which are known to be directed at the signal for manifestation of feeding activity in animals (Karpicke et al, 1977), in the development of defence behaviour in domesticated foxes. Taking into account the alimentary dependence upon man of domesticated animals and of those in the process of domestication (Price and King, 1968), one may think that the role of motivation for food can be found not only in the modulation of expression and variability of defense reactions during ontogenesis, but also in the polymorphism of genetically integrated feeding and defensive reactions to man in domestic animals of different species, including sheep. However, the possible role of feeding behaviour

and of farming factors that influence the variability of manifestation of man-withdrawal reactions, as well as ontogenetic and populational diversity of domestic behaviour in sheep remains unknown.

Breed genotype is an independent factor of diversity of feeding and fear-motivated man-withdrawal reactions in sheep (Kroiter and Akhatov, 1980; Romeyer and Bouissou, 1992). That is why the correlations of domestic behaviour with the live weight and wool yield found in some breeds (Belyaev and Martynova, 1973; Stakan, 1987) can point both to the existence of interbreed differences in this type of behaviour depending on productive characteristics and to the dependence of breed productivity level on behavioural polymorphism. Nevertheless, there have been no interbreed comparisons of domestic behaviour polymorphism in sheep.

The objective of the present work was to compare the influence of environmental factors on the reactions of withdrawal from man and on the polymorphism of domestic behaviour in sheep of different breeds.

MATERIALS AND METHODS

Animals and rearing conditions

Four hundred and sixty seven rams and 1617 ewes of the Soviet meat-and-wool breed at various ages were used for the study of the influence of environmental factors on the manifestation and diversity of withdrawal from man in sheep. The influence of time after feeding on the rate of age-dependent changes of this reaction was investigated on 30 coeval ewes of the Altaian fine-fleece breed.

Polymorphism of domestic behaviour was studied on 2783 ewes of 11 breeds, including the Altaian, Ascanian, Caucasian, North-East Bulgarian fine-fleece breeds, the White Starozagorskaya, East-Friesian, Black-head Pleven and improved Awassi milk breeds, the Ascanian type of polycarpous Karakul and pure-bred Karakul Astrakhan breeds, as well as the native Mongolian breed.

The sheep of the Soviet meat-and-wool and Altaian breeds were kept at the Experimental Farm of the Institute of Cytology and Genetics (Novosibirsk). The sheep of the North-East Bulgarian and White Starozagorskaya breeds were bred in the farm of the Institute of Animal Breeding and Livestock Raising (Stara Zagora, Bulgaria); the sheep of three other fine-fleece and three milk breeds were kept at the breeding farm of the Institute of Animal Breeding (Razgrad, Bulgaria). The sheep of the Ascanian type of polycarpous Karakul and pure-bred Karakul were in the breeding farm of the Institute of Animal Breeding of Steppe Regions (Ascania Nova, Ukraine). The sheep of the Mongolian breed were in the breeding farm of the Institute of Experimental Biology (Ulan-Ude, Buryat Republic).

Sheep breeding conditions were characterized by a high zootechnical level. In all the farms, lambs were reared together with their mothers until the age of 90–100 days. After weaning, ewes and rams were kept separately. All the experimental animals had ear marks (numbers), which made it possible to study their individual behaviour.

Experimental set-up

Estimation of reactions of withdrawal from man in sheep by the method of Belyaev and Martynova (1973) and its modification (Lankin, 1988) was carried out in the premises where the sheep were kept constantly during autumn, winter and spring. The device for estimation of this kind of behaviour consists of several joined stalls built of wooden sheets (1.0 × 4.0 m and 1.0 × 2.0 m) including:

(1) a large pre-testing cage for placing all the animals under study;

(2) a small pre-testing cage (4.0 × 4.0 m) for keeping 30–50 sheep;

(3) the test cage (4.0 × 4.0 m);

(4) a post-testing cage consisting of the remaining free space.

In one corner of the test cage is placed a trough with food for the simultaneous feeding of 10–12 sheep. Behind the trough, the experimenter stands and marks with a long-handled paint-brush the sheep that are eating the food.

The movement of sheep between the cages is done through a sheet gate (1.0 × 2.0 m).

Procedure

General

The technique to measure withdrawal reactions in sheep at different farms was the same. Testing was performed between 0900 and 1200 hours. For estimation of these reactions in 10–12 sheep in the test cage, 9–12 min are necessary. After completion of the test, the sheep are let out into the post-testing cage, and the next group is let into the test cage. The animals move from one cage to another spontaneously and the experimenter only controls the number of animals entering the test cage. In the original method, each animal was tested only once, while in the modified method each one is tested twice.

The experimental conditions minimize uncontrolled stress in sheep. This makes it possible to estimate the sheep behaviour in various farms without any preliminary habituation of animals to the experimental conditions. A necessary prerequisite is the habituation of the animals to being fed with concentrates.

