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An Investigation of Sibling Recognition in a Solitary Sciurid, Townsend's Chipmunk, Tamias townsendii

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AN INVESTIGATION OF SIBLING RECOGNITION IN A SOLITARY SCIURID, TOWNSEND'S CHIPMUNK, TAMIAS TOWNSENDII

by

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(With 3 Figures)
(Acc. 30-V-1989)

Introduction

Numerous animal species can discriminate between heterospecifics and conspecifics (COLGAN, 1983), between their own offspring and same-aged offspring of conspecifics, and between neighbors and strangers (*e.g.* BARASH, 1974; VESTAL & HELLACK, 1978; HARRIS & MURIE, 1982; CALAY & BOUTIN, 1987). These discrimination abilities may have selective advantages: animals can avoid wasted reproductive effort by only mating with conspecifics and caring for their own young or those of close relatives. Neighbors may expend less energy once dominance is established if they can recognize animals they have previously encountered.

The ability to discriminate between kin and non-kin (kin recognition) is another level of discrimination of potential importance in maximizing an animal's fitness (HOLMES & SHERMAN, 1983; HEPPER, 1986; BLAUSTEIN *et al.*, 1987a, b, BLAUSTEIN *et al.*, 1988). Kin recognition may enable animals to direct nepotistic behavior selectively toward kin, which could result in increased inclusive fitness (HAMILTON, 1964). It may also

enable animals to avoid extreme inbreeding (*e.g.* McGUIRE & GETZ, 1981; DEWSBURY, 1982; BOYD & BLAUSTEIN, 1985) or to distinguish degrees of relatedness when choosing a mate, thus facilitating optimal outbreeding (BATESON, 1978, 1983; SHIELDS, 1982, 1983).

Familiarity (direct familiarization, PORTER, 1988) is the most commonly demonstrated mechanism underlying kin recognition in vertebrates (BEKOFF, 1981; BLAUSTEIN *et al.*, 1987a). It occurs when an animal learns to recognize conspecifics to which it has been directly exposed (BEKOFF, 1981; BLAUSTEIN *et al.*, 1987a; WALDMAN, 1987; PORTER, 1988). Because neighbor recognition is also based on familiarity, the question of how animals distinguish familiar kin from familiar neighbors arises. This problem can be resolved if kin recognition through familiarity develops at a time when animals are exposed primarily to kin (*e.g.* lactation in mammals). Familiar animals may be treated as neighbors if they are encountered after this period even if they are kin.

Two mechanisms of kin recognition have been suggested which would allow animals to recognize kin they have never encountered before. These are phenotype matching (indirect familiarization, PORTER, 1988) and recognition alleles. In phenotype matching an animal learns to recognize some aspect of its own phenotype (self-inspection) or the phenotype of related conspecifics, and can subsequently recognize unfamiliar animals (presumably kin) based on that phenotype. If non-kin are present during the period when the phenotypic signal is learned, they also may be treated as kin unless animals only base discrimination on their own phenotype (*i.e.* self-matching, see HOLMES & SHERMAN, 1982). If recognition alleles are operating, both the signal and the perception of the signal would be genetically determined (BLAUSTEIN, 1983). Recognition alleles are difficult to distinguish experimentally from phenotype matching through self-inspection by currently available methods (BLAUSTEIN, 1983; but see BEAUCHAMP *et al.*, 1986).

One way in which we can ascertain the evolutionary and ecological significance of kin recognition is to investigate ecologically similar, closely related species. Comparative studies have been conducted in several species of closely related invertebrate taxa including bees, ants and wasps (BREED & BENNETT, 1987; MICHENER & SMITH, 1987). Among the vertebrates, two groups have been studied most extensively: anuran amphibians and rodents (reviewed by BLAUSTEIN *et al.*, 1987a, b). Studies of kin recognition in the family Sciuridae (Class Mammalia; Order Rodentia) probably represent the most comprehensive comparative work

in mammals. Kin recognition has been studied in at least four North American sciurids (*e.g.* DAVIS, 1982; HOLMES & SHERMAN, 1982; HOLMES, 1984).

Sciurids show varying degrees of sociality (MICHENER, 1983). In the least social species, animals live solitarily, although they may have overlapping home ranges, and pups disperse at weaning. In more social species, daughters tend to settle close to their mothers, pups from neighboring litters interact, and male territories overlap or encompass female territories. The most social species form colonies (MICHENER, 1983). Solitary species tend to be highly aggressive in encounters with conspecifics. In the more social species, amicable interactions are common between related females (MICHENER, 1983).

