AGGRESSIVE BEHAVIOR
Volume 31, pages 283–293 (2005)

Aggression and Commensalism in House Mouse: a Comparative Study Across Europe and the Near East

Daniel Frynta[1]*, Markéta Slábová[1], Hana Váchová[1], Radka Volfová[1], and Pavel Munclinger[1,2]*

[1]Department of Zoology, Faculty of Science, Charles University, Praha, Czech Republic
[2]Institute of Animal Physiology and Genetics, Academy of Sciences of the Czech Republic, Brno, Czech Republic

Species specific differences of house mouse social behavior compared to its closest relatives (aboriginal species *Mus macedonicus, Mus spicilegus,* and *Mus spretus*) have recently been suggested. However, substantial variation of behavioral traits between mouse populations has been also evidenced. Agonistic behavior of laboratory-born house mice from five commensal populations (*Mus musculus musculus*: central Czech Republic, *Mus musculus domesticus*: Bulgaria, Greece, Turkey, and natural *Mus m. musculus/domesticus* hybrids from the Czech part of the hybrid zone) and five non-commensal populations of *M. m. domesticus* (C. Syria, E. Syria, Jordan, Iran, Libya) was studied. Dyadic interactions in a neutral cage were performed and the effects of sex and population on time spent by agonistic behavior evaluated. In all studied populations, the male-male interactions were more agonistic than the female-female ones. Male-male behavior gradually increased from the least agonistic population of *M. m. musculus* from Central Europe to the Near East populations of *M. m. domesticus* exhibiting the highest scores of agonistic behavior. Between-population differences were even stronger when female-female encounters were considered. While females of commensal populations belonging to both *M. m. musculus* and *M. m. domesticus* were tolerant of each other, those coming from non-commensal populations of *M. m. domesticus* were highly agonistic, reaching even the level of aggression between the females of some aboriginal mouse species. This phenomenon may be attributed to increased competition for food in non-commensal populations when compared to commensal ones supplied by superabundant resources. Social behavior of house mice, therefore, appears to be pliable rather than rigid and species specific. It can be changed rapidly according to ecological needs and such adaptability allows house mice to colonize various habitats. Aggr. Behav. 31:283–293, 2005. © 2005 Wiley-Liss, Inc.

Keywords: agonistic behaviour; wild mouse; hybrid zone; *Mus domesticus; Mus spicilegus*; *Mus macedonicus*

Grant support: Grant Agency of the Czech Republic; Grant numbers: 206/01/0989 and 206/03/D148 to P. Munclinger. Grant Agency of the ASCR; Grant number: A6111410 to D. Frynta. Grant support: Ministry of Education Youth and Sport of the Czech Republic; Grant number: MSMT 0021620828.

*Correspondence to: Pavel Munclinger, Daniel Frynta, Department of Zoology, Faculty of Science, Charles University, Viničná 7, 128 44 Praha 2, Czech Republic. E-mail: muncling@natur.cuni.cz, frynta@centrum.cz

Received 22 April 2003; Amended version accepted 1 July 2003

INTRODUCTION

Mouse aggression is a popular model for human violence. While many studies of aggression have been conducted in inbred strains, knowledge of behavioral variation in wild mouse populations is still scant.

The house mouse [*Mus musculus* Linnaeus, 1758] is a well-known inhabitant of human settlements, however, only some populations of this species experience this commensal way of life inside buildings and stores. Other populations of this species, further referred to as non-commensal, are free-ranging, inhabiting fields, shrubs, sandy dunes, etc. outside buildings and urbanised areas. In the Near East, where agricultural societies first developed approximately ten thousand years ago, this non-commensal way of life may be the primary stage in at least some house mouse populations, while non-commensal populations in more recently colonised areas, e.g., the isles around United Kingdom, some populations of America, Australia, and New Zealand, passed through the commensal stage and are usually reported as feral. The closest relatives of the house mouse are three aboriginal species *Mus spicilegus*, *Mus macedonicus*, and *Mus spretus*. They are strictly free ranging, avoid human settlements, and exhibit some peculiar features of ecology and behavior [e.g., Auffray et al., 1990; Cassaing and Croset, 1985; Dobson and Baudoin, 2002; Gouat et al., 2003; Gray and Hurst, 1997; Hurst and Smith, 1995; Patris and Baudoin, 1998; Patris and Baudoin, 2000; Sokolov et al., 1990]. One of the most apparent characteristics of their social behavior is an elevated level of aggression in *M. macedonicus* [Frynta and Čiháková, 1996] and *M. spicilegus* [Suchomelová et al., 1998; Patris et al., 2002]. Surprisingly, not only males but also females of these species are highly agonistic to each other. The high level of aggressiveness in *M. spicilegus* should prevent female aggregation and may lead to female dispersal [Patris et al., 2002]. Moreover, as Suchomelová et al. [1998] suggested, female intolerance in this species can be associated with food hoarding into mounds and cache defense. In contrast, females of *M. musculus* are generally fairly tolerant of each other, notably in neutral cage tests [e.g., Munclinger and Frynta, 2000; Patris et al. 2002], and they became aggressive only under particular circumstances [Palanza et al., 1996; Parmigiani and Palanza, 1994; Parmigiani et al., 1989].