Behavioural tests

The two behavioural tests used (Belyaev and Martynova, 1973; Lankin, 1988) involve mild stressful situations that enhance the phenotypic manifestations of the withdrawal reactions of sheep, such as: (a) isolation of 10–12 animals from the flock during the time of behavioural testing, (b) presence of a man who moves during testing along the trough and touches the sheep with a paint-brush stained with a dye, (c) disturbance of the feeding and gregarious behaviour routines provoked by the two former stimuli.

The experimenter's actions and the behaviour of the sheep in the test cage can be observed by those sheep who are in the second pre-testing cage through wide slits between the wooden sheets.

Original method

Experiments (Belyaev and Martynova, 1973) were carried out in hungry sheep 12–14 h after the evening feeding. For this, all the sheep were driven into the first pre-testing cage and 40–50 sheep were let into the second cage. Into the test cage, 10–12 animals were admitted by the experimenter. Being seen by the sheep, he put food (the feeding stimulus) into the trough and, while remaining behind the trough, stained the sheep that were eating the food with the paint-brush. During the first 3–4 min, he made the first marks on the heads of the animals. During the next 6–9 min, he put the second marks on the back of the sheep, and in the last 9–12 min of testing he put the third marks on the rear backs of animals eating at the trough. As a result, the sheep that had approached the food only once received one staining mark, those who ate during 6–9 min received two marks, and the sheep who ate during the whole feeding time received three marks.

This test was used for the study of the influence of motivation for food and age on the manifestation and variability of withdrawal reactions.

Modification of the original method

In the modified method (Lankin, 1988), the influence of the feeding drive level on the withdrawal reactions in sheep was taken into account. For this, the animals were tested twice: first, these reactions were estimated 12–14 h after feeding and, 3–4 days later, they were tested 2 h after feeding, ie, in animals with a lowered, but not completely absent, feeding motivation (Mamedov, 1958; Segal, 1977). During the second testing, the marks were made with a dye of different colour. The technique was the same as in the original method.

The modified method was used for the study of domestic behaviour variation in sheep of different breeds.

Behavioural records and analysis

Reading of stain marks for all the animals involved in an experiment was performed after completion of the given experiment. The ear number and the number of stain marks of different colours were recorded for each animal.

In the method of Belyaev and Martynova (1973), the number of marks varying from 0 to 3 is the estimate of withdrawal reactions from man expressed in scores. Sheep with a score of 3 are characterized by an absence of withdrawal reaction and represent the most domesticated animals in the flock. These sheep are usually among the heading animals and are the first ones to enter the test cage. Sheeps with a score of 0 show pronounced withdrawal reactions and are represented by the most fearful animals in the flock. During testing, they do not approach food. Sheep with scores of 1 and 2 have a withdrawal reaction intermediate between the above-mentioned types of animals.

In the modified method (Lankin, 1988), behaviour estimates are comprehensive, since they include the score obtained by the animal 12–14 h and again 2 h after feeding. The method makes it possible to distinguish 16 discrete behavioural classes: 3–3, 3–2, 3–1, 3–0, 2–3, 2–2, 2–1, 2–0, 1–3, 1–2, 1–1, 1–0, 0–3, 0–2, 0–1 and 0–0. These estimates reflect the influence of the feeding motivation level on the

manifestations of the withdrawal reaction and can be divided, depending on the character of their change, into three groups. Group 1 includes animals of the 'normal' classes 3–2, 3–1, 3–0, 2–1, 2–0 and 1–0, in which the decrease of the feeding motivation enhances the withdrawal reaction. The second group includes the sheep of the 'stable' classes 3–3, 2–2, 1–1 and 0–0, with a consistent manifestation of the withdrawal reaction independent of changes in their feeding motivation. The third group includes the animals of 'paradoxical' classes 2–3, 1–3, 1–2, 0–3, 0–2 and 0–1 differing in the character of 'conditioned reflectory switch-over' (Asratian, 1951, 1983) of the order of manifestation of feeding and defence reactions to man during the behavioural testing.

Protocols to study the factors of variation

Repeatability of behavioural scores

To estimate the repeatability of the behavioural scores, the same sheep were tested four times consecutively. First, their withdrawal reactions were tested 12–14 h after feeding, and 3 days later, 2 h after feeding. After 10 days, testing was repeated both 12–14 h and 2 h after feeding, with a 3-day interval. The correlation among individual behavioural estimates determined in each of the four tests was studied. In addition, the correlation between the comprehensive estimates obtained by the tests repeated with the interval of 10 days was estimated.

In all these tests, oats were used as the feeding stimulus. In each test, marks were made with a different dye.

Environmental influences

The influence of environmental factors, such as time after feeding or food type used as the feeding stimulus on the man-withdrawal reactions, was investigated. It is known that increasing the time after feeding or the caloric content of food enhances, whereas reducing time after feeding or caloric content of food reduces the feeding motivation in cows and sheep (Khrenov, 1965; Pyanov, 1975; Hutson and Maurik, 1981). That is why, for estimation of the influence of motivation for food on withdrawal reactions, manifestation and diversity of these reactions were observed in sheep 12–14, 7, 2 and 1 h after feeding. In addition as the feeding stimulus, either oats or grass granulates were used, which differ considerably in the caloric content (Modyanov, 1978). Irrespective of the kind of food, the feeding stimulus was always given ad libitum during testing.

