Behavioral and spatial analysis of extraterritorial movements in red foxes (*Vulpes vulpes*)

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Movements away from the natal or home territory are important to many ecological processes, including gene flow, population regulation, and disease epidemiology, yet quantitative data on these behaviors are lacking. Red foxes exhibit 2 periods of extraterritorial movements: when an individual disperses and when males search neighboring territories for extrapair copulations during the breeding season. Using radiotracking data collected at 5-min interfix intervals, we compared movement parameters, including distance moved, speed of movement, and turning angles, of dispersal and reproductive movements to those made during normal territorial movements; the instantaneous separation distances of dispersing and extraterritorial movements to the movements of resident adults; and the frequency of locations of 95%, 60%, and 30% harmonic mean isopleths of adult fox home territories to randomly generated fox movements. Foxes making reproductive movements traveled farther than when undertaking other types of movement, and dispersal movements were straighter. Reproductive and dispersal movements were faster than territorial movements and also differed in intensity of search and thoroughness. Foxes making dispersal movements avoided direct contact with territorial adults and moved through peripheral areas of territories. The converse was true for reproductive movements. Although similar in some basic characteristics, dispersal and reproductive movements are fundamentally different both behaviorally and spatially and are likely to have different ultimate purposes and contrasting effects on spatial processes such as disease transmission.

Key words: animal movement, contact rates, disease transmission, DRAP, gene flow

Animal movement is an essential mechanism underlying ecological processes at many organizational levels (Nams 2006; Nathan 2008), yet at the individual level we know little about variation in movement behaviors and their ecological and evolutionary causes (Doerr and Doerr 2005). Animal movement is constrained by 3 factors: internal factors, such as physiological need, age, or reproductive status; external factors determining availability of resources or perceived risks, or both; and the skills of the individual, including locomotor skills (Bell 1991). A variety of theoretical models has simulated animal movements in search of resources (Turchin 1991; Westcott and Graham 2000), including breeding opportunities, but these are frequently based on multiple assumptions because empirical data are absent (Ruckelshaus et al. 1997) and do not incorporate individual variability into these processes. Models examining dispersal have analyzed the influence of landscape features but have not considered the socio-spatial context of these movements (Kareiva and Shigesada 1983; With 1994). Thus, a critical need exists for empirical data to refine individual and population models and test the ultimate causes and purposes of different movements (Macdonald and Johnson 2001; Wiens 2001).

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In particular, empirical data on extraterritorial movements in search of breeding opportunities or vacant territories are scarce. Extraterritorial movements occur away from the normal (hereafter home) territory and are influenced by constraints and pressures that normally would not affect movements within resident territories. These can include moving through unfamiliar terrain with a reduced ability to detect predators or competitors, or possibly seeking contact with other individuals, for example, for breeding opportunities. As a consequence, extraterritorial movements can be seen as a mixture of competing influences that could have contrasting effects on movement patterns, such as by altering speed of travel or turning angles (Zollner and Lima 2005).

Exploratory or dispersal movements (hereafter dispersal movements) are a fundamental component in the life history of many birds and mammals (Dique et al. 2003; Doerr and Doerr 2005; Gaines and McClenaghan 1980; Van Ballenberghe 1983; Vangen et al. 2001). They occur predominantly when juveniles leave the territory where they were born and search for a vacant territory where they might breed later. In addition, some individuals make temporary forays away from the home territory in search of breeding opportunities (hereafter reproductive movements—Young et al. 2005, 2007).

Despite dispersal and reproductive movements being important movement processes, no data examine key behavioral differences in speed, turning angle, distance, or how these movements are oriented temporally or spatially. Both of these forms of extraterritorial movement have profound implications for the ecology of populations. Dispersal movements can alter gene flow and population structure and regulate population numbers (Bohonak 1999; Pulliam 1988). Reproductive movements have an important role in gene flow and can be an important mechanism to avoid inbreeding (Sillero-Zubiri et al. 1996; Winters and Waser 2003). A clear delineation of these behaviors, therefore, can be used to improve a variety of spatially explicit models, especially those concerning gene flow, the spread of invasive species, and disease epidemiology (White et al. 1995).