Nevertheless, the above studies suggest that behavioral patterns are strictly species specific and not considerably affected by between-population variation. It is known that in species showing extreme adaptability to different local conditions, including the house mouse, such rigidity is unlikely. Mouse aggression is a highly heritable trait [Cairns et al., 1983; Hood, 1988; Hood and Cairns, 1988], exhibiting considerable differences between strains of laboratory mouse [reviewed in Miczek et al., 2001]. The speed of response to artificial selection for attack latency [Sluyter et al., 1996; Van Oortmerssen and Bakker, 1981] suggests that aggression is subjected to natural selection and rapid evolution.

Moreover, differences between some populations have already been shown, e.g., in the north-western part of Europe [Hunt and Selander, 1973; Thuesen, 1977; Van Zegeren and Van Oortmerssen, 1981], where two subspecies of commensal house mice form a hybrid zone. The males from populations from the *M. m. domesticus* side of the zone were more aggressive than those from the *M. m. musculus* side. This conclusion was further supported by the comparison of central European *M. m. musculus* with *M. m. domesticus* from eastern Turkey [Munclinger and Frynta, 2000]. Furthermore, there are other data suggesting within-species variation, e.g., between chromosomal races of *M. m. domesticus* [Ganem and Searle, 1996], island and mainland [Gray and Hurst, 1998], and geographically distant populations of *M. m. musculus* [Krasnov and Chochlova, 1994]. Recently, between-population variation of behavioral traits has been demonstrated in a wide range of animal species [for a review see Foster, 1999]. Such variation has been overlooked in spite of its importance for understanding the evolutionary processes. It is possible that such variation of special interest can also be expected in *M. musculus*, when comparing commensal and non-commensal populations.

The differences between commensal and non-commensal ways of life are sharp and affect almost every aspect of physical and social environment. Commensal populations are supplied with superabundant food and often reach high densities, resulting in very small home ranges and replacement of the territorial system of individuals with hierarchies [Crowcroft and Rowe, 1963; Hurst, 1987; Wolff, 1985]. In contrast, non-commensal populations are usually limited by food or rainfall [Brown and Singelton, 1999; Choquenot and Ruscoe, 2000] and exhibit large home ranges/territories [Krasnov and Chochlova, 1994]. Mouse social behavior, and agonistic behavior in particular, may be affected by different selective pressures in these contrasting environments.

Competition for food is greatly reduced in commensal environment and consequently, there is no reason for female spacing and female-female aggression. Although males compete for females in both environments, the efficiency of social strategies may be changed by, e.g., differences in ability to defend territories (smaller territories are more defendable, but frequency of male-male encounters is higher in a commensal situation), risk of injury, or ability to control female reproduction.

The following main questions were addressed: Is there any between-population variation in the level of agonistic behavior? Is this variation correlated with the level of commensalism of the studied populations?

METHODS

Experimental animals were adult (at least two months old), socially experienced, laboratory born (mostly up to the sixth generation in captivity) mice. The stocks were derived from the following ten populations of different geographic origin (see Fig. 1.): (1) *M. m. musculus* - central Czech Republic, villages: Černošice, Soutice, Satalice; (2) Hybrid zone - villages: Hazlov, Poustka, Podílná in the westernmost Czech Republic. Since the villages are situated close to each other in the centre of the *M. m. domesticus/musculus* hybrid zone [Macholán and Zima, 1994; Munclinger et al., 2002], the trapped animals were undoubtedly natural hybrids of *M. m. musculus* and *M. m. domesticus.* The following stocks were treated as *M. m. domesticus,* but the possibility of introgression of *M. m. castaneus* genes cannot be entirely excluded in the studied mice from Iran and possibly even from Turkey [Gündüz et al., 2000; Karn et al., 2002; Prager et al., 1998]; (3) Bulgaria (Rupite village near the town Petrich, district Blagoevgrad, SW Bulgaria); (4) Greece (vicinity of the town Kilkis, district Kilkis, Northern Greece); (5) Turkey (vicinity of the towns Dogubayazit and Van, Eastern Turkey); (6) Palmyra (the ancient oasis of Palmyra, i.e., present day Tadmor, district Tadmor, Central Syria); (7) Eastern Syria – environs of villages Halabiyah, Doura Europos, and Tell Shaikh Hammad, Euphratus river valley, district Deir az-Zor, Eastern Syria; (8) Iran - environs of Choqa Zanbil village, Khuzestan province, South-western Iran; (9) Jordan - Wadi al-Hidan and vicinity of the Aqaba town, Southern Jordan; (10) Libya - 20 km N of Al-Qusbat, district Tarabulus, Northwest Libya. The above ten stocks are further referred to as

