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Social dynamics and dispersal in free-living prairie voles (*Microtus ochrogaster*)

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Following dispersal from 1 group, individuals may join other established social groups. Such intergroup transfer may increase access to potential mates and decrease mate competition. We used data from 402 individuals to examine patterns of intergroup transfer in prairie voles (*Microtus ochrogaster*). Nearly 32% of established social groups (single female units, male–female pairs, or communal groups of at least 2 adults of the same sex) were joined by 1 or more individuals. Most individuals (76%) that joined social groups were wanderers that were either unmarked, recently marked during grid trapping, or marked transients; 70% were males. Joining a group was not contingent upon recent disappearance of residents. Total number of residents positively affected the probability of a female joining a social group, whereas number of adult female residents and population density negatively affected it. Some individuals (24%) moved directly from one group to another without an intervening wandering stage; we refer to these instances of intergroup transfer as direct transfers. Most direct transferers moved into nearby groups, but not the closest group. Males were more likely than females to directly transfer into groups with potential mates and without potential competitors. Thus, males directly transferred in a manner consistent with maximizing reproductive opportunities. In contrast, 25% of females directly transferred into groups without potential mates and 96% into groups with at least 1 adult female. Females may be less constrained by group composition with respect to potential mates because wandering males, with which females can mate, are prevalent. All-male groups almost never occur in our population, so females probably cannot avoid joining groups with competitors.

Key words: dispersal, intergroup transfer, prairie vole, social dynamics, social group

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Dynamics of social groups include changes in group size and composition over time through the loss or addition of members (Ebensperger and Hayes 2008). Phenomena that drive social dynamics include birth, death, natal philopatry (remaining within the natal social group past weaning—Solomon 2003), natal dispersal (movement between the natal social group and the social group where breeding 1st occurs—Clobert et al. 2001), breeding dispersal (movement between 2 successive breeding sites or groups; also known as secondary dispersal—Clobert et al. 2001), and fission or fusion of social groups. By changing group size and composition, these phenomena influence costs and benefits to group members. Costs may include suppressed reproduction and increased conspicuousness to predators or prey, competition with group members for food or mates, and risk for transmission of diseases and parasites. Benefits may include improved predator detection and defense, and enhanced thermoregulation, care of young, and ability to find and defend food resources (Alexander 1974; Bertram 1978).

Natal and breeding dispersal can result in individuals joining established social groups. In such cases of intergroup transfer, researchers often compare size and composition of groups left and joined. One pattern that has emerged concerns individuals that switch groups to maximize reproductive opportunities. More specifically, intergroup transfers typically result in increased access to potential mates and decreased competition from same-sex conspecifics (Clarke and Glander 2010; Jack and Fedigan 2004; Rood 1983). Intergroup transfer also affects residents' ability to maintain an optimal group size and composition (Anderson 1989; Krebs and Davies 1993). Costs and benefits to residents of accepting a new individual depend on group composition and characteristics of the new individual (Back et al. 2002).

Little information exists on intergroup transfer in rodents, perhaps because individuals of many species are small, short-lived, and difficult to observe under natural conditions. In a review by Ebensperger and Hayes (2008) of group dynamics in 42 species of social rodents, data concerning departures from groups by individuals (that presumably join or form another group) are either not quantified or not available for most species. Especially rare are direct comparisons of groups left and groups joined (Solomon et al. 1998). Such comparisons are needed to elucidate costs and benefits of group living. Some data are available for 3 species: woodland voles (= pine voles; *Microtus pinetorum*), prairie voles (*M. ochrogaster*), and meadow voles (*M. pennsylvanicus*). Woodland voles live in extended families and only a few incidents of intergroup transfer have been documented (FitzGerald and Madison 1983). Transferring males and females tend to enter adjacent social groups that have some members of the opposite sex but no members of the same sex (FitzGerald and Madison 1983; Solomon et al. 1998). Prairie voles also live in extended families, but adults often join families after philopatric offspring reach adulthood (Getz et al. 1990, 1993). Getz et al. (1990) found that only 20% of individuals directly transfer from 1 group to another; the remaining 80% wander for some time before joining a group. Most individuals that leave 1 group to join or form another group enhance their mating opportunities by the move (McGuire and Getz 1995). Data from a field enclosure study in which adult residents (either all adult females or all adults) were removed from groups of prairie voles indicate that vacancies are rapidly filled and that transferring individuals come from nearby groups more often than expected (Jacquot and Solomon 2004). In contrast to woodland voles and prairie voles, meadow voles share nests only in winter for thermoregulatory benefits. Loss of group members prompts meadow voles to transfer groups; aggression does not precipitate or prevent movement between winter groups (Madison and McShea 1987; McShea 1990).