Red foxes (*Vulpes vulpes*) live in groups of 2–10 adults that typically defend exclusive territories (Baker and Harris 2004; Baker et al. 1998). In an urban population in Bristol, United Kingdom, previous work using movement models has shown the importance of intragroup encounters as a mechanism for social cohesion and the limited importance of intergroup encounters in territory defense (Harris and White 1992; White and Harris 1994). Although spatial organization and social behavior of red foxes in urban environments can differ from those in exurban populations (Soulsbury et al. 2010), patterns of extraterritorial movements appear similar. Red foxes can carry out 3 types of extraterritorial movement. Subadults and, to a lesser degree, adults undertake dispersal movements in search of new territories in both urban populations (Harris and Trewhella 1988; Kolb 1984; Woollard and Harris 1990) and exurban populations (Mulder 1985; Storm et al. 1976). Adult males make reproductive movements outside their home territory in search of extrapair mating opportunities in both urban populations (Iossa et al. 2008; White et al. 1996) and exurban populations (Cavallini 1996, 1998). More rarely, some males and females occasionally make extraterritorial movements to access food resources (Tsukada 1997), although this is not seen in all populations. To improve our understanding of the behavioral context for these extraterritorial movements we analyzed fine-scale individual movements within single nights by comparing distance moved, speed of travel, distribution of turning angles, and other parameters of search behavior between dispersal and reproductive movements and, additionally, movements within territories by resident adult foxes to act as a control. We also investigated interaction rates with other territory holders within the population, using a correlated random-walk model to compare the distances between locations of foxes during movements and locations of resident adults, and whether certain areas of fox territories during dispersal and reproductive movements were avoided. Finally, we examined temporal differences in the timing of extraterritorial movements, as indicators of their ultimate purposes, and the number of territories contacted during forays.

MATERIALS AND METHODS

Study site and study animals.—The study was conducted in the northwestern area of the city of Bristol, United Kingdom, between 1977 and 2004 (Baker et al. 1998; Soulsbury et al. 2007; White and Harris 1994). Foxes were captured by netting from den sites or in baited box traps placed in residential gardens (Baker et al. 2001). Animal capture and handling were consistent with guidelines of the American Society of Mammalogists (Gannon et al. 2007). All animals captured were manually restrained and weighed, sexed, aged by incisor wear (Harris 1978), and ear-tagged (Rototags, Dalton Supplies Ltd., Nettlebed, Henley-on Thames, Oxfordshire, United Kingdom). No adverse effects on survival or fecundity were observed from any handling procedures; capture and handling procedures were approved by the University of Bristol ethical review committee.

Throughout this paper we assume that all animals were born on 1 April. Based on month of capture, cubs were 0–6 months old, subadults 6–12 months old, and adults >12 months old. Seasons were defined as: spring, March–May; summer, June–August; autumn, September–November; and winter, December–February. Analyses of dispersal movements were based only on subadults for which the home territory was known. We specifically examined exploratory and permanent movements away from the home territory or temporary home range by animals that eventually left their home territory permanently. Temporary ranges were small, peripheral to adult territories, and occupied for short time periods (<1 season). Dispersing individuals were classified as settled if they used an exclusive area for >2 consecutive seasons. Adults were considered resident if located within the same area for >2 consecutive seasons. Reproductive movements were defined

as movements made by males during winter off their resident territory, to which they subsequently returned; in this part of the study all animals were adults and returned from reproductive movements on the same night.

Radiotracking methods.—Full-grown individuals (full grown ≥6 months of age—Soulsbury et al. 2008a) were fitted with commercial transmitters (Biotrack Ltd., Wareham, Dorset, United Kingdom) or transmitters manufactured at the University of Bristol; collars weighed 1.6–2.5% of body mass. Collars were not removed at the end of this study because other research was ongoing. Each fox was tracked on foot by a single person using a 3-element, handheld Yagi antenna and CE12 receiver (Custom Electronics of Urbana Inc., Nokomis, Florida). Because description of fine-scale movements requires a high degree of accuracy and short interlocation intervals (Doerr and Doerr 2005), animals were tracked between 2000 and 0400 h Greenwich Mean Time, with locations and activity recorded every 5 min. Locations (hereafter fixes) were recorded as 25×25-m grid cells determined using 1:1250 scale Ordnance Survey maps. Activity (active or inactive) was determined from fluctuations in signal amplitude. Most fixes were taken from a distance of <50 m, and locational data easily could be related to specific gardens by taking bearings from nearby roads. By this means individual fixes could be ascribed reliably to a particular garden, or if the fox was in an open area, its position could be confirmed visually. The high density of roads on the study area, combined with the majority of gardens being <625 m^2 (often much less), meant that fixes were both quicker to obtain and far more accurate than is possible in other types of environment. A maximum of 2 foxes on 1 territory was tracked in a single night (by different people) to minimize disruption of behaviors, and we saw no evidence of disturbance of natural behaviors.

