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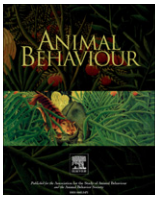

Dear enemy relationships in the subterranean rodent *Ctenomys talarum*: the role of memory of familiar odours

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Individual recognition is expected to enhance fitness by allowing animals to direct appropriate behaviours to specific individuals during interactions with conspecifics. Reduced aggression towards territorial neighbours ('dear enemy phenomenon') is based on the assumption that strangers lacking territories pose a greater threat than territory-holding neighbours. Based on the ability of the subterranean rodent *Ctenomys talarum* (tuco-tuco) to distinguish between familiar and unfamiliar conspecific odours, I assessed whether males, the more aggressive sex, show dear enemy relationships and whether social experience with odour donors affects the memory of conspecific odours. Male–male contests in the laboratory were used to compare the aggressive behaviour of pairs of males. Familiar male tuco-tucos responded less aggressively during contests than unfamiliar males, providing evidence of the dear enemy relationship in *C. talarum*. Memory for familiar odours was affected by social experience since discrimination of known from novel odours lasted longer when males encountered each other in dyadic contests following familiarization with odours. Familiarity by odour cues would represent an important mechanism mediating neighbour recognition and territorial behaviour for tuco-tucos in the wild; intruders may represent a threat of great consequence for territory-holding individuals since they represent the potential loss of their burrow system and their priority of access to neighbouring females.

Individual recognition is critical for the organization and function of relationship networks among individuals. Many aspects of mammalian social relationships, such as dominance hierarchies, pair bonds and group memberships, require the ability to recognize individuals (Halpin 1980). Knowing who an individual is (or at least the ability to discriminate familiar from unfamiliar conspecifics) may alter the nature of the behaviour (e.g. amicable or hostile) directed towards it. Recognizing individuals may prevent males from injuring their mates or offspring, or starting a fight with an individual that, from previous experience, is known to be stronger (Lai & Johnston 2002). Hence, social recognition is expected to enhance fitness by allowing animals to direct appropriate behaviours to specific individuals during interactions with conspecifics.

The ability to use chemical cues in social recognition has been recognized in several rodent species and many other mammals (Halpin 1986; Johnston 1993; Swaisgood et al. 1999; Vaché et al. 2001). Chemical communication may be especially advantageous for territorial species since olfactory signals persist in the territory and do not require the presence of the sender after scent deposition. Discrimination of chemical cues may reduce defence costs since it allows the territory owner to identify itself, and at the same time, to become known to potential intruders and/or neighbours (Bradbury & Vehrencamp 1998). Furthermore, intruders can assess the status of individual conspecifics by comparing territorial scent markings to the odour of possible owners and use that information to evaluate the risk of a direct contest (Gosling 1990; Gosling & McKay 1990). Territory-holding neighbours usually show lower aggression levels towards one another than towards intruders (Temeles 1994). Reduced aggression towards territorial neighbours, termed the dear enemy phenomenon (Fisher 1954), is based on the assumption that strangers lacking territories pose a greater threat in terms of potential loss of territories, resources and/or mates than do territory-holding neighbours. As a consequence, this dear enemy relationship results in mutual benefits for the neighbours, since time and energy spent defending territorial boundaries are saved and costs of territorial defence are diminished (Jaeger 1981; Gosling 1986; Ydenberg et al. 1988; Gosling & McKay 1990).

Dear enemy relationships have been documented in several vertebrate species, mainly songbirds (Stoddard et al. 1990; Mackin 2005), amphibians (Davis 1987), reptiles (López & Martín 2002; Trigosso-Venario et al. 2002), fishes (Leiser 2003) and mammals

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(Vestal & Hellack 1978; Rosell et al. 2008; del Barco-Trillo et al. 2009). However, some territorial animals do not show a dear enemy response (Temeles 1989, 1994). Such differences may be due to the type of territory that is defended (feeding, breeding or multipurpose breeding territories; Temeles 1994), levels of territorial instability in the population (Stoddard et al. 1990; Lachish & Goldizen 2004), or temporal changes in the social environment (Hyman 2005).

The dear enemy relationship involves two cognitive processes, learning and memory; animals must recognize individuals (or at least familiar from unfamiliar individuals) and remember these categories (Johnston & Jernigan 1994; Gheusi et al. 1997; Johnston & Bullock 2001). However, this capacity would probably disappear over time if no reinforcement occurred (Johnston 1993). Memory of aggressive encounters between competitors is expected to affect behavioural responses according to the results of those previous experiences (Lai & Johnston 2002; Petrulis et al. 2004).

Rodents of the genus *Ctenomys* (tuco-tucos) are subterranean herbivores that are widely distributed in temperate South America (Woods 1993). Solitary tuco-tucos concentrate most of their activities in their burrow systems, making direct intraspecific interactions infrequent (Busch et al. 2000). For these species, chemical signals may represent an efficient channel of communication between neighbours since scent cues can persist in the habitat in the absence of the sender and do not require that both sender and receivers be active at the same time (Franchescoli 2000). Furthermore, receivers can avoid agonistic interactions or prepare themselves for a conflict as a result of having encountered the advertising scent marks of a neighbour or potential rival.

