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SHORT COMMUNICATION

Frequency and distribution of *t*-haplotypes in the Southeast Asian house mouse (*Mus musculus castaneus*) in Taiwan

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Abstract

***t*-haplotypes are a meiotic drive system found on the 17th chromosome of the house mouse (*Mus musculus*). They can be found in wild populations of all four genetically differentiated subspecies. The drive phenomenon is male-specific, such that heterozygous males (+/*t*) show non-Mendelian transmission and transmit the *t*-chromosome to > 90% of their offspring. So far the most comprehensive studies on the frequencies of *t*-haplotypes in natural populations have been on just one of the subspecies (*M. musculus domesticus*). We applied molecular methods to accurately screen *t*-haplotypes in a large number of populations of a second subspecies (*M. musculus castaneus*) distributed in Taiwan. We found that the overall *t*-haplotype frequency is low in *M. m. castaneus* (0.108), and the chromosomes are patchily distributed among its populations, closely resembling the situation found in *M. m. domesticus*. Further, we found the frequencies of *t*-haplotypes in our sample did not differ in relation to the sex or age of mice. This resemblance in the frequency and distribution among populations of the two distinct subspecies suggests that similar general mechanisms might be responsible for the low frequencies in both subspecies.**

Keywords: meiotic drive, *Mus musculus*, *M. m. castaneus*, *t*-haplotypes, transmission ratio distortion, wild mice

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Introduction

t-haplotypes are natural mutant forms of chromosome 17 in the house mouse (*Mus muculus*) (Silver 1985, 1993; Hammer *et al*. 1989; Ardlie 1998). They show non-Mendelian transmission from heterozygous +/*t* males, such that 90% of their offspring inherit the *t*-chromosome. Despite this powerful selective advantage in favour of *t*-haplotypes, many surveys of *t*-haplotypes show frequencies, much lower than expected, of around 10–25% +/*t* mice (see Ardlie & Silver 1998), and the mechanisms maintaining *t*-haplotypes in wild mouse populations have been the focus of *t*-haplotype research for decades (Silver *et al*. 1987; Delarbre *et al*. 1988; Hammer *et al*. 1989; Morita *et al*. 1992; Hammer & Silver 1993).

Genetic data from allozymes, mitochondrial DNA (mtDNA), and single nucleotide polymorphism (SNP) indicate that the house mouse contain four major genetic entities—*M. m. musculus*, *M. m. domesticus*, *M. m. bactrianus*, and *M. m. castaneus* (Boursot *et al*. 1993; Bonhomme *et al*. 1994; Yonekawa *et al*. 1994; Lindblad *et al*. 2000), which are largely concordant with their separate geographical ranges (Boursot *et al*. 1996; Din *et al*. 1996). Although house mice of two separate subspecies can interbreed in the laboratory, their genomes are not totally compatible with each other. The most striking illustration of this is the narrow hybrid zone (20–40 km) found in central Europe where the two subspecies, *M. m. musculus* and *M. m. domesticus*, come into contact (Sage *et al*. 1993).

In contrast with the general restriction of gene flow among subspecies, *t*-haplotypes appear to be capable of moving freely across subspecies boundaries. They are found in all subspecies, and *t*-chromosomes retrieved from the different subspecies show an extremely low level of nucleotide variation, even much lower than the variation seen among their wild-type counterparts (Silver *et al*. 1987; Morita *et al*. 1992; Hammer & Silver 1993). Based on the