Territories were delineated using 95% harmonic means (Dixon and Chapman 1980); all adult foxes were radiotracked until an asymptotic territory could be calculated (Harris et al. 1990). Asymptotic size was reached at 200–250 active fixes. Mean number of fixes ($\pm$ *SE*) obtained each night was 77.0 $\pm$ 1.6, and each fox was radiotracked for 4–6 nights to obtain sufficient active fixes. We calculated areas of high use within territories (core areas) using 60% and 30% harmonic mean isopleths (Woollard and Harris 1990). Dispersing foxes do not exhibit an asymptotic territory or range size (Harris et al. 1990). All dispersing foxes were radiotracked until they either settled on a territory in which they were resident for >2 seasons or died before settling. Territories were visualized using TRACKER (Camponotus AB, Radio Location Systems AB, Huddinge, Sweden).

Movement parameters.—We compared mean ($\pm$ *SE*) distance moved per night, speed of travel, and turning angles for all individuals making extraterritorial movements to movements of adult foxes made within their home territory in autumn (hereafter territorial movements). Movements of foxes in autumn were selected as those most representative of territorial movements because adults engage in cub-rearing

during spring and summer, and during winter males undertake reproductive movements (White et al. 1996) and spend time consorting with receptive females. We classified movements into 2 categories, dispersal and reproductive. Dispersal movements were those made away from a home territory or temporary home range by individuals that later dispersed. Temporary home ranges were small ranges used by dispersers at the periphery of adult territories, usually for a limited time period before being abandoned. Reproductive movements were 2-way movements made by individuals that did not change the location of their territory. For both dispersal and reproductive movements we could not categorically exclude movements made by individuals for the purpose of foraging, but given the behaviors exhibited and the temporal timing of movements, it was unlikely that any movements were for the purpose of foraging. Females composed a small component of our extraterritorial movement data set ($n = 9$ males for reproductive movements, and $n = 7$ males and 2 females for dispersal movements), so sex differences were not considered in our analysis and we used only males for territorial movements (9 males) for comparison. Distance moved per night and speed of travel were analyzed using linear mixed effect models (nlme package—Pinheiro et al. 2008) run in R (http://www.r-project.org). This allowed the inclusion of all nights of data, with individual fox as a random grouping variable. Post hoc tests were carried out using the multcomp package (Hothorn et al. 2008).

Distance moved per night was calculated as the sum of straight-line distances between successive 5-min locations. Mean speed of travel (km/h) was calculated using the average distance moved between consecutive active fixes. Bearings were calculated as the relative bearing (on a scale of $-180°$ to $+180°$) of each consecutive fix taken from the previous one, where the direction of each previous movement is $0°$ (White and Harris 1994). We excluded all inactive fixes and consecutive fixes that did not change location. However, because this method generally gives mean bearings close to $0°$ (Baker et al. 2007), we compensated for this by positively transforming all bearings to give a possible range $0–180°$. Bearings were pooled from all nights and individuals into the 3 movement categories. Each bearing was treated as an individual observation although by the nature of movements they are autocorrelated. We compared bearings using a Watson and Williams 3-sample test (F) with $\alpha = 0.05$. Where significant differences occurred, Watson and Williams 2-sample tests between groupings were carried out with α adjusted for multiple testing (Zar 1999).

We analyzed 5 further components of movement using the dispersal range analysis program (DRAP—Doerr and Doerr 2005). These were search area (the area directly encountered, including the assessment corridor of the movement path; see below); linearity (the straight-line distance divided by the total distance of the movement); thoroughness (area assessed directly divided by the total minimum convex polygon area of all fixes for that movement); intensity of search (the mean number of times a location in the assessment corridor was

sampled by the fox); and whether the search was concentrated in 1 area (the *SD* of the intensity of search divided by the mean—Bell 1991; Doerr and Doerr 2005). We analyzed each movement singly, with the assessment corridor set to 25-m width, corresponding with the accuracy of the fixes (White and Harris 1994). DRAP analyses were analyzed using linear mixed-effects models with post hoc tests using the methodology already described.

Intraspecific interactions and movement parameters.—Animal movement is best described as a time series of movement steps (Turchin 1998). Each step is characterized by a bearing and a distance between 2 distinct points in time, which in turn determine a speed value. The distributions of the bearings and distances in a series of steps will determine the type of movement of the animal, from a straight line to a Brownian (random) motion. This principle can be used to generate artificial movements of known characteristics by randomly selecting consecutive bearings and distance values from distributions of real data (Fauchald and Tveraa 2003; Tremblay et al. 2007). To examine whether any spatial avoidance or selection occurred for encounters with territorial adults and for parts of neighboring territories by individuals during dispersal and reproductive movements, we compared real and artificial movements in a real matrix of known fox territories. We selected dispersal movements from 2 years (2002 and 2003) and reproductive movements from 3 years (1990, 2002, and 2003); these were the years for which our knowledge of the spatial distribution of fox territories was >80% (1990— 87% of the study site; 2002—81%; 2003—81%). Data from both autumn and winter periods, and from male and female territories, were used to maximize spatial coverage. Extraterritorial movements are uncommon and unpredictable, so it was not possible to track simultaneously individuals making extraterritorial movements and individuals moving around on home territories. Furthermore, the large number of candidate territories (maximum = 12 territories) precluded tracking all possible individuals every available night.