If kin recognition functions solely to facilitate nepotistic interactions, direct familiarization might be found in species which are only nepotistic toward familiar kin. Indirect familiarization might be found in species which are likely to encounter unfamiliar kin frequently, and which are highly nepotistic. Among the sciurids, amicable interactions in solitary species are primarily restricted to familiar kin (females and their young-of-the-year; MICHENER, 1983). Nepotism among unfamiliar kin may be more important in highly social sciurids (*e.g.* shared resources between sisters from consecutive litters). Thus, if kin recognition facilitates nepotism in these animals, selection might favor familiarity in solitary species and phenotype matching in social species.

If kin recognition functions to facilitate optimal outbreeding, or to enable animals to avoid close inbreeding, the mechanism used to discriminate kin from non-kin should be independent of the level of nepotism and may only depend on the spatial and temporal distribution of animals. Dispersal in many animals is sex-biased and may function in inbreeding avoidance (GREENWOOD, 1980; COCKBURN *et al.*, 1985; WOLFF *et al.*, 1988). Among the sciurids, solitary species often do not have strongly sex-biased natal and breeding dispersal (HOLEKAMP, 1984). These animals might be expected to use phenotype matching to avoid mating with closely related, unfamiliar animals. More social species tend to have strongly male-biased dispersal. In this case, familiarity may be sufficient to allow inbreeding avoidance.

Townsend's chipmunk (*Tamias townsendii*) is a solitary, relatively aggressive sciurid (SHERMAN, 1973). Adults and juveniles of both sexes give alarm calls (BRAND, 1970; WARNER, 1971, pers. obs.), and these calls may function to warn kin of approaching predators. Little is known about dispersal in *T. townsendii*, however, our preliminary data suggest

that dispersal is not strongly sex biased, and that animals may not disperse far enough to completely avoid encounters with close kin. If kin recognition is manifested in this species, it may function both in the facilitation of optimal outbreeding and the direction of nepotistic behavior toward relatives.

To determine whether *T. townsendii* is capable of kin recognition, we experimentally tested laboratory reared juveniles. We addressed the following questions: 1) do juvenile chipmunks recognize their siblings and 2) if so, on which mechanism is kin recognition based?

Methods

Pregnant *T. townsendii* were live-trapped at 3 sites in MacDonald Forest (18 km N of Corvallis, Oregon) and one site at Mary's Peak Campground (42 km SW of Corvallis, Oregon) between 26 April and 2 June, 1987. Females were housed individually in $30.5 \times 35.5 \times 16.5$ cm plastic cages. Each was provided with a nest box and nesting material, and food and water ad libitum. Animals were maintained on a diet of Purina rat and rabbit chow and supplemented with fruit, sunflower seeds, millet, corn and dry dog food.

Nest boxes were checked each evening for pups. Crossfostering of pups was carried out 1-3 days after they first appeared. At this stage, the pups' eyes and ears were still closed (ears open at 24 and eyes at 28 days; FORBES & TURNER, 1972). Cross-fostering produces 4 treatment groups: siblings reared together (SRT), siblings reared apart (SRA), nonsiblings reared together (NSRT), and nonsiblings reared apart (NSRA). If animals only use familiarity to discriminate between kin and non-kin, all familiar animals (SRT and NSRT) should be treated alike, as should all unfamiliar animals (SRA and NSRA). If they use phenotype matching, pups should treat familiar kin (SRT) differently than familiar non-kin, and/or unfamiliar kin differently than unfamiliar non-kin. Paired litters were always born within 48 hours of each other. During the cross-fostering procedure, dams were removed from their home cages and placed in holding cages. All pups were also removed from the cages, weighed, toe-clipped for individual recognition and returned to either the home cage or the foster cage.

An attempt was made to retain the original sex-ratio in each litter, and to switch pups of matched weight. Whenever possible, pups were cross-fostered between females from different sites to avoid the possibility that litters were fathered by the same male, or that dams were closely related. This was not possible for 3/9 pairs of litters, but 2 of these pairs were captured > 140 m apart. Our observations indicate that most male home-ranges had a maximum diameter of < 80 m. Thus, it is unlikely that these litters were paternal half-sibs. The third pair of females was captured approx. 40 m apart. However, these pups were only used in two trials. Pups not born within 48 hours of another litter (n = 4 litters) were weighed, toe-clipped and returned to their dams. Pups were housed with their mothers/foster mothers until testing.

