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Juvenile T. townsendii were tested at 55-62 days of age to determine whether 1) they could distinguish kin from non-kin and 2) whether this ability was based on familiarity or on genetic relatedness. Seventy-three pups were observed in 68 pairwise tests. The frequencies and durations of 8 behaviors as well as the distance between pups were recorded in 10 min. trials. Analyses indicated that pups distinguished familiar animals from unfamiliar animals in the frequency of contacts, and the occurrence of attacks and chases. Pups distinguished animals on the basis of relatedness in the occurrence of chasing. Both relatedness and familiarity probably play a role in the frequency of sniffing and grooming, the duration of grooming and in the mean distance between pups, as shown

by the significant interaction between familiarity and relatedness in a 2-way ANOVA. The sex composition of pairs also affected behavior. Sex influenced the frequency of grooming, the frequency of contact and the mean distance between animals. However, the ability to recognize kin was not limited to one sex. Kin recognition may enable T. townsendii to direct nepotistic behavior (eg. alarm calls) toward kin. It may also function to facilitate optimal outbreeding in this asocial species.

Kin Recognition in Townsend's Chipmunks (Tamias
townsendii)

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TABLE OF CONTENTS

INTRODUCTION	1
MATERIALS AND METHODS	9
Data Analysis	17
RESULTS	20
Frequencies	20
Sex Differences	24
Durations	27
Sex Differences	30
Mean Distance Apart	31
Sex Differences	31
Weights	31
DISCUSSION	34
BIBLIOGRAPHY	41

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1. The cross-fostering procedure and the treatment groups produced by the procedure	10
2. The testing arena	14
3. Means of the significant interaction effects: treatment effects	22
4. Means of the significant interaction effects: sex differences	28

LIST OF TABLES

<u>Table</u>		<u>Page</u>
1.	Behavioral means for all behaviors measured	18
2.	The results of the two-way ANOVAs on frequencies and durations of behaviors, and on the mean distance between pups	21
3.	Chi-square values for three-way contingency analyses and log-linear analyses	25
4.	The results of three-way ANOVAs including the sex composition of pairs	26
5.	Logistic regression results for pup weights	32

KIN RECOGNITION IN TOWNSEND'S CHIPMUNK, (TAMIAS
TOWNSENDII)

INTRODUCTION

Numerous animal species can discriminate between heterospecifics and conspecifics (species recognition; Colgan 1983), between their own offspring and offspring of conspecifics, and between neighbors and strangers (neighbor recognition; e.g. Barash 1974; Vestal & Hellack 1978; Harris & Murie 1982; Caley & Boutin 1987). These discrimination abilities may have selective advantages. For example, animals could avoid wasted reproductive effort by only mating with conspecifics and directing parental care toward it's own young or those of close relatives.

The ability to discriminate between kin and non-kin (kin recognition) is an additional level of discrimination of potential importance in maximizing an animal's fitness (Holmes & Sherman 1983, Hepper 1986, Blaustein et al. 1987a, b). 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 (eg. Dewsbury 1982, Boyd & Blaustein 1985) or to distinguish degrees of relatedness when choosing a mate, thus facilitating optimal outbreeding (Bateson 1978, 1983). Finally, in cannibalistic species, it might be advantageous

to avoid cannibalizing close relatives (Blaustein & O'Hara 1982).

Familiarity (direct familiarization, Porter 1988) is the most commonly demonstrated mechanism underlying kin recognition. It occurs when an animal learns to recognize conspecifics to which it has been directly exposed (Bekoff 1981; Blaustein 1983; 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 direct familiarization develops at a time when animals are exposed primarily to kin (e. g. during lactation in mammals). Familiar animals will be treated as neighbors if they are first encountered after this period. A period during which familiarity develops has been demonstrated in some species. Prairie voles (Microtus ochrogaster) will not mate with conspecifics with which they were reared, but will mate with animals they encounter after weaning, even if these animals are siblings (Gavish et al. 1984). In most species where direct familiarity has been suggested as a mechanism of kin recognition, experiments have not been conducted which would distinguish kin recognition from neighbor recognition. In these species, animals may use familiarity as a means to discriminate between neighbors and strangers, rather than between kin and non-kin.

Two other mechanisms allow animals to recognize kin

they have not previously encountered (ie., unfamiliar kin). 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 phenotypic traits of related conspecifics, and recognizes these same learned traits in unfamiliar animals (presumably kin). If non-kin are present during the critical period when the phenotypic signal is learned, they and their relatives also may be treated as kin unless animals only base discrimination on their own phenotype (ie., self-matching). The phenotypes recognized may have a genetic basis, or may be environmentally determined (e. g. Greenberg 1979; Porter et al. 1981). Environmental cues are acquired from external sources. If recognition alleles operate, both the trait and the perception of the trait would be genetically determined. Thus, there would be no possibility of recognition errors (Blaustein 1983). Recognition alleles are extremely difficult to distinguish experimentally from phenotype matching through self-inspection by currently available methods (Blaustein 1983; but see Beauchamp et al. 1986).

Animals may treat kin differentially without kin recognition per se if location is used as a stimulus for kin related behaviors (Holmes & Sherman 1983). If kin are in a predictable location, and unrelated animals are excluded, animals could direct nepotistic behavior toward conspecifics at that location.

Recently, experimental tests of kin recognition have been conducted across a wide variety of taxa. Experiments usually consist of a behavioral assay to determine whether animals are able to discriminate between various treatment groups of kin and non-kin (Blaustein et al. 1987a, b; Michener & Smith 1987; Breed & Bennett 1987).