In our paper, we use data collected during a 7-year study of prairie vole social organization to examine intergroup transfer in more detail. We consider individuals that share a surface or underground nest to be members of the same social group. Rather than focusing exclusively on communal groups, as in Getz et al. (1990, 1993) and McGuire and Getz (1995), we include data from all 3 types of social groups present in our study population, which are single female units, male–female pairs, and communal groups (at least 2 adults of the same sex, often including 1 or more adults of the opposite sex). In this more comprehensive analysis, we include new information on simultaneous joining by multiple individuals, successive intergroup transfer by single individuals, and the relationship between weekly number of individuals joining social groups and weekly number of adults in the population. We also examine whether joining a group is contingent upon prior disappearance of residents, and how season, group size, and group composition affect patterns of joining. Finally, we examine whether individuals directly transfer into the closest group and whether distance moved varies with sex, season, or population density. Our goals in examining these additional data collected during our long-term study are 2-fold. First, using this very large data set, we provide more comprehensive information on intergroup transfer in prairie voles to increase information available on this phenomenon in social rodents. Second, we test the hypothesis that individual prairie voles transfer groups to maximize reproductive opportunities.

MATERIALS AND METHODS

Study areas.—Our study sites were 2 adjacent 1-ha alfalfa (*Medicago sativa*) fields at the University of Illinois Biological Research Area (Fig. 1), 6 km NE of Urbana, Illinois, (40°15′N, 88°28′W). Other vegetation at the sites included ragweed (*Ambrosia* spp.), goldenrod (*Solidago* spp.), wild parsnip (*Pastinaca sativa*), and bluegrass (*Poa pratensis*). We used 1 site from October 1980 through July 1984, and the other site from June 1983 through May 1987.

Field methods.—We monitored social groups of prairie voles by intensive livetrapping directly at underground and surface nests to identify members of established social groups and adults that joined them (Getz et al. 1993). Social groups included single female units, male–female pairs, and communal groups; young may or may not have been present in each type of group. We located most nests by dusting voles with ultraviolet powder and tracking them back to their nests (Lemen and Freeman 1985) and we found some nests by following radiocollared voles (Hofmann et al. 1984). We placed 4–5 traps either in runways (leading to surface nests) or near burrow openings (for underground nests). We set traps at 0630 h on Monday and checked them at 3–4-h intervals through 2400 h and again at 0630 and 0930 h on Tuesday. This schedule was repeated Thursday morning through Friday morning each week.

A 25-year study (1972–1997) of vole demography at these and nearby sites involved concurrent grid trapping (Fig. 1). We set traps at stations in a 10-m grid pattern once each month (Getz et al. 2001). Traps (1 per station) were set at 1500 h Tuesday and checked at 2000 h, 0800 h, and 1500 h through Friday afternoon. Midway through each period of grid trapping, all stations $\geq$ 15 m from known nests were trapped on the above schedule from 1500 h Wednesday through Friday afternoon. Grid trapping allowed us to capture voles that were not living at or visiting known nests. Livetrapping provides less precise information about movements than methods such as radiotelemetry. However, livetrapping allowed us to monitor many individuals and we improved our precision by combining monthly grid trapping with twice weekly trapping directly at burrows.

For both nest and grid trapping we used wooden multiple-capture live traps (6.5 × 6.5 × 20 cm—Burt 1940). We baited

