

## Role of kinship in the formation of southern flying squirrel winter aggregations

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In winter southern flying squirrels (*Glaucomys volans*) aggregate in large groups. They live on food items individually stored during the fall in their overlapping home ranges. The squirrels gain thermoregulatory benefits from living in aggregations but also face costs of group living, especially nest mates pilfering individually stored food. Other costs include increased predator attraction and a greater vulnerability to parasite infection. The presence of relatives in the group has the potential to increase inclusive fitness by increasing the availability of food, stored in the home area, to related individuals. Using 3 generations of known-relationship squirrels we conducted laboratory experiments to determine whether kin or familiar animals were preferred nest mates during aggregation formation. During 3 time periods, over 2 winters, squirrels were presented with kin and nonkin and familiar and unfamiliar animals and allowed to aggregate over the course of multiple 3-day trials. Kinship was persistently a major factor in the formation of aggregations. Squirrels aggregated with highly related animals (parents, offspring, and siblings) significantly more often than with unrelated animals. Familiarity became significant by the end of the study. Understanding how relatedness and familiarity interact in the formation of aggregations in seasonally gregarious animals sheds light on the processes and factors that lead to sociality.

Key words: *Glaucomys volans*, group nesting, kinship, nest-mate choice, southern flying squirrel, winter aggregation

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Explanations of group structure often are based on kinship, nepotism, and reciprocity (Hamilton 1964; Kutsukake and Clutton-Brock 2006). Living in groups comes with costs and benefits (Alexander 1974; Dickinson and Koenig 2003). The benefits of group living include increases in reproductive fitness (more related offspring surviving to breed), access to additional food or shelter resources, warnings about the presence of predators, and cooperation in rearing young (Alexander 1974; Dickinson and Koenig 2003; Hamilton 1964). The costs and selective pressures that influence aggregation formation, group formation, group cohesion, and fission–fusion societies include loss of resources, predation and parasite pressures, and energetic costs (Alexander 1974; Kerth 2008; Krakauer 2005; Parrish and Edelstein-Keshet 1999; Shimooka 2003). Where animals gain energetic and fitness benefits from group living, this social behavior will persist. When it is more costly than living as a singleton, sociality and long-term aggregations will not occur consistently.

Solitary living is the most common social structure in tree squirrels; this is in distinct contrast to the highly social habits of many ground squirrels (Blumstein and Armitage 1999;

Sherman 1981; Thorington and Ferrell 2006). Southern flying squirrels (*Glaucomys volans*) are small (50–75 g) gliding squirrels. They are unique among the North American tree squirrels for their seasonally gregarious nature, the degree of sociality they display, and nocturnal habits (Arbogast 2007; Dolan and Carter 1977; Heaney 1984; Weigl et al. 1999; Wells-Gosling and Heaney 1984). They do not migrate or hibernate and are active at the coldest, harshest times of year. In winter southern flying squirrels live in groups that confer a thermoregulatory advantage on the group-nesting individual. They are more solitary in warm weather. Females instigate disaggregation in early spring as they become highly defensive of their parturition nest sites and young (Dolan and Carter 1977; Muul 1968, 1969, 1970). In these small squirrels gliding can conserve energy by reducing time spent in foraging and by reducing the energetic costs of transport or aiding predator avoidance (Holmes and Austad 1994; but see Stapp 1994). Despite these benefits for energy acquisition and



conservation, gliding places constraints on physical adaptations to harsh winter conditions, limiting the capacity to increase energy stored as fat or to grow thicker fur for insulation (Stapp 1994). Gliding is a derived characteristic in flying squirrels requiring a significantly different morphology compared to tree and ground squirrels (Thorington and Santana 2007).

Aggregation behavior occurs across the range of the southern flying squirrel, southern Canada to Florida. Group size averages 5–20 animals, and aggregation membership can fluctuate during the winter (Dolan and Carter 1977; Muul 1968). Declining photoperiod drives aggregation formation in the wild, and aggregation size is, in part, temperature dependent (Muul 1968). Relatedness among individuals has been suggested as a potential factor in individual associations between aggregating squirrels (Layne and Raymond 1994). Aggregation formation does not appear to be correlated with nest-site availability because the artificial addition of suitable cavities did not increase population size of the southern flying squirrel (Brady et al. 2000). Winter groups contain kin more often than expected by chance. A minimum one-third to one-half of wild-caught southern flying squirrel groups has a high average relatedness (Thorington 2008; Thorington et al. 2010). Even in springtime, during the height of pup rearing, wild-caught, mixed-age groups are highly related (Winterrowd et al. 2005). Little else is known about the formation of winter groups.

Food is stored in the home area during the declining photoperiod in the fall (Muul 1968; Thomas and Weigl 1998). The storing squirrel has a distinct advantage (storer's advantage) over conspecifics in finding a stored food item (Winterrowd and Weigl 2006). However, during active storing and through the winter, individuals often find and eat or restore food items originally buried by nest mates despite this storer's advantage. This results in a resource overlap where individuals have access to each other's stored food but it in no way implies that these squirrels are intentionally sharing food. Dependence of the southern flying squirrel on stored food is so great that the previous summer–fall mast crop is a good predictor of squirrel abundance the next year (Bowman et al. 2005).

Southern flying squirrels face a dilemma: they gain thermoregulatory benefits from living in winter aggregations (Dolan and Carter 1977; Merritt et al. 2001; Muul 1968; Stapp 1992; Stapp et al. 1991; Tompkins 2003), but group living can be deleterious due to food pilfering and predation risk (Winterrowd 2001; Winterrowd and Weigl 2006). Living in related groups could resolve this apparent conflict. If an individual squirrel dies, its food resources will remain in the home area available to nest mates. If these nest mates are relatives and survive to breed, inclusive fitness can increase. Therefore, southern flying squirrels provide a good model in which to explore the factors that influence formation of aggregations.

We set out to assess the aggregation-formation behaviors of southern flying squirrels under controlled laboratory condi-

tions using 3 generations of known-relationship animals. To address the following questions captive southern flying squirrels were presented with kin and nonkin nest-mate choices in a nonterritorial living situation during the shortest and coldest days of the year: Do southern flying squirrels show a preference for kin when forming aggregations? Do they behave differently when given choices of kin and familiar nonkin individuals as possible wintertime nest mates, potentially preferring highly related animals? Under what circumstances might southern flying squirrels accept unrelated squirrels into their aggregations? If the energetic benefits generated by being in a larger group are enough to outweigh food pilfering losses, relatedness should not matter and all squirrels should aggregate under cold-induced energy stress.