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results, it has been suggested that all present-day *t*-haplotypes are descendants of a single ancestral chromosome that existed recently (subsequent to the divergence of the *M. musculus* subspecies), and this *t*-haplotype then spreads worldwide relatively rapidly, crossing the subspecies boundaries. The transmission bias in favour of *t*-haplotypes is presumed to have favoured their spread across these genetic boundaries, and yet, different genetic backgrounds are known to have a strong effect on the levels of transmission ratio distortion (TRD) in laboratory settings (Gummere *et al*. 1986). Thus, we are interested in determining whether there is any variation in *t*-haplotype properties, such as the frequency distribution, in a subspecies other than *M. m. domesticus*. If similar selective forces are acting on *t*-haplotypes in different subspecific genetic backgrounds, one would expect to see similar patterns in their distribution and frequencies in populations of the different subspecies. So far, the most comprehensive knowledge of *t*-haplotypes in wild populations has been obtained from *M. m. domesticus* (Dunn *et al*. 1960; Anderson 1964; Petras 1967; Klein *et al*. 1984; Figueroa *et al*. 1988; Lenington *et al*. 1988; Ardlie & Silver 1998), with a few limited studies carried out on *M. m. musculus/molossinus* and *M. m. bactrianus* (Tutikawa 1955; Klein *et al*. 1984; Ruvinsky *et al*. 1991). No studies as yet have focused on the Southeast Asian subspecies, *M. m. castaneus*.

In this study we screened a large number of *M. m castaneus* mice inhabiting rice granaries located all over Taiwan (see Chou *et al*. 1998) with recently developed molecular markers (Schimenti & Hammer 1990; Ardlie & Silver 1996). We investigate the geographical distribution and empirical frequencies of *t*-haplotypes in *M. m. castaneus* populations, and determine whether those populations containing *t*-chromosomes are related to one another by geographical location. The relationships of *t*-frequencies to two population parameters, sex and age, are examined as well.

Materials and methods

Sampling and age determination of mice

Since June 1995, we have collected a large number of house mice from rice granaries in 30 townships (Fig. 1; Table 1). We used body weight criterion to determine the age of all field-caught mice (see Chou *et al*. 1998). Mice weighing < 12 g are arbitrarily defined as 'young' mice, and ≥ 12 g as 'old' mice.