The subterranean rodent *Ctenomys talarum* (Talas tuco-tuco; Thomas 1898) provides an excellent study model to examine the role of familiarization by means of odour cues in male–male aggressive interactions. This species is solitary and highly territorial; individuals do not share burrows, except in the case of females and their offspring (up until the time of natal dispersal) and at the moment when mating occurs (Busch et al. 1989). Although both sexes are territorial, only males utter a typical territorial vocalization that informs potential intruders about the owner's presence in a territory (Schleich & Busch 2002). Laboratory studies using seminatural enclosures showed that males are the more aggressive sex, usually engaging in vigorous aggressive interactions with same-sex individuals (Zenuto et al. 2002). Also, presence of scars along the neck in wild males (R.R.Z., unpublished data) suggests the importance of avoiding male–male interactions for this species. Small pieces of plant material contaminated with faeces and urine are usually stored at the burrow entrance both in the field and in captivity (R.R.Z., personal observation); this may serve to provide information at the surface about the owner of each individual burrow. Tuco-tucos perform most of their activities inside their burrows, which measure approximately 18 m^2 for males (Cutrera et al. 2006). Nevertheless, animals venture short distances away from burrow openings to collect above-ground portions of the vegetation that they later eat below ground. Thus, scent cues left on the substrate may be smelled by neighbouring animals during their own foraging trips, patrolling activities and dispersal, thereby providing individuals with information about the identity of neighbours. Metabolic chemical cues in urine and faeces of tuco-tucos provide valuable information about individual identity (Zenuto & Fanjul 2002), gender (Fanjul et al. 2003) and reproductive condition (Zenuto et al. 2004).

Since individual tuco-tucos occupy and defend adjacent territories, familiarity by odour cues may represent an important mechanism mediating neighbour recognition and territorial behaviour. Because of the secretive lifestyle of tuco-tucos, it is difficult to study their territorial behaviour in the wild. For this reason, I staged male–male encounters in the laboratory. A main goal of this study was to determine whether male familiarization with conspecific male odours influences territorial behaviour in the subterranean rodent *C. talarum*. I formulated the following hypothesis concerning the influence of familiarity on territorial behaviour, based on the ability of *C. talarum* individuals to discriminate between familiar and unfamiliar conspecific odours (Zenuto & Fanjul 2002). I hypothesized that familiarity, enabling neighbour recognition, may allow animals to modulate their aggression when they confront each other in direct contests. Hence, I predicted that male familiarization would reduce aggressive behaviour and enhance submissive behaviour.

Moreover, to determine whether social experience with scent donors affects the memory for conspecific odours, I investigated how males responded to scent cues from known males under three conditions: odour familiarization; odour familiarization followed by a behavioural contest; behavioural contest with no prior odour exposure. Discrimination of known from novel male odours at six time intervals after the corresponding experience was assessed to evaluate the duration of memory. I predicted that memory for conspecific odours would last longer when animals were familiar with those odours and had interacted socially with the odour donor.

This is the first study on the dear enemy relationship in subterranean rodents. In addition, the few studies that have examined memory for individual odours and the effects of social experience in rodents have been mainly limited to hamsters, *Mesocricetus auratus* (Johnston 1993), guinea pigs, *Cavia porcellus* (Beauchamp & Wellington 1984) and prairie voles, *Microtus ochrogaster* (Paz y Miño & Tang-Martínez 1999). Hence, the present study represents a valuable opportunity to answer interesting questions regarding the use of odour communication in territorial interactions.

METHODS

I captured wild adult *C. talarum* males in coastal grasslands of Mar de Cobo (37°45′S, 57°26′W, Buenos Aires Province, Argentina) between June and December (during their reproductive season) in 2004–2006. I set plastic live traps at the entry of tunnel systems when fresh surface mounds, indicative of recent burrowing activity, were detected. I transported captured animals to the laboratory in individual plastic tubes containing paper towels and a mix of grasses. Transportation lasted nearly 1 h. In the laboratory, animals were housed individually in plastic cages ($42 \times 34 \times 26$ cm) with wood shavings as bedding and provided daily with a fresh supply of vegetables (carrots, sweet potatoes, lettuce and mixed grasses). Because *C. talarum* do not drink free-standing water, it was not supplied. Photoperiod and temperature were automatically controlled (10:14 h light:dark cycle; 24 ± 2 °C). Individuals ($N = 120$) were allowed to adapt to captivity for 10 days prior to their use in the experiments or as odour donors. Animals were randomly assigned to each odour familiarity treatment. At the end of the experiments, which lasted about 2 months in the more extended situation (10 days for adaptation to captivity, 7 days for odour familiarization, 1 day for contest, 35 days for memory test), the animals were returned to their site of capture. I used latex gloves during all instances of sample odour collection and experimental trials. All equipment used during the study was washed with tap water and odourless glassware cleaner, wiped with alcohol and allowed to air dry to ensure that no trace odours from previous trials remained.

Familiarity

Familiarity was established by housing individuals with conspecific male odours for 8 days. Wood shavings soiled with urine and faeces were collected from the soiled corners of individual cages, in which the bedding was unchanged for 7 days. Odour samples were placed inside male cages in PVC petri dishes (10 cm diameter) that were covered by a wire mesh with an opening (3 cm diameter) that allowed animals to lick or touch the sample. Odour samples (PVC petri dishes filled with wood shavings soiled with urine and faeces) were renovated every 2 days. I assumed that familiarization with the odours of conspecifics effectively occurred in tuco-tucos since, in a previous study that used the same method of odour presentation (Zenuto & Fanjul 2002), animals reached habituation with conspecific odours and distinguished familiar from novel odours. In that study, I used the habituation–discrimination technique (Halpin 1974). Although I did not measure habituation in the current study, based on the earlier study I inferred that familiarization and probably habituation also occurred in the experiments reported here.