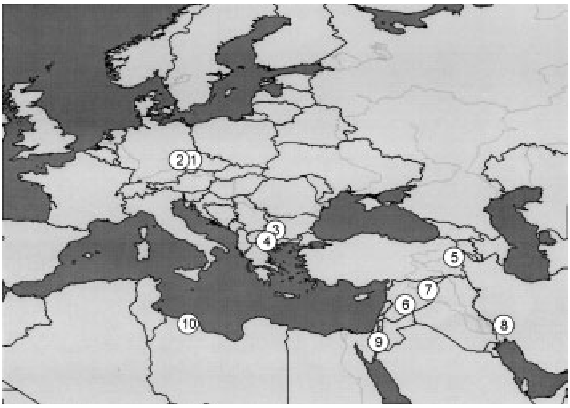

Fig 1. Map of localities from which the studied mouse stocks originated. (1) central Czech Republic, (2) Hybrid zone in the westernmost part of the Czech Republic, (3) Bulgaria, (4) Greece, (5) Turkey, (6) Palmyra (Central Syria), (7) Eastern Syria (8) Iran, (9) Jordan, (10) Libya. See material and methods for details.

populations. The mice from Bohemia, Hybrid zone, Bulgaria, Greece, and Turkey were captured inside buildings (or in the immediate vicinity) and they were consequently considered to be commensal. Those from other localities were captured in outdoor conditions (fields: E. Syria, Iran, gardens and palmerias: Jordan, Palmyra, and Libya) and are referred to as non-commensal.

All animals were kept under an artificial 12 L: 12 D light cycle and housed by heterosexual pairs in plastic cages 30 × 15 × 15 centimeters in size. Water and food (VELAZ ST1 mouse and rat breeder diet, wheat, etc.) were provided ad libitum. Each cage contained sawdust bedding, nesting material (paper), and shelters.

A standard neutral-cage procedure was used. The encounters between mice were carried out in a 50 × 30 × 35 cm glass cage. The cage was divided into two equal parts by a thick card partition. During testing, the cage was illuminated by a single 40 W red light bulb. The mice were tested during the dark phase of their light-dark cycle. At the beginning of each experimental session, two mice were placed in the pen, on the opposite sides of the partition, and left for five minutes. The central partition was then removed and video recording by a single VHS-camera started. The video camera was stopped at the end of the session, i.e., ten minutes after the moment when one or both animals paid attention to the other one for the first time. After each session the cage was thoroughly cleaned using 96% ethanol. Each animal was tested with different opponents two times. Repeated tests of the same individual occurred at least 24 hours apart.

The homogenous-dyad design, i.e., both opponents were of the same sex and population, was applied. Twenty male-male and twenty female-female dyadic encounters were carried out in each of the ten studied populations (Bulgaria: 21 male-male dyads, Palmyra: 19 female-female dyads). In addition, dyads comprising wild caught mice from Eastern Syria (24 male-male and 15 female-female) and Palmyra (12 male-male and 9 female-female) were included to test differences between wild and laboratory born mice. Moreover, the published results of similar experiments with aboriginal mice species, i.e., *M. spretus* (SFM strain, Montpellier, France), *M. spicilegus* (ZYP strain, derived from Pancevo, Serbia), and *M. macedonicus* (wild caught, Krumovo village, SE Bulgaria), that were previously carried out in this laboratory

[Frynta and Čiháková, 1996; Suchomelová et al., 1998] were included to allow between-species comparisons.

