SEXUAL SIZE DIMORPHISM
IN FREE-LIVING POPULATIONS OF *MUS MUSCULUS*:
ARE MALE HOUSE MICE BIGGER?

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We studied sexual size dimorphism (SSD) in captive house mice derived from free-living commensal (inhabitants of buildings and stores) and non-commensal (field and/or semidesert dwellers) populations. While females of commensal populations and most strains of laboratory mice are more or less tolerant to each other, females from non-commensal populations are as highly aggressive as their male conspecifics. As body size considerably contributes to fighting success, we addressed the question whether sexual size dimorphism in commensal mice, with larger males, can be attributed to the switch to the commensal way of life. For this purpose, we performed a laboratory common garden experiment in which non-commensal populations of *Mus musculus domesticus* from Jordan and SW Iran were compared with Greek commensal mice belonging to the same subspecies. *M. m. musculus* and natural hybrids of these subspecies from the Czech Republic were also included. Growth was recorded for 102 litters and 592 juveniles born during the experiments, and SSD calculated on the basis of within litter comparisons between the sexes. Males were considerably larger (SSD = 1.05) at the age of 35 days. Newborn males tended to be larger than newborn females but this tendency rapidly disappeared during the early postnatal period. Starting from a nearly monomorphic state at the age of two weeks, size difference between the sexes was established gradually up to the end of the experimental period. We found no significant differences in SSD among the studied populations at any age. Hence, we suppose that the present SSD in the house mouse could be explained by selective forces operating in the non-commensal way of life, which is ancestral with respect to the commensal one.

Key words: *Mus musculus*, wild mice, sexual dimorphism, commensalism, Middle East

INTRODUCTION

Male and female gender roles and life histories may differ considerably. As a result of opposing selective pressures and sexual conflict (for a review see Arnquist & Rowe 2005), some traits may eventually differ between the sexes. Sexual size dimorphism (SSD), the most frequently studied phenomenon of this kind, is closely associated with social and mating systems in many animal taxa (Anderson 1994, Blanckenhorn 2005, Raihani *et al*. 2006, Serrano-Meneses &

SZÉKELY 2006, FAIRBAIRN 2007, SERRANO-MENESES *et al.* 2007*a, b*, 2008, KRA-
TOCHVÍL & FRYNTA 2002, 2007). Monogamous species are typically mono-
morphic, while males are usually larger in polygynous animals (for a review see
SZÉKELY *et al.* 2007). In mammals (for a review see LINDENFORS *et al.* 2007), this
relationship was studied especially in primates (for a review see PLAVCAN 2004)
and ungulates (JARMAN 1983, PEREZ-BARBERIA *et al.* 2002), but it has also been
found in small rodents, e.g., voles (HESKE & OSTFELD 1990, BOONSTRA *et al.*
1993). SSD may be viewed as a sensitive trait for the detection of evolutionary
changes in mating systems and social organisation. Thus, this trait should be ana-
lysed even in the most frequently studied mammalian model – the house mouse.
Male mice (*Mus musculus* LINNAEUS, 1758) are territorial (CROWCROFT & ROWE
1963) and highly aggressive animals (ZEGEREN 1980), which are also poly-
gynous/promiscuous (DOBSON & BAUDOIN 2002). The territory of the dominant
male usually covers the home ranges of several females (CROWCROFT & ROWE
1963) who are predominantly, but not exclusively, mating partners of the resident
male (HURST 1986, POTTS *et al.* 1991, 1994). As the territory ownership is corre-
lated with reproductive success of a particular male, and fighting ability increases
with physical strength and body size, selection in favour of large male body size
may be expected. Supposing that large body size is less advantageous for females,
which are generally less aggressive, it would be expected that males should exhibit
a larger body size in the house mouse. In accordance with this simplified scenario,
DEWSBURY *et al.* (1980), who studied sexual size dimorphism in 13 species of ro-
dents at 35 and 90 days of age, estimated the ratio of female/male size in a wild-de-
rived house mouse strain to be 0.95 and 0.94, respectively.

