Parentage analysis detects cryptic precapture dispersal in a philopatric rodent

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Abstract
Locating birthplaces using genetic parentage determination can increase the precision and accuracy with which animal dispersal patterns are established. We re-analyse patterns of movement away from the birthplace as a function of time, sex and population density for a sample of 311 banner-tailed kangaroo rats, *Dipodomys spectabilis*. We located birth sites using a combination of likelihood-based parentage analysis with live-trapping of mothers during the breeding season. The results demonstrate that natal-breeding site distances are density dependent in this species; in particular, both sexes emigrate earlier in the year, and females disperse farther than males, at low population densities. Banner-tailed kangaroo rats were chosen as a study system because live-trapping easily detects maternal and offspring locations; nevertheless, parentage analysis reveals that some offspring evade early detection and move substantial distances before their first capture. In a few cases, the approach even detects dispersal out of the natal ‘deme’ prior to first capture. Parentage analysis confirms the extreme philopatry of both sexes but indicates that prior estimates of median dispersal distance were too low. For *D. spectabilis*, more accurate location of individual birthplaces clarifies patterns of sex bias and density dependence in dispersal, and may resolve apparent discrepancies between direct and indirect estimates of dispersal distance. For species in which mothers can be more reliably trapped than juveniles, using offspring genotypes to locate parents is a novel way that genetic techniques can contribute to the analysis of animal dispersal.

Keywords: density dependence, dispersal, kangaroo rats, parentage assignment, philopatry, sex bias

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Introduction
Dispersal distances are commonly of interest to those studying natural populations. The availability of hypervariable markers has produced an explosion of new techniques for inferring dispersal rates and distances. These molecular tools are powerful enough to detect isolation by distance and estimate average dispersal distances using FST-based approaches even at the level of individuals (Rousset 1997, 2000). Assignment tests allow detection of contemporary dispersal among populations (Cornuet et al. 1999; Pritchard et al. 2000; Wilson & Rannala 2003; Paetkau et al. 2004), while sex bias in dispersal can be detected with both FST and assignment approaches (Goudet et al. 2002; Vitalis 2002). Many of these methods allow inference regarding both contemporary animal movements and gene migration rates; coalescence-based approaches (Beerli & Felsenstein 2001; Beerli 2004) further allow inferences regarding historical migration rates.

Measurements of dispersal distance will be inaccurate when juveniles leave their birthplace before they can be captured and individually recognized. Many studies of dispersal mention this problem (e.g. Ribble 1992; Gillis & Krebs 1999; Sumner et al. 2001). Here we discuss the use of parentage analysis to identify the mother of the juvenile. Where mothers are easily observed during the breeding season or tightly attached to particular locations, this approach has the obvious benefit of locating the juvenile’s probable birthplace and thus determining the true distance moved by the juvenile between birth and breeding.

Accurate location of individual birthplaces has an additional benefit: it allows the investigator to distinguish individuals that never leave home from those that emigrate.
but settle nearby. It is increasingly recognized that the probability of emigration from the natal site and the distance moved before settlement by emigrants may respond in different ways to factors like population density. Clearly separating the two might resolve some of the difficulty associated with predicting the impact of dispersal on spatial population dynamics (Bowler & Benton 2005; Matthysen 2005).

The possibility of precapture dispersal may also bear on the fact that estimates of dispersal tendencies produced by ‘indirect’ genetic approaches are not always congruent with those from ‘direct’ approaches based on mark–recapture or radio-tracking techniques (e.g. Galbusera et al. 2004; Wilson et al. 2004). Genetic techniques may underestimate rates of individual movement among populations if not all dispersal results in reproduction, but the reverse pattern is also common. For example, Dobson (1994) found that $F_{ST}$-based estimates of gene flow among populations of Columbian ground squirrels, *Spermophilus columbianus*, were far higher than expected from observed rates of movement by individually marked animals. Dobson used allozymes as markers, but the same pattern has been reported using more informative markers in other mammalian populations (e.g. pikas *Ochotona princeps*, minisatellites, Peacock 1997; water voles *Arvicola terrestris*, microsatellites, Telfer et al. 2003). If juveniles move substantial distances from their birthplaces before capture, dispersal distances would be underestimated by ‘direct’ approaches.