We created artificial fox movements using a correlated random-walk model created in a Visual Basic Macro run in Microsoft Excel (Microsoft Corp., Redmond, Washington). At each movement step distances and turning angles were selected randomly from distances and turning angles generated from the real dispersal and reproductive movement patterns. The number of generated fixes and the start location were matched to each real movement. One night of random data was generated for each night of real data. Dispersal and reproductive movements were examined separately.

To simulate simultaneous tracking between extraterritorial movements and territorial movements a random-number generator was used to select 1 night of real radiotracking for a single fox from each territory. Each extraterritorial movement then was matched temporally to the selected territorial movements within each night. We calculated the distance (m) between the real or simulated extraterritorial fix and the nearest fix of a territorial adult at each time interval. The distances of real and random extraterritorial fixes were

compared using linear mixed-effects models with individual fox included as a factor to examine possible individual-based differences.

To determine which parts of fox territories were intruded on by individuals each territory was split into 2 annuli and 1 central polygon using 95%, 60%, and 30% harmonic mean isopleths to represent areas of different use by the territory holder. Because 95%, 60%, and 30% isopleths of dominant males and females within the same territory overlap extensively (Iossa et al. 2008; Soulsbury 2005), we used data from females if data from the corresponding male were not available. The frequency of intrusions in different parts of each territory then was analyzed using a 1-sample chi-square (χ^2) test with the previously generated simulated data set as the expected value.

Intrusions into adult territories were expressed as coefficients (c) calculated using the formula described in White and Harris (1994):

$$c = (\mathrm{Freq_r} - \mathrm{Freq_s})/\mathrm{Freq_s},$$

where $\mathrm{Freq_r}$ is the frequency of locations in a specific category from the real data and $\mathrm{Freq_s}$ is the frequency of locations in the same category from simulated data. A positive value indicates a higher frequency of separation distances or movements in each annulus and polygon when comparing real and simulated data. Data are presented for each area of the home range.

Last, we counted the total number of territories each dispersal and reproductive movement contacted and compared them using a Mann–Whitney (W) test in Minitab version 14.0 (Minitab, Inc., State College, Pennsylvania). Contact was assigned if the movement entered any part of a territory.

Timing of extraterritorial movements.—To examine the temporal distribution of extraterritorial movements the percentage of extraterritorial movements recorded in each month was calculated for male and female dispersal movements and for reproductive movements (*n* extraterritorial movements in month/total *n* extraterritorial movements × 100). In addition, the frequency of extraterritorial movements in each month in relation to the overall number of nights tracked was calculated to allow comparability with other populations. To increase sample sizes we included additional records of timings of movements made by individuals for which we had incomplete data and that were not used in the previous analyses.

RESULTS

Distances, speeds, and angles moved.—Distance moved per night differed significantly between movement types (Table 1), with dispersal movements and territorial movements being significantly shorter than reproductive movements but not different from one another. Mean nightly speed of travel also was significantly different between movement types (Table 1); both dispersal and reproductive movements were significantly faster than territorial movements but not significantly different from one another.

TABLE 1.—Mean individual ($\pm$ *SE*) distance moved, speed of travel, area searched, thoroughness, linearity, intensity of search, and concentrated search using program DRAP (Doerr and Doerr 2005) for red foxes (*Vulpes vulpes*) making dispersal ($n = 9$ individuals, 23 movements), reproductive ($n = 9$ individuals, 14 movements), and territorial ($n = 9$ individuals, 45 movements) movements. Statistics are for linear mixed-effects models. Different letters in parentheses indicate significant differences ($P < 0.05$) between groupings for a single parameter.