Several taxa have been found to discriminate only between familiar and unfamiliar animals and to treat unfamiliar relatives the same as unfamiliar non-relatives (Bufo boreas, O'Hara & Blaustein 1983; Spermophilus tridecemlineatus, Holmes 1984; Microtus ochrogaster, Gavish et al. 1984; Peromyscus leucopus, Halpin 1987). In other species, results are consistent with the use of both direct and indirect familiarization or, possibly, recognition alleles as mechanisms underlying kin recognition (e. g. Rana cascadae, Blaustein & O'Hara 1981; Spermophilus parryi, Holmes & Sherman 1982; R. sylvatica, Waldman 1984; Acomys caharinus, Porter 1988;). For example, S. beldingi is less aggressive toward familiar non-kin than toward unfamiliar non-kin but is equally amicable toward familiar siblings and familiar non-kin in the field (Holmes & Sherman 1982).

Porter et al. (1981) allowed unrelated unfamiliar juvenile spiny mice (A. caharinus) to nurse from the same female at different times. When placed together in a neutral chamber, these mice treated each other the same as siblings. Thus, recognition is mediated by a cue acquired

from the mother. Worker carpenter ants (Camponotus spp.) will only accept nest-mates into their nests because nest-mates have acquired a pheromone produced by the queen (Carlin & Holldobler 1986, 1987). Recognition also has a genetic component - if workers are raised without a queen they can discriminate between related and unrelated individuals, whether or not these individuals are nest-mates (Carlin & Holdobler 1987, Carlin et al. 1987b).

If the cues used in recognition have a genetic basis, an enormous amount of genetic diversity would be required to produce enough phenotypic diversity for animals to discriminate between individuals or kin classes. Such diversity exists in the major histocompatibility complex (MHC), which also codes for the diversity required for immune response. Both mice and rats can discriminate between conspecifics which differ from each other genetically at only one locus in the MHC (Boyse et al. 1987, Brown et al. 1987). Recognition of these cues in mice is learned between birth and weaning (Yamazaki et al. 1988). Mice reared with foster mothers of a different MHC strain mate with mice of their own strain more often than with mice of their foster mothers strain. Mice raised with mothers of their own strain mate more often with mice of a different strain. Although other portions of the autosomal DNA and the X and Y chromosomes have been shown to be discriminated by mice, discrimination is not based on differences at one locus (Yamazaki et al. 1986).

If kin recognition functions mainly to direct nepotistic behavior toward kin, the ability to recognize kin should vary with the level of sociality. As the social system becomes more complex, the likelihood increases that animals will encounter unfamiliar kin, or kin of varying degrees of relatedness. In this situation, it may be important to recognize unfamiliar kin because opportunities for nepotism are frequent. Thus, less restrictive mechanisms of kin recognition which allow discrimination of unfamiliar kin may be advantageous in highly social, nepotistic species. However, if kin recognition functions mainly to facilitate optimal outbreeding, the mechanism used to discriminate kin from non-kin should be independent of the level of sociality, and may only depend on the spatial and temporal distribution of related animals.

One way in which we can ascertain the evolutionary and ecological significance of kin recognition is to investigate ecologically similar, closely related species. There have been studies of sibling recognition in four North American sciurids (Davis 1982; Holmes & Sherman 1982; Holmes 1984; reviewed in Schwagmeyer 1988). The mechanisms of sibling recognition in these species of ground squirrels have been correlated with the degree of nepotism shown, and with the degree of sociality (Sherman 1980; Sherman & Holmes 1985; Blaustein 1987a, Schwagmeyer 1988). In general, nepotism increases with increasing sociality (Michener 1983) and sibling recognition is achieved through

mechanisms which allow recognition of unfamiliar kin in the highly social sciurids.

Many mammals have strongly male-biased natal and breeding dispersal (Greenwood 1980, Dobson 1982, Cockburn et al. 1984, Johnson 1986, Wolff et al. 1988), and may avoid inbreeding without kin recognition. Holekamp (1984) noted that, although the social sciurids also have male-biased dispersal, it is often not as strongly male-biased in the asocial species. Asocial animals may be opportunistic dispersers and settle on the first available site regardless of whether kin are near enough for inbreeding to occur (Shields 1982, 1983). Thus, kin recognition may be an important mechanism for avoiding inbreeding in asocial sciurids. Direct familiarization must be reinforced continually in several species to be maintained (Porter & Wyrick 1979; McGuire & Getz 1981, Dewsbury 1982, O'Hara & Blaustein 1982, Gavish et al. 1984). Thus, selection for kin recognition in the asocial species may also favor a less restrictive recognition system.

Townsend's chipmunk (Tamias townsendii) are asocial, aggressive sciurids (Sherman 1973; Trombulak 1985) with overlapping home ranges, but non-overlapping centers of activity (Gashwiler 1965). Adults and juveniles of both sexes give alarm calls when disturbed (Warner 1971), and these calls may function to warn kin of approaching predators. Little is known about dispersal in T.

townsendii, however, if they are similar to other asocial sciurids, they may not exhibit strongly male-biased dispersal. If kin recognition is manifested in this species, it may function both in the facilitation of optimal outbreeding and in the direction of nepotistic behavior toward relatives.

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

MATERIALS AND METHODS

Pregnant T. townsendii were live-trapped at 3 sites in MacDonald Forest (18 km N, Corvallis, Oregon) and one site at Mary's Peak Campground (42 km SW, Corvallis, Oregon) between 26 April to 2 June, 1987. Females were housed individually in 30.5 x 35.5 x 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. Cross-fostering of pups was carried out 1-3 days after they were first noticed (see Figure 1 for details of the cross-fostering procedure). 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 produced 4 treatment groups (Figure 1): siblings reared together (SRT), siblings reared apart (SRA), nonsiblings reared together (NSRT), and nonsiblings reared apart (NSRA). If animals only use direct familiarization 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). In nature, it may be likely that familiar animals will be kin. If chipmunks use indirect familiarization, pups should treat familiar kin (SRT) differently than familiar non-kin (NSRT), and/or unfamiliar

Figure 1. The cross-fostering procedure and the treatment groups produced by the procedure. Female A and female B represent two females with pups; a1-a4 and b1-b4 represent A and B's pups, respectively.