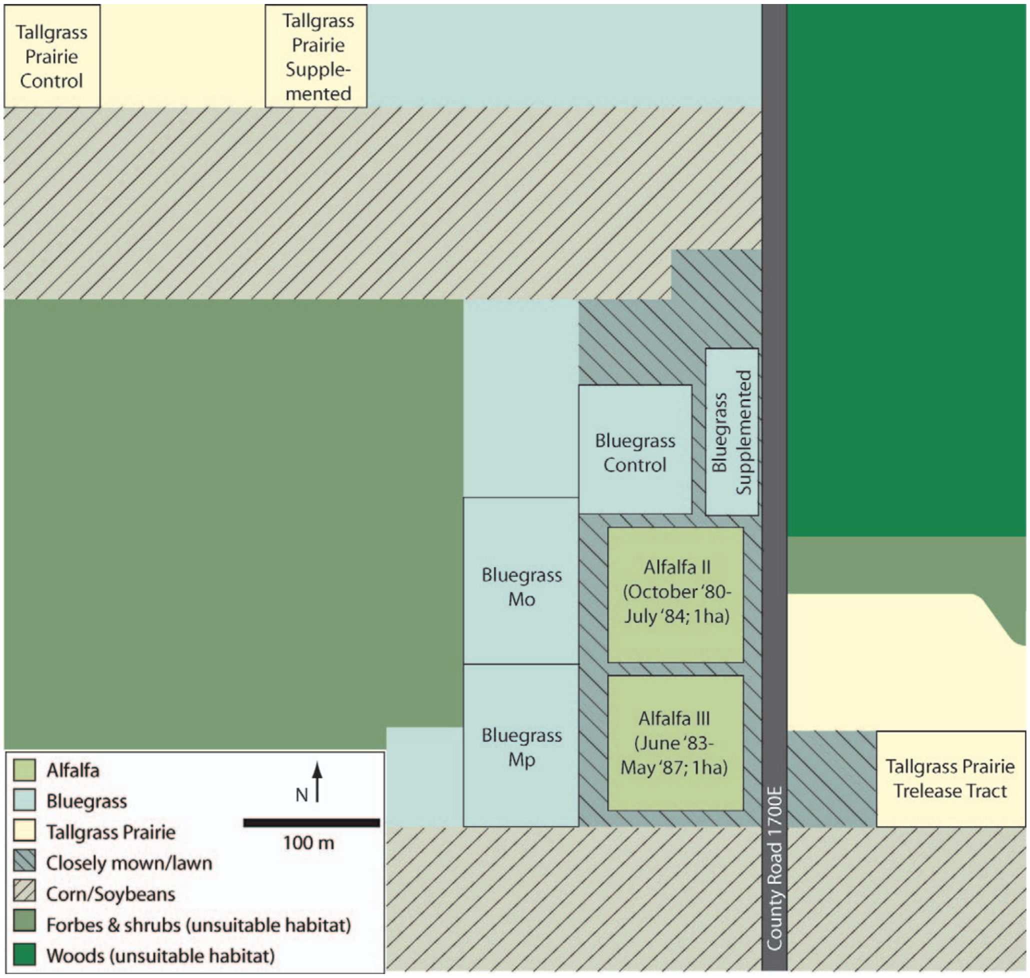

Fig. 1.—Location of alfalfa study sites (Alfalfa II and Alfalfa III) and surrounding study sites at which grid trapping occurred during our study. Dates for nest trapping in the alfalfa sites are shown on the map; dates for concurrent grid trapping were October 1980–July 1984 for Alfalfa II and October 1983–May 1987 for Alfalfa III. Concurrent grid trapping in surrounding sites occurred on the following dates: Bluegrass *Mo* (*Microtus ochrogaster* present but *M. pennsylvanicus* removed; October 1980–May 1987); Bluegrass *Mp* (*M. pennsylvanicus* present but *M. ochrogaster* removed; October 1980–May 1987); Bluegrass Control (October 1980–May 1987); Bluegrass Supplemented (October 1980–December 1983); Tallgrass Prairie Supplemented (October 1980–March 1987); Tallgrass Prairie Control (October 1980–May 1987); and Tallgrass Prairie Trelease Tract (January 1981–November 1983; September 1984–May 1987).

traps with cracked corn and in summer covered them with either vegetation or aluminum shields to provide shade. At 1st capture we weighed each vole to the nearest gram and individually marked it by toe clipping. We recorded location, individual identification, sex, and reproductive condition at each capture (males: testes abdominal or scrotal; females: pregnant, lactating, vagina open or closed). All procedures were approved by the University of Illinois Laboratory Animal Care Committee and meet the current guidelines of the American Society of Mammalogists (Sikes et al. 2011).

Data analysis.—We assigned age classes on the basis of body mass (young, <30 g and adult, ≥ 30 g) using observations of the age and mass at which captive-born prairie voles (descendants of individuals captured at our sites) became reproductive (McGuire et al. 2002). Individuals at 30 g are about 30 days old. Adult males were classified as nonreproductive when testes were abdominal and reproductive when testes were scrotal. Adult females were classified as nonreproductive if the vagina was closed, and reproductive if the vagina was open, or if they were pregnant, lactating, or had recently lactated. For seasonal analyses, we used breeding season (March through November) and nonbreeding season (December through February). As in Getz et al. (2001), we estimated population density of prairie voles for each trapping session using minimum number known to be alive (Krebs 1966).

We defined residents of a social group as individuals captured primarily at the group's nest for at least 10 days (Getz et al. 1993). We classified individuals that joined groups as transferers (individuals that directly transferred from another social group) or wanderers (individuals that left a social group to wander before joining another social group). For individuals with multiple joining events, we used data from their 1st joining event to classify them. Wanderers included transients

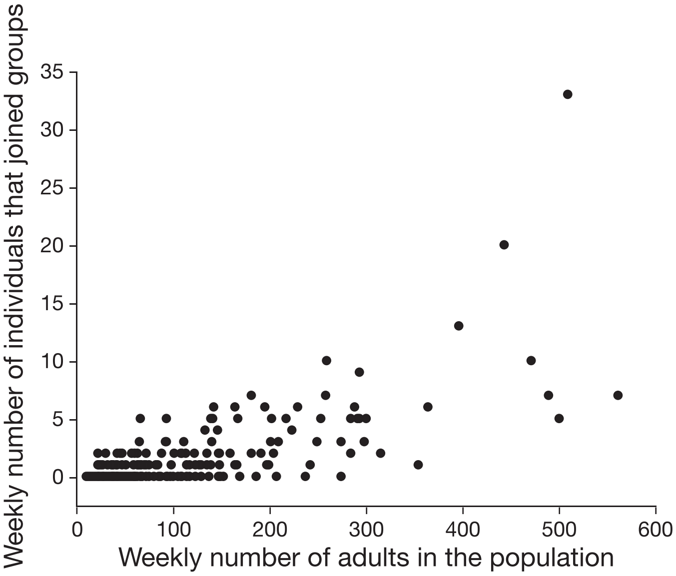

Fig. 2.—Weekly number of individuals that joined groups versus weekly number of adults in the population.