Parameter	Dispersal movements	Reproductive movements	Territorial movements	F	d.f.	P
Distance moved (km)	4.84 ± 0.52 (a)	8.57 ± 0.78 (b)	5.01 ± 0.58 (a)	7.07	2, 58	0.002
Speed of travel (km/h)	1.20 ± 0.08 (a)	1.44 ± 0.14 (a)	0.81 ± 0.06 (b)	33.69	2, 58	< 0.001
Area searched (ha)	12.17 ± 1.04 (ab)	15.01 ± 1.95 (a)	9.29 ± 1.30 (b)	10.97	2, 58	< 0.001
Thoroughness (%)	12.51 ± 2.78 (a)	23.30 ± 3.92 (b)	30.95 ± 3.53 (b)	18.11	2, 58	< 0.001
Linearity	0.25 ± 0.05 (a)	0.11 ± 0.05 (b)	0.11 ± 0.02 (b)	3.18	2, 58	0.049
Intensity of search	1.41 ± 0.09 (a)	1.49 ± 0.05 (a)	1.81 ± 0.08 (b)	9.39	2, 58	< 0.001
Concentrated search (%)	48.95 ± 3.29 (a)	51.09 ± 2.83 (a)	62.90 ± 3.31 (b)	7.17	2, 58	0.002

The bearings of individual movements differed significantly between movement types ($F_{2,3,918} = 110.37$, $P < 0.001$), with dispersal movements (mean angle = 45.2°, variance = 20.2°) being significantly straighter than reproductive movements (66.2°, variance = 19.0°; $F_{1,1,517} = 58.50$, $P < 0.001$) and territorial movements (65.6°, variance = 18.8°; $F_{1,3,168} = 109.47$, $P < 0.001$); reproductive movements were not significantly different from territorial movements ($F_{1,3,151} = 3.83$, $0.10 > P > 0.05$).

The total area searched directly (ha) was not significantly different between movement types, although the thoroughness of search was (Table 1). Foxes making dispersal movements searched less thoroughly than those making reproductive and territorial movements; however, we found no significant difference between reproductive and territorial movements. Movements differed in their degree of linearity (Table 1); dispersal movements were significantly straighter than reproductive and territorial movements, but reproductive and territorial movements did not differ in their linearity. Search intensity differed significantly between movements (Table 1), with foxes during dispersal and reproductive movements searching an area less intensively than during territorial movements. Dispersal and reproductive movements did not differ in search intensity. Dispersal and extraterritorial movements showed similar low levels of concentrated search compared to territorial movements (Table 1).

Spatial patterns of extraterritorial movements.—Dispersal movements were significantly farther away from movements made by resident adults than expected at random (+85.6 $\pm$ 18.2 m; $F_{1,253} = 22.06$, $P < 0.001$). Similar to differences in separation distances, dispersal movements were significantly oriented away from core areas of territories more significantly than expected by chance (Table 2; Figs. 1a and 2a).

In contrast, reproductive movements were significantly closer (-42.4 ± 12.4 m) to neighboring adults than expected by chance ($F_{1,458} = 11.64$, $P < 0.001$). Reproductive movements showed significantly higher rates of intrusion into adult core areas than expected by chance (Table 2; Figs. 1b and 2b). Reproductive movements were found more often in core areas than were dispersal movements ($\chi^2_2 = 71.64$, $P < 0.001$).

Significant differences were found between individuals for both dispersal ($F_{2,251} = 15.67$, $P < 0.001$) and reproductive

($F_{1,457} = 304.08$, $P < 0.001$) movements. However, this might have been predicted because average territory size differed between years in which individuals were tracked, and this ultimately will affect the likelihood of individuals encountering conspecifics. For reproductive movements, separation distances were smaller when territory size was small (mean territory size: 24 ha, separation distance: 219.1 $\pm$ 7.6 m; territory size: 63 ha, separation distance: 532.1 $\pm$ 18.8 m). Similarly, mean separation differences of dispersal movements were slightly smaller in the year when territory size was smaller (2002: territory size: 63 ha, separation distance: 491.3 $\pm$ 14.1 m; 2003: territory size 58 ha, separation distance: 374.2 $\pm$ 31.2 m).

The median total number of home territories contacted per dispersal movement (3.0, interquartile [IQR] range: 2.3–3.8) was significantly higher than the number contacted by reproductive movements (2.0, IQR 1.3–2.0; $W = 91.0$, $n_1 = 8$ reproductive movements, $n_2 = 7$ dispersal movements, $P = 0.01$).

Timing and frequency of movements.—Male dispersal movements ($n = 25$ movements, 8 individuals) occurred mainly during October–December, with a peak in November. In contrast, female dispersal movements ($n = 7$ movements, 4 individuals) showed a peak in January (Fig. 3). Male reproductive movements ($n = 14$ movements, 9 individuals) occurred mainly in January and February (Fig. 3), with 10 of 14 movements occurring during the 2nd half of January.

TABLE 2.—Frequency of intrusions of red foxes (*Vulpes vulpes*) into different regions of other individuals' home territories by real and simulated dispersal ($n = 7$ movements) and reproductive movements ($n = 8$ movements).