Our laboratory chose banner-tailed kangaroo rats (*Dipodomys spectabilis*) as a system for the study of intrapopulation dispersal in the 1980s because of the ease with which individual dens can be located and animals can be captured. These attributes allow us to track the location of individual residences for many individuals throughout their lives, on a scale many times larger than most animals move during their lifetimes (Jones 1987). Small (~125 g) nocturnal residents of desert grassland in the southwestern United States and northwestern Mexico, banner-tailed kangaroo rats den and larder-hoard seeds in large, conspicuous dirt mounds. Each individual is tightly attached to a single ‘primary’ mound, and some also defend one or two immediately adjacent ‘secondary’ mounds (Schroder 1979; Randall 1984).

Jones (1984, 1987) used radio-tracking in combination with saturation live-trapping to show that most juveniles share natal mounds with their mothers until they are 2–3 months of age (weaning occurs at about 1 month) and many for much longer (up to 18 months). When juveniles do leave the natal mound, they often settle in one of their mothers’ secondary mounds. Jones reported that 41% of 195 kangaroo rats that reached maturity at age 1 year did so in their presumed natal mounds. Seventy-nine per cent of these 195 animals dispersed less than 50 m, settling as adults in mounds that are either within or immediately adjacent to the home range their mother originally occupied.

The distribution of natal dispersal distances is approximately geometric; on the study site we describe here, Jones *et al.* (1988) reported a median dispersal distance of only 16.5 m for males and 11 m for females. Jones (1987) and Waser & Elliott (1991) found that male and female dispersal tendencies were extremely similar, an unusual pattern among mammals. Jones also found that philopatry increased in years of high density; when the habitat was ‘saturated’, dispersal distances were lower in both sexes. Female dispersal was more strongly influenced by density than was dispersal by males (Jones 1988; Jones *et al.* 1988).

Recent reports suggesting that ‘direct’ observations can substantially underestimate true dispersal distance in other mammals (e.g. Telfer *et al.* 2003) led us to investigate the disparity between an individual’s first capture location and its probable birthplace in banner-tailed kangaroo rats. Here, we use microsatellite-based parentage determination to detect precapture dispersal and to correct our estimates of natal dispersal distance. Does knowledge of precapture dispersal, even in a species chosen to minimize its magnitude, increase our ability to detect biologically significant dependencies of dispersal on sex and population density? Does it help resolve the small but definite discrepancy (e.g. Rosset 2000) between direct and indirect estimates of dispersal distance in this species?

### Methods

**Field data collection**

*Dipodomys spectabilis* ($N = 663, 564$ of which were first captured as juveniles) were ear-tagged and monitored at three adjacent mound clusters (R1E, R1W, SSW) in southeastern Arizona ($109°15′W, 31°30′N$) from 1990 to 2000. Mound clusters contained 13, 61 and 73 mounds, each separated from its nearest neighbour by a mean of 19 m (range 6–43 m). Mound clusters were separated from each other by several hundred metres of unoccupied habitat. Based on low rates of observed dispersal between them, we have previously referred to these mound clusters as ‘populations’ (e.g. Skvarla *et al.* 2004); but because the degree of genetic linkage among these clusters remains undetermined, we here refer to them as ‘demes’.

Individual locations were recorded during censuses in March (the end of the breeding season) and in May and August, when we captured juveniles that had not emerged from their natal mounds in March. Adult female residences, and those used by offspring during the following March, were determined from trapping locations. Juveniles were distinguished by size and/or lack of reproductive maturity (undescended testes, nipples < 1 mm long). Mounds were ‘owned’ by the adult most frequently captured there (Jones 1984). In some cases, females owned more than one mound; in these cases, the female’s ‘primary’ mound was the one...
at which she was most often captured (Jones 1984). Some females also owned 1–2 secondary mounds; secondary mounds were never more than 30 m from the primary mound.

Between 1990 and 1999, the population density during the July/August censuses fluctuated between 1 and 3 animals/ha, substantially lower than the 4–5 animals/ha during the early 1980s when they were studied by Jones (Waser & Ayers 2003). We therefore refer to densities of 2–3 animals/ha observed during 1994–1998 as ‘medium’ densities, and 1 animal/ha as ‘low’ density (1990–1993 and 1999). The study site and census procedures are described in more detail by Waser & Ayers (2003) and Skvarla et al. (2004).