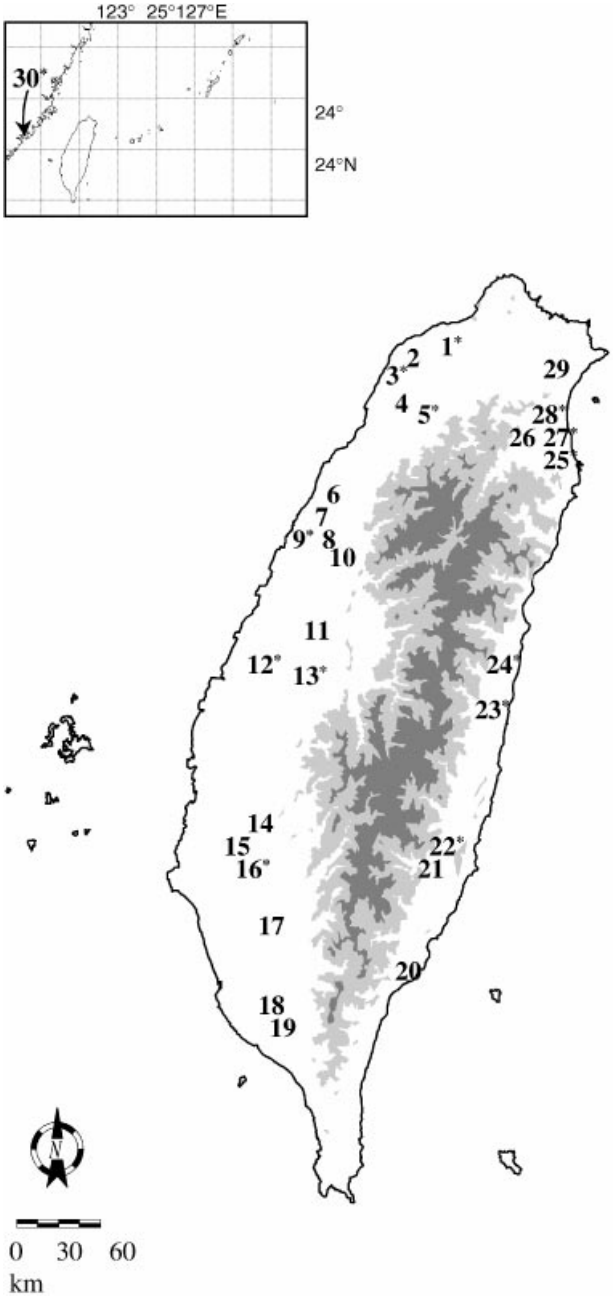

Fig. 1 Map indicating the location of the 39 mouse populations in our survey. Numbers correspond to the localities listed in Table 1. The relative positions of Jin-men (30) are shown in the inset panel. Asterisks indicate the populations with *t*-alleles. Light grey areas, 1000–2000 m; dark grey area, above 2000 m elevation.

Molecular genotyping of t*-haplotypes*

Genomic DNA was prepared following standard protocols (Ausubel *et al*. 1995). We initially screened all mice for the presence of *t*-haplotypes by polymerase chain reaction (PCR). However, the *Hba-ps4* PCR assay is known to incorrectly genotype a small fraction of mice due to gene conversion. Thus, the genotypes of all individuals were further confirmed by restriction fragment length polymorphism (RFLP) analysis (Hammer & Silver 1993; Ardlie & Silver 1996).

A region within the *Hba-4 ps* locus (alpha globin pseudogene) was amplified (Schimenti & Hammer 1990). PCR was performed in a 25 µL reaction containing 200 ng of

Table 1 Frequencies of +/*t* heterozygotes in 39 wild populations of house mouse (*Mus musculus castaneus*) in Taiwan

Geographic range	Locality*		Sample size	no. of +/*t*	
Northwestern	1. Ta-yuan		19	1	(0.05)
	2. Gwan-yin		6	0	
	3. Hsin-wu†		15	1	(0.07)
	4. Hsin-pu		10	0	
	5. Gwan-shi†		22	2	(0.09)
	Pooled		72	4	(0.06)
Central	6. Tung-hsiao		4	0	
	7. Yuan-li		1	0	
	8. Ta-chia		5	0	
	9. Ta-an		1	1	(1.00)
	10. Hou-li		2	0	
	11. Tsao-tun	(#1)	9	0	
		(#4)	9	0	
	12. Shi-jou	(?)‡	16	0	
		(#7)	20	4	(0.20)
		(#8)†	30	7	(0.23)
	13. Lin-nei	(#3)	78	4	(0.05)
		(#9)	23	4	(0.17)
	Pooled	198	20		(0.10)
Southwestern	14. Ma-dou		7	0	
	15. Jia-li		2	0	
	16. Shi-gang		18	4	(0.22)
	17. Mei-nung		2	0	
	18. Ping-dung City		5	0	
	19. Wan-dan		2	0	
	Pooled		36	4	(0.11)
Southeastern	20. Tai-dung City	1	0		
	21. Guan-shan		13	0	
	22. Chr-shang		18	1	(0.06)
	23. Shou-feng		35	12	(0.34)
	24. Ji-an†		3	3	(1.00)
	Pooled		70	16	(0.23)
Northeastern	25. Tung-shan	(#3)	4	0	
		(#6)	12	2	(0.17)
	26. San-hsing	(#17)	5	0	
		(#18)	1	0	
	27. Wu-chiai	(#2)	3	1	(0.33)
		(#6)	9	0	
	28. I-lan City	(#10)	25	1	(0.04)
		(#13)†	16	1	(0.06)
	29. Tou-cheng	(#1)	20	0	
		(#2)	1	0	
	Pooled		96	5	(0.05)
Offshore isle	30. Jin-men†		19	4	(0.21)
Total			491	53	(0.108)

*Each number (1–30) represents one of the townships in our survey. Numbers in parentheses for some townships indicate different rice granaries and therefore different populations.
†Include samples with unknown sex or body weight.
‡The '?' mark indicates rice granary number not specified.

