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First report on social behaviour of *Apodemus hyrcanicus* and *A. witherbyi* (Mammalia: Rodentia) from Iran

Daniel Frynta[1,*)], Jovana Sádlová[2)], Hana Váchová[1)], Eva Cepáková[1,3)] & Pavlína Kuncová[1,4)]

[1)] Charles University, Faculty of Science, Department of Zoology, Viničná 7, CZ–128 43 Praha 2, Czech Republic
[2)] Charles University, Faculty of Science, Department of Parasitology, Viničná 7, CZ–128 43 Praha 2, Czech Republic
[3)] Agency for Nature Conservation and Landscape Protection of the Czech Republic, Kališnická 4, CZ–130 23 Praha 3, Czech Republic
[4)] Ministry of Environment of the Czech Republic, Czech Republic
*) Corresponding author: e-mail: frynta@centrum.cz, daniel.frynta@natur.cuni.cz

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Abstract. We present comparative behavioural data in two yet unstudied wood mice species: *Apodemus hyrcanicus* Vorontsov, Boyeskorov, Mezhzherin, Lyapunova et Kandaurov, 1992, a recently described endemic of the Hyrcanian forest along the southern coast of the Caspian Sea, and the population coming from the Fars Province, Iran, belonging to *A. witherbyi* (Thomas, 1802). Eighty three dyadic interactions in a neutral cage were performed to quantify the behavioural patterns and to assess differences between the species and sexes. *A. hyrcanicus* spent high proportion of time by amicable behaviour and were not aggressive. In this respect, the patterns of their social behaviour resembled those of European populations of *A. uralensis*. In a sharp contrast, males of *A. witherbyi* were considerably more aggressive, and amicable acts were almost absent in both sexes of this species.

Key words. Agonistic behaviour, aggression, mice, *Sylvaemus, Apodemus hermonensis*.

INTRODUCTION

Wood mice of the genus *Apodemus* Kaup, 1829 are widely distributed throughout the Palaearctic region (Musser et al. 1996, Mitchell-Jones 1999). Due to their abundance and important ecological role they have attracted attention of many researchers (for a review see, e.g., Montgomery 1989). More than 2000 papers have been aimed at this genus even before the year 1981 (Jüdes 1982), and the Web of Science database reports more than 3100 hits for the key word *Apodemus* from that year till present. In spite of this, ecology and behaviour of some species, especially those coming from politically hot areas of south Asia has remained virtually unstudied (cf. Musser et al. 1996). It is also the case of the following two *Apodemus* species inhabiting Iran and neighbouring areas of the Middle East (for the exception see Haim et al. 1996).

Recently, *Apodemus hyrcanicus* Vorontsov, Boyeskorov, Mezhzherin, Lyapunova et Kandaurov, 1992 has been described from the Hyrcanian Reserve in southeastern Azerbaijan (Vorontsov et al. 1992, Boyeskorov et al. 1995). In the neighbouring Irani provinces of Gilan and Mazandaran, we found a morphometrically and genetically distinct form of *Apodemus* (Frynta et al. 2001, Macholán et al. 2001, Bellinvia 2004, Frynta et al. 2006, Kuncová & Frynta 2009) which is conspecific with *A. hyrcanicus*. Our site Gichob is only about 80 km from the type locality and both the appearance

of the mouse and morphometric characters support this view. We further confirmed this conclusion by a preliminary comparison of mitochondrial sequence data (Frynta, unpubl. data). Next, morphology, distribution and genetics of *A. hyrcanicus* in Iran has been thoroughly examined (Javidkar et al. 2005, 2007, Siahsarvie & Darvish 2008, Jangjoo 2010, Jangjoo et al. 2011, Darvish et al. 2015). Obviously, this species is restricted to the subtropical Hyrcanian forest along the southern coast of the Caspian Sea. This extremely wet woodland area supported survival of the Tertiary forest species during Quarternary, and consequently exhibits a high degree of endemism in both plant and animal taxa (e.g., reptiles, Anderson 1999). The area is efficiently isolated by seashore in the north, by the Elborz Mts. in the south and by surrounding semidesert and desert areas in the west and east, and its ecological conditions are very specific.