Pups were tested at 55-62 days of age. Pups tested together never differed in age by more than 5 days. Because of litter mortality (7/24 complete litters and one partial litter), the SRA came from 6 litters. SRT and NSRA were obtained by pairing pups from both noncross-fostered (4/17 litters) and cross-fostered litters (13/17). To assess whether pups from cross-fostered litters behaved differently than pups from noncross-fostered litters we compared all behaviors (see below) for pairs consisting of only noncross-fostered pups with pairs which had at least one cross-fostered member. This was done for both SRT
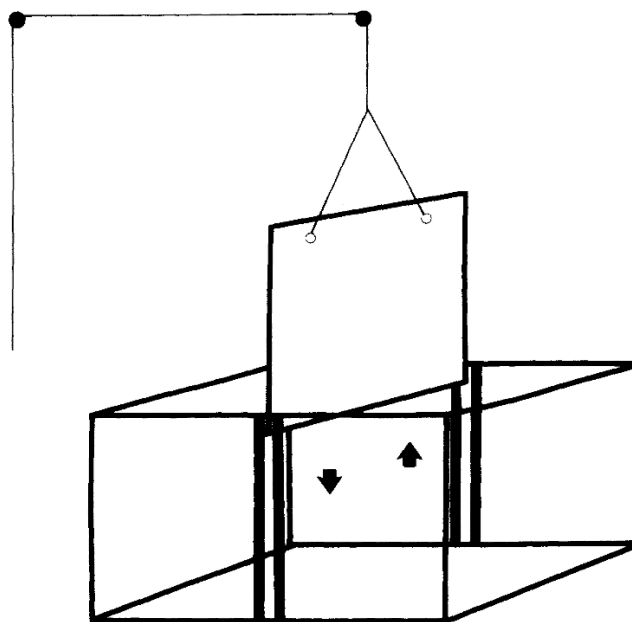
Fig. 1. The testing arena. One pup was placed on either side of the partition. After 5 min, the partition was lifted and the pups interactions were observed. Trials were 10 min.

and NSRA treatment groups (NSRT and SRA consist entirely of cross-fostered pups by definition).

Within the constraints mentioned above, pups were assigned to treatments and partners randomly. Each pup was tested at least once, and 63/73 pups were tested again 1-7 days later. Both pups in second trials had already been tested once. When tested a second time, pups were tested in a different treatment group whenever possible (44/63 trials).

Because we wanted to compare our results to those obtained for other sciurids, we patterned our methods as closely as possible after previous studies of sciurids (*e.g.* Davis, 1982; Holmes & Sherman, 1982; Holmes, 1984). Testing occurred in a $91.5 \times 91.5 \times 56$ cm transparent acrylic arena, which was placed in an observation chamber (Fig. 1). The arena was divided in half by a removable plywood partition. The partition was manipulated from outside the observation chamber by means of a pulley system, and observations were made through a one-way mirror. The bottom of the arena was divided into a 4×4 grid to facilitate recording locations of each animal during trials.

Prior to testing, each pup was given access to the entire arena twice for 20-30 minutes. These familiarization periods usually occurred on the two days immediately prior to testing, and were always within 4 days of the pup's first trial. The arena was rinsed with vinegar water after each pup was removed, as were the cages used to transport the pups between the arena and the home cage. This procedure was also used between actual trials.

On the day of testing, pups were removed from their home cages and places individually in small $26 \times 20 \times 15$ cm holding cages. Pups were placed at least 1 m from neighboring cages, and given water and a small amount of food. Pups were brought in and removed by an assistant, leaving the observer blind to which treatment was being tested in any given trial.

At the beginning of each trial, one pup of a test pair was placed on either side of the partition. They were allowed to acclimate to the arena for 5 minutes before the partition

was lifted. Because pups usually froze for several seconds to several minutes when the partition was lifted, timing of a trial started when one or both pups became active, and trials lasted 10 min. If neither pup moved for 10 min after the partition was lifted, both were removed and retested at the end of the day (n = 7). If the pups still did not interact, the trial was discarded (n = 2).

Frequencies and durations of the following 8 behaviors were recorded into a hand held cassette recorder by one observer (CAF): Approach - an animal moves directly toward a stationary animal; Sniff - an animal contacts another with its naso-oral area; Groom - an animal licks or bites itself; Contact - the two test animals are physically touching but not sniffing; Mount - one animal mounts the other as if copulating; the mounting animal may rub its chin back and forth across the other animal's head; Follow - one animal follows closely (<1 cm) behind the other; both are moving; Fight - one animal jumps on and attempts to bite the other animal; Chase - an animal follows the other; both are running and both have their tails erect. We considered the first six behaviors to be amicable or exploratory and the last two behaviors to be aggressive. In addition to the behaviors, the location of each animal on the 4×4 grid was recorded every 15 sec. by an assistant. This assistant was the same person that placed the animals in the arena, and was not blind to which treatment was being tested. Although pups were individually marked with felt-tipped pen, it was not always possible to keep track of each animal individually. Thus, the data are for test pairs of animals not individuals. We also recorded the sex composition of pairs (male:male, male:female, female:female) and included the variable "sex" in our analyses (see below) to determine whether it affected behavior. Animals were weighed and returned to their home cages after testing.