genomic DNA, 0.5 units of *Taq* polymerase (Promega), 1 μM of each primer, 250 μM dNTP, 12 mM $MgCl_2$, and 2.5 μL of 10× reaction buffer. The reactions were amplified on a thermal cycler (MJ Research PTC-100) for an initial cycle of 95 °C for 5 min, followed by 30 cycles at 95 °C for 30 s, 66 °C for 1 min, and 72 °C for 2 min. This assay amplifies 214 bp and 198 bp fragments on *t*-chromosomes and wild type chromosomes, respectively.

The PCR results were further conformed by RFLP analysis (Hammer & Silver 1993; Ardlie & Silver 1996). Approximately 10 μg of genomic DNA was completely digested with *Taq*I restriction endonuclease (New England Biolabs). Digested DNAs were electrophoresed, blotted, and bound to nylon membranes (Amersham) by UV cross-linking. The membranes were then probed with ^{32}P-labelled Bb-40 clones overnight at 65 °C. Bb-40 defines the locus *D17Leh66b* and reveals four *t*-specific *Taq*I fragments (Schimenti *et al*. 1987). Hybridization and washing of the blots were carried out following standard protocols (Ausubel *et al*. 1995). Only one PCR negative mouse turned out to be RFLP positive, and all other *t*-bearing mice were confirmed by both methods, suggesting satisfaction of the PCR screening protocol.

Results and Discussion

Frequency of t*-haplotypes and population ecology*

Four hundred and ninety-one mice from 39 different populations were screened for the presence of *t*-haplotypes (Table 1). Fifty-three mice were $+/t$ heterozygotes and none were t/t homozygotes, yielding an overall $+/t$ frequency of 0.108. The frequencies of $+/t$ mice among the 39 populations ranged from 0.04 to 0.34 (Table 1), excluding those with frequencies of 0 and 1.

The lower-than-expected frequency of *t*-haplotypes observed among wild mouse populations has long been a paradox (reviewed in Silver 1993; Ardlie 1998), and the population ecology of house mouse has been implied to play a major role in maintaining a low *t*-haplotype frequency in natural populations. However, it is hard to analyse much of the early data from the viewpoint of population ecology, for most of the surveys collected mice across a general region, which often included several disparate localities. In contrast, the mouse populations sampled here are well-defined as mice from the same granary and considered as one population. Our sample sizes reported here usually reflect the relative population sizes (Chou 1996; Chou *et al*. 1998). These granary populations were typically ephemeral and unstable due to regular turnover of grain within a period of 2–3 years (Chou *et al*. 1998). The *t*-haplotype frequencies in them were, therefore, highly variable and greatly affected by genetic drift.

Populations of *Mus musculus castaneus* containing *t*-haplotypes are rare and sparsely distributed in Taiwan, and a similar pattern was found by Ardlie & Silver (1998) for *M. m. domesticus.* In *M. m. domesticus*, the overall frequency of $+/t$ mice was also low (0.062); approximately 55% of the populations did not contain any *t*-haplotypes; and *t*-haplotype-containing populations were scattered in the sampling realm. In addition, the reported *t*-haplotype frequencies for two other subspecies, *M. m. bactrianus* and *M. m. musculus*, were low as well (0.172 and 0.273, respectively) (Ruvinsky *et al*. 1991). Hence, the low frequency of *t*-haplotypes in natural populations appears to be a consistent phenomenon across all subspecies of house mouse.