Age

Beginning from the post-weaning age, and until the age of 60 months, withdrawal reactions were estimated in meat-and-wool sheep both 12–14 h and 2 h after feeding.

The influence of motivation for food on the rate of age-dependent changes in withdrawal reactions was also investigated in sheep of the Altaian breed which had, at the age of 12 months, zero behavioural scores both 12–14 h and 2 h after feeding. In these sheep, the withdrawal reactions were measured at the age of 12, 20, 26 and 40 months.

Statistical evaluation

Distribution of sheep with respect to behavioural scores and classes was compared by means of chi-square test (Rokitski, 1978). Coefficients of correlation between behavioural scores in repeated testings were also calculated (Snedecor and Cochran, 1967).

RESULTS

The influence of food motivation

The reduction of feeding motivation by shortening the time after feeding influences significantly both the manifestation and the population variability of withdrawal reactions in 1-year old sheep (table I). As compared to the 12–14 h interval, testing 2 h after feeding resulted in an enhancement of expression of withdrawal reactions and a change of population distribution with respect to behavioural scores (behavioural structure of the flock) in rams ($\chi^2 = 52.7$, $P < 0.001$) and ewes ($\chi^2 = 15.8$, $P < 0.01$).

Table I. Influence of the time after feeding on manifestation and variation of withdrawal from man in meat-and-wool sheep at the age of 12–13 months.

Sex (number of animals)	*Time after feeding (h)*	*Distribution by behavioural scores (%)*				*Comparison of distributions*	
		0	*1*	*2*	*3*	χ^2	P
	12–14	15	10	23	52		
						3.8	ns
males	7–8	8	7	26	60		
						37.5	0.001
(121)	2	51	8	10	31		
						7.9	0.05
	1	51	19	5	25		
	12–14	29	20	12	39		
						2.6	ns
females	7–8	29	11	14	46		
						13.2	0.01
(373)	2	43	16	10	31		
						79.1	0.001
	1	74	8	2	16		

The negative correlation between food motivation and withdrawal reactions in rams and ewes was confirmed by shortening the time after feeding to 1 h (table I). On the other hand, shortening the time after feeding to 7–8 h did not increase the manifestation of withdrawal reactions in these sheep, as compared to the

12–14 h interval. Probably, when the test occurred 7–8 h after the morning meal, it coincided with the usual time of the evening meal and evoked a manifestation of routine feeding behaviour, which inhibited the reactions of withdrawal from man.

The influence of decreased food motivation on defensive reactions is sex-dependent. A comparison of distributions by behavioural scores shows that, with the exception of testing 2 h after feeding ($\chi^2 = 5.4$, $P > 0.05$), testing 12–14 h ($\chi^2 = 23.8$, $P < 0.001$), 7–8 h ($\chi^2 = 28.9$, $P < 0.001$) and 1 h ($\chi^2 = 24.2$, $P < 0.001$) after feeding resulted in a more pronounced enhancement of manifestation of defensive reactions in ewes than in rams.

Reduction of the caloric content of food influences significantly the manifestation and population diversity of withdrawal reactions in rams (table II). The use of grass pellets instead of oats, when testing 12–14 h after feeding, enhanced the withdrawal reactions. The combination of factors (shortening of the time after feeding to 2 h and use of grass pellets) resulted in an increase in the number of rams with scores of 0 from 20 to 72% ($P < 0.001$) and in a more than four-fold decrease in the number of calm rams with a score of 3. The clear-cut additivity of the effects of these feeding factors points to the dependence of the manifestation of withdrawal reactions on the changes of food motivation in sheep.

Table II. Influence of the time after feeding and the kind of food stimulus on manifestation and variation of withdrawal from man in meat-and-wool rams ($n = 123$) at the age of 12–13 months.

Time after feeding (h)	*Food stimulus*	*Distribution by behavioural scores (%)*				*Comparison of distributions*	
		0	*1*	*2*	*3*	χ^2	P
12–14	oats	20	16	12	52		
12–14	grass pellets	37	19	18	26	18.3	0.001
2	oats	38	20	14	28	2.1	ns
2	grass pellets	72	13	4	11	30.9	0.001

Age

The regulatory influence of food motivation on withdrawal reactions from man can also be found in age-dependent changes of this behaviour in sheep. In meat-and-wool ewes there is an age-dependent decrease of withdrawal reactions and enhancement of feeding reactions. From the age of 3–4 months to 12 months, the number of ewes with a score of 0 when tested 12–14 h after feeding decreased from 35 to 23% ($P < 0.001$), and when tested 2 h after feeding, from 58 to 32% ($P < 0.001$) (table III). Therein, the number of ewes with a score of 3 increased from 34 and 12% to 45 and 30%, 12–14 h and 2 h after feeding, respectively. However, unlike the ewes, the number of rams with a score of 0 remained unchanged during this period of ontogenesis. It also turned out that in 1-year old animals, withdrawal and feeding reactions do not depend on the sex of the sheep (table III).