To determine whether cross-fostering had an effect on growth of pups, we analysed weights at testing. Pups were divided into three treatments: 1) those that were not cross-fostered and were raised with only their own siblings, 2) pups that were cross-fostered and raised with their biological mothers and 3) pups that were cross-fostered and raised with foster mothers. We included age differences and litter size in the analysis to control for these factors.

Data analysis.

Because the 17 variables (8 frequencies, 8 durations and the mean distance apart) were not independent measures of kin recognition, all possible variables were analyzed in two multivariate analyses of variance (MANOVA), one that included only those variables that had been measured in all trials (frequencies and the mean distance apart), and one that included durations. The independent variables in these analyses were sex, relatedness and familiarity. The normality of the dependent variables was assessed using probability plots and histograms. We used an F-max text to determine whether treatments had equal variance. Variables were log- or square root-transformed as necessary to fit the assumptions of parametric analysis of variance. The frequency of mounting, following, fighting and chasing, and the durations of fighting and chasing were not included for reasons discussed below.

The variables that were included in the MANOVA were analyzed individually by a 3-way ANOVA with "familiarity", "kinship" and "sex composition" as the main effects. Thus, the 3-way ANOVAs function as post-hoc tests of the MANOVA (DILLON & GOLDSTEIN, 1984). Table 1 gives the treatment means and standard errors for all behavioral variables.

In 4 cases (frequency of mounting, following, fighting and chasing) the data violated the assumptions of both parametric and non-parametric ANOVAs. In these 4 cases, the data were collapsed into categorical data (*i.e.*, whether or not the behavior occurred in a given trial; Table 1), and analyzed as a three-way chi-square contingency table. If the

TABLE 1. Behavioral means (SE) for all behaviors measured

Treatment	SRT	SRA	NSRT	NSRA
Frequencies (number/min)				
Approach	24.25 (4.76)	23.59 (3.91)	22.22 (2.32)	16.71 (3.81)
Sniff	9.44 (2.17)	9.59 (2.31)	13.78 (2.31)	4.59 (1.48)
Groom	1.83 (0.14)	1.99 (0.16)	2.23 (0.12)	1.33 (0.14)
Contact	1.33 (0.20)	0.81 (0.20)	1.78 (0.21)	0.71 (0.14)
Occurrence (percent)				
Mount	43.7	17.6	50.0	11.8
Follow	43.7	41.2	66.7	29.4
Fight	37.5	64.7	5.6	58.8
Chase	43.7	70.6	5.6	64.7
Mean distance	2.28 (0.10)	2.58 (0.16)	2.07 (0.16)	2.94 (0.11)

Frequencies: mean frequency that a behavior occurred during trials. Occurrence: proportion of trials in which a behavior occurred. Mean distance: mean distance between pups (measured every 15 sec) over the entire trial. Groom and contact were square root and log transformed, respectively. Number of trials per treatment: SRT = 16, SRA = 17, NSRT = 18, NSRA = 17.

chi-square value was significant, log-linear analysis was used to determine which treatment group was the important factor (EVERITT, 1977).

Because the analysis of pup weight contained both continuous (age, weight and litter size) and categorical (treatments) variables, a logistic regression was used (ZAR, 1984).

Results

The first MANOVA (frequency of approach, sniff, groom, contact and the mean distance apart) was highly significant (F [familiarity] = 6.743, df = 1,56, P < 0.001; F [relatedness × familiarity] = 4.545, df = 5,60, P = 0.002), indicating that there were significant differences in the way in which different treatment groups (SRT, SRA, NSRT, NSRA) interacted. Results of the second MANOVA (duration of approach, sniff, groom and contact) showed that the duration of behaviors did not differ across treatment groups. Thus, durations will not be examined further here.

Frequencies and mean distance apart.

Sex composition of pairs.
Results of the 3-way ANOVAs (Table 2) indicate that the sex composition of pairs influenced the mean distance between animals. Scheffe's

TABLE 2. Results of the three-way ANOVAs for the frequency and duration of behaviors, and the mean distance between pups, including the sex of pairs

Variables	Sample size (dfMSE)	Relatedness (1)	Familiarity (1)	Sex (2)	Relatedness × Familiarity (1)	Relatedness × Sex (2)	Familiarity × Sex (2)	Relatedness × Familiarity × Sex (2)
Frequencies								
Approach	68 (56)	0.082	1.661	0.605	0.791	0.427	0.535	1.255
Sniff	68 (56)	0.000	3.357	0.840	4.307*	0.639	1.088	0.051
Groom	68 (56)	0.195	11.040**	0.215	16.156***	3.534*	2.864	1.104
@Groom	67 (55)	1.130	16.208***	0.956	12.421***	2.394	2.961	2.294
Contact	58 (56)	4.185*	23.428***	1.538	5.641*	0.509	3.210*	1.237
@Contact	67 (55)	0.852	13.818***	0.292	1.568	0.641	0.946	0.020
Mean distance								
Apart	68 (56)	0.147	22.534***	3.476*	12.169***	0.607	1.459	2.551