The video recordings of the encounters were then observed, and the duration of behavioral elements was quantified using the computer program package ACTIVITIES [Vrba and Donát, 1993]. The standard catalogue of 34 behavioral elements was used for the purpose of data collection [see Frynta and Čiháková, 1996 for details]. First, the elements were summed into 22 categories and five functional blocks (Agonistic: Threat-Attack, Aggressive upright, Chase, Roll-over fight, Neutral upright, Box, To-fro - repeated approach and avoidance, Tail rattling, Defensive upright-threat, Avoid-Retreat, Flee-Jump avoid, Freeze, Submissive; Introductory: Attend, Approach, Nose-Follow; Amicable: Body Contact, Mutual groom; Exploratory: Loco-explore, Rear-Jump; Individual: Self groom, Sit) and as the behavior of both interacting animals in a particular dyad is obviously inter-correlated, the scores recorded for both members of the dyad were also summed. Subsequently, Principal Component Analysis (PCA) was performed. The first principal component that explained 21 percent of overall variation was highly correlated ($r = 0.968$, $R^2 = 93.7\%$) with the total time spent by agonistic behavior (sum of the former 12 categories, see above). The total time spent by agonistic behavior was further used as a measure of agonistic behavior, because it is easier to interpret and less sensitive to mistakes of the observer. It was, however, natural log transformed to achieve normality. Surprisingly, the analysis of covariance revealed no effect of mean body weight ($p = 0.065$) and/or relative difference of body weight between the interacting mice ($p = 0.118$) on the time spent by agonistic behavior. Consequently, these factors were excluded from the final model. A slight effect of repeated testing was detected in male-male ($F_{1,228} = 4.14$, $p = 0.043$) but not in female-female ($F_{1,216} = 1.62$, $p = 0.204$) dyads. Nevertheless, there was no interaction between the repeated testing and the studied factor (population). The time spent in agonistic behavior in wild caught and laboratory born mice from Palmyra and E. Syria was compared by analysis of variance (ANOVA) in which sex and population were also included as factors. The effects of population on the time spent by agonistic behavior in the overall data set were examined separately in male-male and female-female dyads by ANOVA. The factor of repeated testing was maintained in the final model. As Scheffe multiple range tests are supposed to be most conservative and robust when homogeneity of variances is violated, they were used for subsequent comparisons of individual populations. Scheffe tests produced the same or even more conservative results than their non-parametric alternative, the Bonferoni adjusted Mann-Whitney U-tests. The latter tests were also applied to comparisons between male-male and female-female dyads in each studied population.

RESULTS

The analysis of variance revealed significant between-population variation in the time spent by agonistic behavior both in male-male ($F_{12,241} = 14.61$, $p < 0.0001$) and female-female ($F_{12,216} = 29.12$, $p < 0.0001$) encounters.

Male-male encounters were apparently the least agonistic in *M. spretus* and *M. m. musculus* (see Fig. 2 and APPENDIX). *M. spretus* males were significantly less agonistic than males of *M. spicilegus, M. macedonicus,* and males of *M. m. domesticus* from Turkey and from all non-commensal populations, with the exception of Libya (Scheffe $p < 0.05$). Males of *M. m. musculus* were less agonistic than males of *M. spicilegus, M. macedonicus,* and males of

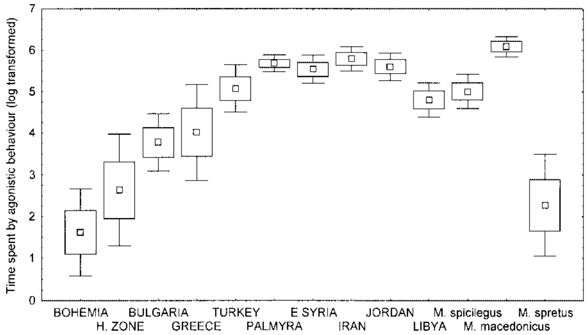

Fig. 2. Time spent by agonistic behavior in male-male dyads. Means, S.E., and 95% confidence intervals are given for each population.

Appendix. Mean Duration (in Seconds) of Main Function Blocks of Behavior

	Agonistic	Amicable	Introductory	Exploratory	Individual
females					
Bohemia	5.0	3.1	223.2	729.3	239.4
Hybrid zone	6.8	1.3	127.5	598.7	465.7
Bulgaria	10.0	2.7	192.3	720.6	274.4
Greece	0.5	0.9	97.0	837.8	263.8
Turkey	45.6	0.7	224.6	754.3	174.9
Palmyra	111.8	3.0	246.1	640.7	198.3
E Syria	84.7	1.2	243.9	687.5	182.7
Iran	161.2	0.6	145.1	697.2	195.9
Jordan	188.1	0.0	107.2	597.9	306.9
Libya	51.3	6.3	340.4	611.7	190.3
males					
Bohemia	37.5	18.2	319.5	518.1	306.7
Hybrid zone	137.8	4.5	201.5	465.2	391.0
Bulgaria	99.6	2.0	216.9	637.8	243.6
Greece	190.5	0.2	110.6	524.3	374.4
Turkey	225.1	1.0	115.3	387.1	471.4
Palmyra	318.6	0.0	150.6	495.9	234.9
E Syria	310.4	0.0	136.2	601.5	151.9
Iran	386.5	0.0	21.7	466.0	325.8
Jordan	334.7	0.0	31.1	439.9	394.3
Libya	170.8	3.1	275.4	480.0	270.7

M. m. domesticus from Turkey and from all non-commensal populations, including Libya (Scheffe $p < 0.05$). Despite the fact that the hybrid zone males were slightly more agonistic than *M. m. musculus*, they were still significantly less agonistic than males from all non-commensal *M. m. domesticus* populations and *M. macedonicus* males (Scheffe $p < 0.05$).