Table III. Influence of age and of time after feeding on manifestation and variation of withdrawal from man in meat-and-wool ewes.

Age, months gender (number of animals)	*Time after feeding (h)*	*Distribution by behavioural scores (%)*				*Comparison of distributions*	
		0	*1*	*2*	*3*	χ^2	P
3–4							
ewes	12–14	35	17	14	34	172.4	0.001
(800)	2	58	20	10	12		
rams	12–14	23	26	18	33	14.4	0.01
(223)	2	35	20	20	25		
7–8							
ewes	12–14	26	21	16	37	9.4	0.001
(709)	2	36	22	10	32		
rams	12–14	22	25	16	36	17.4	0.001
(200)	2	38	14	10	38		
12–13							
ewes	12–14	23	19	13	45	5.6	0.05
(717)	2	32	20	12	36		
rams	12–14	23	17	8	52	5.2	0.05
(196)	2	36	16	6	42		
36							
ewes	12–14	22	12	13	53	1.7	ns
(90)	2	26	14	8	52		
60							
ewes	12–14	13	9	8	70	2.2	–
(96)	2	19	10	4	67		

In meat-and-wool ewes, further changes with increasing age were of smaller magnitude (table III). At the age of 36 months, the number of sheep with a behavioural score of 3 when estimated 12–14 h and 2 h after feeding increased from 45 and 36% to 53 and 52% ($P < 0.05$), respectively. On the whole, from the age of 3–4 to 60 months, the number of ewes with a score of 0 decreased by 22 and 39% ($P < 0.001$), and the number of ewes with a score of 3 increased by 36 and 55% ($P < 0.001$), respectively.

Food motivation and age

The significant dependence of the decrease of withdrawal reactions on food motivation found in meat-and-wool sheep before 12 months of age (tables III and IV) prompted us to study in more detail the influence of this factor on the rate of age-dependent changes of these reactions.

In ewes of the Altai breed, who had at 12 months a behavioural score of 0, it was found that the age-dependent formation of adaptive phenotype at the period of 12–40 months also depends significantly on the level of food motivation (table IV). It

Table IV. Influence of time after feeding on the age-related extinction of reaction of withdrawal from man in ewes of the Altai fine-fleece breed, with a score of 0 at 12 months of age.

Age, months (*number of animals*)	*Time after feeding* (*h*)	*Distribution by behavioural scores* (*%*)				*Comparison of distributions*	
		0	*1*	*2*	*3*	χ^2	P
12	12–14	100	0	0	0		
(30)	2	100	0	0	0		
20	12–14	4	20	44	32		
(25)	2	92	4	0	4	39.3	0.001
26	12–14	0	8	24	68		
(25)	2	48	20	16	16	21.7	0.001
40	12–14	0	13	5	82		
(22)	2	27	23	0	50	9.2	0.05

turned out that the rate of decrease of withdrawal reactions with age, as estimated by the increment in the number of sheep that acquire with age a behavioural score of 3 when tested 12–14 h after feeding, was higher (during the period 12–20 months by 28% ($P < 0.001$), and during the period 20–26 months, by 24% ($P < 0.001$)) than the increment for sheep at the same age periods when tested 2 h after feeding (table III). It is only from the age of 26 months (ie, after the completion of formation of adaptive behavioural phenotype to 82% in sheep with a high food motivation) that the rate of age-related reaction decrease became higher (by 20%) in sheep with a low food motivation (tested 2 h after feeding).

These data demonstrate that food motivation and its interaction with farming factors is one of the mechanisms of environmental control of both manifestation and ontogenetic variability of the withdrawal reaction. An elevated level of food motivation not only inhibits the manifestation of such reactions, but is also positively correlated with a high rate of age-dependent decline of withdrawal reactions from man in sheep.

Repeatability of withdrawal reactions

The repeatability of estimates of withdrawal reactions also depends on the level of food motivation. So, estimates of behaviour obtained 12–14 h after feeding are 62% repeatable, whereas estimates of withdrawal reactions obtained 2 h after feeding are 79% repeatable (table V).

Comprehensive estimates of behaviour take into account both the influence of the environment and of food motivation on withdrawal reactions and are therefore not only more representative, but also well repeatable (table VI). These properties of comprehensive estimates demonstrate the objectivity of the proposed method of detection and measure of population variability of coupled feeding and withdrawal reactions that compose the domestic behaviour in sheep (Lankin, 1988).

Table V. Repeatability of individual scores of withdrawal reactions in meat-and-wool ewes at the age of 12 months, studied in 444 animals.

Tests considered	*(Time after feeding, h)*	*Coefficient of correlation between behavioural scores in different tests*
1–2	(12–14) – (2)	0.56*
2–3	(2) – (12–14)	0.63*
3–4	(12-14) – (2)	0.53*
1–3	(12-14) – (12–14)	0.62*
1–4	(12-14) – (2)	0.52*
2–4	(2) – (2)	0.79*

* $P < 0.001$.

Table VI. Repeatability of comprehensive estimates of behaviour in meat-and-wool ewes at the age of 12 months, studied in 443 animals.