While *A. hyrcanicus* is known from only a few specimens and its distribution area seems to be very restricted, *A. witherbyi* (Thomas, 1902) has much broader distribution in the Middle East (for a review see Kryštufek & Vohralík 2009). Filippucci et al. (1989) recognized *A. witherbyi* as a distinct species from high elevations of Mt. Hermon in Israel. They described it as *A. hermonensis* Filippucci, Simson et Nevo, 1989 which is currently treated as a junior synonym of *A. witherbyi*. Later on, conspecific populations have been found in Turkey (Filippucci et al. 1996, Bellinvia et al. 1999, Macholán et al. 2001, Kryštufek & Vohralík 2007), the Mediterranean island of Bozcaada/Tenedos (Özkan & Kryštufek 1999), Armenia (Balasanyan et al. 2018) and Iran (Frynta et al. 2001, Macholán et al. 2001, Hosseinpour et al. 2009, Darvish et al. 2015). The species was thoroughly examined by genetic methods, e.g., Filippucci 1992, Bellinvia et al. 1999, Bellinvia 2004, Macholán et al. 2001, Filippucci et al. 2002, Michaux et al. 2002, Darvish et al. 2015, Balasanyan et al. 2018). The conspecificity of Caucasian, Ukrainian and south-Russian populations assigned to *A. fulvipectus* Ognev, 1924 with the Middle East ones has been hypothesised (for molecular confirmation see Hoofer et al. 2007, but see Reutter et al. 2003), and the prior available name *A. arianus* (Blanford, 1881) has been suggested for this species (Mezhzherin 1997, Zagorodnyuk et al. 1997). Nevertheless, Kryštufek (2000) examined the type specimen of *A. arianus* morphologically and concluded that it belongs probably to *A. flavicollis* (Melchior, 1834). Thus, he suggested the name *Apodemus iconicus* Heptner, 1948 for this taxon. Finally, the name *A. witherbyi* (Thomas, 1902) described right from the Fars Province of Iran was adopted for this species.

Our stock came from the surroundings of the Shiraz town in the Fars Province, i.e., the south-eastern limit of known range of *A. witherbyi*, and its species determination was unequivocally proved by multivariate morphometrics (Frynta et al. 2001).

Behavioural tests performed under standardised laboratory conditions have been successfully used in comparative studies of numerous species of small rodents, in particular voles and deer mice of North America (e.g., Wilson et al. 1976, Dewsbury et al. 1978, Evans et al. 1978, Webster et al. 1979, 1981, Baumgardner et al. 1980, Dewsbury 1980, 1981, Wynne-Edwards & Lisk 1987). They may help us to assess the adaptive profile of studied species and predict some features of its social or mating systems. Such tests are especially useful in the case of rare species.

In the Palaearctic mice of the genera *Mus* Linnaeus, 1758 and *Apodemus*, comparative studies have been focused on the exploratory (e.g., Frynta 1992, 1994, Meshkova et al. 1999, Simeonovska-Nikolova 2000, Frynta et al. 2018) and agonistic behaviour (e.g., Thuessen 1977, Montgomery 1978, van Zegeren & van Oortmerssen 1981, Ivantcheva & Cassaing 1999, Patris et al. 2002), and the behavioural traits associated with mating systems like mate choice and paternal care (Patris & Baudoin 1998, 2000, Dobson & Baudoin 2002, Frynta et al. 2010).

We performed dyadic interactions in a neutral-cage in five species of house mice (Frynta & Čiháková 1996, Suchomelová et al. 1998, Munclinger & Frynta 2000, Volfová et al. 2002, Frynta et al. 2005) and five species of wood mice (Čiháková & Frynta 1996, Frynta et al. 1995,

Suchomelová & Frynta 2000, Váchová & Frynta 2004). In both genera, a surprising variation in the observed behavioural patterns was found. There are almost non-aggressive species as well as those highly aggressive. Males are usually more aggressive than conspecific females, however, there are some species or populations exhibiting elevated female aggression (Frynta et al. 2005). In the case of the genus *Apodemus*, the central European populations of *A. uralensis* are extremely peaceful while *A. flavicollis*, *A. mystacinus* (Danford & Alston, 1877) and *A. agrarius* (Pallas, 1771) exhibited high scores of agonistic behaviour.

We studied social interactions of *A. hyrcanicus* and *A. witherbyi* in a standard laboratory situation permitting quantification of observed behavioural patterns. The aim of this study was: (1) to describe behaviour of these species for comparative purposes, (2) to assess the effects of sex and (3) to discuss the results in the context of similar studies performed in other *Apodemus* species.