## MATERIALS AND METHODS

*Study animals and facilities.*—Southern flying squirrels readily adapt to and prosper in captivity (Stapp and Mautz 1991; Svihla 1930). They breed and exhibit other behaviors similar to those observed in the wild, based on cues, such as temperature and photoperiod, given to them in captivity (Muul 1969). In the fall of 2002 the captive colony at Wake Forest University was composed of 2 distinct groups. One, NC Piedmont B, was a group of 12 animals that were trapped from a Winston–Salem, North Carolina, residence. The other was a group of 20 individuals of various origins; some were born in captivity prior to the start of this study, and others were wild-caught at the Savannah River Ecology Laboratory, South Carolina, at Archbold Biological Station, Florida, or locally in Winston–Salem. These 2 groups were used to breed our known-relationship animals. During the course of this study colony size increased from these 32 animals to an average of 60, with births far outnumbering deaths (Thorington 2008). The care of these squirrels conformed to guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998; Gannon et al. 2007) and the regulations of the Wake Forest University Animal Care and Use Committee (protocols A03-117 and A06-212).

Captive squirrels were housed in an outdoor facility at Wake Forest University under ambient conditions. Squirrel housing consisted of 7 welded wire-mesh cages measuring 2 m wide  $\times$  4 m long  $\times$  2.6 m high, with a divider creating 2 equal-sized cages that shared a wall, for a potential total of 14 individual 10.4-m<sup>3</sup> units. Wire mesh cage tops were covered by a slanted plastic roof. The cage bottoms were raised off the concrete to facilitate cleaning and prevent accumulation of water and ice. Squirrels were provided with plywood nest boxes measuring 15 cm wide  $\times$  15 cm deep  $\times$  26.25 cm high, with a 4.5-cm-diameter round entrance hole. Boxes can easily hold more than 15 squirrels at a time. We used wooden boxes because their thermoregulatory properties were closest to those of the natural tree cavities used by wild squirrels (Merritt and Zegers 2002; Tompkins 2003). Boxes were filled with shredded paper towel bedding before being placed in the cage. Squirrels were fed ad libitum with a combination of LabDiet

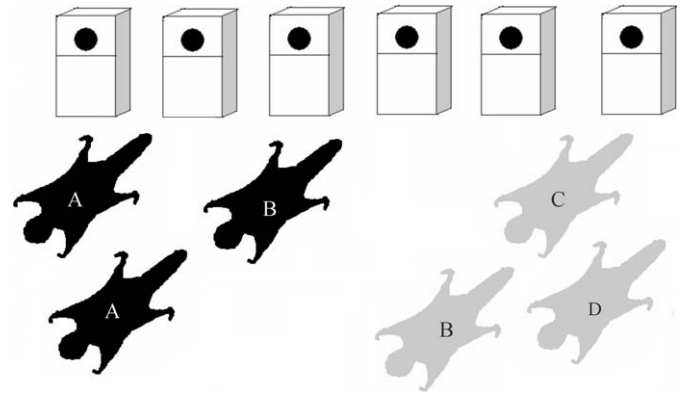
5P00 Prolab RMH 3000 rodent chow (PMI Nutrition International, LLC, Brentwood, Missouri) and hazelnuts.

Southern flying squirrels are naturally gregarious animals. Therefore, between experiments they were housed in groups of 3–10 animals. During the study colony size more than doubled while the number of cages was constant. Housing groupings and group size were based on breeding, relatedness and familiarity needs for experiments, and logistical constraints. Within cage groups squirrels were free to nest with whichever individuals they chose. We maintained a minimum of 1 nest box per 4 animals in each cage during nonbreeding and nonexperimental housing. Breeding groups consisted of 1 male and 3 or 4 females. Nest boxes were removed from cages, emptied, and washed as needed. Experimental nest boxes were washed after each trial (see Thorington [2008] for additional care, handling, and breeding data). Squirrels often used 1 nest box for food storage and another for sleeping when 2 or more boxes were provided for multiple squirrels.

**Experimental design.**—Known-relationship captive southern flying squirrels were exposed to living situations in which they could form aggregations during the winter months. The squirrels were given nest-mate choices of kin, nonkin, familiar, and unfamiliar squirrels. Nesting associations were used to determine nest-mate choices during individual trials. A trial was defined as the 3-day exposure period in which groups of squirrels were allowed to form aggregations, potentially choosing nest mates of different kinship or familiarity categories.

**General procedures.**—Groups of squirrels were introduced into neutral cages—those not previously used by trial group members—for the course of 3-day behavioral association trials. The neutral cage was identical to the squirrels' home cage and was free of scent or other territorial markings associated with the individuals in the trial. For each trial a neutral cage was arranged such that it contained unrestricted food and water and 1 clean, dry nest box per squirrel (Fig. 1). We numbered all nest boxes and placed each box in the same location on the cage wall for the duration of the trial.

Squirrels and boxes were introduced into the test cages during daylight hours, the afternoon before the 1st night of exposure. Squirrels were allowed to interact throughout their active period each of the 3 trial nights and to aggregate in the nest boxes without human observers present. During most trials they were observed for 1 h during the 1st evening (sunset to approximately 2100 h) of exposure. Each morning during these trials we removed all squirrels from all nest boxes, recording which individuals were together and which, if any, were nesting alone. We returned the boxes and squirrels to the cage and repeated the procedure for the following 2 nights. The natural response of southern flying squirrels to this kind of disturbance is to switch nest boxes. Under nonexperimental conditions winter groups tend to be stable, moving into a new box as a group. We saw no box preferences during any trials: 13% of the time aggregations were found in the same box during any 2 days of the trial (consecutive nights = 10%). Aggregations never were found in the same box for all 3 days



**FIG. 1.**—Experimental arrangement for aggregation formation trials. For each of the 17 trials an equal number of southern flying squirrels (*Glaucomys volans*) and nest boxes were placed in the cage. The number of squirrels in a trial varied between 5 and 14 individuals. In this example there are 2 family groups coded by the black or gray silhouettes. Letters on the silhouettes indicate operational familiarity.

of a trial. At the end of the trial squirrels were returned to their original cages. We used individual animals in multiple trials during each time period.