Behavioural classes	*Coefficient of correlation between behavioural scores in repeated tests*	*Proportion of animals in each class (%)*
all 16 classes	0.73 ± 0.02*	100.0
10 'normal' and 'stable' classes	0.74 ± 0.02*	90.3
4 'stable' classes	0.88 ± 0.03*	62.3
6 'paradoxical' classes	0.54 ± 0.11*	9.7

* $P < 0.001$.

Interbreed diversity of domestic behaviour

With the exception of the Ascanian and Caucasian fine-fleece breeds, the population structure with respect to domestic behaviour in ewes is significantly different among the 11 breeds studied (table VII). This character is also significantly different between the Black-headed Pleven and the polycarpous Karakul breeds ($\chi^2 = 18.30$, $P < 0.01$), improved Awassi and Mongolian ($\chi^2 = 25.3$, $P < 0.001$), Ascanian and North-Eastern Bulgarian ($\chi^2 = 13.2$, $P < 0.05$) breeds.

A distinctive character of behavioural polymorphism in low-specialized breeds such as the Mongolian and Awassi (Esaulov and Litovchenko, 1963; Khinkovski et al, 1979) is the low intrabreed variability of behaviour and prevalence of 'wild' class 0–0 animals. The number of animals of the 0–0 class is as large as 77 and 94% in these breeds and decreases to 3% in the East-Friesian breed. Opposite to this is the variation of 'domestic' classes 3–3, 3–2, 3–1 and 3–0 characterized by prevalence of feeding reactions over the reactions of withdrawal from man. Characteristic of commercial breeds such as the Altaian and East-Friesian is the extension of the diversity range which includes the class 3–3 and the increase in the number

Table VII. Variation of domesticated behaviour in different sheep breeds (at the age of 16–18 months.

Breed, number of animals	*Distribution (%) by classes*				
	3–3	*3–2, 3–1 3–0*	*2–2, 2–1, 2–0 1–1, 1–0*	*0–1, 0–2, 0–3 1–2, 1–3, 2–3*	*0–0*
East-Friesian, 201	20.0	66.0	10.5	0.5	3.0
Pleven, 309	28.0	3.0	27.0	7.0	36.0
Askanian, 242	2.0	25.0	16.0	3.0	54.0
Altaian, 356	17.0	9.0	35.0	2.0	37.0
Caucasian, 255	0.0	26.0	23.0	1.0	50.0
North-East Bulgarian, 262	4.0	16.0	18.0	1.0	61.0
Starozagorskaya, 84	7.0	12.0	34.0	6.0	41.0
Polycarpous Karakul, 160	14.0	5.0	17.0	4.0	60.0
Karakul, 493	3.5	12.4	6.8	6.0	71.3
Mongolian, 110	0.0	5.0	18.0	0.0	77.0
Awassi, 206	0.0	2.4	2.4	0.5	94.7

of animals in classes characteristic of domestic behaviour. Taking the number of animals in the 'domestic' classes (3–X) as the criterion of interbreed differences, it is possible to estimate the behavioural rank of breeds in the following decreasing order: East-Friesian, Pleven Black-head, Askanian, Altaian, Caucasian, North-Eastern Bulgarian, Starozagorskaya, Polycarpous Karakul, Karakul, Mongolian and improved Awassi (table VII). The number of sheep of these classes was maximal (86%) in the East-Friesian breed.

The significance of differences in the breed structure with respect to domestic behaviour points to breed specificity of behavioural polymorphism and to the dependence of interbreed and intrabreed diversity on breed genotype.

DISCUSSION

The data obtained in the present experiments point to the existence of a negative relationship between the food motivation level and the manifestation of withdrawal reactions from man in sheep of various breeds. Indeed, a reduction of time after feeding and of food caloricity, which lower the food motivation in sheep (Pyanov, 1975), brought about an enhancement of withdrawal reactions in rams and ewes of meat-and-wool and Altaian breeds. Conversely, an enhancement of food motivation by increasing the time after feeding or food caloricity resulted in a reduced manifestation of withdrawal reaction in these sheep (tables I, II, V). The negative dependence of withdrawal reactions on food motivation points to the existence of a negative relationship between feeding and passive-defensive (or withdrawal) reactions in sheep, which exists also in other animal species (Kozlovskaya, 1974; Petryaevskaya and Andreev, 1974; Hind,1975; Lozovskaya and Kassil, 1977; Shephard et al, 1985). It is also noteworthy that data from electrophysiological and neuropharmacological experiments have demonstrated the existence of antagonistic

reciprocal relations between hypothalamic centres of control of feeding and defensive behaviour in laboratory animals (Kalyuzhny, 1962, 1964; Kozlovskaya, 1967).

The effect of such a physiological relationship on the manifestation of coupled feeding and withdrawal reactions in sheep is probably limited by the age of the animals and depends on the breed. So, it turns out that in ewes of the meat-and-wool breed, from the age of 22–24 months, the manifestation of the withdrawal reaction does not depend on changes at the level of food motivation (table III). On the other hand, the modulating influences of food motivation on the manifestation of withdrawal reactions in ewes of class 0–0 of the Altaian breed were clearly expressed at 40 months of age (table IV).