Nevertheless, the ecology and consequently also social organisation of house
mouse populations have been considerably changed during the last ten thousand
years, since the appearance of agriculture in the Fertile Crescent. Most populations
studied by researchers are those that have already adopted a commensal way of
life; they live inside buildings and have access to concentrated and superabundant
food resources. In contrast, food resources in ancestral non-commensal conditions
were probably rather scarce and dispersed, and may have favoured female spacing
to avoid exploitation competition. Present day populations inhabiting fields and
semideserts of the Fertile Crescent may serve as a model of this non-commensal
way of life. We demonstrated that not only males, but also female mice from non-
commensal populations are usually highly aggressive when subjected to dyadic
encounters with an unfamiliar opponent of the same sex (FRYNTA *et al.* 2005).
This supports the view that female-female interference competition may consider-
ably contribute to fitness in house mice (especially in non-commensal populations)
and therefore should not be overlooked (PALANZA 1993, RUSU & KRACKOW 2004).

SSD evolves as a result of conflicting selective pressures affecting male and female body size. Thus, we hypothesise that the reduction of female-female aggression accompanying adoption of the commensal way of life may be an ultimate cause for house mice males being larger. Alternatively, the observed SSD in this species may have evolved much earlier, before their penetration into buildings, and may not be further explained by ecological and social factors operating in current commensal populations.

The aim of this study was to (1) perform a common garden experiment to examine SSD from an ontogenetic perspective, and (2) assess differences in SSD among house mice populations with respect to the possible effect of commensalism.

MATERIAL AND METHODS

The studied mice were laboratory born outbred descendants (F1–F4 generations) of mice collected by the authors and other colleagues in the field. All animals were kept under an artificial 12 L: 12 D light cycle in breeding rooms at the Faculty of Science of the Charles University in Prague. They were housed by heterosexual pairs in plastic cages $30 \times 15 \times 15$ centimetres 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.

Pairs were controlled every day to detect newborns from September 1997 till June 1998. Juveniles were weighed to the nearest 0.1 g on the day of birth and then regularly every week using electronic scales. Juveniles were not individually marked, but their sex was determined on the first day.

Altogether, we studied 102 litters (592 juveniles) derived from the following regions (Fig. 1): (1) Czech Republic: Černošice (49°58' N, 14°19' E) and Soutice (49°45' N, 15°05' E) in the Central Bohemian Region, Czech Republic, (17 litters; the captive population was derived from 20 pairs of wild founders caught during winter 1993–1994).

(2) The Balkans: most animals came from N Greece in the vicinity of Kilkis (41°00' N, 22°53' E), distr. Kilkis, (18 litters; the captive population was derived from 8 pairs of wild founders caught in May 1995). The parents of four litters came from an adjacent part of Bulgaria: Rupite near the town Petrich (41°47' N, 23° 09' E), distr. Blagoevgrad, SW Bulgaria (the captive population was derived from two pairs of wild founders caught during summer 1996).

(3) Iran: environs of Choqa Zanbil (32°00' N, 48°30' E), distr. Khuzestan, SW Iran (25 litters; the captive population was derived from three males and four females of wild founders caught during May 1996).

(4) Jordan: Wadi al Hiddan and Aqaba (29°32' N, 35°00' E), S Jordan (26 litters; the captive population was derived from a pair from the former site and a male from the latter locality caught during summer 1995). For further information concerning populations 1–4 see SLÁBOVÁ & FRYNTA (2007).

(5) Hybrids: The centre of the hybrid zone between *M. m. musculus* and *M. m. domesticus*, Hazlov, Poustka and Podílná (surroundings of 50°09' N, 12°19' E), W Czech Republic (12 litters; the captive population was derived from five pairs of wild founders caught during 1995); for further information see MUNCLINGER *et al*. 2002, VOLFOVÁ *et al*. 2002, BOŽÍKOVÁ *et al*. 2005, MACHOLÁN *et al*. 2007.

The founders of our colonies from regions 1, 2 and 5 were captured in populations perma-
nently living in buildings and/or stores; hereafter these stocks are further referred to as commensal.
Those from regions 3 and 4 were captured in open landscapes (on fields or surrounding semi-deserts).
Although it cannot be excluded that some animals of these populations may temporarily migrate to
buildings during the short winter period, these populations were apparently independent of human
settlements; these are further referred to as non-commensal.