The pattern found in female-female dyads (see Fig. 3) is even more distinctive, females of non-commensal populations of *M. m. domesticus* as well as those of *M. spicilegus* and *M. macedonicus* were highly agonistic, while females coming from populations of commensal *M. m. musculus, M. m. domesticus,* and free-ranging *M. spretus* were peaceful. Scheffe tests

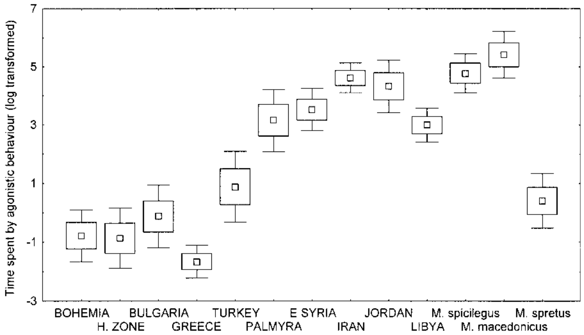

Fig. 3. Time spent by agonistic behavior in female-female dyads. Means, S.E., and 95% confidence intervals are given for each population.

proved differences between the following populations at a significance level $p < 0.05$: Females from the central Czech Republic, the hybrid zone, Bulgaria, and Greece are less agonistic than females from Palmyra, E. Syria, Jordan, Iran, and Libya, and females of *M. spicilegus* and *M. macedonicus*. Females of *M. m. domesticus* from Turkey have been found less agonistic than *M. m. domesticus* females from Iran and Jordan, and females of *M. spicilegus* and *M. macedonicus. M. spretus* females are less agonistic than *M. m. domesticus* females from E. Syria, Iran, and Jordan and females of *M. spicilegus* and *M. macedonicus.*

Laboratory born and wild caught mice from Palmyra and E. Syria exhibited almost the same scores of agonistic behavior ($F_{1,131} = 0.0306$, $p = 0.8612$).

DISCUSSION

Substantial differences were demonstrated between *M. musculus* populations of different geographical origin. The most interesting finding is a high level of aggression in non-commensal populations of *M. m. domesticus* from the Near East and Libya, where female-female interactions reach even the extreme level previously attributed only to free-ranging species *M. spicilegus* and *M. macedonicus* [Frynta and Čiháková; 1996; Patris et al., 2002; Suchomelová et al., 1998].

Female aggression in rodents is usually interpreted as competition for food or as a strategy to avoid infanticide [cf. Labov, 1984]. In the house mouse it has long been a neglected phenomenon. Although repeatedly noticed, it has been restricted either to pup defense or cohabitation with a territorial male [e.g., Hood, 1988; Parmigiani et al., 1989; Parmigiani and Palanza, 1994; Soroker and Terkel, 1988]. Female house mice usually showed only low levels of agonistic behavior in neutral-cage conditions [e.g., Munclinger and Frynta, 2000; Patris et al., 2002]. However, the female of aboriginal species of mice, *M. macedonicus* and *M. spicilegus*, behave aggressively towards their female conspecifics when tested in a neutral-cage [Frynta and Čiháková, 1996, Suchomelová et al., 1998; Patris et al., 2002]. Female-female dyads in these species were equally as agonistic as male-male ones. Female aggression may be associated with food hoarding and cache defense. *M. spicilegus* is a well-known food hoarder [Muntyanu, 1990; Von Festetics, 1961] and *M. macedocicus* hoards seeds in laboratory experiments [Frynta and Ambrozková, unpubl. data]. Unfortunately, comparative evidence concerning food-hoarding behavior in the genus *Mus* is not available. These authors assume that hoarding is not essential in commensal populations surrounded by superabundant food sources. Such sources are too concentrated to be economically defendable and female territoriality is unlikely. Female aggression may therefore be reduced in such habitats. This hypothesis relating resource defense to the level of aggression may explain the low level of aggression in commensal females in these experiments. However, it does not predict territoriality in every non-commensal population, e.g., in habitats where resources are dispersed and effective hoarding is not possible. May Island [Gray and Hurst, 1998], where elevated female aggression has not been reported, may serve as an example.

The low levels of agonistic behavior in both females and males of *M. spretus* seem rather surprising, yet it fits very well with the finding of Hurst et al. [1996] that dominance over suitable sites is more important than investment in fierce aggression to drive competitors away in this free-ranging species. In other words, while fighting for scattered food is profitable and yields essential gains, it is probably wiser to find one's own shelter than to risk injuries associated with driving other mice out from already occupied shelters.