CROSS-FOSTERING PROCEDURE

BEFORE:

Female A: Pups a_1, a_2, a_3, a_4 Female B: Pups b_1, b_2, b_3, b_4

AFTER:

Female A: Pups a_1, a_2, b_1, b_2 Female B: Pups a_3, a_4, b_3, b_4

TREATMENTS

Siblings Reared Together (SRT) - a_1, a_2

Siblings Reared Apart (SRA) - b_1, b_3

Nonsibs Reared Together (NSRT) - a_3, b_4

Nonsibs Reared Apart (NSRA) - a_4, b_2

Figure 1

kin (SRA) differently than unfamiliar non-kin (NSRA). Paired litters were always born within 24 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. My data indicate that most male home-ranges a maximum length of < 80 m (pers. obs.). Thus, it is unlikely that a single male mated with both females of a pair and that paired litters consisted of paternal half-sibs. The third pair of females was captured approximately 40 m apart. 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. SRT and NSRA were obtained by pairing pups from both noncross-fostered (4/17 litters) and cross-fostered litters (13/17). To control for the possibility that cross-fostering had

some effect on pups ability to recognize kin, approximately half of the SRT and NSRA (20/32 SRT and 14/36 NSRA) were obtained from cross-fostered litters, and half from noncross-fostered litters. Because of litter mortality (7/24 complete litters and one partial litter), the SRA came from 6 litters.

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).

Testing occurred in a 91.5 x 91.5 x 56 cm transparent acrylic arena (Figure 2), which was placed in an observation chamber. 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 x 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

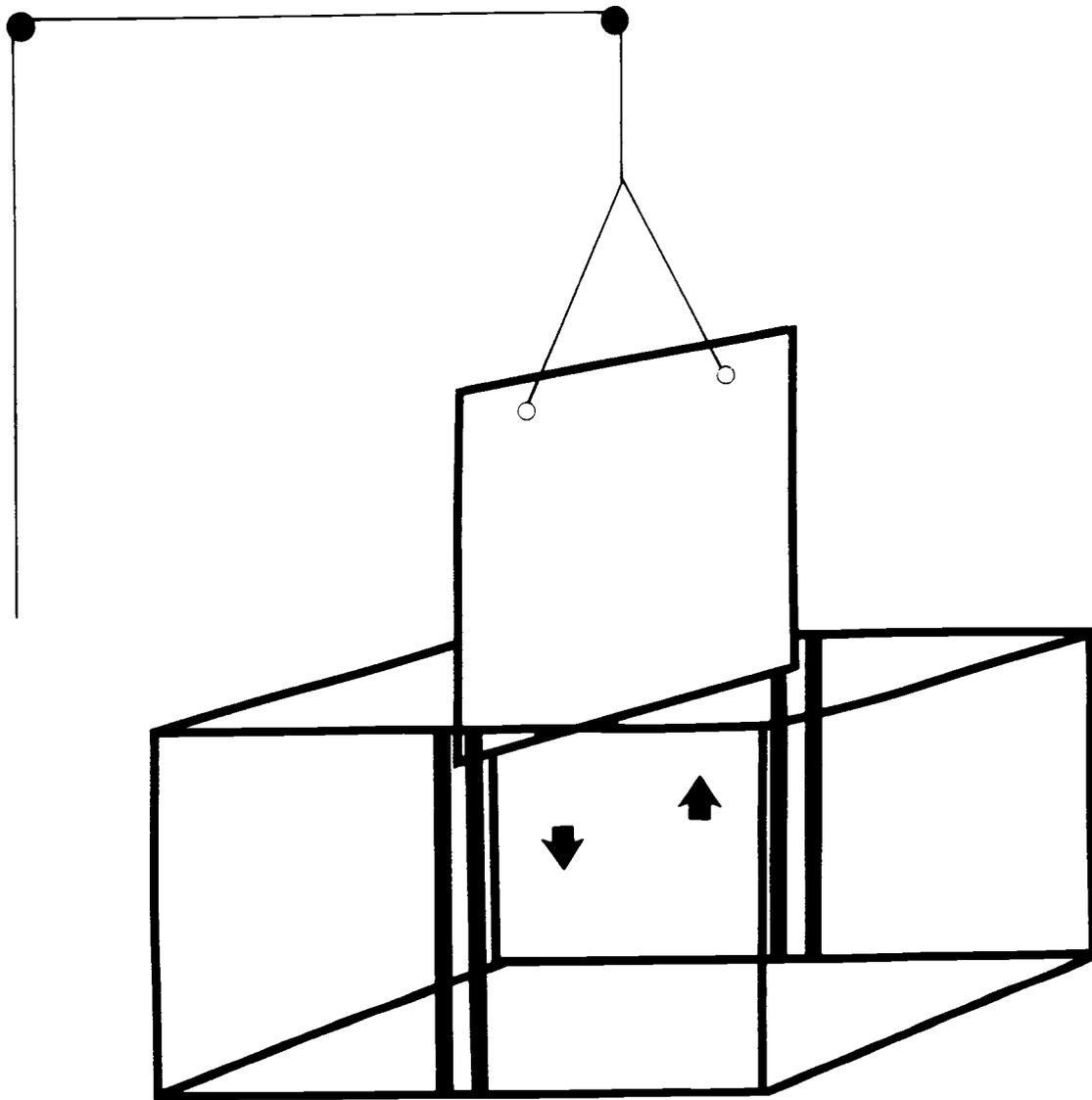


Figure 2: The testing arena.

each pup was removed to mask odors from previous pups, as were the cages used to transport the pups between the arena and the home cage.