(marked individuals that moved throughout the study area rather than establishing residency at a nest), immigrants (individuals marked at another study site and then captured at a nest in the alfalfa sites), individuals that were marked at a nearby grid trap within the past month, and individuals 1st captured and marked as an adult at a social group. We did not conduct genetic analyses; thus, we regarded individuals weighing ≥30 g when captured for the 1st time at a group as unrelated to group members. Given the intensity of livetrapping directly at nests, we consider it unlikely that an individual would reach adulthood without ever being captured at its natal nest. Trappability of prairie voles at our study sites was estimated at 92% on the grid (Getz et al. 2001) and should be even higher at nests.

We examined joining in relation to the disappearance of a resident. Jacquot and Solomon (2004) found that 41% of new females moved into experimentally created vacancies within 24 h of removal of residents, with an average interval of 4.6 days. Given their findings, we set 1 week as the interval after disappearance of residents in our study. We also examined factors that might influence successful joining by individuals, including characteristics of the individual joining (sex and reproductive condition), characteristics of the group joined (type of social group, total number of residents, number of adult male residents, and number of adult female residents), season, and population density (see logistic regression analysis below).

We examined several characteristics of the group left and the group joined for individuals that directly transferred groups. We compared size of the group left with that of the group joined, with group size defined as the total number of residents (adults and young) living at a nest. To characterize age and sex composition of the group joined, we defined potential mate as any adult of the opposite sex and potential competitor for mates as any adult of the same sex. We also examined distance moved (m) by individuals in relation to sex of the individual directly transferring, season, and population density.

Finally, using maps of nest locations and distance (m) from group left to group joined, we examined whether individuals directly transferred into the closest group. We used the distance from the group left to the group joined as the radius of a circle around the group left and counted all existing groups within that circle to estimate the number of closer groups that the transferer could have joined. Unfortunately, we cannot describe the composition of potential groups for each animal to join because group composition changed frequently due to mortality during the time the transferer would have encountered other groups.

We examined the relationship between weekly number of individuals joining groups and weekly number of adults in the population using linear regression analysis, with log (weekly number of individuals joining groups + 1) as a response variable and weekly number of adults in the population as a predictor variable using SAS 9.3 (Cary, North Carolina). Given potential sex-specific differences in reproductive strategies, factors influencing successful joining of groups by males and females may differ. Thus, we used logistic regression to model the probability that an individual joining a group is female using LOGISTIC procedure in SAS. We first used stepwise variable selection procedure to identify variables that significantly influenced the response variable; we then fitted the logistic regression model using only those variables identified to have a significant effect. We analyzed some data involving counts of individuals using either chi-square goodness-of-fit tests or chi-square tests of association with Yates correction when appropriate; typically, we compared patterns of joining by males and females. We used a general linear model (SAS procedure GLM) to test for the effect of season, population density, and sex of the transferer on distance moved; we also examined all 2-way interactions of these variables. In some cases we simply present descriptive data in either the text or a figure.

Results

Overall description of joining.—Weekly number of adults in the population positively influenced weekly number of individuals that joined groups (Fig. 2; $\beta \pm SE = 0.0054 \pm 0.0003$, $P < 0.001$; $r^2 = 0.544$). The overall mean monthly sex ratio (males : females) for prairie voles living in alfalfa habitat was 0.51 ($SE = 0.18$, $n = 275$ months). Of 402 individuals that joined social groups, 280 (69.7%) were male and 122 (30.3%) were female ($X^2_1 = 55.96$, $P < 0.001$).

Most individuals that joined groups were wanderers (75.9%; 305/402). Of these, most were first marked at the group joined ($n = 185$), marked at a nearby grid trap within the past month ($n = 54$), or were marked transients known to be visiting nests throughout the study site ($n = 63$); a few individuals (3 males) were immigrants from another study site. Only 24.1% (97/402) of individuals that joined social groups were recorded as direct

Table 1.—Results of logistic regression modeling the probability that a prairie vole (*Microtus ochrogaster*) joining a group is a female.

Effect	*d.f.*	Wald X^2	*P*
Reproductive condition	1	4.70	0.0301
Group type	2	9.02	0.0110
Total residents	1	12.12	0.0005
Total adult female residents	1	10.01	0.0016
Population density	1	11.33	0.0008

transfers from another group. Of these, only 2 males and 4 females transferred from their natal group. Therefore, most instances of direct transfer (93.8%; 91/97) represented breeding dispersal; of the 91 individuals, 68 were males and 23 were females. For 65 of the 97 direct transfers, we had body mass data from grid trapping the month before their switching groups. Most (96.9%; 63/65) were adults, with body masses ranging from 30 to 55 g. We previously reported that most young (70–75%) remain at home until death; further, of those that do disperse, most (90–95%) leave their natal group after reaching adulthood (McGuire et al. 1993).