Although the behavioral distinctions between females from different populations in these experiments are correlated with the level of commensalism, the similarity caused by common ancestry cannot be completely excluded, as the selection of localities was obviously biased. All non-commensal populations examined come from the Near East or Libya. In addition, mice from the Mediterranean area can probably switch between commensal and non-commensal ways of life. For this reason, other populations secondarily adapted to comparable steppe or semi-desert habitats (e.g., American or Australian) and strictly commensal Near East or Mediterranean populations (e.g., from large towns) should be studied. However, it should be noted that females from E. Turkey (the only commensal locality studied from the Near East) exhibited the lowest level of aggressiveness among the Near East females. As densities, dispersal, intra-sexual, or inter-specific competition could also intervene when explaining space use and, consequently, female aggressiveness, experimental manipulations with food resources are also needed to validate the influence of food defense on aggression. Nevertheless, Gray et al. [2002] showed that both sexes of *M. domesticus* exhibit more aggression towards intruders in areas containing valuable resources.

As far as male-male encounters are concerned, males from non-commensal stocks exhibited the highest scores of agonistic behavior among *M. musculus*. Furthermore, results supported the findings of earlier studies [Hunt and Selander, 1973; Munclinger and Frynta, 2000; Thuesen, 1977; Van Zegeren and Van Oortmerssen, 1981] that *M. m. musculus* males are less agonistic than *M. m. domesticus* males. The general validity of this conclusion is, however, limited by great between-population variation in the time spent by agonistic behavior found in *M. m. domesticus*. In addition, there are published data supporting the existence of similar variation also among populations of *M. m. musculus.* Krasnov and Chochlova [1994] reported higher scores of aggression in Moscow population when compared with another commensal population in Chukotka and non-commensal population in Kalmykia. Nevertheless, genetic purity of the experimental animals from Moscow was not checked and possible introgression of *M. m. domesticus* genes cannot be excluded. Moscow is a densely-populated urban area, and can be seen as an international port with extensive transport of commodities, and, possibly, mice. Such human-mediated transports for long distances have already been proven at Lake Casitas in California, where Orth et al. [1998] found substantial contribution of Asian *M. m. castaneus* genes in mouse populations.

Male mice from the hybrid zone examined in this study showed intermediary values between *M. m. musculus* and European populations of *M. m. domesticus,* as expected. In contrast, males of F_2 and especially F_1 hybrid generation of *M. m. musculus* (Czech Republic) and *M. m. domesticus* (Greece) were highly agonistic, reaching or even exceeding the scores of their *M. m. domesticus* parents [Volfová et al., 2002]. This discrepancy may be explained by the fact that while simple F_1 hybrids do not occur in the hybrid zone, the animals in the zone result from multiple crosses between hybrids [Boursot et al., 1993; Munclinger et al., 2002].

Foster [1999] claimed that behavioral patterns are hardly invariant within species and characterization of species based only on single populations is elementarily inappropriate. Results demonstrated that the differences between a single population of *M. m. domesticus* and a single population of *M. spicilegus* found by Patris et al. [2002] may be more adequately interpreted as differences between non-commensal and commensal *M. m. domesticus*. Moreover, the *M. m. domesticus* DDO strain used in the study by Patris et al. [2002] comes from the close proximity of the hybrid zone in Denmark and thus the lower level of defensive behavior may also be seen as a possible result of an introgression of *M. m. musculus* genes across the hybrid zone into the *M. m. domesticus* gene pool. It is worth noting that substantial introgression at several loci has already been evidenced in the DDO strain [Barbara Dod, personal communications].

Every behavioral trait exhibiting vast within-species variation, heritability, and rapid response to artificial selection is likely to exhibit variation within a species inhabiting an extensive range and/or showing contrasting ecological or social strategies. This study demonstrated that this is precisely the case of agonistic behavior in house mouse. Earlier authors interpreting the results obtained in a single *M. m. domesticus* population as representative of this species/subspecies as a whole omitted the most interesting source of interpretable data. Apparently, mice aggression is subject to recent and rapid evolutionary change and may serve as an excellent natural model for studies of adaptive processes on population level.

ACKNOWLEDGEMENTS

The helpful comments of Lukáš Kratochvíl, Barbara Dod, Markéta Malá, and an anonymous referee are greatly appreciated. The authors thank colleagues Eva Suchomelová and Jovana Sádlo-Čiháková for the original data concerning aboriginal species of house mice, and Theodora Sofianidou, Vladimír Vohralík, Petra Nová, Pavlína Mikulová, Jaroslav Flegr, Petr Benda, Miloš Macholán, Jovana Sádlo-Čiháková, and other colleagues for their kind help in catching mice in the field.