Genotyping

Upon first capture, we collected a pencil-point-sized snap of the pinna from each individual and stored it in liquid N₂ within a few hours of collection. DNA was obtained using standard phenol–chloroform extraction procedures as described in Winters & Waser (2003).

To supplement the suite of five loci available for D. spectabilis (Davis et al. 2000), we created a genomic library and screened it for novel microsatellite sequences using an enrichment procedure briefly described in Williams & DeWoody (2004). A detailed version of the protocol can be found at www.agriculture.purdue.edu/hrn/html/faculty/DeWoody/DeWoodyweb/pdfs/msatclngprtl.pdf. We sequenced approximately 150 recombinant clones from our enriched genomic library, and over 85% contained microsatellites. Polymerase chain reaction (PCR) primers were designed for 58 unique microsatellite sequences and screened for polymorphism using individuals from our study site. Amplifications for all loci were conducted in 8-µL PCRs consisting of 0.5 µM each primer, 250 µM dNTPs, 1.25x reaction buffer (Promega), and 0.75 U Taq DNA polymerase (Promega). Thermal profiles consisted of an initial denaturation of 94 °C for 2 min followed by 35 cycles of 94 °C for 30 s, a locus-specific annealing temperature (Table 1) for 30 s, and 72 °C for 30 s. A final 5-min extension at 72 °C concluded the thermal profile. As noted during the development of an independent microsatellite library (Davis et al. 2000), an unusually low proportion of microsatellite sequences yielded specific PCR products. We wonder whether this difficulty might be related to the high proportion of satellite DNA in this species (Mazrimas & Hatch 1972; Stock 1974) and the large-scale repeats reported from kangaroo rats more generally (Keim & Lark 1987; Kursar 1988).

From our library, 19 primer pairs successfully yielded PCR products, of which only eight were polymorphic (Table 1). Two of these were not fully characterized because low polymorphism was observed at our study site. Allelic diversity at these six novel loci was moderate, with a mean of 8.2 alleles per locus. As gauged by cervus (Marshall et al. 1998), null alleles occurred at very low frequencies and did not compromise the parentage analyses. Individual genotypes were determined by PCR amplification with the above conditions using a single end-labelled primer for each locus (Table 1), and electrophoresis in a 4.75% polyacrylamide gel with an ABI377. GENESCAN 3.1 and GENOTyper 2.1 software from ABI were used to assign locus-specific genotypes.

Parentage analysis

We assessed parentage using a combination of exclusion and likelihood-based inference. As candidate parents for each juvenile, we started by including all adults whose primary residence was within 100 m of that juvenile’s first capture location, either during the March census of the juvenile’s birth year or the preceding August census. Our inclusion of adults present the preceding August accounts for the possibility that some could have survived long enough to produce offspring early in the breeding season, but then disappeared before the March census. We chose a 100-m cut-off because live-trapping and radiotelemetry data, as well as behavioural observation, suggested that adults spend virtually all their time within a few tens of

**Table 1** Microsatellite primers developed for this study. When possible, we ran duplex PCRs for pairs DS107/109 and DS98/163. DS222 and DS281 were always amplified singly. DS222 is presumably sex-linked because every heterozygous individual in the data set is a female. DS92 and DS108 are known to be polymorphic in our population, but were not fully characterized. Tₐ, annealing temperature; A, number of alleles detected in a sample of several hundred individuals