* $P < 0.05$; ** $P < 0.005$; *** $P < 0.001$. @ Excluding one outlier from the analysis (see text). The values given are F-values, the numbers in parentheses are degrees of freedom for the variables and for the error term.
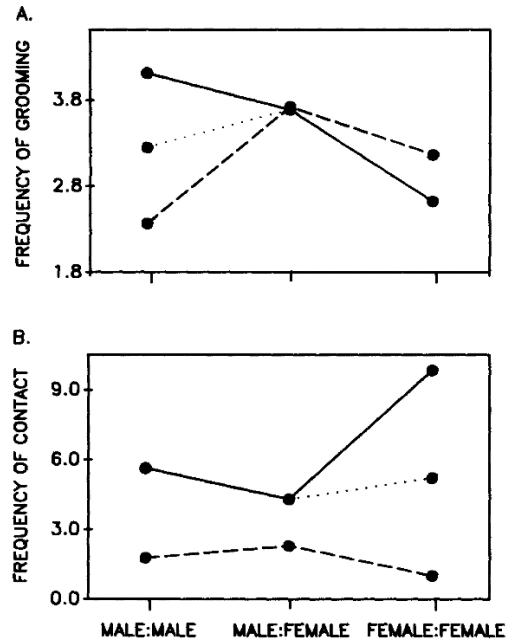
Fig. 2. Means of the significant interaction effects when the sex composition of pairs was a factor: 2a - relatedness × sex interaction term for the frequency (mean number of grooming/10 min trial) of grooming; (—) related, (--) unrelated, (····) related without the outlier. 2b - the familiarity × sex interaction term for the frequency of contacts; (—)familiar, (--) unfamiliar, (····) familiar without outlier.

multiple contrasts indicate that male:male pairs did not differ significantly from female:female pairs with respect to the mean distance apart $(F = 0.092, \; df = 1,56, \; P = 0.073)$, but that male:female pairs remained farther apart than either male:male $(F = 6.288, \; df = 1,56, \; P = 0.015)$ or female:female pairs $(F = 5.402, \; df = 1,56, \; P = 0.024)$. In two cases (the relatedness × sex effect of groom and the familiarity × sex effect of contact), interaction terms which include sex were significantly different than random (Table 2, Fig. 2). However, when box plots were used to determine whether any data points were outliers, one was discovered in each data set. When these outliers were removed, the interaction terms no longer had a significant influence $(P > 0.05$; Fig. 2; Table 2). In the case of the relatedness × sex interaction term for the frequency of grooming, the removal of one male:male point resulted in a change in the standard deviationfrom 3.06 $(X = 4.11, \; n = 9)$ to 1.75 $(X = 3.25)$. The removal of the outlier for the familiarity × sex interaction term for the frequency of contact resulted in a change in SD from 11.00 $(X = 9.7; \; n = 6)$ to 5.22 $(X = 5.6)$. This strongly suggests that sex did not influence the frequency of grooming and contact, but that the effects were caused by one pair in each case.

Familiarity and relatedness.