**Trials and trial groupings.**—Seventeen trials were conducted during 3 time periods. Period 1 was 29 January through 20 February 2004 and included 7 trials; period 2 was 8 November through 3 December 2004, 6 trials; and period 3 was 20 January through 11 February 2005, 4 trials. Trials were conducted in the winter months to best mimic natural aggregation timing and ambient conditions, which are stressful due to cold. The number of trials and number of squirrels within a trial reflects the constraints of known-relationship animals and cage associations that affect familiarity. Each trial had a minimum of 5 and a maximum of 14 squirrels. The variability in group size allowed us to control the availability of relatives, nonrelatives, and familiar animals for each animal within a trial, given initial limitations on numbers of known-relationship squirrels. This facilitated our explorations of the effects of kinship and familiarity on choice of nest mate, based on the relationship between squirrels in particular dyads (pairs of squirrels), not the total number of squirrels in a trial (Fig. 1). Dyadic relationships are often studied within social groups to elucidate behavioral preferences for kin or familiar animals (Holekamp et al. 1997; Shimooka 2003; Wahaj et al. 2004; Willis and Brigham 2004). Dyad numbers were similar across time periods because of the different trial group sizes.

In the trial groups individuals were either related or unrelated to each other and either familiar or unfamiliar with each other. This resulted in 4 categories of dyad with familiarity and relatedness scored as follows. Animals were considered operationally familiar when they had lived together in the same cage with access to the same nest boxes for a minimum of 1 month prior to the start of a trial. For the course of this experiment relatedness was treated categorically using theoretical (Hamiltonian) pedigree  $r$ -values (Table 1). For example, full siblings and parent–pup pairs are recorded as

**TABLE 1.**—Categorical relationships possible for an individual dyad of southern flying squirrels (*Glaucomys volans*). Operational familiarity (F) is based on the definition: those squirrels that have lived in the same cage with access to the same nest boxes for a minimum of 1 month prior to the trial start date. Relatedness is based on whether the animals were related to each other measured in pedigree-derived Hamiltonian  $r$ -values.

	Familiar (access to shared nest boxes for a minimum of 1 month prior to trial)	Unfamiliar (no access to shared nest boxes in the month prior to trial)
Related $r \geq 0.125$	F+/r+	F-/r+
Unrelated $r \leq 0$	F+/r-	F-/r-

having  $r = 0.5$  and half siblings have  $r = 0.25$ . In each trial squirrels were presented with a situation in which they could choose nesting associations with combinations of operationally familiar (F+), operationally unfamiliar (F-), relatives (r+), and nonrelatives (r-) as nest mates. Results were recorded at the dyad level (scores are based on associations and relationships between each unique pair of squirrels). In a single dyad the relationship between the 2 squirrels could be F+/r+, F+/r-, F-/r+, or F-/r- (Table 1).

During the 1st time period we ran 7 trials (groups of 5–8 squirrels). These trials involved 27 individuals resulting in 119 dyads. In this time period 40% of squirrels did not have a relative in the cage and half of those (20%) also were lacking a familiar animal. The 2nd period consisted of 6 trials (6 squirrels each, 22 individuals, 90 dyads). In this time period all animals had relatives in the cage but 60% did not have an operationally familiar animal in the cage. In the 3rd time period all 4 trials were arranged so that most squirrels (80%) had F+/r+, F+/r-, F-/r+, or F-/r- relationship choices available at all times (3 trials had 8 squirrels each and 1 trial had 14 squirrels, resulting in a total of 20 individuals and 176 dyads). In the course of all 3 time periods we used 39 total individual squirrels to produce 385 total dyads.

**Statistics.**—Known relatedness values (Hamilton's  $r$ , hereafter  $r_H$ ) were determined using pedigrees of colony squirrels (Hamilton 1964). Genetic relatedness is based on microsatellite markers (hereafter  $r_M$ ) analyzed in Thorington et al. (2010). Average relatedness of the NC Piedmont B group (resident in the captive colony,  $n = 12$  animals,  $r_M = 0.041$ ) was high based on a randomization test, but the 20 mixed-origin animals were not significantly related ( $r_M = 0.013$ —Thorington 2008; Thorington et al. 2010). Therefore, the original colony animals from which we bred known-relationship animals were not significantly inbred. We kept NC Piedmont B animals out of the same breeding groups to avoid inbreeding effects on the relatedness of our known-relationship squirrels used in this experiment. In 2004 we had 2 generations of known-relationship squirrels; by 2005 we had 3 generations in 2 separate lineages. For each dyad an  $r_H$ -value between 0 and 0.5 was calculated from our breeding (pedigree) records. We scored the operational familiarity

(familiar or unfamiliar) of each dyad of squirrels at the time of each trial. Association of squirrels during a trial was scored in a pairwise (dyad) fashion to calculate a double-weight association index  $AI = R/(P + Q + R)$  (Cairns and Schwager 1987; Shimooka 2003; Wahaj et al. 2004). Given the dyad of squirrels A and B in a particular trial, R is those aggregations in which both A and B are present, P is those aggregations that include A but not B, and Q is those aggregations that include B but not A. AI varies from 0 (never in the same aggregation) to 1 (always in the same aggregation).

We created a hierarchical regression equation in SPSS 15.0 (SPSS Inc., Chicago Illinois) to predict the AI based on the amount of variance particular factors explained. This variance for individual factors is measured in terms of  $\Delta R^2$ , which is the change in the fit of the equation occurring with the addition of each factor. Hierarchical regression was used because it allowed us to control for a number of factors other than kinship and familiarity that can affect aggregation behavior, and therefore the AI, and includes these factors in the equation. Decreasing ambient temperature and daylight drive the winter aggregation tendencies of southern flying squirrels (Muul 1968; Sawyer and Rose 1985). Animal age and sex also could affect aggregation tendencies. Both were included as categorical variables; a squirrel was either juvenile, yearling, or adult at the time of the trial, and either male or female. Age was based on birth date. All squirrels were  $\geq 4$  months old, weaned, and capable of dispersal at the start of a trial. Whether an animal has kin available in the cage will affect its capacity to aggregate with kin and was scored as a categorical variable, yes or no, regardless of the degree of kinship. Because the AI does not include a direct term for nonassociation, nesting alone was included in the regression. Therefore, variance due to these variables was accounted for by entering them into the equations before the factors in question, kinship (Hamilton's  $r_H = 0, 0.125, 0.25, \text{ or } 0.5$ ) and familiarity (F+, F-). Factors were entered into the hierarchical regression in the following order: trial mean low temperature, animal ages, animal sexes, kin present in the cage, nesting alone, kinship, and familiarity category. The regression was run with order of kinship versus familiarity switched to examine which factor order explained the most variance.