At the same time, the data obtained show that the manifestation and population variability of withdrawal reactions in sheep are under the influence of farming factors which affect their feeding behaviour. Depending on the changes in food motivation which they provoke, these widespread factors may be divided into: (a) those enhancing the withdrawal reactions in sheep when their food motivation decreases due to shortening of the time after feeding, reduction of caloricity, worsening of food taste, or during pasture (Pyanov, 1975; Hutson and Maurik, 1981), and (b) those decreasing the withdrawal reactions when the food motivation is enhanced. The effectiveness of modulatory influences of food motivation on the manifestation and variability of withdrawal reactions permits one to suppose that food motivation may play the key role in the environmental control of variation of negatively correlated feeding and withdrawal reactions to man in sheep.

Finding a regulatory interdependence between food motivation and withdrawal reactions demonstrates that domestic behaviour in sheep has a two-factor motivational basis. However, one may think that this conclusion is the result of the method of estimating the behaviour, which includes the effect of the feeding stimulus in combination with the presence of man (Belyaev and Martynova, 1973; Lankin, 1988), who induces fear in them (Leopold, 1944; Krushinsky, 1991). From this point of view, the involvement of feeding motivation in the modulation of instinctive withdrawal reactions in sheep is not typical of domestic behaviour, which is usually considered as unitary fear reactions to man in animals of various species (Belyaev and Trut, 1964; Belyaev and Martynova, 1973; Romeyer and Bouissou, 1992). Nevertheless, the plausibility of the concept of two-factor motivational nature of domestic behaviour is corroborated by the opinion of Manteufel (1987), who believed that behaviour of wild animals in interspecies contacts is determined by an interaction of defensive (D) and feeding (F) reactions. If the mutual proportion of these factors in normal conditions is 1 ($D/F = 1$), it becomes less than one as the feeding motivation is enhanced ($D/F << 1$) and it exceeds unity ($D/F >> 1$) during danger. It follows from this notion that: (1) domestic behaviour, as a typical form of interspecific activity (McBride, 1984), has a heterogeneous motivational determination, and (2) there exists a physiological regulatory relationship between defensive and feeding reactions that compose this kind of behaviour. The correctness of these deductions is confirmed by our own data and by results from the literature previously cited. All this confirms the objectiveness of the detection and description of mutually related withdrawal and feeding reactions in sheep as carried out in this work, but their role in domestication of animals of other species remains unstudied.

The heterogeneous motivation of domestic behaviour was clearly manifested in silver foxes in the process of breeding for absence of withdrawal reactions from man (Belyaev and Trut, 1982; Vasilyeva, 1991). This domestication phenomenon, that has not been explained so far, clearly demonstrates that the nature of the behaviour of domestic animals towards man remains obscure, as well as the laws of diversity and evolution of animal behaviour in domestication.

Our data point to the level of feeding motivation being an independent factor of control of the rate of age-dependent modification of withdrawal reactions in sheep (table III). At the same time, the common direction of development of adaptive domestic behaviour in different breeds presupposes the existence of a universal physiological mechanism of ontogenetic inhibition of fear of man in animals. It is possible that such a mechanism may be the age-dependent enhancement of feeding drive caused by animal growth and development of productive properties, pregnancy and lactation (Aminov, 1956; Modyanov, 1978), which inhibits the manifestation of withdrawal reactions in older sheep. This process can be supplemented by feeding motivation-dependent development of positive conditioned reflexes to stimuli associated with feeding, including man as a key stimulus in controlled feeding, which also inhibits the manifestations of fear reactions in animals (Sudakov, 1971; Karpicke, 1978; Hutson, 1985; Grandin, 1989; Vasilyeva, 1991).

The laws of ontogenetic variation of domestic behaviour in sheep can be expressed in the following hypothetical diagram (fig 1). The diagram takes into account the existence of ten basic behavioural classes representing more than 90% of animals in the population (table VI). The arrows indicate the most probable age-dependent changes of phenotypes determined by: (a) a common direction of development of adaptive behavioural phenotypes and (b) a higher rate of extinction of withdrawal reactions in sheep with high feeding motivation (when tested 12–14 h after feeding, horizontal arrows) than in those with lowered feeding motivation (when tested 2 h after feeding, vertical arrows). The rank values corresponding to the more probable age-dependent phenotype changes reflect at the same time the increase in the 'share' of feeding reactions and decrease in the 'share' of withdrawal reactions in the behavioural phenotype.

As a result of realization of the above-mentioned age pattern, it is found that there exists an organized ontogenetic and populational diversity of domestic behaviour. It is characterized by the absence of simple linear relationships between behavioural phenotypes, there being a special discreteness of classes 0–0, 1–1, 2–2 and 3–3. Direct age-characteristic transitions between these classes, that require a simultaneous increase of the first and the second values of the comprehensive behaviour estimate, turn out to be 'forbidden'. The diagram points to the existence of an environmental control of behaviour which brings about an age-dependent modification of the 'wild' 0–0 phenotype into its opposite domestic phenotype 3–3, with respect to the state of feeding and withdrawal reactions.