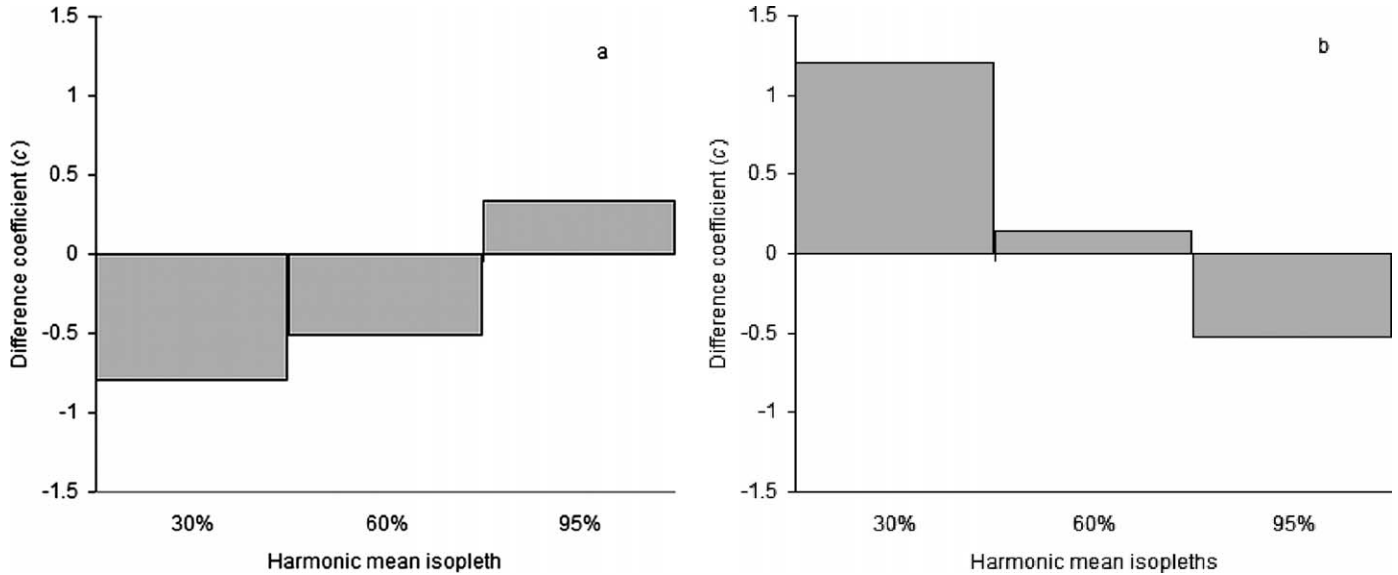|	Harmonic mean isopleth				
	30%	60%	95%	Total χ^2_1	P
Dispersal movements (♂ and ♀)					
Real data	11	22	172		
Simulated data	52	45	129		
Partial χ^2	32.33	11.76	14.33	58.42	< 0.001
Reproductive movements (♂)					
Real data	44	87	101		
Simulated data	20	76	119		
Partial χ^2	28.80	1.59	64.22	94.61	< 0.001

Fɪɢ. 1.—Differences between frequencies of real versus random movements of red foxes (*Vulpes vulpes*) for a) dispersal and b) reproductive movements within 95%, 60%, and 30% harmonic mean isopleths of adults. Differences are expressed as the coefficient, *c* (for details, see text). A positive difference indicates a higher frequency than expected and a negative difference a lower frequency than expected.

Overall, male dispersal movements were recorded on 10.5% of all tracked nights (*n* = 238), with the highest rate of 21.4% of all tracked nights in November. Female dispersal movements were recorded on 9.1% of all tracked nights (*n* = 77), with the highest rate of 21.7% of tracked nights in January. Male reproductive movements were recorded on 8.8% of all tracked nights (*n* = 160), with the highest rate of 19.6% of tracked nights in January.

DISCUSSION

The behaviors exhibited by a dispersing animal should be strongly influenced by the environment in which it travels and