The 3 time periods were analyzed separately to allow detection of the influences of increasing overall colony familiarity, and as cage-mate familiarity of animals changed between time periods due to separation of squirrels for breeding. The separation of time periods also allowed us to reduce the number of repeated measures of individual dyads. To assess the influence of individual dyads participating in multiple 3-day trials during 1 time period the regression was run with only the first 3-day trial during that time period for each dyad entered (1st trial data set). The regression also was run with all dyads from all trials entered (full data set). Because each group was unique (no repeated groups) the context in which each pair of squirrels was encountering each other was fundamentally different and therefore the full data set provides a more inclusive picture of nest-mate choice. It

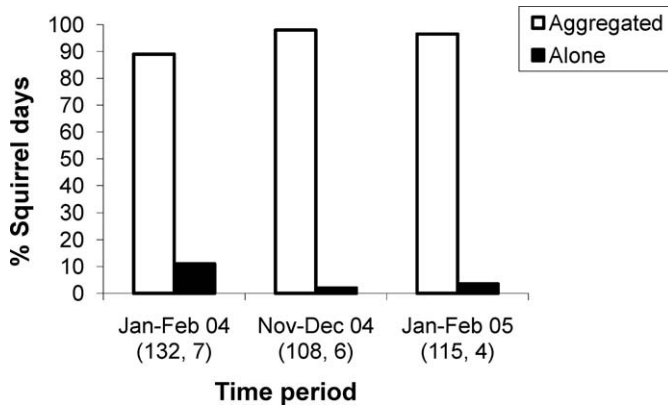


FIG. 2.—Aggregation of southern flying squirrels (*Glaucomys volans*) during 3-day trials in captivity. Squirrel days are the number of squirrels in all trials times the number of trial days. A group of 4 squirrels in a single 3-day trial would result in 12 squirrel days. Numbers under the trial designations are (dyads, trials).

should be emphasized that familiarity of the entire colony also increased with time.

RESULTS

General observations.—During winter southern flying squirrels aggregate in captivity as they do in the wild (Fig. 2). Squirrels inspected multiple nest boxes when they initially were released into the neutral cage (during daylight), but they settled quickly, generally within 30 min to 1 h, without much interaction among individuals. On the 1st night of a trial the squirrels spent additional time exploring the cage, sniffing the tops and bottoms of all nest boxes, and interacting with other individuals in the cage. Squirrels repeatedly entered all boxes that were not defended vigorously by another squirrel, and box switching was frequent during the active period. Direct food pilfering was common, and squirrels stored, stole, and re-stored food items multiple times in quick succession, such that 1 hazelnut might have been stored by most of the squirrels in a cage before it was eaten. Eating often was interrupted by cage mates, and individual squirrels regularly hung by their hind toes from the top of the cage to

avoid disturbance. Some interactions were extremely aggressive. On multiple occasions we saw 2 or more squirrels perform stereotypic, highly aggressive nose-to-tail foot-stomping displays (Muul 1968). Some displays lasted  $\geq 45$  min and were associated with food.

Analyses.—We present the full data set in the text because the results from both the full data set (Tables 2 and 3) and 1st trial data set (Appendix I) showed the same patterns. We found that kinship is consistently a significant factor explaining choice of nest mates in the winter aggregation behavior of southern flying squirrels. Familiarity with potential nest mates increases in importance as experience with those nest mates increases. Squirrels show a consistent pattern, choosing familiar kin (F+/r+) over unfamiliar nonkin (F-/r-) as nest mates (F+/r+ mean AI  $\pm$  SE = 0.9  $\pm$  0.11 to 0.97  $\pm$  0.03; F-/r- mean AI  $\pm$  SE = 0.37  $\pm$  0.04 to 0.64  $\pm$  0.06). When either kinship or familiarity is present alone, unfamiliar related (F-/r+) or familiar unrelated (F+/r-) animals are preferentially accepted as nest mates over F-/r- individuals but less than F+/r+ individuals (Fig. 3).

In the 1st time period the degree of dyad kinship ( $r_H$ ) was the predominant factor predicting associations (Table 2). In the 2nd and 3rd time periods kinship remained significant, although it explained less of the variance than in the 1st time period (Table 2). Operational familiarity was not a significant predictor of associations in period 1, became significant in period 2, and remained significant in period 3, explaining more of the variance than kinship in this final time period (Table 2). The degree of kinship also can have an effect when squirrels are operationally unfamiliar and have a choice between related animals of different degrees of relatedness. In these situations squirrels preferentially nested with their familiar or unfamiliar  $r_H = 0.5$  relatives over unfamiliar  $r_H = 0.25$  relatives (Fig. 4).

Other significant contributors to the model were inconsistent across the 3 time periods. These predictions of association include animal ages, significant in periods 1 ( $\Delta R^2 = 0.12$ ,  $F_{3,115} = 5.421$ ,  $P \leq 0.001$ ) and 3 ( $\Delta R^2 = 0.06$ ,  $F_{3,172} = 10.675$ ,  $P = 0.002$ ); individuals nesting alone, significant in periods 1 ( $\Delta R^2 = 0.17$ ,  $F_{8,110} = 5.186$ ,  $P \leq 0.001$ ) and 2 ( $\Delta R^2 = 0.15$ ,  $F_{8,81} = 4.413$ ,  $P \leq 0.001$ ); and mean low temperature,

TABLE 2.—Variance explained by the kinship and familiarity components in the best-fitting hierarchical regression equation for captive southern flying squirrels (*Glaucomys volans*). The full data set numbers include repeated measures for some squirrel dyads. Model step  $R^2$  values indicate the total variance explained by all factors in the model to that step (kin or familiar).  $\Delta R^2$  values indicate the amount of variance explained by the factor in that step (kin or familiar). Boldface type indicates a significant effect.