Experiment 1: Male–Male Contests

To assess whether male familiarization with conspecific male odours influences aggressive behaviour in tuco-tucos, I staged male–male contests between: (a) individuals that were previously familiarized with the odours of their opponents (opponent odour ‘familiar’; $N = 15$ pairs), (b) individuals that were previously familiarized with the odour of a male that was not the one that acted as his opponent (opponent odour ‘unfamiliar’; $N = 15$ pairs), (c) individuals that were not exposed to any conspecific male odour prior to the contest (‘unfamiliar/no odour’; $N = 15$ pairs). Housing of individuals under the last treatment included exposure to a PVC petri dish filled with clean shavings for the same time period as the familiarized groups. Pairs of males were randomly assigned to each treatment, but two conditions were required to assign two males to a dyad: (1) individuals must not have been neighbours in the wild (distance between their respective sites of captures had to exceed 50 m) and (2) the body mass of the individuals must not differ by more than 5%. Animals participated only once as test animals and once as odour donors, hence 90 individuals were used during male–male contests.

Male–male contests occurred the day after familiarization concluded (see above). The experimental apparatus consisted of three acrylic cages (45 × 30 × 30 cm) that were connected to each other by an acrylic tube (10 cm diameter × 20 cm length). To distinguish each contestant, one of them, randomly chosen, was marked with a nontoxic dye (Creameches™, Ľoreal, Paris, France) on the back. Each test animal was individually confined for 30 min (acclimation time) in one of the apparatus cages, which contained shavings from its own housing cage. At the start of each trial, both animals were allowed to enter the central cage (provided with clean shavings), and they interacted freely for 15 min along the test apparatus. Using this set-up, each individual was expected to show territorial behaviour in the cage that contained its own odour (own territory) but to be submissive in the central cage or in the opponent's cage. Although this species shows arrhythmic patterns of activity, both in captivity (Luna et al. 2000) and in field (Cutrera et al. 2006), all trials were performed during mid-mornings and videotaped under white light. Afterwards, I observed the videotapes and recorded agonistic behaviours, following early descriptions of Zenuto et al. (2002). Relevant behaviours were categorized according to their apparent motivational similarity (see Table 1 for a complete description). For each treatment, the frequency of each behaviour (i.e. total number of acts per 15 min test) was recorded for both members of each interacting pair. The sum of these frequencies was then computed for each dyad and averaged for each treatment. However, for ‘wrestle’ and ‘rounds’, interactions rather than individual behaviours by each animal were recorded and averaged for each treatment. Also, latency of the first aggressive and submissive behaviours in a contest was recorded.

Table 1
Agonistic behaviours recorded during male–male contests of *C. talarum*

Behaviour	Description
Aggressive-low	Male raises his head and shows his incisors, or defeats an opponent making pounces
Reject	Quick approach and retreat by a male from a nearby opponent
Threat	Male raises his head and shows his incisors
Aggressive-high	Risk of physical injury. Male bites, or attempts to bite or mount, opponent
Bites	Male bites or attempts to bite opponent
Wrestle	Both males bite each other's neck while rolling
Mount	One male mounts the other
Rounds	Both males try to mount each other
Submissive	One male flees from the other or shows his rump during an encounter
Rump	Male turns rump towards an approaching opponent
Evasion	One male avoids the other
Escape	Male attempts to leave the test apparatus as a direct consequence of an interaction

Because the behavioural data did not conform to the assumptions required for parametric analysis, Kruskal–Wallis tests were performed for each type and level of behaviour. If the Kruskal–Wallis tests yielded significant differences, the differences between groups were further tested by a multiple comparison Dunn's test (Zar 2009).

Experiment 2: Memory

This experiment was aimed at assessing whether memory for odours in male tuco-tucos is affected by the type of experience a subject has with odour donors. To accomplish this objective, *C. talarum* males were presented with odours from individuals that they had previously been exposed to under three conditions: (a) odour familiarization alone ($N = 30$); (b) odour familiarization and behavioural contest ($N = 30$; subject and stimulus animals from experiment 1a); and (c) behavioural contest alone ($N = 30$; subject and stimulus animals from experiment 1c). To verify whether individuals can discriminate between known and novel odours, both odours were presented simultaneously and the responses to both samples were recorded. A known odour in this study represented the odour from a male that the subject had experienced during either a familiarization treatment (treatments ‘a’ and ‘b’) or a contest treatment (treatment ‘c’). Novel odours were from an unfamiliar animal that the subject had not been exposed to either directly or indirectly. To assess the duration of memory, I conducted these discrimination tests at six time intervals (2, 7, 14, 21, 28 and 35 days) after each respective treatment. For each treatment, five individuals were randomly assigned to one of those time intervals. Selection of these time intervals was based on previous studies available for rodents (Beauchamp & Wellington 1984; Johnston 1993).