The first step of data processing was to remove the within-litter component of variation by cal-
culating mean body weight of males and females for each litter and age. These mean values were used
as the data in further analyses. Because body weight exhibited a log-normal distribution, we em-
ployed geometric means instead of the simple ones.

Alternatively, we performed all analyses described below based on simple means; neverthe-
less, both procedures produced almost the same results. Therefore, we report only the analyses based
on the geometric means.

Next we calculated between-litter geometric means of these within-litter values for each com-
bination of age, sex and population. These between-litter mean values allowed us to compare body
size between the sexes and express the SSD. For reasons discussed in detail by SMITH (1999), we de-
cided to employ the LOVICH–GIBBONS revised two-step ratio (i.e., if M = F, dimorphism = M/F, if F =
M, dimorphism = 2 – F/M; further abbreviated as LG; LOVICH & GIBBONS 1992). Significance of par-
tial SSDs was estimated using pair-wise t-tests.
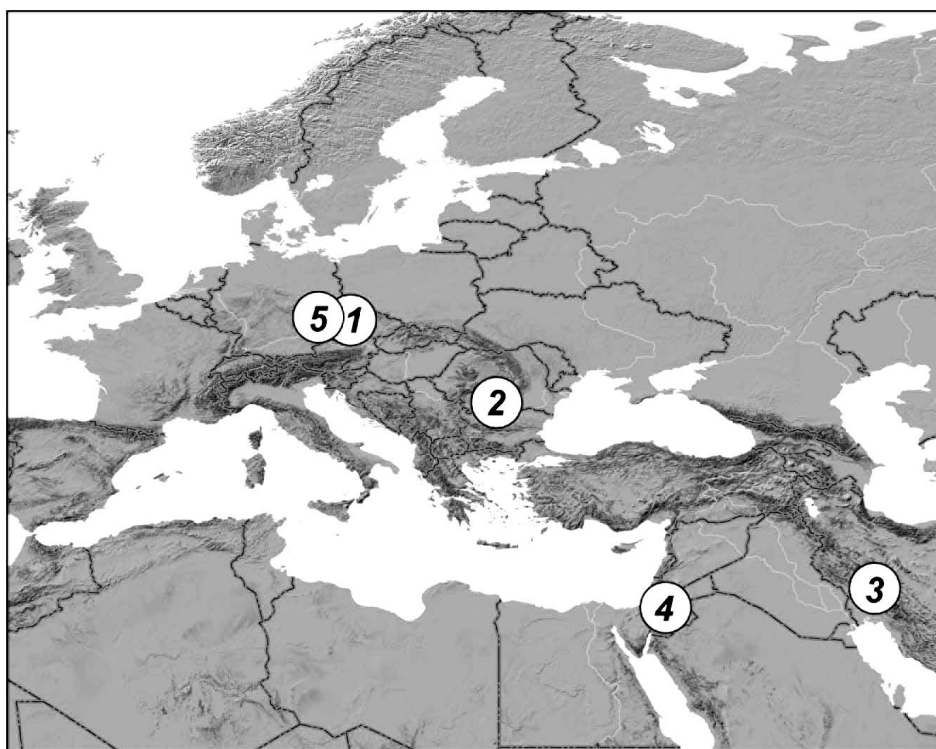
Fig. 1. Map of the studied localities: 1 = Czech Republic, 2 = The Balkans, 3 = Iran, 4 = Jordan, 5 =
hybrids. See Material and Methods for coordinates of the localities

In order to avoid statistical problems associated with the use of ratios, we used the non-parametric Kruskall-Wallis test to compare SSD among the populations.

STATISTICA Analysis System (version 6.0) was used for most calculations. In addition, we performed GLMM to assess the effects of fixed factors population, age and their interaction on SSD; litter identity was included as a random factor and litter size as a covariate. These calculations were performed using SPSS (Statistical Package for the Social Sciences, version 16.0).

The experiments were performed in accordance with current Czech law and regulations and were approved by the Institutional Animal Care and Use Committee of the Charles University.

RESULTS

Males were the larger sex in all studied populations. Almost all Lovich-Gibbons ratios of body mass calculated separately for every combination of age and population were higher than one (Table 1, Fig. 2).