Full data set variance due to:	Time period		
	January–February 2004	November–December 2004	January–February 2005
Model step Kin $R^2$	0.565	0.375	0.247
Kin $\Delta R^2$	0.268	0.072	0.069
Kin $F_{d.f.}$	15.740 <sub>9,109</sub>	5.336 <sub>9,80</sub>	6.053 <sub>9,166</sub>
Kin $P$	$\leq$ <b>0.001</b>	$=$ <b>0.003</b>	$\leq$ <b>0.001</b>
Model step Familiar $R^2$	0.569	0.419	0.338
Familiar $\Delta R^2$	0.004	0.044	0.091
Familiar $F_{d.f.}$	14.239 <sub>10,108</sub>	5.707 <sub>10,79</sub>	8.412 <sub>10,165</sub>
Familiar $P$	$=$ 0.35	$=$ <b>0.02</b>	$\leq$ <b>0.001</b>

**TABLE 3.**—Variance explained by all factors entered in the best-fitting hierarchical regression equation, their contributions, and significance using the full data set for captive southern flying squirrels (*Glaucomys volans*). Factors in boldface type explain significant portions of the variance in the particular time period.

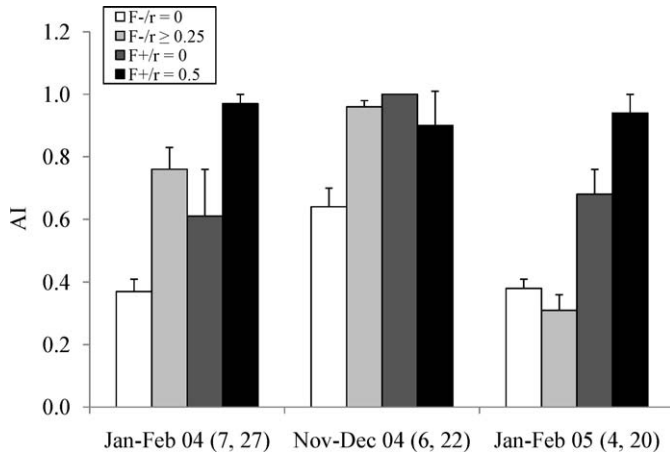
Time period	Factor	Adjusted $R^2$	$\Delta R^2$	$\beta$	$F_{d.f.}$	$P \leq$
January–February 2004	Mean low temperature	−0.009	0.000	−0.435	0.002 <sub>1,117</sub>	0.966
	<b>Age A, B</b>	<b>0.101</b>	<b>0.124</b>	<b>0.037</b>	<b>5.421</b> <sub>3,115</sub>	<b>0.000</b>
				<b>−0.256</b>		
	Sex A	0.086	0.001	−0.032	3.227 <sub>5,113</sub>	0.934
	Sex B			0.062		
	Kin available	0.073	0.003	−0.123	2.321 <sub>7,111</sub>	0.840
				−0.968		
	<b>Not aggregated</b>	<b>0.246</b>	<b>0.170</b>	<b>−0.455</b>	<b>5.816</b> <sub>8,110</sub>	<b>0.000</b>
	<b>Degree of kinship</b>	<b>0.529</b>	<b>0.268</b>	<b>0.928</b>	<b>15.740</b> <sub>9,109</sub>	<b>0.000</b>
	Familiarity	0.529	0.004	0.072	14.239 <sub>10,108</sub>	0.349
November–December 2004	<b>Mean low temperature</b>	<b>0.068</b>	<b>0.079</b>	<b>−0.174</b>	<b>7.516</b> <sub>1,88</sub>	<b>0.007</b>
	Age A, B	0.096	0.048	0.124	4.151 <sub>3,86</sub>	0.101
				0.361		
	Sex A, B	0.095	0.019	0.166	2.860 <sub>5,84</sub>	0.397
				0.016		
	Kin available	0.085	0.011	−0.051	2.176 <sub>7,82</sub>	0.583
				0.189		
	<b>Not aggregated</b>	<b>0.235</b>	<b>0.147</b>	<b>−0.399</b>	<b>4.413</b> <sub>8,81</sub>	<b>0.000</b>
	<b>Degree of kinship</b>	<b>0.305</b>	<b>0.072</b>	<b>0.282</b>	<b>5.336</b> <sub>9,80</sub>	<b>0.003</b>
	<b>Familiarity</b>	<b>0.346</b>	<b>0.044</b>	<b>0.225</b>	<b>5.707</b> <sub>10,79</sub>	<b>0.016</b>
January–February 2005	<b>Mean low temperature</b>	<b>0.088</b>	<b>0.093</b>	<b>−0.169</b>	<b>17.859</b> <sub>1,174</sub>	<b>0.000</b>
	<b>Age A, B</b>	<b>0.142</b>	<b>0.064</b>	<b>0.145</b>	<b>10.675</b> <sub>3,172</sub>	<b>0.002</b>
				<b>0.146</b>		
	Sex A, B	0.135	0.003	−0.019	6.464 <sub>5,170</sub>	0.756
				0.059		
	Kin available	0.138	0.013	0.079	4.996 <sub>7,168</sub>	0.282
				−0.126		
	Not aggregated	0.138	0.005	−0.005	4.512 <sub>8,167</sub>	0.295
	<b>Degree of kinship</b>	<b>0.206</b>	<b>0.069</b>	<b>0.176</b>	<b>6.053</b> <sub>9,166</sub>	<b>0.000</b>
	<b>Familiarity</b>	<b>0.298</b>	<b>0.091</b>	<b>0.376</b>	<b>8.412</b> <sub>10,165</sub>	<b>0.000</b>

significant in periods 2 ( $\Delta R^2 = 0.08$ ,  $F_{1,88} = 7.516$ ,  $P = 0.007$ ) and 3 ( $\Delta R^2 = 0.09$ ,  $F_{1,174} = 17.859$ ,  $P \leq 0.001$ ; Table 3). Although animal age was a significant factor in 2 time periods, littermate sibling dyads aggregated regardless of age (adult mean AI = 0.91; juvenile mean AI = 0.97;  $n = 7$  litters, 11 unique dyads). Relatedness persists in being a significant factor predicting association behavior throughout the 3 time periods, explaining more variance in periods 1 and 2 than familiarity, whereas operational familiarity increases in significance with the passage of time (Table 3). In later trials squirrels showed an increased tendency to associate with familiar nonkin (F+/r−; Fig. 3). Over the course of this experiment squirrels were encountering each other repeatedly and living in close proximity even when they did not share nest-box access in a cage. Therefore, increased familiarity with the passage of time is inherent in the laboratory system and potentially in natural populations.

