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Frontier disputes between the West- and East-European house mouse in Schleswig-Holstein, West Germany

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Abstract

In the framework of a comparative behaviour study of the house mice *Mus m. domesticus* and *Mus m. musculus* mice were trapped in East Holstein (W. Germany), through which the borderline between the areas of both subspecies could be established rather accurately: viz, leading from Plön to Lütjenburg. In the laboratory a behavioural study was performed with descendants of these mice, as well as with descendants of *domesticus* and *musculus* mice caught in Holland respectively Poland. No clear or systematic differences were found in their way of life, in their exploratory and social behaviour, with the exception of a difference in tolerance between adult males. The aggressive behaviour of dominant males led in *domesticus* to a higher mortality among subordinate males than in *musculus*. In confrontations between male *domesticus* and *musculus* the heavier *domesticus* males always became the winners. This result may explain the shift of the borderline between both subspecies in an eastward direction.

Introduction

The borderline between the areas of the West-European (*Mus musculus domesticus* Rutty) and East-European house mouse (*Mus musculus musculus* L.) goes right across Europe, from Denmark to the Adriatic Sea (see Fig. 83 in REICHSTEIN 1978). In all probability both subspecies have spread over Europe mainly in connection to the spreading of the human grain cultures: *domesticus* via North Africa and Spain over western Europe, *musculus* (as a split off of *spicilegus*) from the South East over Central and East Europe (FREYE and FREYE 1960; SCHWARZ and SCHWARZ 1943; ZIMMERMANN 1949). Presumably about 3000 B. C. (see below) *domesticus* and *musculus* met each other, and since then there has been a zone of contact between both subspecies. Not much is known concerning the exact position of this zone through the ages. HUNT and SELANDER (1973), who made an extensive investigation of allozyme-frequencies in *domesticus* and *musculus* populations at both sides of their border line in Jütland (Denmark), supposed that this border had been located much more westerly ("several hundred miles") in earlier times. Their assumption is based on an article of WATERBOLK (1968) about (among other things) the spreading of the farming cultures in prehistoric Europe. According to WATERBOLK these cultures are of twofold origin: on one hand the "Danube" cultures which spread over Central and East Europa via the Balkan, and on the other hand the "West-Mediterranean" cultures which dispersed from the South-West over western Europe. About 3000 B. C. these western and Danube cultures should have made contact, presumably in an area extending from the French Alps to the North Sea. However, not much can be said about the question where the principal regions of contact were: these may have been in France, the Netherlands or North-West Germany (WATERBOLK 1968).

The contact between western and eastern European cultures will have led to contact between *domesticus* and *musculus*. It seems reasonable as well to suppose (as HUNT and SELANDER 1973 do) that the border between both subspecies has been located more westerly formerly but as long as no more is known about the original regions of contact one can hardly say something reliable about the extent of the shift. Anyway, hybridization between both subspecies may have taken place already during some 5000 years. In the laboratory both forms prove to cross-breed: if not at random, at least without a clear tendency for assortative mating (HUNT and SELANDER 1973).

In nature, however, only a narrow "hybrid zone" is found. URSIN (1952), performing morphometric research on mice from Jütland, mentions that he found populations of hybrid character in a zone of about 50 kilometers wide, running almost east-west across South-Jütland. Only in a zone of a few kilometers wide he observed mice with such characters that he could not judge anymore which subspecies they resembled most (some characters being identical to those of the one subspecies, some identical to those of the other, and some in between). HUNT and SELANDER (1973), sampling mice in the same area for the determination of isozyme frequencies, found that for many enzymes investigated the two subspecies possess different allozymes. The nearer the borderline, the more decreases the frequency of the allozyme of the one subspecies, and the more increases that of the other. In a part of their study area, 90 % of the transition in genetic respect proved to occur over a distance of about 20 kilometers.

So, with regard to morphology as well as genetics, no gradual transition exists in the border area between both subspecies: on the contrary, it is rather abrupt. The occurrence of narrow zones of hybrid animals between two populations, that live allopatric for the rest, is a wellknown phenomenon, and usually it appears when two populations of one and the same origin meet each other again after a long period of isolation ("secondary intergradation"; MAYR 1963). Often both populations have not yet diverged so far for selective mating to take place, and the absence of a gradual transition between the two

populations can (or must) be ascribed to incompatibility between both parental genotypes. In addition it is possible that other, behavioural or ecological, isolation mechanisms are operating, inhibiting the production of hybrids because behaviour and way of living of both subspecies may have diverged so much that encountering and mating chances between individuals of both subspecies diminished (see VAN OORTMERSEN 1971).