MATERIAL AND METHODS

Experimental animals were: (1) *Apodemus hyrcanicus.* Eight males and eight females captured on 16–17 May 1997, Gichob village 12 km W of Asalem, Gilan Province, Iran (coordinates: 37° 41' 12" N, 48° 50' 55" E, 297 m a. s. l.), and five males and two females captured on 13–14 May 1997 near Now Kandeh, Mazandaran Province, Iran (36° 40' 47" N, 53° 52' 17" E, 280 m a. s. l.). They were tested in August 1997. (2) *Apodemus witherbyi.* Twelve males and twelve females of the first or second laboratory-born generations. They were descendants of the mice captured at the locality Dasht-e Arzhan, vicinity of Shiraz, Fars Province, Iran, 21–22 April 2000 (29° 34' 64" N, 51° 56' 89" E, 2000 m a. s. l). The experiments were carried out in July 2001.

Mice were housed in heterosexual pairs in standard cages (30×15×15 cm). Each cage contained sawdust bedding, nesting material and a shelter. Cages were placed in a room with natural light-dark cycles. Mice were provided with ad libitum water and food (mouse and rat breeder diet ST1, sunflower seeds, bread, apples, etc.).

A standard neutral-cage procedure (with minor changes adopted from Gurnell 1977 and Montgomery 1978, for details see Čiháková & Frynta 1996) was used. Encounters between mice were studied in a 50×30×35 cm glass cage illuminated with a single 40 W red-light bulb. The cage was divided by a thick card partition into two equal parts. 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, each on the opposite side of the partition, and left for five minutes. Then the central partition was removed and video recording started. The camera was stopped ten minutes after the moment when one or both animals paid attention to the other for the first time (e.g,, oriented head movement, approaching, sniffing the opponent). The cage was thoroughly cleaned using 96% ethanol after each session.

At the time of testing the experimental animals were adult (more than four months old), males had large testes in scrotal position and also females showed signs of sexual activity (open vagina), nevertheless, they were neither pregnant nor lactating.

Overall, 23 male-male and 12 female-female encounters were performed in *A. hyrcanicus,* and 24 male-male and 24 female-female encounters in *A. witherbyi*. Each animal was tested with different opponents up to four times. Repeated testing of the same dyad (a unique combination of animals) was avoided. Testing of the same individual occurred no earlier than 24 hours after the preceding test.

Video records were subsequently observed and quantified, using the computer program package ACTIVITIES (Vrba & Donát 1993). The following categories of behaviour were distinguished: Agonistic behaviour (i.e., threat, aggressive upright, attack, chase, roll-over fight, neutral upright, box, ambivalent, submissive, defensive upright and/or threat, avoid-retreat, flee-jump avoid), Amicable behaviour (social grooming and body contact), Introductory behaviour (attend--approach, nose-follow), Exploratory behaviour and Individual behaviour (for description and grouping of behavioural elements see Čiháková & Frynta 1996). Sums of time spent by both animals of a dyad by particular categories of behaviour were computed (total time of each observation is 1200 seconds, i.e., ten minutes for each of two opponents) and further analysed.

The total duration of agonistic and amicable behaviours were log-transformed to meet the requirements of ANOVA and/or ANCOVA. Because no effects of repeated testing, mean body weight and weight difference of the interacting mice were found ($P>0.1$), these variables were excluded from the models and only the effects of Sex and Species were further examined. As homogenity of variance was violated by inclusion of both species into a single analysis, non-parametric Mann-Whitney tests were adopted to validate the ANOVA results. Significant comparisons which passed the requirements of Bonferroni correction (α was divided by the number of comparisons concerning single data set) were exactly the same as those obtained by *post hoc* Scheffe tests given below under the Results. Calculations were carried out using Statistika version 6.0 software.

RESULTS

The studied species and sexes clearly differed in patterns of neutral cage behaviour (Appendix 1). *Apodemus hyrcanicus* dyads were characterised by high proportion of amicable behaviour and low aggression. In contrast, *A. witherbyi* exhibited almost no amicable behaviour and the representation of agonistic behaviour was much higher, particularly in males. Concerning non-social behaviour, *A. witherbyi* were markedly more active, spending more time by exploratory than by individual behaviour (grooming, sitting).