Nearly 32% (226/711) of established social groups were joined by 1 or more individuals. Whereas 57.5% (130/226) of these groups were joined by a single individual, 42.5% (96/226) were joined by 2 or more individuals (range, 2–9 adults; range in time from joining of the 1st individual to joining of last, 1–130 days). For the 96 groups joined by 2 or more individuals, joining events were confined to the breeding season at 50 groups, the nonbreeding season at 22 groups, and spanned breeding and nonbreeding seasons at 24 groups. At 31 groups we recorded more than 1 individual joining on the same day: at 22 of these groups, 2 individuals joined and at 9 groups, 3 individuals joined. At 3 (9.7%) of the 31 groups, all individuals had transferred from the same social group; the remaining instances involved joining by all wanderers (at 14 groups; 45.2%), a mix of transferers and wanderers (at 12 groups; 38.7%), and transferers from different social groups (at 2 groups; 6.4%). Finally, at 16 (51.6%) of 31 groups, all simultaneously joining individuals were male; the remaining instances involved joining by all females (at 5 groups; 16.1%) or a mix of males and females (at 10 groups; 32.3%).

Individuals that joined social groups almost always joined only 1 group (96.5%; 388/402). However, 14 individuals (13 males and 1 female) joined 2 or 3 groups in succession. Of the 13 males, 11 joined 2 groups and 2 joined 3 groups; the female joined 2 groups. Most (11/14) moved directly from 1 group to another; however, 3 of the males joined a group, left it to wander for a period of time, and then joined another group. Most of the 14 individuals that engaged in successive intergroup transfer were residents of a group for 1–2 months before transferring again.

Joining was not contingent upon prior disappearance of an adult resident from that group. Only 13.2% (53/402) joined a group after 1 or more residents disappeared the previous week. Of these 53 individuals, 24 (45.3%) joined after at least 1 resident of the same sex disappeared; 21 (39.6%) joined after at least 1 resident of the opposite sex disappeared; and 8 (15.1%) joined after at least 1 resident of each sex disappeared.

Table 2.—Type of social group joined by male and female prairie voles (*Microtus ochrogaster*). Values within each row represent percentages for each sex, with number of individuals in parentheses.

	Group		
Sex	Single female	Male–female pair	Communal group
Male	29.6 (83)	9.7 (27)	60.7 (170)
Female	15.6 (19)	11.4 (14)	73.0 (89)

Factors influencing successful joining.—Stepwise variable selection procedure revealed that the following variables significantly influenced the probability that an individual joining a group is female: reproductive condition, group type, total number of residents at the group, total number of adult females at the group, and population density. Hosmer-Lemeshow test did not reveal lack of fit of the logistic regression model using the aforementioned variables ($X^2_8 = 8.856$, $P = 0.355$). Results from the logistic regression analysis are presented in Table 1. Total number of residents positively affected the probability of a female joining a social group (slope ± $SE = 0.234 \pm 0.067$), whereas total number of adult female residents (–0.424 ± 0.134) and population density (–0.003 ± 0.001) negatively affected it. Type of social group affected the probability of a female joining (–0.650 ± 0.234) in that females were less likely than males to join single females (Table 2). Finally, reproductive condition affected the probability of a female joining (odds ratio: 1.78): females (59.0%; 72/122) were more likely than males (45.7%; 128/280) to be nonreproductive at the time of joining a group.

Comparison of the size and composition of groups left and groups joined.—We recorded direct transfer for 104 individuals (76 males and 28 females; this number is slightly higher than the 97 transferers described previously because we included 7 individuals originally classified as wanderers because their 1st joining event followed a period of wandering; however, their 2nd joining event involved a direct transfer, so we included data on their 2nd event here). Males and females differed in patterns of direct transfer with respect to group size: whereas 78.6% (22/28) of females transferred into a group larger than the group they left, only 50.0% (38/76) of males did so ($X^2_1 = 5.72$, $P = 0.02$). Whereas all 76 males that directly transferred entered a group that contained at least 1 potential mate, only 75.0% (21/28) of female transferers did so ($X^2_1 = 16.58$, $P < 0.0001$). Of the 7 females that transferred into a group without a potential mate, 5 did so during the breeding season and 2 during the nonbreeding season. Additionally, females (96.4%; 27/28) were more likely than males (32.9%; 25/76) to directly transfer into a group that contained at least 1 potential competitor for mates ($X^2_1 = 30.54$, $P < 0.0001$). Given our finding that total number of adult female residents negatively affects the probability of a female joining a group, we examined these direct transfer data for females in more detail. Of the 27 females that directly transferred into a group with at least 1 adult female resident,

TABLE 3.—Results of general linear model testing for the effects of season, population density, and sex of the prairie vole (*Microtus ochrogaster*) transferring groups and all 2-way interactions of these variables on the distance moved.