In this study we have tried to detect differences in behaviour between the subspecies, which may possibly give some insight in the existence of a behavioural isolating mechanism between them. For this purpose apart from *domesticus* mice from Holland and *musculus* mice from Poland, mice of both subspecies have been studied which were caught in their border region in Holstein.

Materials and methods

Mice

All mice studied descended from wild caught mice. Concerning the Dutch and Polish mice, all were caught on one locality (Groningen, respectively Warsaw); the mice from Holstein came from several places. The founder mice from Germany were trapped in November-December 1973, for the larger part in corn sheds belonging to country-estates, sometimes on farms. *Domesticus* and *musculus* can be easily distinguished in the field: *musculus* has a whitish belly fur with a "demarcation line" on the flanks; *domesticus* usually has a gray coloured belly without such a side line. The fur of *domesticus* is on the whole more grayish, that of *musculus* more brownish. Furthermore *domesticus* mice are usually a little larger and heavier, with a relatively larger tail and more tail rings (see for morphology FREYE and FREYE 1960; REICHSTEIN 1978; SCHWARZ and SCHWARZ 1943; ÜRSIN 1952; ZIMMERMANN 1949).

In all our experiments we compared mice from four localities: Dutch and German *domesticus*, and German and Polish *musculus*. In the experiments in which the behaviour of individual mice was observed, only male mice were used; 15 males of each locality were always compared.

Experimental conditions

Experiment (1): A habitat choice test and a study of individual exploratory behaviour.

In cages of 150 × 80 × 80 cm exploratory behaviour of individual mice was studied. After that, the mice were left in the cages to do a habitat choice: in the cages possibilities were offered for nestbuilding and living underground as well as overground. Frequencies or durations were scored of various behaviour elements like: upright posture, sniffing, attention posture, grooming, digging, climbing.

Experiment (2): A comparative study of the social behaviour.

Groups were always started with 3 males and 3 females, either descending from one nest (called "litters"), or all from different nests and placed together at three weeks, the age of weaning (called "samples"). They were placed in small barns (4 × 4 m), in which food and nesting opportunities were present ad lib, but without possibilities for emigration. The groups were placed in these barns at ages of 8–12 weeks; each had only half such a barn to its disposal. Nature and frequencies of interactions were studied with help of a tape-recorder and a computer program. Of all four localities two litters and two samples were tested.

Experiment (3): Confrontations between individual *domesticus*- and *musculus*-males on the borderline between their adjacent territories.

These confrontations took place in cages of 60 × 30 cm, with two compartments: each mouse was placed in its compartment 24 hours before the test, and was probably not able to perceive the other mouse at all.

Experiment (4): Confrontations between groups of *domesticus* and *musculus* mice.

These groups were first involved in exp. (2), in which each of two groups had disposed of half a barn. Now the barrier between the living areas of two groups was removed, and the mice could interact freely.

Results

Catches in Holstein

The places where *domesticus*, *musculus* and hybrid mice were caught in Holstein, are shown in Fig. 1. The border between *domesticus* and *musculus* lies in the valley that connects the cities Plön and Lütjenburg. At Breitenstein, near Plön, 24 mice were caught,

12 of which had a dark belly, 10 had a light belly, and 2 with a fur colour and colour distribution that was somewhere between those of both subspecies. Later measurements on other morphological features, generally used in distinguishing the subspecies (see Materials and Methods), confirmed that a number of these mice indeed could be considered as hybrids. At Lammersshagen, some kilometers west of the line Plön–Lütjenburg, 7 large, dark bellied and longtailed *domesticus*-mice were caught; at Mühlenfeld, some kilometers

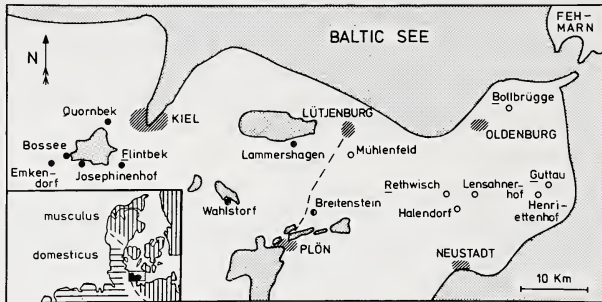


Fig. 1. Catching sites of house mice in East Holstein. Most catches are from country-estates, the others of farms in villages. In the latter cases, the first letter of the name of the village has been underlined. For sake of orientation, large towns have been drawn in as well. ● *Mus m. domesticus*; ○ Hybrids; ○ *Mus m. musculus*; - - - -: borderline between both subspecies

east of this line, 6 smaller, lightbellied and shorttailed *musculus* mice were found. (The distance between Lammersshagen and Mühlenfeld amounts to 10 kilometers as the crow flies.) Apart from the catches at Breitenstein (10 males, 14 females), a total of 22 *domesticus* mice (14 males, 8 females) were caught on seven different places, and 29 *musculus* mice (15 males, 14 females), also on seven places.