The main effect, "familiarity" significantly influenced the frequency with which chipmunks groomed and contacted each other and the mean distance between animals. In three cases (frequency of sniffing, grooming and the mean distance apart) the kinship × familiarity interactions term was significant, indicating that familiarity and kinship do not act independently. In each case, siblings acted similarly, but the behavior of nonsiblings depended on whether they were familiar or not. In general, NSRT sniffed and groomed more often than siblings and remained closer together (whether reared together or apart), while NSRA sniffed and groomed least and remained farther apart (Fig. 3a, b, c). Although the main effects "relatedness" and "familiarity" and the relatedness by familiarity interaction term are significant in the first ANOVA for the frequency of contact, only the main effect "familiarity" is significant when one outlying point is removed (see above). This suggest that only familiarity influenced the frequency with which pups contacted each other. Although the main effect "relatedness" never significantly influ-
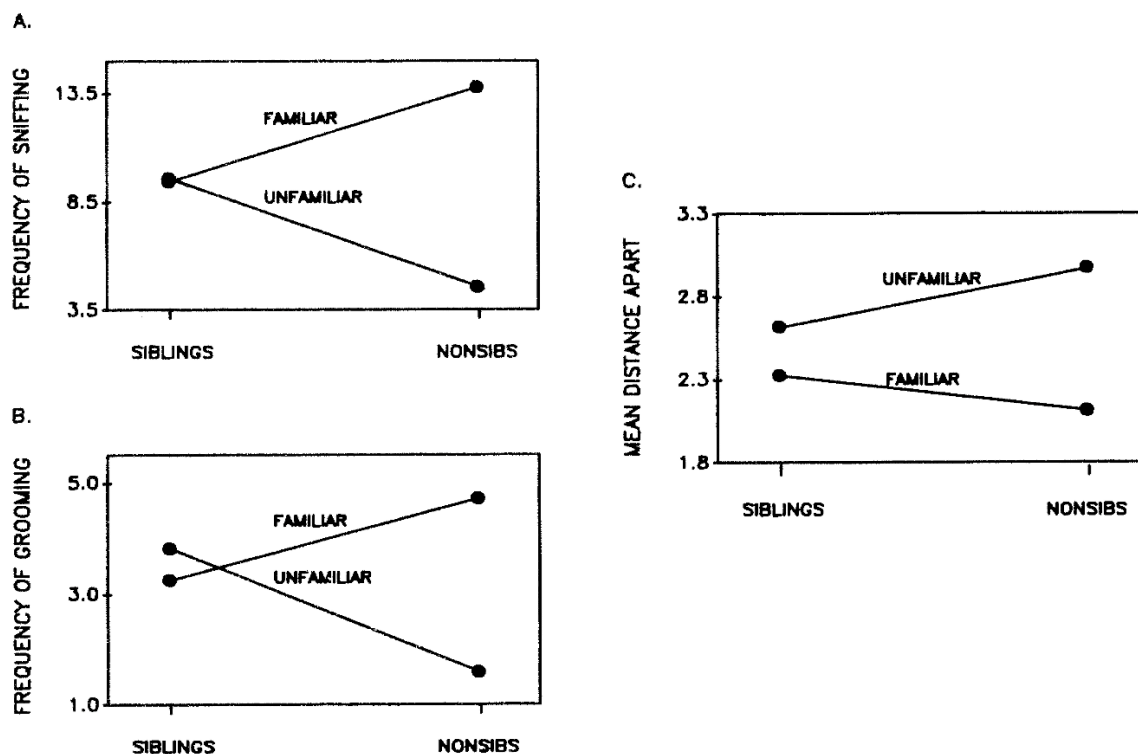

Fig. 3. Means of significant interaction effects: 3a - frequency (mean number of sniffs/10 min trial) of sniffing; 3b - frequency of grooming; 3c - the mean distance between animals in grid units (where 0 is the minimum and 5.66 is the maximum distance apart).

enced behaviors by itself, a significant interaction term suggests that kinship did influence the behavior of the animals. However, the significant main effects are difficult to interprete when the interaction terms are significant.

The three-way contingency analyses (Table 3) indicate that familiarity

TABLE 3. Chi-square values for three-way contingency analyses and log-linear analyses for frequencies of mounting, following, fighting and chasing

Variables	Three-way Chi-square	Log-linear variables		
		Relatedness	Familiarity	Relatedness × Familiarity
Degrees of freedom	4	2	2	1
Mount	8.64a	—	—	—
Follow	5.29	—	—	—
Fight	15.98**	5.41a	13.95***	2.57
Chase	18.90***	7.00*	17.67***	3.20a

a $P < 0.10$; * $P < 0.05$; ** $P < 0.005$; *** $P < 0.001$.

strongly influenced the occurrence of fighting and chasing. Furthermore, kinship significantly influenced the occurrence of chasing.

The effect of cross-fostering.

In no case was there a significant difference in behavior between cross-fostered and noncross-fostered pups when comparing the behavior of SRT or NSRA (Mann-Whitney U, $p > 0.17$).

Pups that were from cross-fostered litters were significantly heavier at testing than pups that were not cross-fostered but did not differ in weight regardless of whether they were raised by their own or a foster mother (Table 4; treatment 1: mean = 63.4 g, SE = 4.5; treatment 2: mean = 67.4 g, SE = 5.6; treatment 3: mean = 66.0 g, SE = 5.5). The factor ''age'' was initially included in the model but had no effect on weight, and was dropped from the analysis. Although litter size had no significant effect when included in the model, it became significant (Model: weight = litter size + constant, $F = 4.424$, $df = 1,65$, $p = 0.039$) when rearing regimen was dropped. This suggests that the effects of litter size and rearing regimen are highly correlated, but that rearing regimen is more important.

TABLE 4. Logistic regression results for pup weights: Students t values for the terms in the regression model

Model	Sample size	Overall F	Df	Age	Litter size	Cross-fostered	Mother
1) Weight at testing	67	3.064*	3,63	—	−1.651	2.120*	1.101
2) Weight at testing	48	5.168**	4,43	1.800a	−2.724**	3.209**	0.615

a $P<0.10$; * $P<0.05$; ** $P<0.01$. Model 1: Weight = constant + litter size + cross-fostered + mother. Model 2: Weight = constant + litter size + age + cross-fostered + mother.