There was a clear pattern of SSD during postnatal growth which was almost the same across the studied populations (Fig. 1). Males were slightly larger in newborns (N = 77 litters; LG = 1.0579; t = –4.92, P < 0.0001) and partially also in one week old juveniles (N = 84 litters; LG = 1.0346; t = –2.16, P = 0.033). At the age of two weeks, no significant SSD was recorded (N = 81 litters; LG = 1.0185; t = –1.87, P = 0.065). The SSD then gradually increased starting from weaning attempts at the age of three weeks (N = 79 litters; LG = 1.0267; t = –2.69, P = 0.009; four weeks: N = 74 litters; LG = 1.0601 and N = 65 litters; LG = 1.1140; t = –6.64 and t = –8.85; at the age of four and five weeks, respectively; both P < 0.0001).

No significant effect of population on SSD (within litter Lovich-Gibbons ratio in body mass) was found by Kruskall-Wallis tests performed separately for each age (all P > 0.34). Consequently, there was good agreement between the above tests of SSD in pooled material and those evaluating individual populations.

The above partial comparisons were clearly supported by GLMM in which the LG-ratio was taken as the dependent variable and litter identity included as the random factor. The results revealed an age effect ($F_{5,92.1}$ = 10.29; P < 0.001; for estimates see Table 2), but showed no effect of population ($F_{4,94.4}$ = 0.79; P = 0.538) nor their interaction ($F_{20,96.7}$ = 0.71; P = 0.81). A covariate also had no significant effect (litter size: $F_{1,80.4}$ = 1.94; P = 0.17).

DISCUSSION

We found no significant differences in SSD among the studied populations. Thus, SSD is comparable in commensal populations with fighting males and peaceful females, and in non-commensal populations where both sexes are highly

Table 1. Mean male and female weights, Lowich-Gibbons ratios (LG) and statistical significance of SSD (revealed by pair-wise t-test). N = number of litters; W = mean body weight in grams; CI = confident interval (see under Material and Methods).

Population	Age (days)	Females				Males				LG	T – test	
		N	W	CI –95%	CI +95%	N	W	CI –95%	CI +95%		t	p
Iran[1]	0	14	1.19	1.065	1.333	14	1.24	1.098	1.410	1.044	–1.25	0.2324
	7	19	3.26	2.922	3.533	18	3.33	3.022	3.660	1.035	–1.26	0.2256
	14	18	5.33	4.811	5.630	17	5.35	4.939	5.796	1.028	–1.03	0.3189
	21	18	7.54	6.915	8.227	18	7.6	6.906	8.373	1.008	–0.34	0.7365
	28	15	9.55	8.947	10.192	15	10.1	9.493	10.747	1.058	–2.78	**0.0148**
	35	14	11	10.211	11.528	13	12.3	11.293	13.444	1.136	–3.91	**0.0021**
Jordan[1]	0	13	1.21	1.098	1.305	12	1.24	1.134	1.347	1.032	–1.38	0.1957
	7	18	3.78	3.436	4.175	17	3.82	3.472	4.212	1.01	–0.77	0.451
	14	17	6.34	5.782	6.914	16	6.42	5.851	7.033	1.015	–1.09	0.2922
	21	15	8.01	7.336	8.692	14	8.07	7.468	8.711	1.01	–0.56	0.5828
	28	16	9.14	8.517	9.844	15	9.56	8.791	10.392	1.044	–2.09	0.0558
	35	14	10.2	9.696	10.637	14	11.2	10.318	12.062	1.099	–3.59	**0.0033**
The Balkans[2]	0	22	1.21	1.113	1.302	19	1.26	1.178	1.344	1.045	–2.04	0.0567
	7	22	2.93	2.621	3.261	19	3.1	2.766	3.485	1.062	–1.08	0.2943
	14	22	4.59	4.370	5.213	19	4.82	4.343	5.357	1.011	–0.53	0.6006
	21	22	6.41	6.138	7.050	19	6.83	6.252	7.453	1.038	–1.69	0.1075
	28	21	8.22	7.802	9.012	18	9.03	8.347	9.778	1.077	–3.91	**0.0011**
	35	18	9.12	8.274	9.904	15	10.2	9.358	11.093	1.126	–3.87	**0.0017**

Table 1 (continued)