its ultimate purposes (Bowler and Benton 2005). Dispersal movements familiarize an individual with an area by allowing it to gather information on neighboring animals, thereby increasing the likelihood of finding a vacant territory or breeding opportunity, or both (Haughland and Larsen 2004; Holekamp 1986). One way of increasing the likelihood of finding a vacancy is to increase the area searched. However, the area directly searched by dispersing foxes in this study was found to be no greater than either reproductive or territorial movements, and the thoroughness of search was found to be low, as in dispersing wolves (*Canis lupus*—Bascompte and Vilà 1997). Although the area searched directly was low, the spatial configuration of dispersal movements showed that they
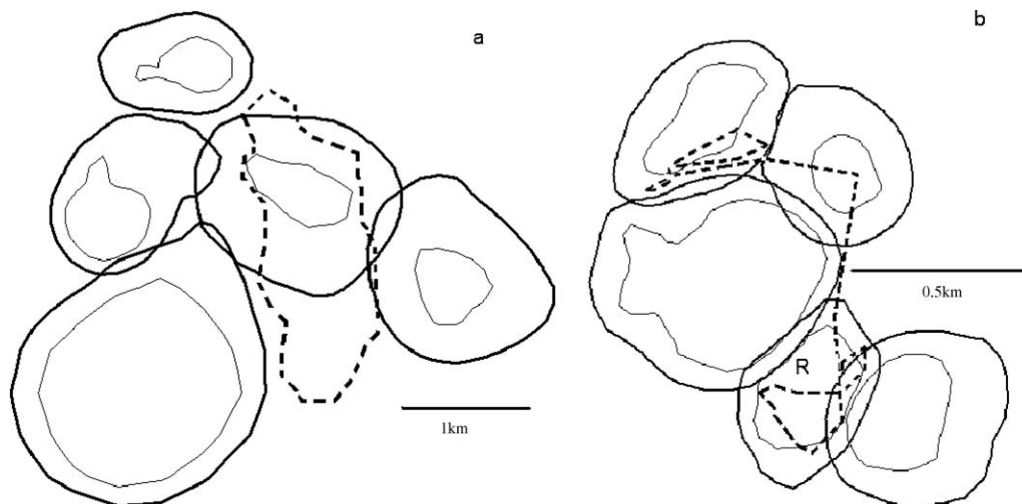

Fɪɢ. 2.—Examples of a) a single exploratory movement of a dispersing red fox (*Vulpes vulpes*) from a temporary range (start and end point marked by a diamond), and b) a male reproductive movement (both denoted by dashed lines) in a matrix of resident home territories denoted by 95% (thick line) and 60% (thin line) harmonic mean isopleths. The home territory of the male making the reproductive movement is indicated with **R**. For clarity, the spatial coverage of all resident home territories is not shown.
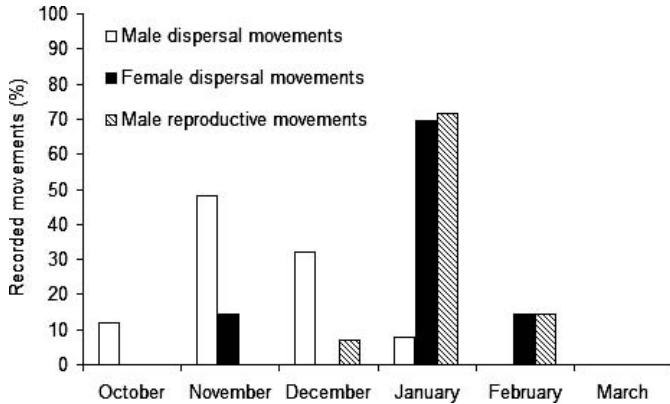
Fig. 3.—The percentage of all recorded male (*n* = 25 movements, 8 individuals) and female (*n* = 7 movements, 4 individuals) dispersal and reproductive movements (*n* = 14 movements, 9 individuals) of red foxes (*Vulpes vulpes*) detected at monthly intervals during October to March.

contacted a greater number of territories than did reproductive movements and therefore had the potential to acquire information about a greater number of territories than did reproductive movements. Additionally, the use of olfactory or vocal communication by territory holders could have conveyed information about vacancies, thereby reducing the necessity to search an area directly.

Dispersal movements often are noted as being faster and straighter than other types of movements (del Mar Delgado et al. 2009). Low speeds can increase the ability to detect predators or competitors (Zollner and Lima 2005); however, reduced speed might increase certain forms of risk by increasing the time spent on conspecific territories, so faster, straighter movements might be the best method for traversing resident territories, as we found. Furthermore, theoretical models show that straight or nearly straight search strategies are more effective than random movements at finding vacant territories (Zollner and Lima 1999). Consequently, straighter movements are favored by dispersing individuals (Bascompte and Vilà 1997; Storm et al. 1976).

Dispersal movements clearly were oriented away from adult core areas, something that has been suggested for foxes (Macdonald 1980; Meia and Weber 1996) but never tested quantitatively. The separation distance between dispersing foxes and territorial adults was greater than expected at random, and the costs of encounters with adults through mortality (Harris and Smith 1987) or increased injuries (Soulsbury et al. 2008b) could be sufficient to maintain this avoidance behavior. However, the analysis also indicated that the spatial pattern of our population, particularly the average territory size, will alter the likelihood of encounters. As a consequence, the degree to which dispersers avoid encounters may be density-dependent. Dispersers probably can orient away from core areas using resident scent marks, because areas used more frequently have higher rates of scent marking (Frafjord 2004). Avoidance of interactions with residents appears to be a key dispersal tactic. Studies on other species also report dispersing or transient

individuals avoiding core areas, thereby reducing the risk of direct interactions with residents (Kamler and Gipson 2000; Loveridge and Macdonald 2001).