Within each time period distinct patterns of aggregation behavior were apparent from day 1 of a trial through day 3. In trials from January and February 2004 squirrels were most likely to aggregate with familiar relatives 1st and least likely to aggregate with unfamiliar nonrelatives (Fig. 5A). In November and December 2004 relatedness and familiarity

both played a role; time within the trial did not (Fig. 5B). In January and February of 2005, when familiarity might have played an equal or greater role than relatedness in the squirrels' aggregation choices, differences in behavior over the 3 days suggest that when animals have the choice of highly related ( $r_H = 0.5$ ) familiar animals and unfamiliar less-related ( $r_H = 0.25$ ) animals, relatedness combined with familiarity becomes a determining factor (Fig. 5C). Squirrels aggregated with their familiar full siblings and parents or offspring but not with unfamiliar half siblings or unfamiliar nonrelatives (Fig. 4). With increasing overall familiarity the amount of exposure within the trial also becomes a factor, in that the occurrence of associated F−/r− dyads increased from day 1 to day 3 in time 3, which did not occur during the January through February 2004 time period when overall colony familiarity was less (Fig. 5).

Nesting alone was an uncommon event in these experiments (Fig. 2). Squirrels were most often alone on the 1st day of a trial (Fig. 6), or when they did not have kin as nest-mate options. Squirrels failed to aggregate 10% of the time in the 1st time period (Fig. 2). In the 2nd time period all animals had kin as nest-mate options and nested alone 2% of the time. In the 3rd time period nesting alone (3% occurrence) was not a

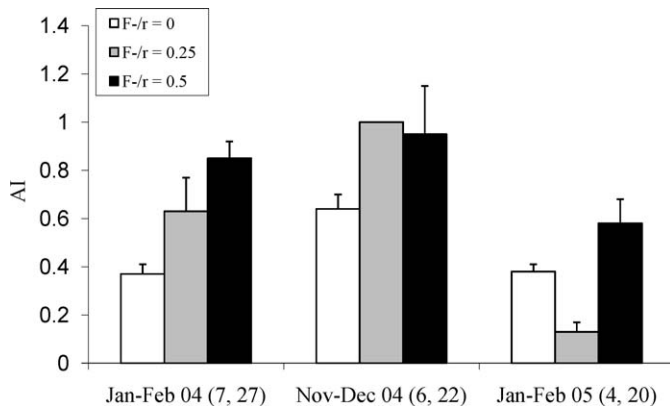


**FIG. 3.**—Association (mean AI  $\pm$  SE) of southern flying squirrel (*Glaucomys volans*) dyads in aggregations based on dyad relatedness and familiarity. F+ = operationally familiar dyads, F- = operationally unfamiliar dyads, and r = the degree of relatedness. No  $r_H = 0.25$  familiar dyads were tested throughout the 3 time periods.

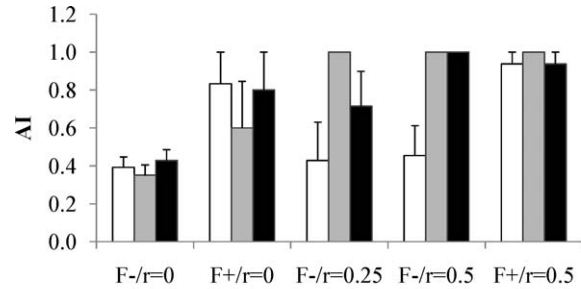
significant factor. This mirrors the increase in significance of familiarity.

**DISCUSSION**

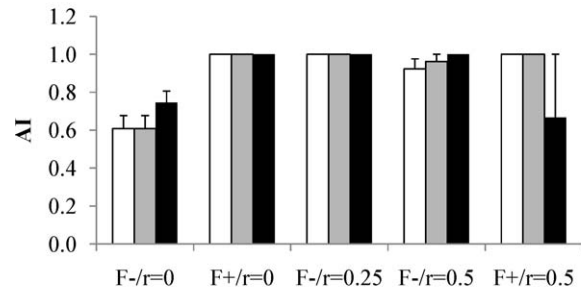
We have shown that southern flying squirrels show a marked preference for kin when forming winter aggregations in captivity and that under certain circumstances familiar but unrelated animals are incorporated into these kin-based aggregations. Also, southern flying squirrels differentiate between classes of individuals based on kinship and, with extreme increased exposure, familiarity. Wintertime preferences for related nest mates, as seen here, have the potential to mitigate these energetic costs of group living by increasing inclusive fitness and the amount of food stored in the home area (Doby 1984; Muul 1969). If an individual dies, its food stores also can help nest mates survive the winter. Reaching the breeding season in better condition increases the potential



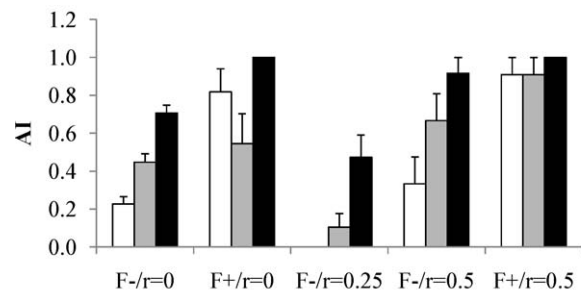
**FIG. 4.**—Association (mean AI  $\pm$  SE) of unfamiliar (F-) southern flying squirrel (*Glaucomys volans*) dyads by  $r_H$  category.