The data obtained, that point to the obligatory involvement of feeding reactions in the modulation of withdrawal from man in sheep, show at the same time the necessity of taking into account the ecological significance of man as a signal for the

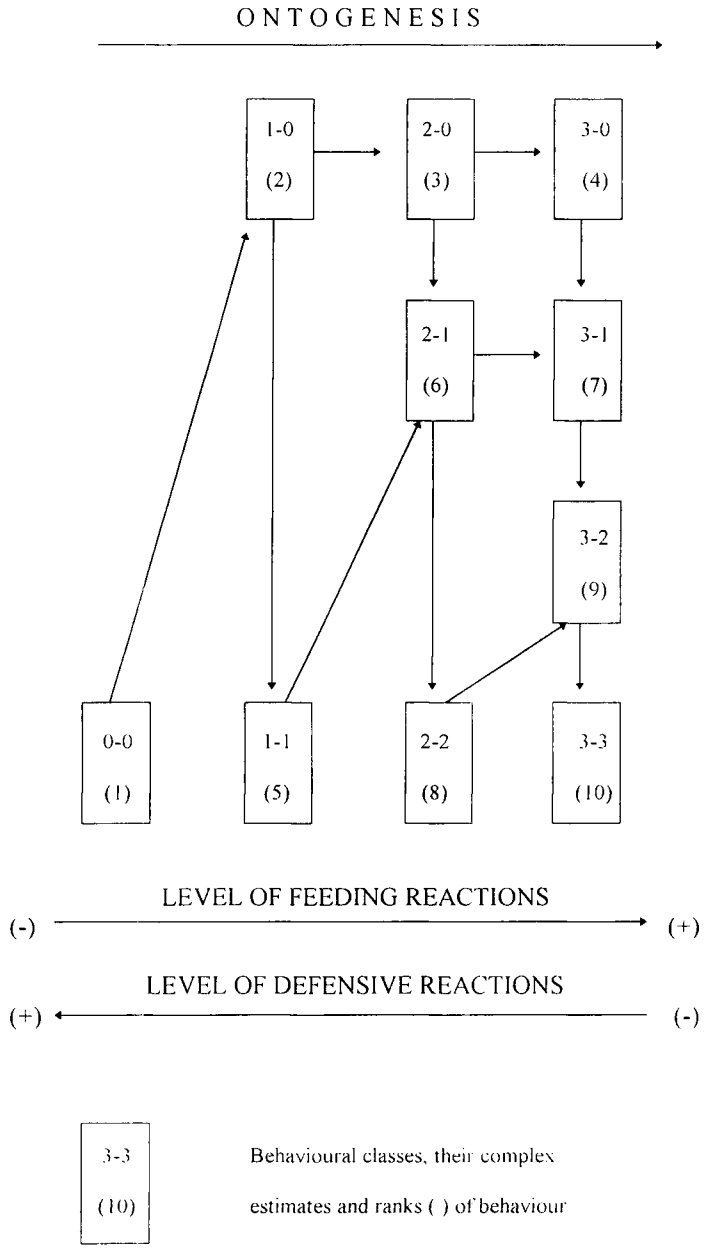

Fig 1. Organized ontogenetic and population diversity of domestic behaviour.

manifestation in domestic animals not only of fear, but also of feeding reactions. In this connection, one may suppose that the bisignal ecological significance of man is a unique property that arose from the first stage of domestication as a consequence of a new 'domestic' feeding chain of animals which made them dependent on man to the degree of possible starving (Kislovsky, 1937; Bogdanov, 1977). Having created an artificial feeding chain which has rigidly attached the animals' defensive and feeding reactions towards man, the latter has created a new 'domestication' vector of natural selection acting on the adaptation of animals to stressful man-controlled conditions of feeding and keeping. Under these conditions, the effectiveness of ontogenetic and evolutionary adaptations of behaviour could be determined by the above-mentioned patterns of physiological interaction between feeding reactions and the fear of animals towards man, who was transformed into a constant ecological signal for a combined manifestation of these heterogeneous behavioural activities in domestic animals and animals in the process of domestication.

The specificity of breed structure with respect to the domestic behaviour that was found and the differences in characteristics between lowly-specialized and commercial breeds make it possible to put forward some hypotheses on evolutionary factors of development of polymorphism of this behaviour in domestic sheep (fig 1).

The common direction of the ontogenetic and interbreed variation of domestic behaviour points to the existing pressure of selection for fitness (Kislovsky, 1937; Lobashov, 1955; Mair, 1968) of sheep to farming conditions including the 'domestication' vector of selection for absence of withdrawal from man and enhancement of feed-motivated approach to man in these animals. However, it has been directed to the opposite direction of the vector of selection by negative environmental factors that have been dominant by their intensity under primitive farming conditions (Price and King, 1968) thus 'protecting' the 'wild' behavioural phenotype in low-specialization breeds (such as Mongolian and Awassi shown in fig 2). An evolutionary result of the disruptive action of these vectors of natural selection could have been the development of ecological polymorphism with respect to a complex of coupled viability and fitness characteristics (Mettler and Gregg, 1972), including defensive and feeding behaviour, in domestic sheep.