ANOVA has revealed highly significant effects of the Species (F=48.11, P<0.0001), Sex (F=12.42, P=0.0007), but not of the Species-Sex interaction (F=0.01, P=0.9155) on time spent by agonistic behaviour (Fig. 1). Consequently, *post hoc* Scheffe tests (P<0.05) showed that *A. hyrcanicus* females spent less time by agonistic behaviour than *A. witherbyi* of either sex, *A. hyrcanicus* males less than *A. witherbyi* males, and *A. witherbyi* females less than *A. witherbyi* males.

In contrast, the time spent by amicable behaviour (Fig. 2) was affected by the Species (F=295.14, P<0.0001), but not by the Sex (F=0.23, P=0.6331) nor Species-Sex interaction (F=1.51, P=0.2215). *Post hoc* comparisons revealed that *A. hyrcanicus* of both sexes were more amicable than *A. witherbyi* of either sex.

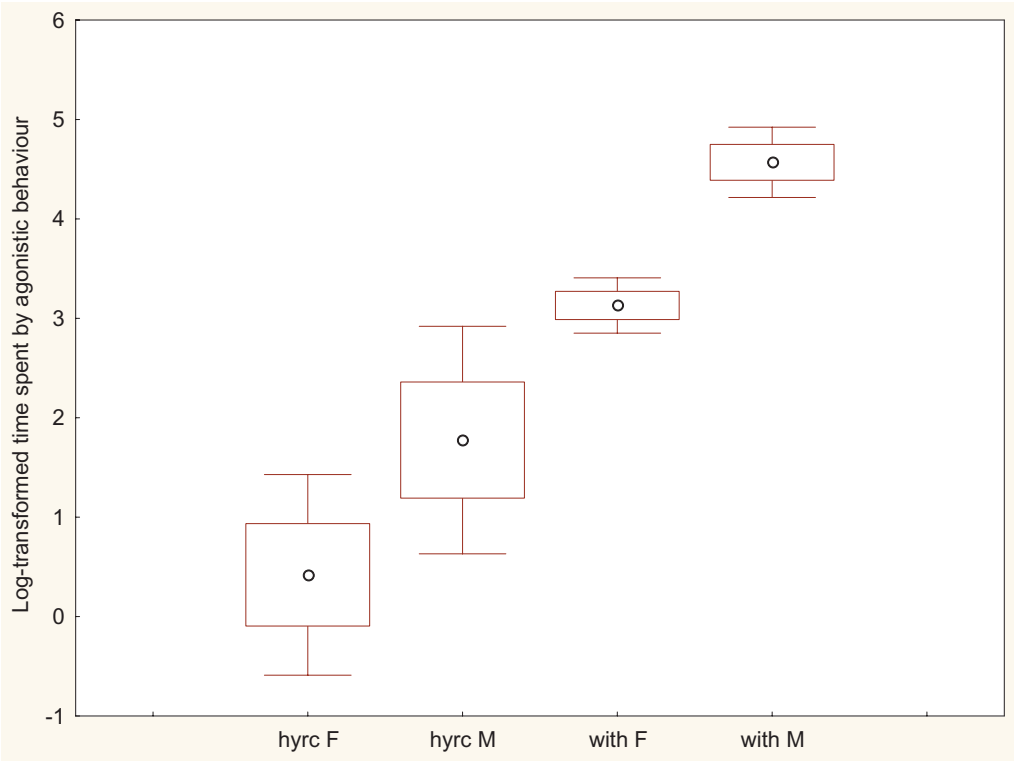

Fig. 1. Time spent by agonistic behaviour (in seconds natural log-transformed) in female-female (F) and male-male (M) dyads in *Apodemus hyrcanicus* and *A. witherbyi*. Median, quartils, non-outlier range, and outliers are provided. Abbreviations: hyrc = *Apodemus hyrcanicus*; with = *Apodemus witherbyi.*