The variables cross-fostered and mother are indicator variables. Cross-fostered indicates whether or not pups came from litters which had been cross-fostered, mother indicates whether pups were raised by their own or by foster mothers.

To determine whether these differences in weights existed prior to cross-fostering, we also analysed pup weights at cross-fostering. The litter sizes used in this analysis were those of each pup's natural litter. Cross-fostered pups were again found to be significantly heavier than noncross-fostered pups (Table 4; treatment 1: mean = 3.72 g, SE = 0.53; treatment 2: mean = 4.17 g, SE = 0.512; treatment 3: mean = 4.25 g, SE = 0.74). In addition, litter size was also significant. Thus, cross-fostering probably did not cause the differences in weights between groups. The differences were probably a pre-existing condition, perhaps caused by litter size differences.

Discussion

Our results indicate that Townsend's chipmunks can discriminate between kin and non-kin. The most likely mechanism for sibling recognition was familiarity established during rearing because overall, pups were more amicable and less aggressive toward familiar animals than toward unfamiliar animals. However, familiarization can not fully account for sibling recognition because in four analyses (the frequency of sniffing, grooming, chasing and the mean distance apart (Tables 2, 3), kinship also had a significant influence on behavior.

Although siblings that were reared apart experienced each other in utero and up to 72 hours post-partum, this early association may not completely explain the differential behavior toward unfamiliar related animals. If familiarity alone were responsible for kin recognition, and the

cues mediating recognition can be learned post-partum in addition to in utero, pups might be expected to treat SRT and NSRT alike. If recognition can only be learned before cross-fostering takes place, pups should treat NSRT and NSRA alike. Because in some cases, pups discriminated between NSRT (familiar non-siblings) and siblings (whether reared together or apart), but did not treat NSRT and NSRA alike (Fig. 2), it seems likely that a mechanism other than familiarity (phenotype matching or recognition alleles) was also operating.

By raising females with from zero to two siblings and from one to three non-siblings, HOLMES (1986a) showed that female Belding's ground squirrels (*Spermophilus beldingi*) recognized kin by phenotype matching through self-inspection. Siblings raised only in the presence of non-siblings were still significantly less agonistic toward unfamiliar siblings than toward unfamiliar non-siblings. Because all of our SRA were reared with at least one sibling, we were unable to test directly for recognition by self-inspection. Nevertheless, pups discriminated between familiar siblings and familiar nonsiblings which suggests that recognition may be achieved by self-inspection. If pups used all litter-mate phenotypes as a basis for kin recognition, they should treat all litter-mates alike. If they compare animals to their own phenotype, they should be able to discriminate between litter-mate siblings and litter-mate non-siblings on the basis of this comparison.

The sex of pair members only affected the mean distance between pups (Table 2). This may be a random effect because only 1 of 15 variables which included sex had a significant effect on behavior. If this is not due to random variation, it does not change the interpretation of the significant "familiarity" and "familiarity × relatedness" variables. Although members of male:male and female:female pairs were closer to each other than members of male:female pairs, within each of these groups NSRT were closest to each other, sibs (whether raised together or apart) were an intermediate distance apart, and NSRA were farthest apart (Fig. 3c).

Experimental tests of sibling recognition in four species of ground squirrels have demonstrated differences in the ability to discriminate between kin and non-kin (SHEPPARD & YOSHIDA, 1971; DAVIS, 1982; HOLMES & SHERMAN, 1982; HOLMES, 1984). *S. tridecemlineatus* used familiarity alone to discriminate between siblings and non-siblings (HOLMES, 1984). In *S. parryii* and *S. beldingi*, familiarity influenced kin recognition but females of both species can also distinguish kin on the basis of relatedness (HOLMES & SHERMAN, 1982). Female *S. beldingi* can distinguish full sisters from maternal half-sisters (HOLMES & SHERMAN,

1982, HOLMES, 1986a) and from paternal half-sisters, suggesting that kin recognition can occur in the absence of familiarity (HOLMES, 1986b). *S. richardsonii* behaved more amicably toward kin than non-kin, whether or not they were familiar and only differentiated between familiar and unfamiliar kin by the frequency of approaches (DAVIS, 1982). In addition, animals only differentiated between familiar and unfamiliar non-kin in one out of five behaviors. Thus, *S. richardsonii* relies primarily on phenotype matching or recognition alleles for kin recognition. Although familiarity plays a role, it is not the sole mechanism on which kin recognition is based.