I used a clean cage (45 × 30 × 45 cm) connected to a Y-maze (10 cm diameter) that consisted of a base (20 cm long) and two arms (10 cm long) with petri dishes containing the stimulus scents located at the end of each arm. The two-choice test is considered a suitable method to determine the limits of an animal's abilities to discriminate scents with the additional advantage of controlling for other confounding motivational factors (Halpin 1974). Each subject was confined for 30 min in the cage, which contained soiled

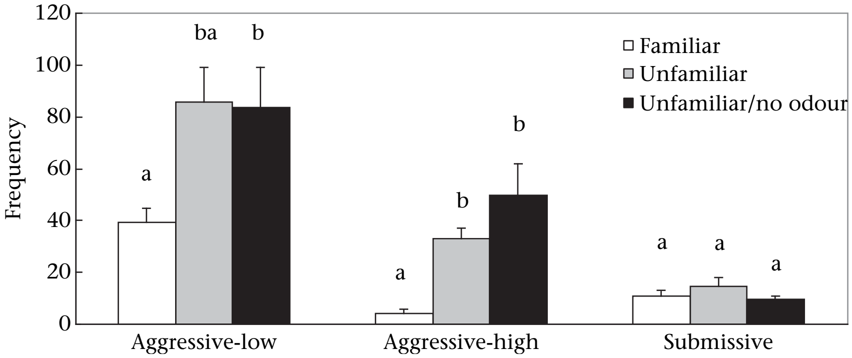

Figure 1. Mean + SE frequencies of high and low aggressive behaviours and of submissive behaviours during 15 min paired encounters between *C. talarum* males in three familiarization treatments: familiar—opponent odour familiar; unfamiliar—opponent odour unfamiliar; unfamiliar—no odour exposure. Different letters denote significant differences ($P < 0.05$).

shavings from its own home cage. At the start of the trial, the subject was allowed to enter the maze (by removing a Plexiglas door) and investigate by sniffing the petri dishes containing soiled bedding from a pair of males (known versus novel). The unscented petri dish (control) was not provided since in a previous experiment we found that animals rarely sniffed them (Zenuto & Fanjul 2002). The position of each odour sample (right or left) was selected at random. Time spent sniffing or in direct contact with each scent sample was recorded with stopwatches during a 7 min trial.

A two-way MANOVA (general linear model, Statistica, Statsoft, Tulsa, OK, U.S.A.) was performed on data for time spent sniffing; because both scent samples (known and novel) were presented simultaneously, they were treated as paired measures. Factors were: odour treatment (‘odour familiarization’, ‘odour familiarization + contest’, and ‘contest’) and time interval since odour treatment (2, 7, 14, 21, 28 and 35 days). Furthermore, paired *t* tests were used to compare time spent sniffing the known and novel male odours at each time interval for each odour treatment. To control for type I error, standard Bonferroni correction was used (Rice 1989). Each treatment was considered a family of tests that was considered collectively, hence the alpha level was divided by the number of comparisons included in each treatment (0.05/6). Only those tests with probabilities of 0.008 or less were considered statistically significant.

Results are reported as means ± SE. In all cases, the critical significance level was set at $P < 0.05$.

Ethical Note

I adhered to the *Guidelines for the Use of Animals in Research and Teaching* (ASAB/ABS 2003). During male–male interactions, I was prepared to interrupt the trial if a threat to the health of either animal was detected. However, such threats never occurred.

RESULTS

Experiment 1: Male–Male Contests

Most male–male interactions started with animals sniffing the bedding of the opponent's cage, sometimes showing head-bobbing behaviour. When contestants approached each other more closely, anogenital sniffing occurred. Because bedding from the home cages was provided in the end cages of the apparatus where I recorded interactions, marking with urine and faeces could not be detected and, therefore, was not recorded. Nevertheless, marking with urine and faeces was seldom observed in the central clean cage or in the tubes that connected the cages, and anogenital dragging was never observed. Likewise, countermarking was not evident.

Familiarization with odour cues affected male–male contests in *C. talarum*. Total agonistic (both aggressive and submissive) activity displayed by interacting pairs of males was affected by odour treatment ($H_2 = 19.216$, $P < 0.001$); familiar males showed lower frequencies of agonistic behaviours than unfamiliar/no odour males (multiple comparison Dunn's method: $q = 3.753$, $P < 0.05$) or unfamiliar males ($q = 3.837$, $P < 0.05$; Fig. 1). However, no differences were detected between the latter two groups ($q = 0.083$, $P > 0.05$). Furthermore, total frequency of both low ($H_2 = 7.471$, $P < 0.05$) and high ($H_2 = 24.555$, $P < 0.005$) aggressive behaviours differed between treatments (Fig. 1). Familiar males showed lower frequencies of low aggressive behaviours than unfamiliar/no odour individuals ($q = 2.599$, $P < 0.05$) and unfamiliar males, but in this latter case no significant differences were found ($q = 2.030$, $P > 0.05$). As expected, unfamiliar/no odour males showed similar frequencies of low aggressive behaviours as unfamiliar males ($q = 0.570$, $P > 0.05$). High aggressive behaviours were seldom detected in males in the familiarization treatment, but were used more frequently in contests that involved unfamiliar/no odour individuals ($q = 4.372$, $P < 0.05$) or unfamiliar individuals ($H_2 = 24.555$, $P < 0.005$). No significant differences were detected for the latter two groups ($q = 0.195$, $P > 0.05$). Submissive behaviours were similar among treatments ($F_{2,42} = 1.246$, $P > 0.05$; Fig. 1).