REFERENCES

Auffray J-C, Tchernov E, Bonhomme F, Heth G, Simson S, Nevo E. 1990. Presence and ecological distribution of *Mus "spretoides"* and *Mus musculus domesticus* in Israel. Circum-Mediterranean vicariance in the genus *Mus*. Z Saugetierk 55:1–10.

Boursot P, Auffray J-C, Britton-Davidian J, Bonhomme F. 1993. The evolution of house mice. Annu Rev Ecol Syst 24:119–152.

Brown PR, Singleton GR. 1999. Rate of increase as a function of rainfall for house mouse *Mus domesticus* populations in a cereal-growing region in southern Australia. J Appl Ecol 36:484–493.

Cairns RB, MacCombie DJ, Hood KE. 1983. A developmental-genetic analysis of aggresive behavior in mice: I. behavioral outcomes. J Comp Psychol 97:69–89.

Cassaing J, Croset H. 1985. Organisation spatiale, competition et dynamique des populations sauvages de Souris (*Mus spretus* Lataste et *Mus musculus domesticus* Rutty) du Midi de la France. Z Saugetierk 50:271–284.

Choquenot D, Ruscoe WA. 2000. Mouse population eruptions in New Zealand forests: the role of population density and seedfall. J Anim Ecol 69:1058–1070.

Crowcroft P, Rowe EP. 1963. Social organization and territorial behavior in the wild house mouse (*Mus musculus*). Proc Zool Soc Lond 140:517–531.

Foster SA. 1999. The geography of behavior: an evolutionary perspective. Trends Ecol Evol 14:190–195.

Frynta D, Čiháková J. 1996. Neutral cage interactions in *Mus macedonicus* (Rodentia: Muridae): an aggressive mouse? Acta Soc Zool Bohem 60:97–102.

Ganem G, Searle JB. 1996. Behavioral discrimination among chromosomal races of the house mouse (*Mus musculus domesticus*). J Evol Biol 9:817–830.

Gouat P, Katona K, Poteaux C. 2003. Is the socio-spatial distribution of mound-building mice, *Mus spicilegus*, compatible with a monogamous mating system? Mammalia 67:15–24.

Gray SJ, Hurst JL. 1997. Behavioral mechanisms underlaying the spatial dispersion of commensal *Mus domesticus* and grassland *Mus spretus*. Anim Behav 53:511–524.

Gray SJ, Hurst JL. 1998. Competitive behavior in an island population of house mice, *Mus domesticus*. Anim Behav 56:1291–1299.

Gray SJ, Jensen SP, Hurst JL. 2002. Effects of resource distribution on activity and territory defense in house mice, *Mus domesticus*. Anim Behav 63:531–539.

Gündüz I, Tez C, Malikov V, Vaziri A, Polykov A, Searle JB. 2000. Mitochondrial DNA and chromosomal studies of wild mice (*Mus*) from Turkey and Iran. Heredity 84:458–467.

Hood KE. 1988. Female aggression in mice: development, social experience, and the effects of selective breeding. J Comp Psychol 2:27–41.

Hood KE, Cairns RB. 1988. A developmental-genetic analysis of aggressive behavior in mice. II. Cross-sex inheritance. Behav Genet 18:605–619.

Hunt WG, Selander RK. 1973. Biochemical genetics of hybridisation in European house mice. Heredity 31:11–33.

Hurst JL. 1987. The function of urine marking in free-living population of house mice, *Mus domesticus* Rutty. Anim Behav 35:1433–1442.

Hurst JL, Hall S, Roberts R, Christian C. 1996. Social organization in the aboriginal house mouse, *Mus spretus* Lataste: behavioral mechanisms underlaying the spatial dispersion of competitors. Anim Behav 51:327–44.

Hurst JL, Smith J. 1995. *Mus spretus* Lataste: a hygienic house mouse? Anim Behav 49:827–834.

Ivantcheva A, Cassaing J. 1999. Male-female interactions and socio-sexual isolation of *Mus spicilegus* toward two other species of east-Europaean mice, *Mus macedonicus* and *M. m. musculus*. C R Acad Sci Paris, Sciences de la vie 322:597–605.

Karn RC, Orth A, Bonhomme F, Boursot P. 2002. The complex history of a gene proposed to participate in a sexual isolation mechanism in house mice. Mol Biol Evol 19:462–471.

Krasnov BR, Chochlova JS. 1994. Spatial ethological structure of groups. In: Kotenkova E, Bulatova NS, editors. The House Mouse: Origin, distribution, systematics, behavior. Moskva: Nauka. p 188–214.

Macholán M, Zima J. 1994. *Mus domesticus* in Western Bohemia: a new mammal for the Czech Republic. Folia Zool 43:39–41.

Manning CJ, Wakeland EK, Potts WK. 1992. Communal nesting patterns in mice implicate MHC genes in kin recognition. Nature 360:581–583.