Source	*d.f.*	*F*	*P*
Season	1	1.52	0.2217
Sex	1	0.10	0.7470
Density	1	0.00	0.9451
Season × sex	1	0.81	0.3707
Density × season	1	0.33	0.5681
Density × sex	1	0.00	0.9542

19 transferred into a group with more adult females than the group they had left. However, 9 of these 19 females had been living alone.

Distance between groups left and groups joined.—Distances moved were available for 76 of the 104 individuals that directly transferred groups. However, 3 males simultaneously transferred from 1 group to another. To avoid problems associated with lack of independence, we used data from only 1 of these males, leaving a total of 74 individuals with distance data. Our general linear model analysis revealed that distance moved by transferers was not affected by sex, season, population density, or the 2-way interactions involving these variables (Table 3). Mean distance moved (± *SE,* in m) was 27.5 ± 3.0 for males ($n = 47$) and 22.1 ± 4.6 for females ($n = 19$). Only 5 (4 males and 1 female) of the 74 transferred into a group that was unusually far from their original group (>65 m; Fig. 3). Excluding these 5 individuals from the previous analysis did not appreciably change the results.

We used data from 69 individuals for our examination of whether direct transferers joined the closest group. We did not include the 5 individuals with unusually long transfer distances because the area enclosed by their radii included most groups in the field. Most individuals that directly transferred into groups did not join the closest group; for 92.8% (64/69) of direct transferers there was at least 1 other group, and often many more, closer than the group they joined (Fig. 4).

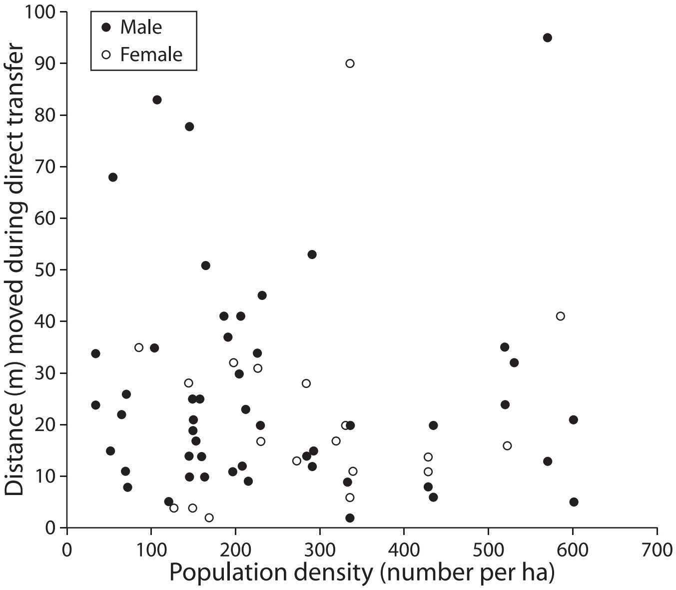

FIG. 3.—Distance moved during direct transfer versus population density.

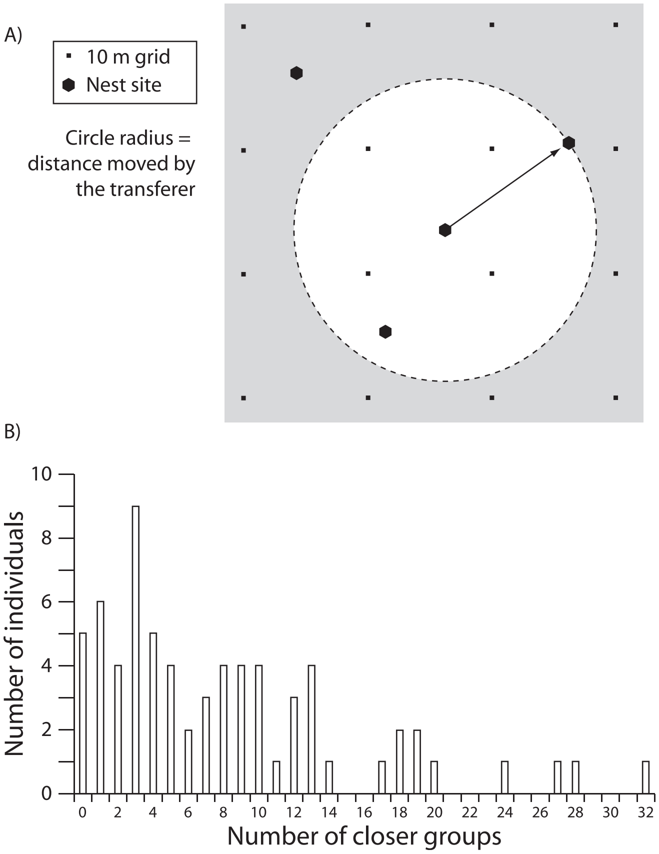

FIG. 4.—A) Method used to determine number of groups closer than the one into which the individual directly transferred. Arrow indicates movement of transferer from one group to another. B) Number of individuals that directly transferred into groups in relation to number of groups closer than the one into which the individual transferred. When number of closer groups equals zero, an individual transferred into the group closest to the one it left.