Familiarity particularly affected some of the behaviours recorded during encounters (Fig. 2). Males rejected contestants to a similar degree regardless of the odour treatment ($H_2 = 0.389$, $P > 0.05$), but the occurrence of threatening behaviour differed between treatments ($H_2 = 12.492$, $P < 0.005$) and was significantly more frequent between males in the unfamiliar/no odour and unfamiliar treatments than between males in the familiarized treatments (unfamiliar/no odour versus familiar: $q = 2.467$, $P < 0.05$; unfamiliar versus familiar: $q = 3.413$, $P < 0.05$). Familiarized males were less aggressive while interacting than males in the unfamiliar/no odour or unfamiliar treatment. Bites and wrestle were rarely seen in familiarized males but frequently displayed in the other two groups (bites: $H_2 = 12.755$, $P < 0.005$; wrestle: $H_2 = 24.233$, $P < 0.001$). Males from the unfamiliar/no odour and unfamiliar treatments showed a similar frequency of bites ($q = 0.188$, $P > 0.05$). However, these two groups showed significantly higher frequencies of bites than did familiarized males (unfamiliar/no odour versus familiar: $q = 2.982$, $P < 0.05$; unfamiliar versus familiar: $q = 3.169$, $P < 0.05$). A riskier behaviour, which consisted of both males rolling while biting each other's neck (wrestle), was seen almost exclusively in the nonfamiliarized

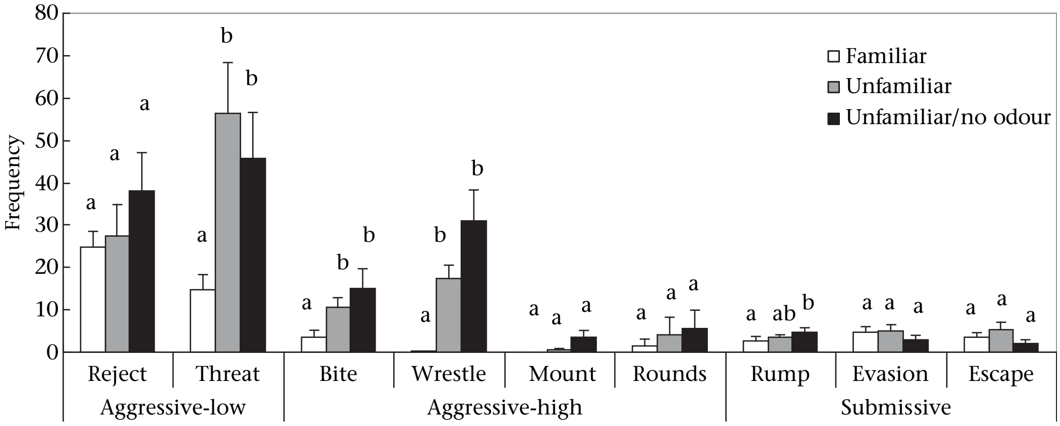

Figure 2. Mean + SE frequencies of high and low aggressive behaviours and of submissive behaviours (see Table 1 for definitions) during 15 min paired encounters between *C. talarum* males in three familiarization treatments: familiar—opponent odour familiar; unfamiliar—opponent odour unfamiliar; unfamiliar—no odour exposure. Different letters denote significant differences ($P < 0.05$).

groups (unfamiliar/no odour versus familiar: $q = 4.240$, $P < 0.05$; unfamiliar versus familiar: $q = 4.080$, $P < 0.05$). Mounts and the number of rounds displayed when both animals tried to mount each other were highly variable (mount: $H_2 = 5.493$, $P > 0.05$; rounds: $H_2 = 2.042$, $P > 0.05$). Males engaged in submissive behaviours to a similar degree regardless of the odour treatment (evasion: $H_2 = 1.896$, $P > 0.05$; escape: $H_2 = 5.251$, $P > 0.05$). However, unfamiliar/no odour males showed their rumps more frequently than did familiar males ($H_2 = 7.500$, $P < 0.024$; $q = 2.697$, $P < 0.05$).

Latency to the first type of agonistic behaviour displayed in a contest was variable in all treatments (Table 2). Only low aggressive behaviour differed between groups, with familiar males displaying rejection or threatening behaviour later than unfamiliar/no odour males ($H_2 = 6.702$, $P < 0.05$; $q = 2.585$, $P < 0.05$). No differences were detected in latencies to the first high aggressive behaviour ($H_2 = 2.022$, $P > 0.05$) or the first submissive behaviour ($H_2 = 4.302$, $P > 0.05$).

Experiment 2: Memory

Memory experiments revealed that time spent sniffing known and novel odours was affected by odour treatment (main effect odour treatment: $F_{2,72} = 4.464$, $P < 0.05$; Fig. 3); subjects in the 'contest' condition spent more time sniffing samples (99.49 ± 6.85 s) than did subjects in 'odour familiarization' (77.87 ± 6.51 s; Tukey post hoc test: $P < 0.05$) and 'odour familiarization + contest' (78.76 ± 5.54 s; Tukey post hoc test: $P < 0.05$) conditions. Also, the time interval elapsed since the odour treatment also affected the time spent sniffing odour samples; a clear decrease in the interest of animals investigating the samples was detected over time (main effect time treatment: $F_{5,72} = 4.237$, $P < 0.005$; time intervals 2, 7 and 21 days differed from 35 days; Tukey post hoc test: $P < 0.05$). Whether odour samples were known or novel affected time spent sniffing samples since animals spent more time investigating novel odours (52.79 ± 2.89 s) than familiar odours (32.58 ± 2.63 s) (within-subjects factor: $F_{1,72} = 33.73$, $P < 0.001$). Furthermore, an interaction was found between odour treatment and whether the odour sample was known or novel ($F_{2,72} = 12.814$, $P < 0.001$). Novel odours were more interesting than known odours for animals from 'odour familiarization' (novel odour: 49.73 ± 5.34 s; known odour: 28.14 ± 2.74 s; Tukey post hoc test: $P < 0.01$) and 'odour familiarization + contest' (novel odour: 59.92 ± 4.89 s; known odour: 18.84 ± 2.39 s; Tukey post hoc test: $P < 0.005$) conditions, while animals from the 'contest' condition devoted similar amounts of time to both odours (novel odour: 48.74 ± 4.68 s; known odour: 50.76 ± 5.67 s; Tukey post hoc test: $P > 0.05$). Time spent sniffing odour samples was not affected by the interaction between odour treatment and time elapsed since odour treatment ($F_{10,72} = 1.095$, $P > 0.05$), the interaction between odour type (novel or known) and time ($F_{2,72} = 2.059$, $P > 0.05$), or the interaction between odour type, odour treatment and time ($F_{10,72} = 1.276$, $P > 0.05$).