At the same time, the increased number of more adaptive and more productive sheep of domesticated classes (Belyaev and Martynova, 1973; Stakan, 1987) in commercial breeds suggests that their behavioural structure has been formed under the influence of coinciding selection (Schmalhausen, 1940): the domestication vector of natural selection and selection for productivity (such as Altaian and East-Friesian shown in fig 2). The influence of these selection vectors on adaptation to increasing pressure of stressful 'domestication' conditions (Kislovsky, 1937, 1965; Ovsyannikov, 1969; Belyaev, 1983) must have resulted in the formation of the behavioural polymorphism characteristic of commercial breeds. It is possible that the effect of this form of selection has reached its 'limit' result in the historically ancient East-Friesian breed conspicuous with its productivity and characterized not only by the very low incidence of the 'wild' 0–0 class, but also by the loss of gregarious behaviour (Maimone et al, 1965; Novitsky, 1981).

The proposed hypothesis of development of ecological behavioural polymorphism in commercial breeds assumes logically that the domestic behaviour may be an integral character of general fitness that 'marks' physiological and morphophysiolog-

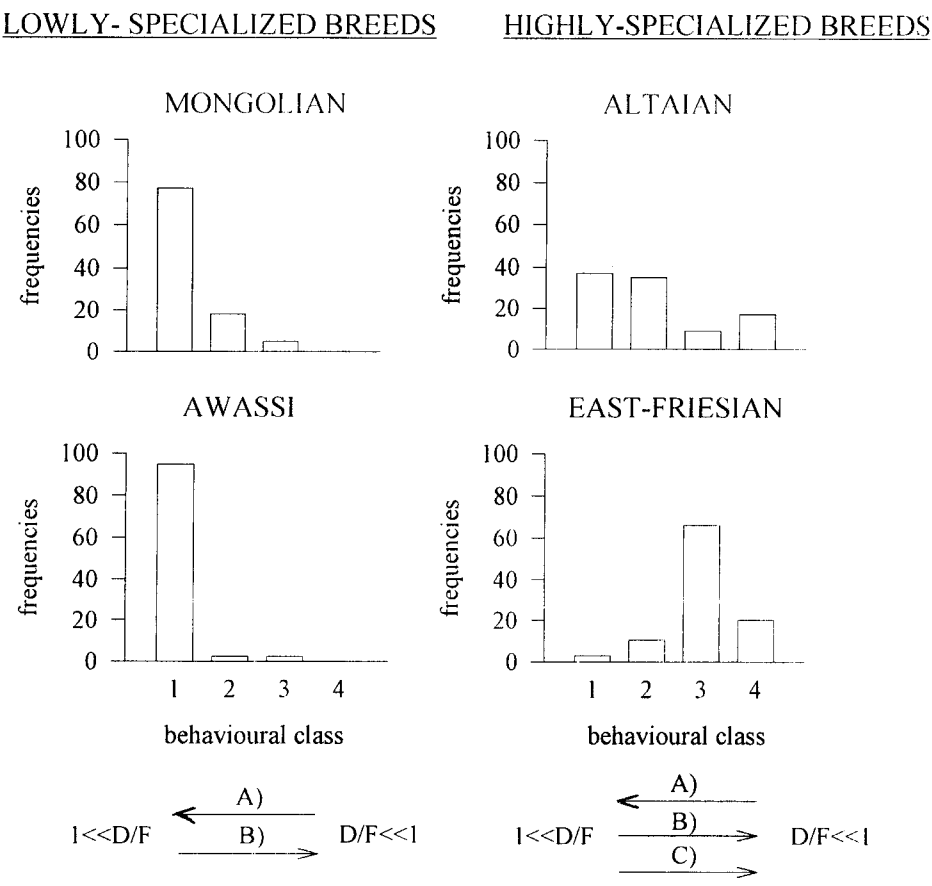

Fig 2. Structure of lowly-specialized and highly-specialized breeds with respect to domestic behaviour, and factors forming the behavioural polymorphism in domestic sheep. Behavioural classes: (1) animals with a 0–0 score; (2) 2–2, 2–1, 2–0, 1–1 and 1–0 scores; (3) 3–2, 3–1, 3–0 scores; (4) 3–3 score. D/F, defensive to feeding reactions ratio. (A) Selection by negative natural factors: food deficit, cold, all-year-round pasture keeping; (B) selection by 'domestication' environmental factors: stress induced by contact with man, population and 'technological' stresses, controlled feeding and breeding; (C) selection for productivity.

ical features coupled with it and determines viability and adaptation in domestic sheep. In this case, the domestic behaviour may be a factor controlling the range of intrabreed diversity of the complex of coupled adaptive physiological and productive characteristics that compose the 'constitutional type' of animals, and the behavioural structure of breeds being a specific trait of adaptability and productivity level. It is to elucidate these sequences of the hypothesis having directly to do with solution of questions of controlling the adaptiveness in productive animals that our following experiments are directed.

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