Males made the majority of dispersal movements in November, whereas females made most dispersal movements in January, something observed in other urban and rural fox populations (Hough 1980; Lloyd 1980; Phillips et al. 1972; Woollard and Harris 1990). Adult female mortality peaks during January and February (Harris and Smith 1987), so dispersing females might make dispersal movements to locate newly vacant breeding opportunities. Most female dispersal distances are short and often into neighboring groups (Iossa et al. 2009; Trewhella et al. 1988), suggesting that females could be making these movements to assess opportunistic vacancies in the local area. In contrast, the peak of male dispersal movements does not coincide with peak adult male mortality in January and February (Harris and Smith 1987). Intragroup aggression increases toward the end of October (Ahola and Mononen 2002) and can trigger more subordinate or disassociated littermates to leave the natal territory (Harris and Trewhella 1988; Harris and White 1992). Thus, it would appear that sexual differences in the causes of dispersal exist, with male dispersal in November being forced but female dispersal in January being opportunistic.

Males of many avian and mammalian species trespass on neighboring territories during the breeding season to try to acquire extrapair matings (Christian 1995; Iossa et al. 2008; Naguib et al. 2001; White et al. 2000), but in red foxes reproductive movements were very different from dispersal movements. They were as fast as dispersal movements and longer, but they did not show any trend toward linearity. Male foxes on reproductive movements searched a smaller area more thoroughly. Territorial movements of adults showed a more intense search and concentration of movements, which is consistent with animals foraging in patchy environments (Bell 1991; Fauchald and Tveraa 2006; Mellgren and Roper 1986). The lack of any concentration of movements suggests that males do not forage during reproductive movements; males making reproductive movements lose more body fat than males that do not (Cavallini 1998). Increasing speed and distance moved appear to be common strategies for males during the reproductive period (Arthur and Krohn 1991; Jędrzejewski et al. 2002; Schmidt et al. 2003), and this might increase encounter rates with receptive females.

Rather than showing avoidance, reproductive movements of adult males tended to select for neighboring core areas and were found closer to neighboring adults than by chance. Many studies have observed that reproductive movements are energetically costly (Cavallini 1998; Young et al. 2005) and so are generally carried out only by larger males (Cavallini 1998; Iossa et al. 2008). Prior interaction between neighbors can allow the establishment of a dominance hierarchy between territories (Barash 1974) so that intruding males preferentially can select territories with weaker territory holders. Because a dominance hierarchy can occur only through direct interactions, this limits possible knowledge of dominance to the

surrounding neighboring males. In accordance with this hypothesis, the trespassing males traveled approximately 1 territory from the boundary of their home territory (Iossa et al. 2008) and contacted a low number of territories during reproductive movements. If males preferentially intrude into territories of smaller males, they should show no avoidance of core areas. Instead, they should positively select these areas because dominant male and female core areas overlap considerably, and this may increase the likelihood of encountering an estrous female, which is consistent with our findings.

Reproductive movements appear to be driven by 1 principal factor, maximizing reproductive fitness. This is achieved by increasing encounter rates with estrous females and thus the chances of fertilizing a female. Consistent with this hypothesis, reproductive movements occurred mainly in late January, the period when most females are in estrus (Lloyd and Englund 1973). Similarly, extraterritorial movements of male meerkats (*Suricata suricatta*) coincide with the period of peak female fertility (Young et al. 2007).

In conclusion, dispersal and reproductive movements differ significantly from territorial movements. Although both occur away from the home territory, they differ behaviorally and spatially. We have shown that dispersers use behaviors that reduce the likelihood of encounters with resident adults and maximize the chances of finding a vacant territory by contacting multiple territories. In contrast, reproductive movements occur in neighboring territories, and males search an area thoroughly during the peak period of female fertility to maximize the likelihood of an encounter with an estrous female.

These results have important implications for modeling animal movements. They indicate that incorporating fine-scale individual movements will allow better prediction of animal search models and, in turn, improve understanding of how species disperse across landscapes and how gene flow can occur within and between populations. In addition, we have shown that contact probabilities differ between dispersal and reproductive movements. For foxes, dispersal movements likely play little role in the spread of diseases at a local level, although they can transport infections over wider areas, whereas reproductive movements appear most important for spread among neighboring groups (Vos 2003; White et al. 1995).

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