Miczek KA, Maxson SC, Fish EW, Faccidomo S. 2001. Aggressive behavioral phenotypes in mice. Behav Brain Research 125:167–181.

Mikeš M. 1971. Ekološka prouèvana na mišu-chumkašu (*Mus musculus hortulanus* Nord.) u Vojvodini (Ecological investigations on *Mus musculus hortulanus* Nordmann in Vojvodina). Zbornik za prirodne nauke matice Srpske 40:52–129.

Munclinger P, Božíková E, Šugerková M, Piálek J, Macholán M. 2002. Genetic variation in house mice (*Mus*, Muridae, Rodentia) from the Czech and Slovak Republics. Folia Zool 51:81–92.

Munclinger P, Frynta D. 2000. Social interactions within and between two distant populations of house mouse. Folia Zool 49:1–6.

Muntyanu AI. 1990. Ecological features of an overwintering population of the hillock mouse (*Mus hortulanus* Nordm.) in the south-west of the U.S.S.R. Bilo J Linn Soc 41:73–82.

Orth A, Adama T, Din W, Bonhomme F. 1998. Hybridization naturelle entre deux sous-espèces de souris domestique, *Mus musculus domesticus* et *Mus musculus castaneus*, près du lac Casitas (Californie). Genome 41:104–110.

Palanza P, Re L, Mainardi D, Brain PF, Parmigiani S. 1996. Male and female competitive strategies of wild house mice pairs (*Mus musculus domesticus*) confronted with intruder of different sex and age in artificial territories. Behavior 133:863–882.

Parmigiani S, Palanza P. 1994. Social behavior of wild house mice: the role of the neglected female. Boll Zool 61:47–48.

Parmigiani S, Palanza P, Brain D. 1989. Intraspecific maternal aggression in the house mouse (*Mus domesticus*): a counterstrategy to infanticide by male? Ethol Ecol Evol 1:341–352.

Patris B, Baudoin C. 1998. Female sexual preferences in *Mus spicilegus* and *Mus musculus domesticus*: the role of familiarization and sexual experience. Anim Behav 56:1465–1470.

Patris B, Baudoin C. 2000. A comparative study of parental care between two rodent species: implications for the mating system of the mound- building mouse *Mus spicilegus*. Behav Processes 51:35–43.

Patris B, Gouat P, Jacquot C, Christophe N, Baudoin C. 2002. Agonistic and sociable behaviors in the mound-building mice, *Mus spicilegus*: A comparative study with *Mus musculus domesticus*. Aggressive Behavior 28:75–84.

Prager EM, Orrego C, Sage RD. 1998. Genetic variation and phylogeography of central Asian and other house mice, including a major new mitochondrial lineage in Yemen. Genetics 150:835–861.

Sluyter F, van Oortmerssen GA, Ruiter AJHd, Koolhaas JM. 1996. Aggression in wild house mice: Current state of affairs. Behav Genet 26:489–496.

Sokolov VE, Kotenkova E, Lyalyukhina SI. 1990. Biology of house and mound-building mice. Moskva: Nauka.

Soroker V, Terkel J. 1988. Changes in incidence of infanticidal and parental responses during the reproductive cycle in male and female wild mice *Mus musculus*. Anim Behav 36:1275–1281.

Suchomelová E, Munclinger P, Frynta D. 1998. New evidence of pseudosexual behaviour and female aggression in mice: neutral cage interactions in *Mus spicilegus* and *Mus spretus*. Folia Zool 47:241–247.

Thuesen P. 1977. A comparison of the agonistic behaviour of *Mus musculus musculus* L. and *Mus musculus domesticus* Rutty (Mammalia, Rodentia). Vidensk Meddr dansk naturh Foren 140: 117–128.

Van Oortmerssen GA, Bakker TCM. 1981. Artificial Selection for Short and Long Attack Latencies in Wild *Mus musculus domesticus*. Behav Genet 11:115–126.

Van Zegeren K, van Oortmerssen GA. 1981. Frontier disputes between the West- and East-European house mouse in Schleswig-Holstein, West Germany. Z Saugetierkunde 46:363–369.

Volfová R, Munclinger P, Frynta D. 2002. Aggression in reciprocal crosses of two subspecies of wild house mouse. Folia Zool 51:17–22.

Von Festetics A. 1961. Ärenmaushügel in Österreich. Z Saugetierk 26:112–125.

Vrba I, Donát P. 1993. Activities version 2.1. *Computer programme for behavioural studies.*

Wolff RJ. 1985. Mating behavior and female choice: their relation to social structure in wild caught house mice (*Mu*s *musculus*) housed in a semi-natural environment. J Zool Lond 207:43–51.