**A. Jan-Feb 2004**



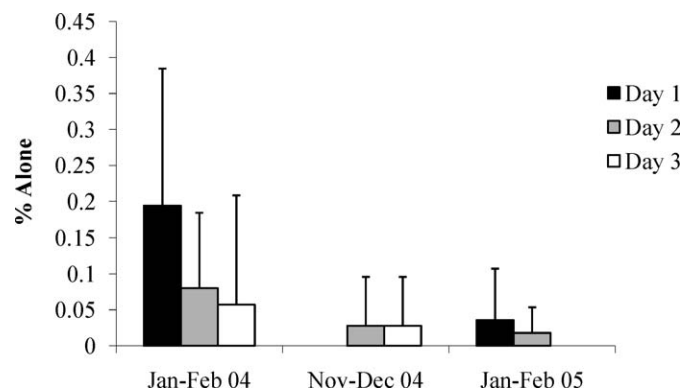
**B. Nov-Dec 2004**



**C. Jan-Feb 2005**

**FIG. 5.**—Daily mean association (mean AI  $\pm$  SE) by southern flying squirrel (*Glaucomys volans*) dyad type for each time period. F+ = operationally familiar dyads, F- = operationally unfamiliar dyads, and r = the degree of relatedness.

for each animal to produce more offspring (Bowman et al. 2005; Sullivan 1990). The individual that has a large litter or has a relative with a larger litter, or both, has more of its genes represented in succeeding generations.



**FIG. 6.**—Percent ( $\pm$  SD) of southern flying squirrels (*Glaucomys volans*) nesting alone each night by trial time period.

In general, earlier studies suggested that kinship is a component of winter aggregation structure of southern flying squirrels. Layne and Raymond (1994) suspected that their estimates of the number of 1st-order relatives in the aggregations they studied were low (16% of aggregations contained 1st-order relatives) because their marked litters were a small subsample of the local breeding population. Winterrowd et al. (2005) found a pattern of highly related family groups, highly related subadult groups, and minimally related adult-only nest groups, as would be expected in the late spring, postparturition, when breeding females and their pups avoid and behave agonistically toward other squirrels. Disturbance due to management for red-cockaded woodpeckers (*Picoides borealis*) by squirrel removal could have reinforced this pattern of reduced background relatedness shown by Winterrowd et al. (2005). The hierarchy of nest-mate choice we show here is consistent with the aggregation patterns of highly related groups from undisturbed, high-quality habitat (Thorington 2008; Thorington et al. 2010). In conditions where resource availability is high a tolerance for less-related and unrelated familiar nest mates seems reasonable. This tolerance could promote outbreeding, creating a situation in which the unrelated animal dyads in an aggregation share relatives. For example, an aggregation might consist of an unrelated male and female together with their offspring from last summer.

The probability of high relatedness between animals encountering each other in a woodlot is unclear and might be dependent on time of year (Thorington et al. 2010; Winterrowd et al. 2005). Also, postnatal dispersal distances are not well documented. Home ranges of flying squirrels within natural areas have high overlap, and squirrels in a woodlot are using many of the same nest sites (Holloway and Malcolm 2007; Sonenshine et al. 1979). Examination of trapping data shows that southern flying squirrel populations are distributed in patches. In good habitat where squirrels are found they are found in large groups, multiple groups, and have multiple active nests (Doby 1984). Within a season the composition of these groups fluctuates, and groups will be larger during colder weather (Muul 1968). We found that adult littermate siblings were associated within the same aggregation when given the opportunity. This preference for siblings would lead to high relatedness within aggregations if dispersal distances were limited or littermates disperse in similar directions. Examination of molecular data suggests that in high-quality habitat populations have a high degree of relatedness (Thorington 2008; Thorington et al. 2010). We would predict that winter groups will undergo compositional changes (fission and fusion) based on kinship, and if resources become scarce, the observed tolerance for unrelated animals might decrease. Further study of wintertime interactions among group members in the wild would increase our knowledge and understanding of any such patterns.

Familiarity of individuals is important and positively correlated with the choice of nest mates. The marked preference for kin, and the definition of kinship as a crucial factor in aggregation behavior, does not eliminate the potential

impacts of familiarity. Familiarity probably facilitates aggregation formation in general, because we observed that familiar animals were treated less aggressively during initial encounters. Additionally, close relatives generally are familiar in the wild. The role of familiarity seen here has implications for mechanisms responsible for recognition. In these experiments familiarity became a factor, but in the laboratory setting squirrels become more familiar with each other than they would be in the wild due to physical proximity and prior exposure in captivity. In the 1st trial period operational familiarity was not a significant factor. Additionally, the presence of a few animals that did not have kin available in the trial but were familiar with potential nest-mate squirrels did not explain aggregation behavior. It was only after repeated physical encounters through the experimental and breeding situations that operational familiarity influenced choice of nest mates. In the wild repeated physical encounters are likely to be less common because an excluded animal will attempt to find a different nest and other nest mates. When repeated physical encounters do occur, the result should be decreasing aggressive behaviors such as home-range and dominance marking because highly aggressive interactions or chasing individuals away from the nest are energetically costly behaviors.

A tolerance of familiar neighbors can facilitate advantageous behaviors. For example, solitary kangaroo rats (*Dipodomys ingens*) accept neighboring individuals as mates (Lovell and Lein 2005; Ralls 1971; Randall et al. 2002). Neighbor recognition has been seen both within and between species, and in some species neighboring groups contain closely related animals (Barash 1974; Ralls et al. 2001). Given the overlapping summer home ranges seen in southern flying squirrels (Bendel and Gates 1987; Holloway and Malcolm 2007; Sawyer and Rose 1985) and their propensity to nest with kin shown here, we predict that animals with summer range overlaps might be more likely to share a winter nest, and more closely related than those animals that do not have overlapping home ranges. This should be further explored in the field using mark-recapture techniques and additional microsatellite sampling (Thorington 2008; Thorington et al. 2010; Winterrowd et al. 2005). In cases where squirrels are being actively relocated for management practices, relocation could disrupt population structure, potentially lowering the availability of kin and known neighbors for winter aggregation. Despite these possibilities, Winterrowd et al. (2005) found high relatedness in their mixed-age squirrel groups.