Geographical distribution of populations containing t*-haplotypes*

To examine whether there was any general geographical or clinal variation in *t*-haplotype frequencies, we performed spatial autocorrelation analyses (Koenig & Knops 1998; Bjørnstad *et al*. 1999; Koenig 1999) for 10 western townships and eight eastern townships, respectively. In these analyses, frequencies were calculated for each township and small samples ($n \leq 5$) were excluded. The analyses did not show synchrony declines with distance ($P = 0.674$ western townships; $P = 0.265$ eastern townships), suggesting no obvious geographical pattern of the *t*-haplotypes. However, when data were pooled according to geographical regions (Table 1), the $+/t$ frequency of the southeastern populations was found to be the highest (0.23), significantly different from the other four regions combined (0.08) ($P = 0.0002$). Removal of the small samples ($n \leq 5$) without *t*-alleles did not alter this conclusion ($P = 0.0006$). Finally, the offshore isle also showed a high frequency of $+/t$ frequency (0.21).

One possible explanation of the significantly higher *t*-frequency of southeastern populations than other parts of Taiwan is that they harboured a higher diversity of *t*-haplotypes (complementary groups). In natural populations where a greater variety of lethal and semi-lethal *t*-haplotypes coexist, higher frequencies of *t*-haplotypes can be found (Ardlie & Silver 1998), because t/t homozygotes can survive and such females can also breed, transmitting *t*-haplotypes to their offspring. It has been shown that there is considerable population structure at the level of six geographical regions (Table 1) (Peng 1998). In particular, the southeastern populations stand out as being most differentiated from those of the other regions. Furthermore, mitochondrial D-loop sequence data have shown that the southeastern region harbours a high frequency of an older mtDNA lineage, which is distinct and separated by a deep branch from the other mtDNA haplotypes (Yang 1998). As a more ancient and the other newly intrusive mouse lineages coexist, it is plausible that southeastern Taiwan may have a higher diversity of *t*-haplotypes than that of other parts of Taiwan. Currently the types and diversity of *t*-haplotypes in Taiwanese *M. m. castaneus* are undetermined and will be pursued in future studies.

Frequencies of +/t *heterozygotes in relation to sex and age*

Since reduced fitness in $+/t$ heterozygotes is often implicated to contribute to the low *t*-haplotype frequency in nature (Young 1967; Johnston & Brown 1969; Durand *et al*. 1997),

we measured two major population parameters, sex and age, to determine their effect on *t*-haplotype frequency.

Our data do not show any evidence for differences in *t*-haplotype frequencies between two sexes in 16 of 17 populations (one population, Ji-an, sex unrecorded) containing *t*-haplotypes. In eight of these 16 populations, the $+/t$ frequencies were higher in males, while in the other eight populations the $+/t$ frequencies were higher in females. The mean frequencies of *t*-haplotypes in two sexes (for the 16 populations with *t*-alleles) were the same, which were 0.14 for both males ($n = 177$) and females ($n = 177$). The goodness-of-fit test showed no significant difference in $+/t$ frequency between sexes ($P = 0.9700$), implying no differential fitness existing between $+/t$ males and $+/t$ females as suggested by Lenington *et al*. (1988).

We then examined whether there was any relationship of $+/t$ frequency with age. All mice were placed into one of two age categories (young or old) based on their body weight. The overall frequency of $+/t$ heterozygotes among old mice was 0.18 (25/142), which was slightly higher than the frequency of 0.11 (22/193) among young mice; however, the difference was not significant ($P = 0.2678$). Therefore, it suggested that if any age-related fitness components act against *t*-haplotypes, they must be manifested prenatally, such as embryonic lethality or fertility differences (e.g. Johnston & Brown 1969; Lenington *et al*. 1994; Ardlie & Silver 1996) and not as postnatal survival rates.

Origin and rapid expansion of t*-chromosomes in house mouse*

Here we have shown a considerable similarity in the low *t*-haplotype frequency, in two genetically differentiated subspecies of the house mouse: *M. m. domesticus* and *M. m. castaneus*. The similarity, which involved populations of two subspecies inhabiting disparate geographical ranges, suggests that not only are these chromosomes of the mouse subspecies closely related, but also the selection forces on them are similar. There may exist general mechanisms to prevent the spread of *t*-haplotypes in natural populations despite of their high transmission advantages.

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