Discrimination of known from novel odours was statistically significant for day 7 following familiarization (paired *t* test: $t_4 = 6.253$, $P < 0.008$; Fig. 3). When behavioural contests followed familiarization with odours, memory of known odours lasted until day 14 after that treatment (paired *t* test: day 2: $t_4 = 5.838$, $P < 0.008$; day 7: $t_4 = 11.264$, $P < 0.008$; day 14: $t_4 = 5.544$, $P < 0.008$; Fig. 3).

Table 2
Mean ± SE latency (s) to the first type of agonistic behaviour during male–male contests of *C. talarum* under different odour treatments (sample sizes in parentheses)

Treatment	Aggressive-low	Aggressive-high	Submissive
Familiar	101.20±29.15 (15)	211.11±81.63 (9)	182.53±29.39 (15)
Unfamiliar	39.67±6.78 (15)	188.33±38.51 (15)	102.93±24.85 (15)
Unfamiliar no odour	22.07±1.79 (15)	135.20±35.88 (15)	158.13±46.91 (15)

DISCUSSION

Individual recognition can enhance fitness by directing appropriate behaviours to specific individuals in interactions with conspecifics. One mechanism for individual recognition is the use of odours or chemical cues. I found that familiar male tuco-tucos responded less aggressively during contests than unfamiliar males, providing evidence for a dear enemy relationship in *C. talarum*. Males that were familiarized with odours from a conspecific male before they interacted with a different male behaved similarly to individuals that were not exposed to conspecific male odour prior to the contest, reinforcing the evidence that tuco-tucos recognize individual scents. Familiar individuals were slower to initiate and showed fewer aggressive behaviours during contests while the frequency of submissive behaviours was similar in males from all three conditions. Specifically, unfamiliar males threatened, bit and wrestled contestants more frequently than did familiar males.