Population	Age (days)	Females				Males				LG	T – test	
		N	W	CI –95%	CI +95%	N	W	CI –95%	CI +95%		t	p
Hybrids[3]	0	12	1.29	1.143	1.422	11	1.37	1.217	1.536	1.072	-2.46	**0.0336**
	7	11	3.69	3.060	4.232	10	3.67	3.144	4.280	1.019	-1.18	0.269
	14	11	5.98	5.034	6.710	10	5.8	5.020	6.700	0.998	0.17	0.8696
	21	11	7.52	6.638	8.099	10	7.66	6.911	8.489	1.045	-1.68	0.1268
	28	11	9.23	7.894	10.247	10	9.69	8.427	11.131	1.077	-4.36	**0.0018**
	35	10	10	8.593	11.060	9	10.8	9.572	12.162	1.107	-3.58	**0.0072**
Czech Republic[4]	0	17	1.13	1.067	1.206	17	1.24	1.163	1.323	1.093	-4.91	**0.0002**
	7	16	2.83	2.663	3.010	16	2.94	2.767	3.124	1.039	-2.57	**0.0214**
	14	16	4.22	3.762	4.587	15	4.3	3.929	4.714	1.036	-2.72	**0.0165**
	21	15	6.02	5.434	6.431	14	6.15	5.749	6.579	1.04	-2.27	**0.0411**
	28	15	7.88	7.195	8.145	13	7.93	7.269	8.654	1.036	-1.79	0.0985
	35	12	8.85	8.269	9.409	10	9.68	8.851	10.587	1.098	-3.93	**0.0035**

[1]non-commensal *M. domesticus*
[2]commensal *M. domesticus*
[3]hybrid zone of *M. musculus* and *M. domesticus*
[4]*M. musculus*

Table 2. Estimates of age effect found by GLMM (dependent variable – LG-ratio, random factor – litter identity). CI = confident interval (see under Material and Methods).

Age (days)	Estimate	CI –95%	CI +95%
0	–0.0106	–0.0843	0.0630
7	–0.0694	–0.1725	0.0336
14	–0.0709	–0.1368	0.0050
21	–0.0694	–0.1358	0.0030
28	–0.0632	–0.1274	0.0010
35	0		

aggressive. The commensal way of life in Middle East populations is obviously a derived state and has only a short history of about ten thousand years (AUFFRAY *et al.* 1988, 1990*a, b*, CUCCHI *et al.* 2002). This period may be too short to allow for a substantial increase in SSD. If this is the case, the low degree of SSD found in house mouse populations should be analysed in the light of social and ecological factors operating in ancestral house mice populations that obviously lived in
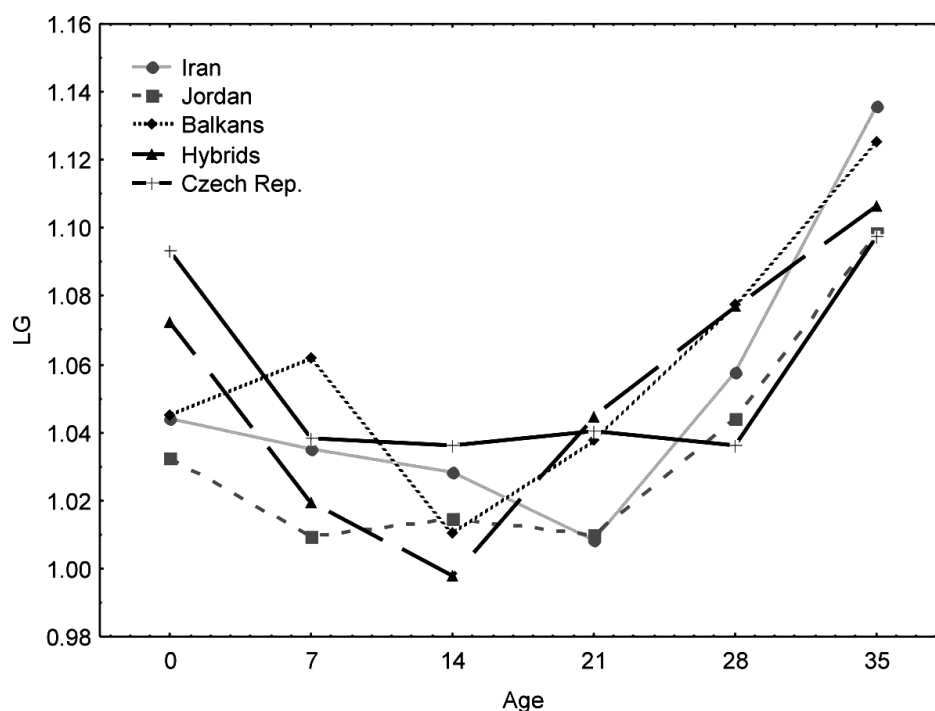
Fig 2. Variation in SSD during the first five weeks of postnatal development in five mice populations. SSD is expressed as Lowich-Gibbons ratios of mean body weight (see under Material and Methods)