DISCUSSION

Characteristics of individuals that join groups.—Nearly all individuals that join established social groups are adults. This agrees with our previous finding that most individuals reach adult body mass before leaving their natal group (McGuire et al. 1993) as well as with Jacquot and Solomon (2004), who found that 98% of prairie voles that joined established groups in field enclosures were adults. Data on age at transfer are conflicting for woodland voles. Whereas FitzGerald and Madison (1983) documented 6 cases of intergroup transfer for woodland voles and all involved adults, Solomon et al. (1998) found evidence that young woodland voles switched groups (2 of 10 males and 9 of 15 females). Arvicolines vary in the relationship between age and dispersal: in some species, dispersal is more common in adults; in others, it is more common in young; in others, there is no detectable age difference (Le Galliard et al. 2011).

Most individuals that joined social groups were wanderers (76%) rather than direct transferers (24%). Our results agree with Jacquot and Solomon (2004), who found that many individuals that joined established groups were either unmarked (43%) or captured infrequently (27%). Only 30% directly transferred from other social groups. Wanderers have been identified in both open (Getz et al. 1993; McGuire and Getz 2010) and enclosed populations of prairie voles (Ophir et al. 2008; Solomon and Jacquot 2002), and are comparable with individuals that display the alternative reproductive strategy described as "nonterritorial" for some mammals (Wolff 2008).

About 70% of individuals that joined established social groups were male. This probably reflects the greater proportion of males in the pool of individuals likely to join groups. For example, even though the sex ratio for prairie voles in alfalfa habitat is only slightly male-biased (0.51 males), at any given time 32–46% of adult males are wanderers as compared with 19–24% of females (Getz et al. 1993). About one-half (51%) of wandering males eventually join or form a social group (McGuire and Getz 2010). Possibly, residents of established groups preferentially accept males, which might work as follows. Many female mammals compete for resources and mates to gain reproductive benefits (Stockley and Bro-Jørgensen 2011). Such female–female competition might make females in a group less likely to accept another female. Field- and laboratory work with Damaraland mole-rats (*Cryptomys damarensis*) show that foreign females are less readily accepted than foreign males into existing colonies (Hazell et al. 2000), although reasons for this preference are unknown. We found that the total number of adult female residents negatively affected the probability of a female joining a group, although some of our data concerning direct transfers by females somewhat contradict these findings (see below). Thus, we conclude that the 70% prevalence of males joining established groups probably reflects more males than females in the pool of individuals likely to join groups, and possibly preferential acceptance of males by resident adult females.

We previously reported no significant sex difference in natal dispersal in our study population, with about 30% of males and 25% of females leaving their natal group (McGuire et al. 1993). Here, we report male-biased breeding dispersal in the population, which may reflect greater reproductive benefits to males than females of wandering and moving between social groups. This is consistent with our finding that males were more likely than females to be reproductive at the time they joined a social group. Lactation, in particular, is inconsistent with wandering. We found no significant sex difference in distances moved by male and female natal dispersers (McGuire et al. 1993) or between males and females that directly transferred between groups (present study), although male dispersal distances tended to be longer than those of females. Most arvicolines display male-biased natal and breeding dispersal, with a more pronounced male bias for breeding dispersal, and males tend to move longer distances than females (Le Galliard et al. 2011).

Many wanderers were unmarked at the time they joined a group ($n = 185$) and only a few were marked immigrants ($n = 3$). Getz et al. (2005), using data from all months of the 25-year study, reported a mean ($\pm$ *SE*) of 4.5 ± 0.5 immigrants into the alfalfa sites per month. Additionally, McGuire et al. (2009) found that density of conspecifics at a site positively influenced rates of immigration to that site. During months with adult population densities $\geq$50/ha in the alfalfa sites, 31.3% ± 3.6% (range 7.0–56.2%) of adults were immigrants (L. L. Getz, pers. comm.). Given the small number of marked immigrants in the present study and the relatively high population densities recorded in the alfalfa sites during many months of the study (number of months with adult population densities $\geq$50/ha at the 2 alfalfa sites were 18/38 and 29/44 for Alfalfa II and Alfalfa III, respectively), we suggest that many of the 185 unmarked individuals that joined groups were immigrants. Although we conducted grid trapping in many surrounding sites, some adjacent sites could have been sources for unmarked voles. For example, while trapping at nests and on the grid in Alfalfa II, unmarked individuals could have moved in from Alfalfa III, which was not trapped during the same time period, except for an initial period of overlap (Fig. 1).