The mechanisms of recognition may be correlated with sociality and life-history traits in the sciurids (HOLMES, 1984; SHERMAN & HOLMES, 1985; HOLMES, 1986b; BLAUSTEIN, 1987a; SCHWAGMEYER, 1988). Recognition without direct familiarization has been demonstrated in the three colonial species tested (*S. beldingi*, *S. parryii*, HOLMES & SHERMAN, 1982; and *S. richardsonii*, DAVIS, 1982). Presumably, these three species are the most nepotistic (SHERMAN, 1977; McLEAN, 1982; DAVIS, 1984). If kin recognition is primarily used to direct nepotistic acts, phenotype matching (or recognition alleles) might be found in species which frequently encounter unfamiliar kin. In the most social sciurids, several generations of related females may use the same burrow system and encounters between unfamiliar kin may be likely (MICHENER, 1984). *S. tridecemlineatus*, a solitary species, only discriminated between familiar and unfamiliar animals in laboratory tests (HOLMES, 1984). In this species, nepotism is probably only manifested between litter-mate siblings and between females and their young-of-the-year (SCHWAGMEYER, 1980). All four sciurids in which kin recognition has been studied have strongly male-biased dispersal (HOLEKAMP, 1984). Because sexually active, related males and female do not generally overlap spatially, inbreeding avoidance may occur without kin recognition.

Tamias townsendii is similar to *S. tridecemlineatus* because it is solitary but dissimilar in that it is capable of using both direct and indirect familiarization to discriminate between kin and non-kin. Townsend's chipmunks probably do not interact frequently and interactions are typically aggressive (SHERMAN, 1973; pers. obs.) but its alarm calling behavior may have a nepotistic function. In addition, chipmunks may be passively nepotistic: they may be less aggressive toward kin than non-kin.

Finally, if dispersal in *T. townsendii* is not highly sex-biased, kin recognition may function in optimal outbreeding avoidance.

Summary

We tested juvenile Townsend's chipmunks (*Tamias townsendii*) to determine whether 1) they could distinguish kin from non-kin and 2) to assess if this ability was based on familiarity or on genetic relatedness. Seventy-three pups between the ages of 55-62 days were observed in 68 pairwise tests. The frequencies (number/trial) and durations (length in seconds) of 8 behaviors as well as the mean distance between pups were recorded in 10 min. trials. Analyses indicated that frequencies of behaviors varied depending on relatedness (related/unrelated) and familiarity (familiar/unfamiliar) but durations of behaviors did not. Pups discriminated between familiar and unfamiliar animals in the frequency of contacts, and the occurrence of attacks and chases. Pups discriminated between animals on the basis of relatedness in the occurrence of chasing. Both relatedness and familiarity played a role in the frequency of sniffing and grooming and in the mean distance between pups, as shown by the significant interaction between familiarity and relatedness in 2-way ANOVAs. The sex composition of pairs (male-male, male-female or female-female) influenced the mean distance between pups. We can only speculate on the functions of kin recognition in Townsend's chipmunk. It may enable animals to selectively direct nepotistic behavior toward kin or facilitate optimal outbreeding.

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Zusammenfassung

Wir untersuchten ob 1) junge Townsend's Streifenhörnchen (*Tamias townsendii*) zwischen verwandten und unverwandten Tieren unterscheiden können (Verwandtschaftserkennung) und 2) ob diese Fähigkeit auf Bekanntheit oder genetischer Verwandtschaft basiert. Es wurden 73 Jungtiere im Alter zwischen 55-62 Tagen untersucht. Sie wurden in 68 Einzelversuchen jeweils paarweise in einer Arena beobachtet. In diesen 10-minütigen Versuchen wurden die Häufigkeit (Anzahl/Versuch) und die Dauer (Sekunden) von acht verschiedenen Verhaltensweisen, sowie der durchschnittliche Abstand zwischen den Tieren, gemessen. Die statistischen Analysen zeigten, dass die Häufigkeit der Verhaltensweisen in Abhängigkeit von Verwandtschaft (verwandt/nicht verwandt) und Bekanntheit (bekannt/unbekannt) variierten, nicht jedoch die Dauer der Verhaltensweisen. Eine Unterscheidung von bekannten oder unbekannten Tieren zeigte sich in der Häufigkeit der Individualkontakte und im Auftreten von Angriffsverhalten oder Jagdverhalten. Jagdverhalten zeigte sich ebenfalls unterschiedlich bei verwandten und nicht verwandten Tieren. Die Tests zeigten weiter, dass beide, Bekanntheit und Verwandtschaft, eine Rolle in die Häufigkeit von Schnüffeln, Putzverhalten, und dem durchschnittlichen Abstand zwischen den Tieren, spielte. Die Geschlechtszusammensetzung in den Paaren (männlich-männlich, männlich-weiblich, weiblich-weiblich) beeinflusste ebenfalls den Durchschnittsabstand. Über die Funktion der Verwandschaftserkennung in Townsend's Streifenhörnchen können wir leider nur spekulieren. Vielleicht befähigt es die Tiere, nepotistisches Verhalten direkt auf ihre Verwandten zu richten oder es soll Inzucht verhindern.