Mechanisms of kin recognition are not fully understood in southern flying squirrels. Squirrels could rely on odor, sound, sight, or some multimodal combination. In Belding's ground squirrels (*Spermophilus beldingi*) an experiment involving habituation to a neutral odor stimulus, followed by a discrimination task with nonneutral odors, resulted in the demonstration of kin preferences (Mateo 2003; Mateo and Johnston 2000a, 2000b). If southern flying squirrels are relying predominantly on 1 cue type such as odor or sound, a similar experiment could reveal mechanisms responsible for



recognition, which could explain further the patterns of kin-based sociality seen here.

In the wild many factors can influence choice of nest mates by squirrels. Many young squirrels do not survive much past weaning, and squirrels that do mature might not survive beyond their 2nd or 3rd year (Doby 1984). Older squirrels are likely to have fewer living littermate siblings, therefore relatedness of temporally overlapping descendants and relatedness at lower  $r$ -values (e.g., half siblings, cousins, or grandchildren) could play a greater role in nest-mate choice (Sherman 1981). Food availability in the fall also can impact aggregation behavior, because the mast crop in an area can be used to predict squirrel abundance in that area the next summer (Bowman et al. 2005; Doby 1984). When food is scarce, squirrels either move or die. Over the course of a winter, as food availability and temperatures change, aggregations form and disband repeatedly in the wild (Doby 1984; Muul 1968). We saw fluctuations in temperature-related aggregation size regularly in the captive colony during our study.

Ultimately, the factors that will influence choice of nest mates are going to be the thermoregulatory constraints, availability of kin and other nest mates, and availability of food. Therefore, we predict that under adequate food conditions, when kin are available, southern flying squirrels will nest with kin, but they also will demonstrate a tolerance for familiar unrelated animals. Unrelated animals add heat energy to the aggregation, and tolerance of these animals would promote outbreeding. However, in a food-limited situation a kin-based group might be much less tolerant of unrelated individuals. Southern flying squirrels show a marked preference for their relatives when forming aggregations in captivity. A kin-based core is common in wild-caught wintertime aggregations (Thorington et al. 2010). Combined, these results suggest that kinship is a crucial component of aggregation behavior in southern flying squirrels.

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## APPENDIX I

Variance explained by all factors entered in the best-fitting hierarchical regression equation, their contributions, and significance using the 1st trial data set for captive southern flying squirrels (*Glaucomys volans*). Factors in boldface type explain significant portions of the variance in the particular time period. As for the full data set, kinship is the only consistent factor across time

periods, explaining a high portion of variance throughout. Familiarity becomes significant in the 2nd period and remains so for the 3rd. Other factors are not consistent in explaining a significant portion of the variance. The 1st trial data set removes all repeated exposures of individual dyads within a time period so each dyad is represented only once in the regression for each time period.

Time period	Factor	Adjusted $R^2$	$\Delta R^2$	$\beta$	$F_{df}$	$P \leq$
January–February 2004	Mean low temperature	−0.009	0.000	−0.439	0.004 <sub>1,107</sub>	0.949
	<b>Age A, B</b>	<b>0.052</b>	<b>0.078</b>	<b>−0.018</b> <b>−0.217</b>	<b>2.970</b> <sub>3,105</sub>	<b>0.014</b>
	Sex A	0.033	0.000	−0.047	1.749 <sub>5,103</sub>	0.999
	Sex B			0.053		
	Kin available	0.016	0.002	−0.164	1.258 <sub>7,101</sub>	0.900
	<b>Not aggregated</b>	<b>0.198</b>	<b>0.177</b>	<b>−0.467</b>	<b>4.329</b> <sub>8,100</sub>	<b>0.000</b>
	<b>Degree of kinship</b>	<b>0.508</b>	<b>0.291</b>	<b>0.847</b>	<b>13.367</b> <sub>9,99</sub>	<b>0.000</b>
	Familiarity	0.508	0.005	0.083	12.168 <sub>10,98</sub>	0.282
	<b>Mean low temperature</b>	<b>0.063</b>	<b>0.075</b>	<b>−0.141</b>	<b>6.246</b> <sub>1,77</sub>	<b>0.015</b>
	<b>Age A, B</b>	<b>0.123</b>	<b>0.082</b>	<b>0.087</b> <b>0.414</b>	<b>4.642</b> <sub>3,75</sub>	<b>0.031</b>
November–December 2004	Sex A	0.145	0.043	0.174	3.640 <sub>5,73</sub>	0.148
	Sex B			−0.065		
	Kin available	0.125	0.004	−0.042	2.588 <sub>7,71</sub>	0.848
				0.176		
	<b>Not aggregated</b>	<b>0.261</b>	<b>0.133</b>	<b>−0.411</b>	<b>4.440</b> <sub>8,70</sub>	<b>0.000</b>
	<b>Degree of kinship</b>	<b>0.316</b>	<b>0.058</b>	<b>0.246</b>	<b>5.002</b> <sub>9,69</sub>	<b>0.012</b>
	<b>Familiarity</b>	<b>0.372</b>	<b>0.058</b>	<b>0.260</b>	<b>5.681</b> <sub>10,68</sub>	<b>0.009</b>
	<b>Mean low temperature</b>	<b>0.089</b>	<b>0.095</b>	<b>−0.168</b>	<b>14.308</b> <sub>1,136</sub>	<b>0.000</b>
	<b>Age A, B</b>	<b>0.146</b>	<b>0.070</b>	<b>0.139</b> <b>0.037</b>	<b>8.834</b> <sub>3,134</sub>	<b>0.005</b>
	Sex A	0.140	0.007	0.005	5.471 <sub>5,132</sub>	0.595
January–February 2005	Sex B			0.111		
	Kin available	0.136	0.008	0.156	4.080 <sub>7,130</sub>	0.513
				−0.274		
	<b>Not aggregated</b>	<b>0.130</b>	<b>0.001</b>	<b>0.072</b>	<b>3.570</b> <sub>8,129</sub>	<b>0.674</b>
	<b>Degree of kinship</b>	<b>0.201</b>	<b>0.072</b>	<b>0.158</b>	<b>4.831</b> <sub>9,128</sub>	<b>0.001</b>
	<b>Familiarity</b>	<b>0.332</b>	<b>0.127</b>	<b>0.472</b>	<b>7.794</b> <sub>10,127</sub>	<b>0.000</b>