Experiment 1: Habitat choice and exploratory behaviour

Clear and systematic differences between *domesticus* and *musculus* were not found, nor indications for the occurrence of "character displacement" (the phenomenon that when the regions of two, otherwise allopatric living species or subspecies overlap each other partly, the differences between both are stressed in the zone of coexistence: see BROWN and WILSON 1956). In our test-situation, most mice of both subspecies preferred to settle underground (*Mus m. domesticus*: 27 out of 30 males, *Mus m. musculus*: 22 out of 30).

Experiment 2: Social behaviour

In this experiment, too, no clear differences between mice from the four localities were found, with the exception of the degree of tolerance of adult males towards each other. This difference in tolerance led to differences in mortality of subordinate males: see Table. In all groups, of both subspecies, a hierarchical dominance structure developed: one male became the dominating territory holder, the other two got wounded and became outcasts. In the *domesticus* samples all subordinate males died within 14 days after the start of the experiment. This only happened in one *musculus* sample (a German one); in the other three *musculus* samples the outcast males stayed alive much longer: in the two Polish samples till the end of the experiment (3 respectively 8 weeks from the start), while in the other West-German *musculus* sample both outcast males died at last after about 8 weeks. In one *domesticus* litter both subordinates were dead within 24 hours, while in the other three litters only one subordinate died within 14 days, and the other stayed alive till the end of

Table

Mortality among subadult males

SAMPLES	
day:	1 2 3 4 5 6 7 8 9 10 11 12 13 14
N :	2 2 1 1 0 0 0 0 0 0 0 0 0 0
	2 2 2 2 2 2 1 1 0 0 0 0 0 0
G ^d :	2 2 1 1 1 0 0 0 0 0 0 0 0 0
	2 2 2 2 2 2 2 1 1 1 1 1 0 0
G ^m :	2 2 2 0 0 0 0 0 0 0 0 0 0 0
	2 2 2 2 2 2 2 2 2 2 2 2 2 2
P :	2 2 2 2 2 2 2 2 2 2 2 2 2 2
	2 2 2 2 2 2 2 2 2 2 2 2 2 2

LITTERS	
day:	1 2 3 4 5 6 7 8 9 10 11 12 13 14
N :	0 0 0 0 0 0 0 0 0 0 0 0 0 0
	2 2 2 2 2 2 2 2 2 1 1 1 1 1
G ^d :	2 2 1 1 1 1 1 1 1 1 1 1 1 1
	2 2 2 2 2 1 1 1 1 1 1 1 1 1
G ^m :	2 2 2 1 0 0 0 0 0 0 0 0 0 0
	2 2 2 2 2 2 2 2 2 2 2 2 2 2
P :	2 2 2 2 2 2 2 2 2 2 2 2 2 2
	2 2 2 2 2 2 2 2 2 2 2 2 2 2

The number of subordinate males, alive on the 14 consecutive days from the start of the experiments, are indicated. Of each of the four origins, in the "sample" as well as in the "litter" series (see text), two replicas were studied. N = *domesticus* mice from the Netherlands, G^d = *domesticus* mice from West-Germany, G^m = *musculus* mice from West-Germany, P = *musculus* mice from Poland

the experiment (after 8 weeks). In both Polish *musculus* litters the outcasts stayed alive; in one German *musculus* litter the same thing happened, while in the other one both subordinates died within 5 days.

The difference between *domesticus* and *musculus* concerning the mortality of subordinate males within two weeks after the start of the experiments, is significant with Fisher's exact probability test on the .05 level: see Fig. 2. Clearly, *domesticus* subordinates have smaller chances for survival than *musculus* subordinates.

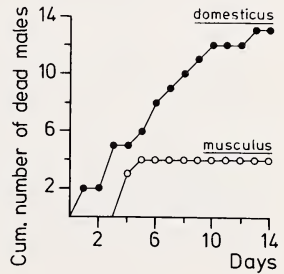


Fig. 2. Cumulative number of subordinate males deceased during the first 14 days after the start of the experiments

Experiment 3: Confrontations between *domesticus* and *musculus* males

In 2 out of 15 confrontations no aggressive interactions were observed, but in all other 13 tests the *domesticus* male became the winner. This male was also always the heavier one: the weights of the *musculus* males used varied between 20–25 g while all *domesticus* males were heavier than 25 g.