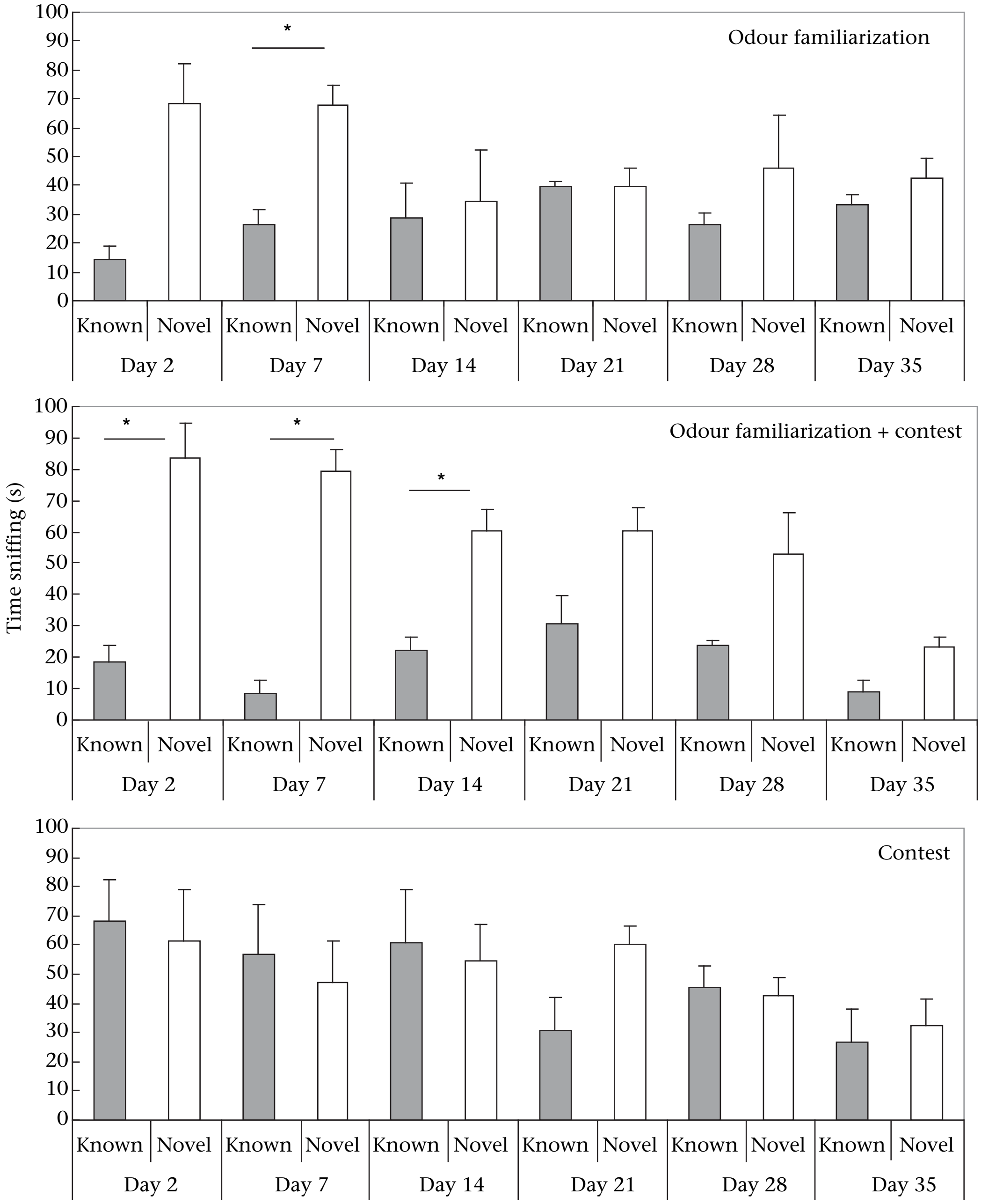

Figure 3. Mean + SE time (s) that *C. talarum* males spent sniffing known and novel male odours 2–35 days after experiencing the odour familiarization, the odour familiarization + contest and the contest conditions. $^*P < 0.05$.

Two key hypotheses have been used to explain the relationships between territorial competitors relative to the dear enemy relationship: the familiarity hypothesis and the threat hypothesis. The familiarity hypothesis proposes that repeated interactions between neighbours lead to low aggression towards one another to conserve time and energy inherent in risky contests (Wilson 1975). These repeated interactions reinforce the recognition of neighbouring individuals, making it less likely to confuse a neighbour with a stranger (Ydenberg et al. 1988). Neighbours may also be expected to fight less because identity has been previously established, with no new information to be gained from further interactions (Getty 1989). Alternatively, the threat hypothesis suggests that, because neighbours and strangers compete for different resources, dispersers or wandering animals without territories represent a greater risk to territory holders (Temeles 1994). Although these two hypotheses are not necessarily mutually exclusive, the relative importance of familiarity versus threat in the aggressive behaviour of a territory holder is difficult to determine.

While familiarity leads to reduced aggression between neighbours in some species, in others, competition between neighbours is intensified. For instance, Müller & Manser (2007) showed that in a social carnivore, the banded mongoose, *Mungos mungo*, neighbours represent potential usurpers of territories and elicit a stronger aggressive response than strangers because transient animals appear to be a lesser threat that may not be encountered again. In another study, male meadow voles, *Microtus pennsylvanicus*, were more aggressive towards neighbours than strangers, presumably because of increased mate competition and the threat of infanticide (Ferkin 1988).

Individuals defend territories to gain exclusive access to resources, but defence often comes with substantial costs (Bradbury & Vehrencamp 1998). One mechanism to minimize defence costs is to reduce aggression towards individuals that pose a low threat, such as neighbours holding their own territories (Jaeger 1981). Aggression towards neighbours or strangers may depend on how the territory is used. For example, Temeles (1994) found that territory owners were much more aggressive towards strangers than towards neighbours when the territory was used as a breeding or multipurpose territory but not when it was used as a feeding territory. The author reviewed 65 studies, which focused mostly on birds but included 12 mammals. The dear enemy relationship was demonstrated in five species of rodents (Temeles 1994). Additional work in rodents has demonstrated dear enemy relationships in male *Gerbillus dasyurus* (Gromov et al. 2001), *M. oeconomus* (Rosell et al. 2008), *Mesocricetus brandti* (del Barco-Trillo et al. 2009) and the subterranean rodent *C. talarum* (this study).

Recognition of familiar and unfamiliar odours in *C. talarum* (Zenuto & Fanjul 2002) may play a key role in distinguishing neighbours from strangers in this solitary species, which occupies exclusive multipurpose burrows that provide protection from predators and harsh external conditions (Busch et al. 2000; Antinuchi et al. 2007). Each neighbouring male tuco-tuco represents a potential competitor for mating opportunities, since, in this species, males are polygynous (Zenuto et al. 1999) and burrow systems are spatially distributed such that individual males are surrounded by several females (Busch et al. 1989). Strangers, however, may pose a greater threat since they could be dispersing individuals looking for a new territory. Although the potential to disperse may be low for many adult subterranean rodents (reviewed in Busch et al. 2000), *C. talarum* adults often disperse, particularly those males in areas of high population densities (Malizia et al. 1995). While dispersing individuals may acquire a new burrow system by either digging a new burrow or finding an unoccupied burrow, burrow systems are costly to excavate (Luna & Antinuchi 2006), and unoccupied burrows are difficult to find. Displacing individual territory holders may represent the best option for dispersers, increasing the threat to territory holders. A displaced individual not only loses his burrow and accompanying access to females but is exposed to increased risk of predation because he is forced above ground to find another burrow. Therefore, for tuco-tucos and other individuals that occupy and defend adjacent territories, using odour cues to distinguish neighbours from strangers may prevent costly interactions with low-threat individuals (i.e. neighbours) and conserve energy for high-threat individuals (strangers).