On the day of testing, pups were removed from their home cages and placed individually in small 26 x 20 x 15 cm holding cages. Pups were placed at least 1 m from neighboring cages, and given water and a small amount of food. Each pup was marked with a black felt-tipped marker or hair dye in one of three places (head, back or rump) to facilitate identification in the arena. 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. If the pups still did not interact, the trial was discarded ($n = 2$). The arena and holding cages were rinsed with vinegar water (as above).

Frequencies (number of occurrences per trial) and durations (in seconds) of the following 8 behaviors were recorded into a hand held cassette recorder by one

observer: 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. I considered the first six behaviors to be amicable or exploratory and the last two behaviors to be aggressive. All behavioral observations were recorded by the same observer (CAF). In addition to the behaviors, the location of each animal on the 4 x 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. Animals were and weighed 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) for differences among the four treatment groups, 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 variables used in these analyses were log-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 duration of following and mounting were not included because these variables occurred very infrequently in trials.

The variables that were included in the MANOVA were analyzed individually by a 2 x 2 ANOVA with familiarity (SRT and NSRT versus SRA and NSRA) and kinship (SRT and SRA versus NSRT and NSRA) as the main effects. Thus, the 2 x 2 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

TABLE 1: Behavioral Means (SE) for all behaviors measured

Treatment	SRT	SRA	NSRT	NSRA
Frequencies (number/min)				
Approach	24.25 (19.06)	23.59 (16.02)	22.22 (9.85)	16.71 (14.94)
Sniff	9.44 (8.64)	9.59 (9.70)	13.78 (9.85)	4.59 (6.15)
Groom	3.25 (1.95)	3.82 (2.79)	4.72 (2.61)	1.59 (1.54)
Contact	4.06 (3.91)	2.35 (3.71)	7.33 (6.94)	1.35 (1.73)
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
Duration (sec)				
Approach	1.12 (0.82)	0.91 (0.39)	0.92 (0.27)	0.92 (0.38)
Sniff	2.66 (1.78)	2.70 (2.39)	2.92 (1.01)	3.30 (2.01)
Groom	5.85 (2.57)	4.79 (1.83)	4.29 (1.24)	5.47 (1.88)
Contact	5.62 (6.17)	5.30 (7.47)	5.34 (3.76)	2.30 (1.51)
Mount	1.31 (0.99)	1.03 (0.84)	2.17 (1.30)	0.75 (0.35)
Follow	1.56 (0.89)	1.00 (0.52)	1.83 (1.01)	1.55 (1.44)
Fight	0.67 (0.26)	0.70 (0.32)	0.50 (-)	0.65 (0.20)
Chase	2.47 (2.05)	1.50 (0.75)	1.50 (-)	1.85 (1.22)
Mean Distance	2.28 (0.41)	2.58 (0.64)	2.07 (0.66)	2.94 (0.45)

Means and SE are for untransformed data. Frequencies: mean frequency that a behavior occurred during trials. Occurrence: proportion of trials in which a behavior occurred. Duration: mean length (sec) of behavior in trials.

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 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 weights contained both continuous (age, weight and litter size) and categorical (treatments) variables, a logistic regression was used (Zar 1984).

RESULTS

Results of the first MANOVA (frequencies and the mean distance apart) was highly significant, indicating that there were significant differences in the way in which different treatment groups interacted ($df = 5,60$; F [relatedness x familiarity] = 3.589; $P = 0.007$). Results of the second MANOVA (duration of approach, sniff, groom and contact) showed that durations of behavior did not differ across treatment groups ($df = 4,37$; F [relatedness x familiarity] = 0.848; $P = 0.504$).

Frequencies

Results of the two-way analyses of variance (Table 2) indicated that "familiarity" significantly influenced the frequency with which chipmunks contacted each other. In two cases (sniffing and grooming) the kinship x familiarity interaction term was significant, indicating that familiarity and kinship do not act independently. Siblings acted similarly in both cases, but the behavior of nonsiblings depended on whether they were familiar or not. In general, NSRT sniffed and groomed more often than siblings (whether reared together or apart), while NSRA sniffed and groomed least (Fig. 3 a, b). Although the main effect "relatedness" never significantly influenced behaviors by itself, a significant interaction term suggests that kinship did influence the behavior of the

TABLE 2: The Results of Two-Way ANOVAs on Frequencies and Durations of Behaviors, and on the Mean Distance Between Pups. The values represent F-values, the numbers in parentheses degrees of freedom for the variables and the error term.