non-commensal conditions. Although females are somewhat less aggressive than males even in non-commensal populations (FRYNTA *et al*. 2005), unlike in commensal house mice, this difference is small and thus it conforms to the limited SSD found in house mice. Nevertheless, one may argue that ten thousand years is enough time for morphological change and the low SSD in house mice is due to constraints. This interpretation may be supported by the small body size of the house mouse (cf. Rensch's rule suggesting that male to female body size ratio increases with body size; see FAIRBAIRN 1997, LINDENFORS *et al*. 2007, POLÁK & FRYNTA 2009, 2010) and limited variation in SSD in rodents (WOLF & SHERMAN 2007). Current literature emphasise that SSD is a dynamic phenomenon resulting from sex differences in growth and development (BADYAEV 2002).

This approach was fruitfully applied in reptilian (COX & JOHN-ALDER 2007), bird (BADYAEV *et al*. 2001*a, b*, 2003) and mammalian models (ATMOKO & HOOFF 2004 and references herein). We analysed ontogenetic trajectories of mice SSD within the period of early postnatal development and demonstrated consistent sex differences in growth patterns. With the notable exception of birth weight, body weight was least dimorphic during the first three weeks of life when the pups are fully dependent on the nest due to thermoregulatory demands and mother's milk (KONIG & MARKL 1987). This suggests that male and female pups receive about the same amount of parental effort. The observed difference between male and female weight at birth was completely compensated, and disappeared at the end of the nesting period. This, together with other reasons (large litter size), may disprove the usefulness of house mice as model species for testing some predictions of sex ratio theory (e.g. TRIVERS & WILLARD 1973, for a review see HARDY 1997) requiring unequal investment to male and female offspring (see KRACKOW 1997).

Earlier studies performed on laboratory mice (reviewed by GLUCKSMANN 1974) reported that the difference between mean male and female weights is restricted to particular age classes. Males are about 5% heavier at the age of six weeks, while both juvenile and old mice are nearly monomorphic. We studied SSD up to the age of considerable life history decisions associated with sexual maturation. We confirmed that males are the larger sex at the age of 35 days and obtained SSD values similar to those reported by DEWSBURY *et al.* (1980). However, this finding does not necessarily mean that house mice are also dimorphic in adulthood. Morphometric studies performed on adult house mice (MACHOLÁN 1996*a, b*, 2001, SLÁBOVÁ & FRYNTA 2007) usually reported no significant SSD and treated this species as monomorphic.

Nevertheless, the question whether house mice exhibit SSD is further complicated by the following two factors: (1) like other small mammals (VOHRALÍK 1975, FRYNTA & ŽIŽKOVÁ 1992), mice continue to grow throughout their life, and

(2) growth may be affected by phenotypic plasticity (sensu WEST-EBERHARD 2003) and therefore life-history decisions may alter SSD. For example, most authors studied individually housed animals, i.e. they compared males in reproductive conditions with virgin females. Such an approach results in considerable underestimation of female body size (see DEWSBURY 1992 in *Peromyscus maniculatus*). Sexual size dimorphism reported for laboratory rodents can therefore be just an artefact of differential ontogenetic timing of growth and its regulation in males and females. Thus, a full understanding of factors affecting trajectories of SSD during the entire postnatal ontogeny requires experimental manipulation of life history decisions. Although the house mouse is probably the most studied mammalian species, to the best of our knowledge, such experiments are still missing in this model species.

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