Two main criticisms have emerged from previous studies on the dear enemy relationship. First, laboratory studies, employing the use of neutral arenas in which to stage male–male confrontations, lacked a critical component, defence of a valuable resource. Resources characterize the ‘benefit’ in the cost–benefit relationship central to territory defence (Fox & Baird 1992). Because of the limitation of the neutral arena method, additional studies of free-living animals were deemed necessary. However, a second criticism emerged from those studies because they tended to disregard the role of relatedness. In many mammal species, neighbours are also relatives. Ignoring relatedness between individuals creates confusion about whether animals distinguish neighbours from strangers or relatives from nonrelatives. If neighbours are closely related individuals, low aggression between neighbours may function to increase benefits acquired from those neighbours via indirect fitness, as has been found in beavers, *Castor fiber* (Rosell & Bjørkøyli 2002). Consequently, studies testing the dear enemy relationship should include knowledge of genetic relatedness to be complete.

To date, only one study on a mammal species (*M. oeconomus*) investigated territorial behaviour using a field arena test involving individuals raised in captive conditions with a known pedigree (Rosell et al. 2008). In the present study, field-captured animals were tested in laboratory conditions using an experimental condition where each individual was provided a cage with wood shavings from its home cage to resemble its own territory to be defended. Additionally, the possibility that test animals were relatives was minimized since males are the more dispersive sex (Malizia et al. 1995) and low coefficients of relatedness between males were found for the same population in another study (Zenuto et al. 1999). Moreover, by pairing males only from sites that were more than 50 m apart, I maximized the likelihood that the subjects were both unrelated and unfamiliar.

Other factors that could affect territorial behaviour include resource-holding capacity and ‘prior resident advantage’ (Kokko et al. 2006). I controlled for resource-holding capacity by matching males of similar body mass for all contests. Since all experimental males were provided with their own ‘territory’ in the experimental set-up at the same time, no individual had prior resident advantage.

With individual recognition, animals can modify their behaviour when they encounter conspecifics or scent as an associate cue. However, recognition requires the capacity to remember specific individuals with their respective cues. It was shown in prairie voles that the recognition of individually distinctive phenotypes rather than genetic relatedness per se is responsible for the higher frequency of amicable behaviours and lower frequency of aggression seen between siblings (Paz y Miño & Tang-Martínez 1999). Although few studies have examined memory for odours, rather long intervals between trials in some habituation studies suggest that rodents have a good memory for individual scents. Earlier data for hamsters (Johnston 1993) demonstrated that males remember the odour of another male for 10 days, while Beauchamp & Wellington (1984) showed that memory for odours lasted 4 weeks in guinea pigs. Paz y Miño & Tang-Martínez (1999) found that prairie voles remember the individual odours of siblings for approximately 3 weeks. After that, recognition is maintained only by limited occasional encounters after separation. In all these cases, since memory for odours lasts longer than hours or days, long-term memory must be involved (Kogan et al. 2000). The results of the present study show that memory for familiar scents in tuco-tucos is similar to that found in hamsters. Furthermore, memory was enhanced when combined with experience with the scent donor, as also occurs in prairie voles. Tuco-tucos that also interacted with the scent donor in a contest distinguished odours through the first week, but continued to investigate the novel odour until the fifth week. Note, however, that a single interaction with another individual did not result in familiarization. Males given no prior experience with an odour did not differ in the amount of time they spent sniffing the odour of an individual that they had previously encountered and the odour of a novel individual.

Memory performance should be improved when multiple cues are used. Animals that were familiarized with the odours of an individual that they later encountered in a contest associated the scent with a specific competitor. Other sensory cues (visual, tactile and acoustic signals) might reinforce chemical cues during the contest and enhance subsequent recognition during the discrimination test. In the present study, I tested male tuco-tucos responses to odours from male conspecifics that they had previously encountered during a contest without considering the result of the contest (loser or winner). In golden hamsters, *Mesocricetus auratus*, physical contact between the subjects and stimulus animals was necessary to develop integrated, multi-odour memories of familiar individuals (Johnston & Peng 2008). Furthermore, the result of an initial aggressive encounter affected the subsequent response to the competitor's odour; losers avoided scents of winners for 1 week after the interaction experience (Lai & Johnston 2002). In a more recent study, Petrulis et al. (2004) found that individual hamsters not only recognized familiar males but that losers also distinguished familiar winners from novel winners. Individuals learned to fear the familiar winner, but they had no fear of other familiar, but neutral, males (Lai et al. 2005). Hence, hamsters appear to recognize opponents from a single fight and modify their behaviour according to past experiences. It is likely that tuco-tucos in the present study were not able to recognize an opponent's odour as 'familiar' following a single previous contest with that individual, or that they effectively recognized them, but treated them as strangers rather than as territory-holding neighbours because they posed a similar threat.

Fighting for limited resources may be costly (including energy and time spent during a contest) and risky (injuries received, enhanced predation risk or death); thus, it is expected that selection should favour a suite of mechanisms involved in the assessment of contestants (Arnott & Elwood 2009). In this study, familiarity by odour cues diminished aggressive behaviour in tuco-tucos, suggesting that it may represent a key mechanism mediating neighbour recognition and territorial behaviour in *C. talarum*. Furthermore, social experience with scent donors improved the memory for their odours; memory for conspecific odours lasted longer when animals were familiar with those odours and when they interacted socially with the odour donor. For territory-holding individuals, strangers may represent both the potential loss of a male's burrow system and priority access to neighbouring females. Thus, this is the first study to demonstrate both a dear enemy relationship in a caviomorph burrowing rodent as well as the importance of memory for odours in the territorial system of *C. talarum*. Future studies should focus on the interaction among familiarity, body mass asymmetry, outcome of previous fights and health-state-defining fighting strategies.

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