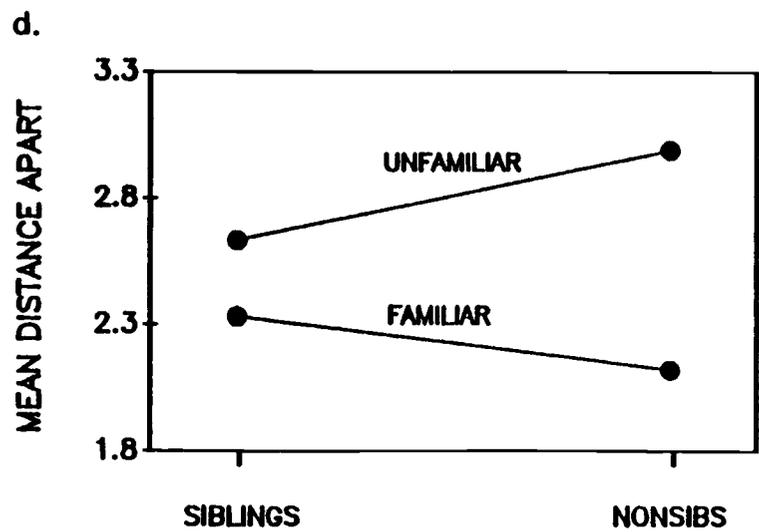
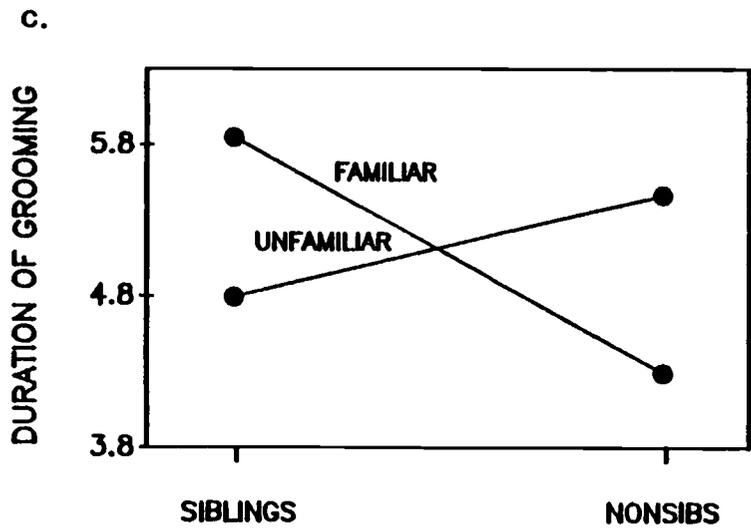
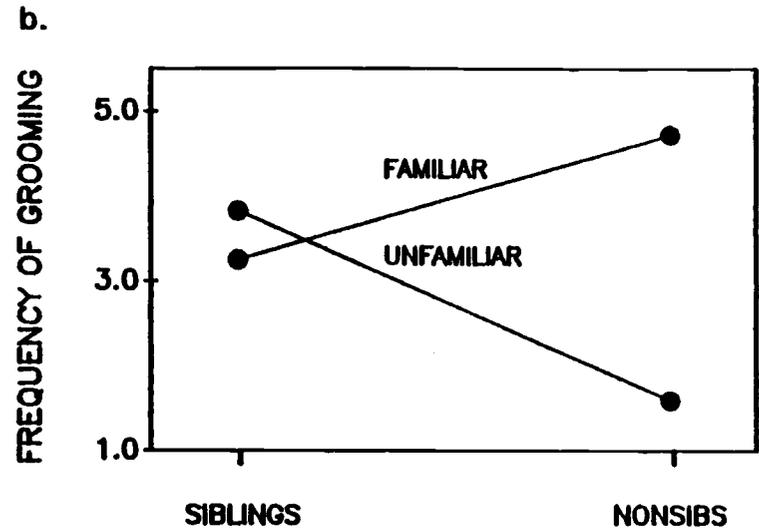
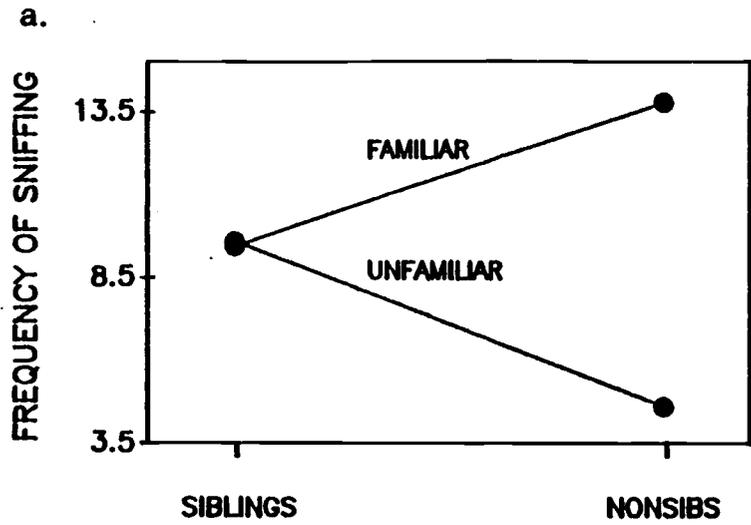
Variable	Sample Size (dfMSE)#	Relatedness (1)	Familiarity (1)	Relatedness x Familiarity (1)
Frequencies				
Approach	68 (64)	0.147	0.844	1.756
Sniff	68 (64)	0.024	4.547	4.855
Groom	68 (64)	1.564	9.143	13.260
Contact	68 (64)	0.745	17.311	2.851
Durations				
Approach	67 (63)	0.258	0.530	0.364
Sniff	60 (56)	2.079	0.001	0.039
Groom	59 (55)	0.427	0.084	4.247
Contact	51 (47)	0.185	4.727	1.021
Mount	19 (15)	0.245	2.093	0.948
Follow	31 (27)	0.851	1.887	0.077
Mean Distance Apart	68 (64)	0.286	18.865	4.466

* P < 0.05 ** P < 0.005 *** P < 0.001

dfMSE = error degrees of freedom

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

Figure 3



animals. However, the main effects are difficult to interpret when the interaction terms are also significant.

The three-way contingency analyses (Table 3) indicate that familiarity strongly influenced the occurrence of fighting and chasing. Furthermore, kinship significantly influenced the occurrence of chasing and showed a nonsignificant trend in fighting ($P = 0.067$). Familiar animals fought and chased in fewer trials than unfamiliar animals. In addition, Familiar siblings fought more often than familiar non-siblings (Table 1).