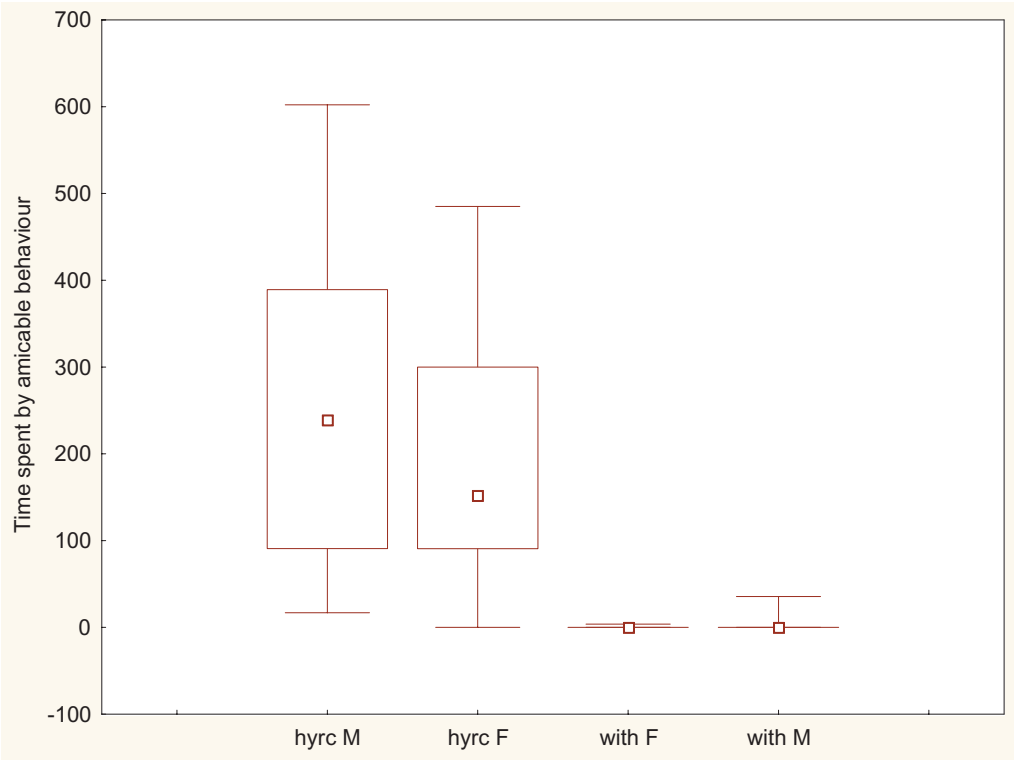

Fig. 2. Time spent by amicable behaviour (in seconds) in male-male (M) and female-female (F) dyads in *Apodemus hyrcanicus* and *A. witherbyi*. Median, quartils, non-outlier range, and outliers are provided. Abbreviations: hyrc = *Apodemus hyrcanicus*; with = *Apodemus witherbyi.*

DISCUSSION

Behavioural patterns exhibited by *A. hyrcanicus* in our experiments were clearly distinct and uncommon among small muroid rodents subjected to the neutral-cage procedure so far (e.g., Frynta et al. 1995, Čiháková & Frynta 1996, Frynta & Čiháková 1996, Suchomelová et al. 1998, Frynta et al. 2003). Nevertheless, they resembled those reported in central European populations of *A. uralensis* (Suchomelová & Frynta 2000), the species that seems to regularly exhibit active peace-keeping strategy involving "cooperate first" when exposed to unfamiliar conspecifics (Suchomelová & Frynta 2000). This kind of active cooperative strategy is a rare phenomenon in animal societies (for a review see Dugatkin 1997) and *A. uralensis* was therefore used as a model for studies dealing with social cooperation (Stopka & Graciasová 2001).

Like *A. uralensis*, *A. hyrcanicus* also spent enormous proportion of the total time by amicable behaviour: 15.9% in male-male and 21.5% in female-female dyads, respectively. These percentages exceeded many times (4.3 and 73.4 times in males and females, respectively) the corresponding values of agonistic behaviour. Thus, most neutral-cage interactions in *A. hyrcanicus* were apparently not only peaceful, but even amicable. There were, however, three exceptional male-male

dyads with high proportion of agonistic behaviour (10.3%, 18.3% and even 24.2% of total time). To exclude the potential effect of season and/or sexual activity, we repeated some dyadic encounters of *A. hyrcanicus* after several months and found exactly the same amicable pattern as before. In addition to peaceful interactions in a neutral cage, *A. hyrcanicus* (like *A.uralensis*) behaved markedly non-aggressively also when handled.