Most joining events by prairie voles involved single individuals. Nevertheless, we documented 2 or 3 adults joining on the same day at 31 social groups, a finding we term simultaneous joining. Simultaneous departures from social groups, known as parallel dispersal, have been reported for a few species of rodents (*Cynomys ludovicianus*—Hoogland 1995; Manno et al. 2007; *Hydrochoerus hydrochaeris*—Herrera et al. 2011; *Heterocephalus glaber*—Braude 2000; Brett 1991), but information on simultaneous joining is lacking. Parallel dispersal occurs in some large mammals where it is hypothesized to reduce dispersal costs (especially those related to predation, starvation, and aggression from conspecifics), increase success of taking over a new group, and serve as a way to retain kinship among new group members (Handley and Perrin 2007; Jack and Fedigan 2004; Pusey and Packer 1987). The benefits, if any, to prairie voles of parallel dispersal and simultaneous joining are unknown. Only a few individuals in our study displayed successive joining events. Prairie voles have a short life span (typically <3 months in natural populations—Getz et al. 1997), so most individuals probably die before having a chance to disperse again.

Characteristics of groups joined.—Most prairie voles directly transferred into nearby groups, but not necessarily into the closest group. For about 93% there was at least 1 group, and often several groups, closer than the group joined. Mean distance moved was about 27 m for males and 22 m for females; on the basis of typical size of home ranges at our study site (Getz and Hofmann 1986; Getz et al. 1986), these distances represent transfer into nearby groups. Similarly, Jacquot and Solomon (2004) found that prairie voles transferring into a group moved from nearby groups more often than expected by chance. Transfers between nearby groups have been reported for other mammals, including woodland voles (FitzGerald and Madison 1983) and Eurasian badgers (*Meles meles*—Macdonald et al. 2008), and transfers between groups with overlapping ranges have been reported for dwarf mongooses (*Helogale parvula*—Rood 1987) and horses (*Equus caballus*—Linklater and Cameron 2009). Limiting distance is hypothesized to minimize dispersal costs (Linklater and Cameron 2009). Finally, we found no relationship between the distances moved during direct transfer and either season or population density.

In some species, loss or experimental removal of residents leads to increased immigration. Intergroup transfer in woodland voles occurred exclusively when voles of the immigrant's sex were absent from the group due to death, disappearance, or group fission (FitzGerald and Madison 1983). Large-scale experimental removal of resident small mammals from a site can result in increased immigration into the site (see papers cited in Brandt 1992). Similarly, targeted experimental removals of particular individuals from social groups can increase immigration into those groups. Jacquot and Solomon (2004) found that experimental removal of all adults from groups of prairie voles in field enclosures stimulated rapid arrival of new adult females, and that more females moved into these groups than into intact groups (movement of females into groups at which all adult females had been removed was intermediate but did not differ from intact groups). In contrast, we found that disappearance of 1 or more adult residents from an established group was not a necessary prerequisite for joining by other adults. Most individuals (87%) joined groups that had not experienced loss of adult residents the previous week. The difference between our findings and those of Jacquot and Solomon (2004) might reflect different degrees of vacancies; whereas we considered the disappearance of 1 or more adult residents (i.e., most of our social groups still had adult residents present), Jacquot and Solomon (2004) found effects when they removed all adult residents.

Males were more likely than females to directly transfer into groups that contained at least 1 potential mate and lacked potential competitors for mates. Thus, males switched groups in a manner consistent with maximizing reproductive opportunities, a pattern reported in many mammals (Clarke and Glander 2010; Jack and Fedigan 2004; Rood 1983; Solomon et al. 1998) and consistent with our hypothesis. Our hypothesis does not, however, explain patterns of direct transfer for females. In particular, about 25% of females directly transferred into a group that did not contain a potential mate and 96% directly transferred into a group that contained at least 1 potential competitor for mates. Jacquot and Solomon (2004) also found that presence of a potential mate was not critical in determining movements into groups by female prairie voles. We suggest that directly transferring female prairie voles are less constrained by group composition because wandering males are common. Wandering males frequently visit nests of social groups, especially groups without resident males (Getz et al. 1993; McGuire and Getz 1998), and some fertilize females in enclosures (Ophir et al. 2008). Thus, a female that directly transfers into an all-female group can produce offspring by mating with wandering males. The rarity of single male residents and all-male communal groups in our population (Getz et al. 1993; McGuire et al. 2002) likely explains why most females transferred into groups with at least 1 adult female resident. Additionally, of those females that directly transferred into a group with more adult females than the group they had left, about half had been living alone. For these females, potential benefits of group living may outweigh costs of competition with resident females. Finally, most transferers moved into nearby groups, so resident females may have been familiar with directly transferring females and more readily accepted them.

Conclusions.—The results of this study advance our knowledge of mammalian social dynamics in several areas. By using the largest data set yet reported to analyze patterns of intergroup transfer of any species of *Microtus*, we confirmed and extended some previously reported patterns, and detected differences in joining behavior of males and females. Our study revealed that joining a group is not contingent upon recent disappearance of adult residents, a finding that suggests more flexibility and complexity in the interactions between residents and immigrants than previously reported. There is a need for studies of social behavior of free-living prairie voles that include detailed analyses of relatedness of residents and immigrants to examine the role of genetic relatedness in social group dynamics.

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