Sex Differences. A third variable was added to the ANOVA model to determine if the sex composition of pairs influenced behavior. This was analysed separately because further partitioning of the data resulted in extremely small cell values. In this case, extremely large or small values may have a large effect on overall means, and the power of the model will decrease. Thus, the value of these analyses is somewhat questionable. Sex had a significant effect on only two variables (Table 4). All three two-way interactions were significant for the frequency of grooming, although the kinship x familiarity interaction had the strongest effect. The sex x familiarity interaction was significant for the frequency of contacts. Figure 4 presents the mean of each treatment for each significant interaction effect. If each interaction is examined separately, a few trends emerge. Relatedness x Sex:

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 x Familiarity
Degrees of Freedom	4	2	2	1
Mount	8.64 ^a	---	---	---
Follow	5.29	---	---	---
Fight	15.98 ^{**}	5.41 ^a	13.95 ^{***}	2.57
Chase	18.90 ^{***}	7.00 [*]	17.67 ^{***}	3.20 ^a

^a P < 0.10

* P < 0.05, ** P < 0.005, *** P < 0.001

TABLE 4: Results of the Three-Way ANOVAs for the Frequency and Duration of Behaviors, and the Mean Distance Between Pups, Including the Sex of Pairs. The values given are F-values, the numbers in parentheses are degrees of freedom for the variables and for the error term.

Variables	Sample Size (dfMSE)	Relatedness (1)	Familiarity (1)	Sex (2)	Relatedness x Familiarity (1)	Relatedness x Sex (2)	Familiarity x Sex (2)	Relatedness x Familiarity x Sex (2)
Frequencies								
Approach	68 (56)	0.110	1.839 ^a	0.664	0.891 [*]	0.506	0.474	1.292
Sniff	68 (56)	0.000	3.350 ^{***}	0.882	4.411 ^{***}	0.628	1.143 [*]	0.025
Groom	68 (56)	0.113 [*]	12.312 ^{***}	0.343	15.369 [*]	3.258	3.291 [*]	0.921
Contact	68 (56)	3.827 [*]	23.237 ^{***}	1.583	6.658 [*]	0.456	3.249 [*]	0.956
Durations								
Approach	67 (55)	0.261	0.251	0.697	0.579	1.248	0.314	2.231
Sniff	60 (48)	0.527	0.489	1.132	0.287 [*]	0.623	1.188	1.645
Groom	59 (47)	0.626	0.333	0.282	5.114 ^a	1.792	0.293	1.173
Contact	51 (39)	2.504 ^a	2.032	0.003	3.151 ^a	1.549	2.867 ^a	2.110
Follow	31 (19)	3.529 ^a	0.668	0.288	0.250	2.959 ^a	1.928	0.111
Mean Distance Apart	68 (68)	0.236	24.629 ^{***}	4.407 [*]	12.499 ^{***}	0.439	1.393	2.716 ^a

* P < 0.05 ** P < 0.005 *** P < 0.001

^a 0.10 > P > 0.05

Note: it was not possible to analyse the duration of mounting because not all categories were represented.

male:male sibling pairs groomed most frequently whereas nonsibling male:male pairs rarely groomed (Fig. 4a). Other sex combinations differed only slightly. The Relatedness x Sex interaction is difficult to interpret in general because relatedness did not have a strong influence on any behavior, thus one group (NSRT) may account for most of the differences. Familiarity x Sex: 1) familiar animals always groomed more often than unfamiliar animals (Fig. 4b). Here, female:female pairs seem to cause the major differences: familiar females groom the most and unfamiliar females groom the least of any other group. 2) Familiar animals also contacted each other more frequently than unfamiliar animals (Fig. 4c). In all cases, male:female pairs acted similarly, whether or not they were familiar or related.

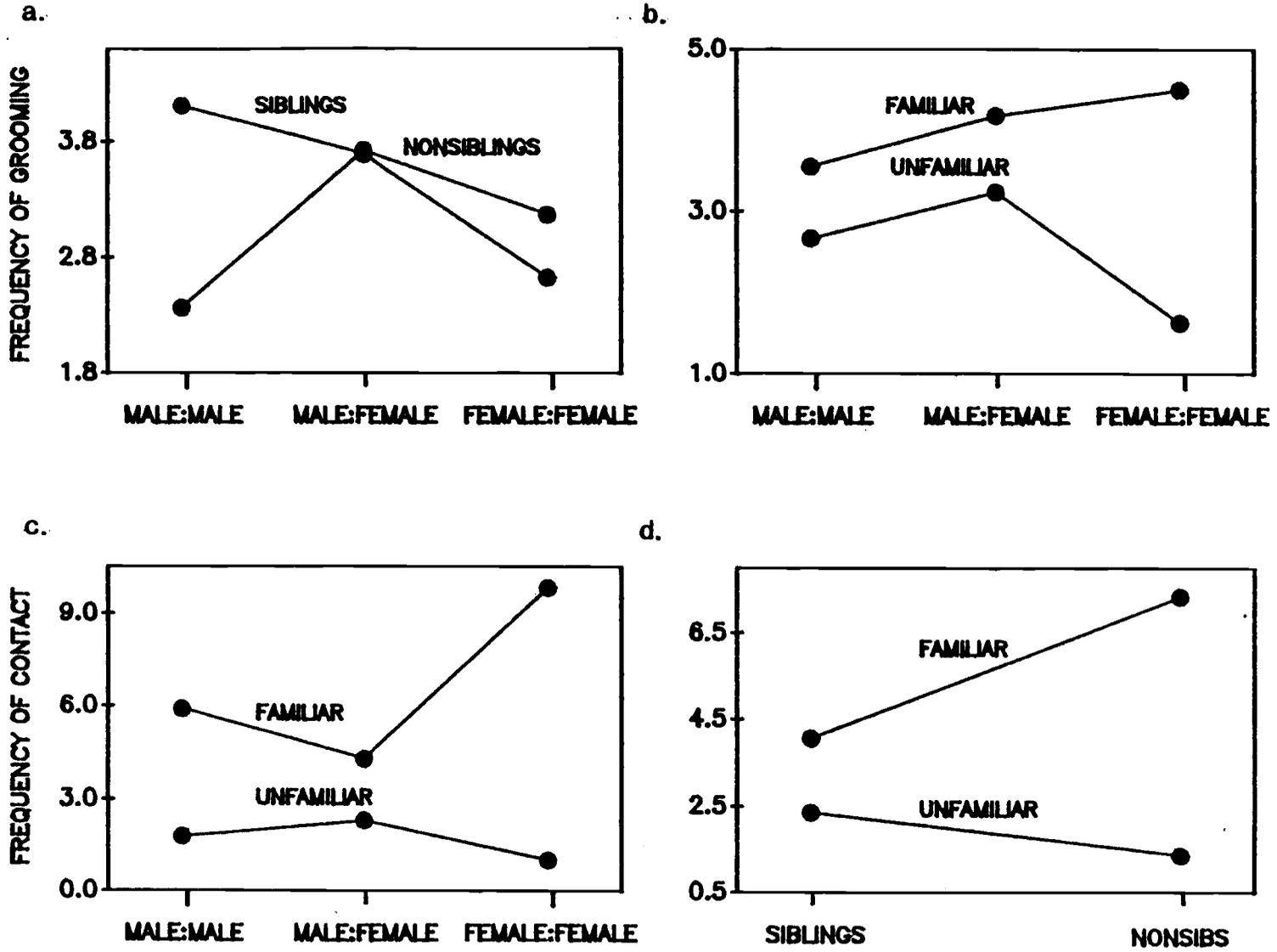
When the effects of sex were removed from the frequency of contacts, the familiarity x relatedness interaction effect became significant (Table 4; Figure 4d). NSRT contacted each other most often, NSRA contacted each other least often, and siblings contacted an intermediate amount.