Experiment 4: Confrontations between *domesticus* and *musculus* groups

Two experiments have been performed. In the experiment in which confrontations between West-German *domesticus* and *musculus* mice were studied, only one male in each group, viz, the dominant one, had survived in exp. (2). After the removal of the barrier between the living areas of both groups, the *musculus* male was found dead within 24

hours. In the experiment in which Dutch *domesticus* (1 dominant male left) and Polish *musculus* (3 males) were confronted, the dominant *musculus*-male died within 24 hours, and the *musculus*-subordinates followed within a few days. In both experiments the *musculus*-females (3 per group) became outcasts, and were only tolerated in a single nest cage. Such a repudiation process, however, also occurs when the mice should have belonged to the same subspecies. In both experiments the clear advantage of the *domesticus* males was coupled to a higher body weight.

Discussion

Several animal species and subspecies show a North-South directed region of contact through Central-Europe (THORPE 1979; WHITE 1978). Our mousetrapping in Holstein has led to a more precise localization of the border line between *domesticus* and *musculus* in this area: up till now it was known of only one mouse with hybrid characters caught at Plön in 1930 (MOHR 1931). The location of the borders between both subspecies in South-Jütland and East-Holstein seems to indicate that *domesticus* has driven a wedge in the *musculus* area as a result of which the *musculus* of Jütland were separated from the German *musculus*. This agrees well with the data of HUNT and SELANDER (1973) that introgression of *domesticus* alleles in *musculus* populations is larger than in the reverse direction. It agrees also with their suggestion that the border between both subspecies has been shifted in eastward directions. The differential winning chances of the two subspecies in agonistic interactions give an explanation for how this shift could have taken place. Although we are still uncertain about the origin of the differences between *domesticus* and *musculus* (probably a consequence of adaptations to different environments, see e. g. HUNT and SELANDER 1973), we now know the consequences of contact between both. Where *domesticus* mice have established themselves, no *musculus* male will be able to settle down. But, whenever a *domesticus* male arrives in *musculus* area, a fair chance exists that sooner or later the *musculus* mice will be driven away. It remains uncertain to which degree mixing up with *musculus* females will happen.

Further study is needed on the problem whether the greater competitive abilities of *domesticus* males are connected to a higher aggressivity (VAN OORTMERSEN 1971), or are a consequence of their higher body weight (the influence of body weight on chances of winning fights and establishing territories in *domesticus* is evident: VAN ZEGEREN 1980). A better understanding of the isolation mechanisms operating between the two subspecies and leading to the narrowness of the hybrid zone, will be derived from further field research in situ and more extensive behavioural observations in the laboratory, concerning hybrid mice as well.

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Zusammenfassung

Grenzstreitigkeiten zwischen der west- und der ost-europäischen Hausmaus in Schleswig-Holstein, Bundesrepublik Deutschland

Die Grenze zwischen den Hausmaus-Unterarten *Mus musculus domesticus* und *M. m. musculus* wurde in Ost-Holstein untersucht und verläuft hier über Plön und Lütjenburg (Fig. 1). Die Vermischungszone zwischen beiden Formen ist schmal. Vergleiche der Lebensweise, des Erkundungs- und Sozialverhaltens im Laboratorium zeigten nur einen Unterschied zwischen Angehörigen der beiden

Unterarten aus den Niederlanden und Holstein bzw. aus Holstein und Polen: Bei *domesticus* führten die Angriffe dominanter Männchen häufiger zum Tode der unterlegenen Männchen als bei *musculus*. In Konfrontationen zwischen Männchen der verschiedenen Unterarten siegten immer die (schwereren) *domesticus*-Tiere. Ihre Überlegenheit könnte die Verschiebung der Unterartgrenze nach Osten erklären.

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The African rodent *Colomys goslingi* Thomas and Wroughton, 1907 (Rodentia: Muridae) – a predator in limnetic ecosystems

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Abstract

The African rodent *Colomys goslingi* (Muridae) nearly always lives close to running waters. In this study the feeding biology of this species, based mainly on the morphology of the intestinal tract, on stomach contents, and on observation of its preying behaviour is investigated.

Evidently *Colomys* is a predator in limnetic ecosystems, as running water invertebrates heavily predominate in the stomach contents. In the laboratory *Colomys* also fed on vertebrates (fishes, tadpoles), which were actively hunted. High sensory performances of *Colomys* can be expected in