Nevertheless, neutral-cage behaviour of *A. uralensis* and that of *A. hyrcanicus* differ in important details: the mean proportion of amicable behaviour in *A. uralensis* was even higher (27.8–29.6% of the total observation time; Suchomelová & Frynta 2000), and mutual grooming (i.e., the "altruistic" element of amicable behaviour) was more represented in *A. uralensis* (from 4.5 to 9.7% of the total time spent by amicable behaviour, Suchomelová & Frynta 2000) than in *A. hyrcanicus* (1.8 and 2.2%). We can conclude that amicable character of dyadic encounters is somewhat less expressed in *A. hyrcanicus* than in *A. uralensis.*

In a sharp contrast to *A. hyrcanicus,* both sexes of the Fars population of *A. witherbyi* exhibited less exceptional patterns of neutral-cage behaviour. Mean proportions of time spent by agonistic behaviour (11.5% in males and 2.3% in females) were similar to corresponding values in European *A. sylvaticus* (Linnaeus, 1758) (9.9% and 4.8% Čiháková & Frynta 1996), i.e., the species sharing both similar body size and ecological requirements with *A. witherbyi*. Although the level of aggression in *A. sylvaticus* is much higher than in *A. uralensis,* it is usually considered to be rather low (e.g., Bovet 1972, Hoffmeyer 1973, Garson 1975, Gurnell 1977, Montgomery 1978, Lambin 1988). The proportions of agonistic behaviour reported in most aggressive *Apodemus* species such as *A. agrarius*, *A. mystacinus* and *A. flavicollis* are, however, somewhat higher (Frynta et al. 1995, Čiháková & Frynta 1996, Váchová & Frynta 2004).

The proportion of amicable behaviour we found in *A. witherbyi* (<0.2% of the total time) was unusually low (e.g., *A. sylvaticus*: 2.2% in males and 8.2% in females, Čiháková & Frynta 1996). Since it contradicts our experience concerning the wild-caught *A. witherbyi* from eastern Turkey and western Iran (Frynta & Cepáková, unpubl. data), we prefer to interpret the low representation of amicable acts in our experiments as a side-effect of high locomotion and exploratory activity of studied mice. They were laboratory born individuals, well familiarised with the laboratory conditions, and consequently exhibited no fear when placed into the experimental pen. Nevertheless, they spent considerable proportion of time by social behaviour, and therefore, the nearly complete absence of amicable behaviour is still worth of attention.

We can conclude that the studied species exhibited clearly different behavioural patterns in a standardised situation. Although the relevance of the experiments performed in an artificial environment to the behaviour in nature may be questioned, our results might indicate differences in social strategies of these nearly forgotten species.

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APPENDIX 1

Mean duration (in seconds) of individual behavioural categories. Means are calculated per encounter (dyad)

	Apodemus hyrcanicus		*Apodemus witherbyi*	
	F	M	F	M
N dyads	12	23	24	24
threat-attack	0.0	4.5	0.7	5.3
aggressive upright	0.0	0.8	0.0	4.9
chase	0.0	0.8	0.0	10.3
roll-over fight	0.0	1.4	0.2	10.9
neutral upright	0.0	1.2	6.2	9.1
box	0.0	0.1	1.0	0.0
tofro	0.0	2.9	7.8	12.5
tail-rattle	0.0	0.0	0.1	0.7
avoid-retreat	3.3	8.7	10.4	14.6
defensive	0.0	18.0	1.2	53.8
flee and jump-avoid	0.2	0.9	0.0	12.6
freeze	0.0	5.1	0.0	0.2
submissive	0.0	0.3	0.0	2.5
agonistic	3.5	44.6	27.5	137.5
SE	0.9	15.5	3.1	25.0
body contact	252.8	186.9	0.5	0.4
mutual groom	5.7	3.5	0.0	1.7
amicable	258.4	190.4	0.5	2.1
SE	57.3	29.1	0.2	1.5
attend	1.5	1.9	2.0	3.3
approach	1.3	2.8	3.9	4.3
nose-follow	63.6	65.8	84.3	100.1
introductory	66.4	70.5	90.3	107.7
SE	11.6	6.7	8.9	9.8
loco-exploratory	191.9	164.2	432.6	344.2
rear-jump	95.8	52.9	218.1	140.5
exploratory	287.7	217.1	650.7	484.6
SE	45.5	24.3	38.8	31.8
selfgroom	107.9	133.7	172.2	188.7
sit	476.1	543.7	258.9	279.4
individual	584.0	677.4	431.0	468.1
SE	38.4	21.3	42.8	30.1