Durations

Although the overall MANOVA was not significant for durations of behaviors, I conducted 2-way ANOVAs on individual variables. This was done because only 44/68 trials could be included in the MANOVA (see above). Analyzing each variable separately allowed me to include

Figure 4. Means of the significant interaction effects when the sex composition of pairs was a factor: 4a - relatedness x sex interaction term for the frequency (mean number of grooming/ 10 min trial) of grooming; 4b - the familiarity x sex interaction effect for the frequency of grooming; 4c - the familiarity x sex interaction term for the frequency of contacts; 4d - the familiarity x relatedness interaction effect of contact when the affect of sex is removed.

Figure 4



all data available for each, and thus may be a better analysis for these variables. The durations of behaviors differed in only two cases (Table 2). Familiar animals spent more time in contact with each other than unfamiliar animals, and the kinship x familiarity interaction was significant for the duration of grooming (Figure 3c). In this case, SRT and NSRA showed similar behavior, and SRA and NSRT showed similar behavior.

Because fighting and chasing only occurred in one instance in NSRT, this treatment was excluded from the duration analysis, and these behaviors were analyzed using a one-way ANOVA. Neither the duration of fighting or chasing differed across the three treatments (fight: $F = 0.055$, $n = 26$, $P > 0.5$; chase: $F = 0.572$, $n = 30$, $P > 0.5$).

Sex Differences. The sex of the pair members never significantly influenced the duration of chipmunk behavior (Table 4). This may be due in part, to small sample sizes, since the kinship x sex interaction for follow and the familiarity x sex interaction for contact showed non-significant trends ($P = 0.076$ and $P = 0.084$, respectively). Fighting and chasing were again analyzed separately as a 2-way ANOVA because NSRT could not be included. There was no significant "sex" effect on the duration of fighting or chasing (FIGHT: $F(\text{trmt}) = 0.073$, $F(\text{sex}) = 1.039$, $F(\text{trmt} \times \text{sex}) = 0.384$, $n=26$; CHASE: $F(\text{trmt}) = 0.221$, $F(\text{sex}) = 0.981$, $F(\text{trmt} \times \text{sex}) = 0.391$, $n=30$; $P > 0.35$ for all F values).

Mean Distance Apart

There was a significant ($P < 0.05$) kinship x familiarity interaction effect on the distance between animals during trials (Table 2). NSRT remained the closest, siblings (whether reared together or apart) remained somewhat farther apart, and NSRA remained farthest from each other (Figure 3d).

Sex Differences. The main effect "sex" was significant for the mean distance apart (Table 4). I used Scheffe's multiple contrasts to determine which treatments were different from the others. 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 ($F = 5.402$, $df = 1, 56$, $P = 0.024$).

Weights

Pups that were from cross-fostered litters were significantly heavier ($P < 0.05$) 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 5; treatment 1, not cross-fostered: mean = 63.4 g, SE = 4.5; treatment 2, cross-fostered and raised with the biological mother: mean = 67.4 g, SE = 5.6; treatment 3, cross-fostered and raised with a foster

TABLE 5: Logistic Regression Results for Pup Weights: Students T Values for the Terms in the Regression 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 Birth	48	5.168 **	4,43	1.800 ^a	-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.

mother: 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 ($P > 0.05$) effect when included in the model, it became significant ($F=4.424$, $df=1,65$, $p=0.039$) when rearing regimen was dropped. This suggests that the effects of litter size and rearing regimen are highly correlated, but that rearing regimen is the more important factor.

To determine whether these differences in weights existed prior to cross-fostering, I also analyzed pup weights at the time of 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 5; 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, the effect of litter size was also significant. Thus, cross-fostering probably did not cause the differences in weights between groups. The differences were probably a preexisting condition, perhaps caused by litter size differences.

DISCUSSION

The results indicate that Townsend's chipmunks can discriminate between kin and non-kin. Furthermore, the most important mechanism for sibling recognition in this laboratory situation was probably familiarity established during rearing because overall pups were more amicable and less aggressive toward familiar animals than toward unfamiliar animals. However, familiarization cannot fully account for kin recognition because in 6 of 8 significant analyses (Tables 3 and 4: frequency of sniffing and chasing, frequency and duration of grooming, the mean distance apart, and the frequency of contacting when the effect of sex is removed), kinship also significantly influenced 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 and siblings (whether reared together or apart), but did not treat NSRT and NSRA alike (Figure 4),

an additional mechanism (phenotype matching or recognition alleles) must be operating.

By raising females with from zero to two siblings and from one to three non-siblings, Holmes (1986a) was able to establish that female Belding's ground squirrels recognized kin by phenotype matching through self-inspection. He found that 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, I was 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 affected chipmunk behavior (Table 4), but this effect was relatively weak compared with that of familiarity, and did not have a predictable effect. In part, the data were difficult to interpret because we were unable to record each individual's behavior during most trials. Thus, the data for sexes represent interactions within pairs of animals, rather than for individuals. Despite these difficulties, it seems clear

that kin recognition in T. townsendii is not limited to one sex or the other because sex did not affect interactions strongly in most cases (Table 4).

Experimental tests of sibling recognition have been conducted in four other species of sciurids (Sheppard & Yoshida 1971; Davis 1982; Holmes & Sherman 1982; Holmes 1984). Spermophilus 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 direct familiarity (Holmes 1986b). Spermophilus 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 on the basis of one out of five behaviors measured. Thus, S. richardsonii relies primarily on phenotype matching or recognition alleles for kin recognition in the laboratory, and familiarity is relatively unimportant.

Both male and female T. townsendii give alarm calls (pers. obs.), and calling increases dramatically around the

time of juvenile emergence and dispersal (Brand 1970). The increase in calling may be due to calls given by juveniles (Warner 1971). Warner (1971) showed that calls alert chipmunks to approaching predators, but it was not known whether callers were related to the alerted animals. Tamias striatus females generally move young to another nest at the edge of their home ranges one to 14 days after emergence and do not interact with them thereafter (Elliot 1978; Yahner 1978). Juveniles often remain in this new nest until the time of dispersal. If the majority of alarm calls are given by juveniles, they may function to warn siblings of approaching predators.

Schwagmeyer (1980) found that S. tridecemlineatus alarm calls were given primarily by parous females and their young of both sexes. Adult female S. beldingi call more frequently than other age and sex classes (Sherman 1977). Because males disperse as juveniles and after breeding and females are generally philopatric, adult females tend to have more close relatives near enough to benefit from alarm calls than males. Adults of both sexes of S. richardsonii give alarm calls and animals with offspring or siblings nearby call most frequently (Davis 1984). In this species males do not disperse after breeding and thus, may also benefit by alarm calling.

Kinship significantly influenced the occurrence of chasing during trials, and showed a non-significant trend in the occurrence of fighting - familiar non-kin fought and

chased less than familiar kin. This suggests that chipmunks may avoid aggressive behavior toward kin. Lower aggression toward kin has been demonstrated in S. beldingi (Holmes & Sherman 1982), S. parryii (McLean 1982) and may facilitate food sharing or allow animals to avoid seriously injuring kin in territorial disputes in some species (Porter et al. 1980; Kareem & Barnard 1982).

It is not known whether dispersal is sex-biased in T. townsendii. In closely related species, dispersal is probably not strongly sex-biased (T. amoenus, States 1976). In these species, even when males disperse farther, they may not disperse far enough to avoid related females. In a recent review of sciurid dispersal, Holekamp (1984) found that only one asocial sciurid (S. tridecemlineatus) out of those studies has strongly male-biased dispersal.

There are several potential disadvantages to both close inbreeding and extreme outbreeding (Bateson 1983). If animals mate with close relatives, inbreeding depression may result or animals may lose advantages of heterozygosity. Outbreeding with animals that are very different genetically may result in the break-up of co-adapted gene complexes. If animals must disperse far to outbreed, the cost of dispersal may increase with the distance traveled. It is possible that T. townsendii uses kin recognition to facilitate optimal outbreeding. NSRT were more amicable and less aggressive than siblings, and siblings were more amicable than NSRA. Chipmunks might

choose mates that are familiar but unrelated over unfamiliar unrelated animals. Familiar unrelated animals may be perceived as different enough to make good mates, whereas unfamiliar unrelated animals may be too different.

The mechanisms of recognition may be correlated with sociality and life-history traits in the sciurids (Holmes 1984; Sherman & Holmes 1985; Holmes 1986b; Blaustein et al. 1987a; Schwagmeyer 1988). Recognition without direct familiarization has been demonstrated in the three most social species (S. beldingi, S. parryii, Holmes & Sherman 1982; and S. richardsonii, Davis 1982). These three species are also the most nepotistic (Sherman 1977; McLean 1982; Davis 1984). If kin recognition is mainly used to direct nepotistic behavior toward related animals, the mechanism of kin recognition should be less restrictive in species that are likely to encounter and be nepotistic toward unfamiliar kin. This is generally the case in the highly social sciurids where several generations of related females may use the same burrow system (Michener 1984). The least social species, S. tridecemlineatus, can only discriminate between familiar and unfamiliar siblings (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). Kin recognition without direct familiarization may not have evolved in S. tridecemlineatus because individuals are nepotistic only toward familiar animals. All four species

probably avoid inbreeding by spatial and temporal distribution (Holekamp 1984). T. townsendii is asocial and may only direct nepotistic behavior toward familiar animals, as in S. tridecemlineatus. However, in T. townsendii, kin recognition may be achieved in the absence of direct familiarity. If kin recognition is used to facilitate optimal outbreeding, it should be independent of sociality. Thus, T. townsendii may have evolved the ability to recognize kin in the absence of direct familiarity to facilitate optimal outbreeding.

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