<table>
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<th>Primer name</th>
<th>Sequence</th>
<th>Tₐ</th>
<th>A</th>
</tr>
</thead>
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<tr>
<td>DS92F</td>
<td>5'-GAGGCTTCTTCTCCAGATCCA-3'</td>
<td>47 °C</td>
<td>&gt;1</td>
</tr>
<tr>
<td>DS92R</td>
<td>5'-GCTTACGGAAACCTGACA-3'</td>
<td>47 °C</td>
<td>&gt;1</td>
</tr>
<tr>
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<td>5'-GCCATCTCCCTCCGATACG-3'</td>
<td>50 °C</td>
<td>9</td>
</tr>
<tr>
<td>DS98R</td>
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<td>50 °C</td>
<td>9</td>
</tr>
<tr>
<td>DS107F</td>
<td>HEX 5'-CATCATCTCATTGTCTCA-3'</td>
<td>47 °C</td>
<td>16</td>
</tr>
<tr>
<td>DS107R</td>
<td>5'-CTGGATATAATGTGAGTCA-3'</td>
<td>47 °C</td>
<td>16</td>
</tr>
<tr>
<td>DS108F</td>
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<td>47 °C</td>
<td>&gt;2</td>
</tr>
<tr>
<td>DS108R</td>
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<td>&gt;2</td>
</tr>
<tr>
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<td>47 °C</td>
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</tr>
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<td>DS109R</td>
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<td>DS163F</td>
<td>HEX 5'-CATCATCTCATTGTCTCA-3'</td>
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<td>DS163R2</td>
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<tr>
<td>DS222F</td>
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<td>DS222R</td>
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<td>7</td>
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<tr>
<td>DS281F</td>
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metres of their primary residence (Winters & Waser 2003). Our first step was exclusionary based on two X-linked loci, DS19 and DS22; for each juvenile, we eliminated all candidates (fathers for juvenile females, mothers for juveniles of both sexes) that were incompatible at both loci. We then used CERVUS (Marshall et al. 1998) to infer parentage based on nine autosomal loci. As recommended by Morrissey & Wilson (2005), we set the error rate for likelihood calculations at 0.001, below the observed genotype error rate of ~0.01. As in Winters & Waser (2003), we started with two analyses (maternity and paternity) assuming that neither parent was known. We then performed two further analyses, maternity with a known father and paternity with a known mother, using the same strict criteria. We accepted a parental candidate only if CERVUS assigned both parents a confidence > 95% and if there was at most one mismatch between the candidate pair and the juvenile (e.g. a mutation, scoring error, or null allele).

If CERVUS did not find parents within 100 m, we repeated the analysis including as candidates all adults with residences < 250 m (approximately the radius of a deme) from the juvenile’s first capture location. If we found no parents within 250 m, we searched using candidate parents within 500 m. In these latter cases, however, we accepted parents only if CERVUS assigned them at > 95% confidence, genotype comparisons were based on eight or more loci, and there were no mismatches. Finally, if we were unable to find both parents, we accepted CERVUS assignments of the mother alone, again using the > 95% confidence criterion.

**Dispersal distances**

In previous analyses, we defined natal-breeding site dispersal distance as the distance between the mound at which a juvenile was first captured, and its residence during the following March census. Here, we refer to these distances as first capture-breeding (FCB) distances (Fig. 1). A better indication of the distance moved by genes from one generation to the next is the distance between the juvenile’s inferred natal mound (the primary residence of its genetically determined mother during the March census of its birth year) and its primary residence during the following March census when it first breeds itself (Jones 1984). We refer to these distances as mother–offspring (MO) distances. Precapture dispersal distances were the distances between the mound at which a juvenile was first captured and its inferred natal mound. Each mound was mapped to an accuracy of ± 1 m using a theodolite. FCB and MO distances were used to look for relationships of dispersal to sex, density, age, and season of year.

**Results**

**Precapture dispersal**

Our CERVUS analyses identified mothers for 306 juveniles; we identified the mothers’ primary residence for 303 of these. One hundred thirty-four of these 303 (47%) were still in their mothers’ primary residence when they were first trapped. On the other hand, 109 juveniles (36%) had already moved more than 30 m, so that they were no longer in either the primary or a secondary mound of their mother. Even within demes, a few juveniles had moved very long distances; 19 (6%) had moved more than 100 m and the maximum precapture dispersal distance was 193 m (Fig. 2).

Precapture dispersal distances increased significantly with age, as indexed by weight at first capture (a regression
of distance on weight was significantly positive, \( t = 4.86, P < 0.001 \). In addition, they differed slightly by sex; median female precapture dispersal distance was 19 m, compared to 10 m for males (\( U_{158,145} = 13223, P = 0.02 \)). Precapture dispersal was equally extensive during low- and medium-density years (13 m vs. 16 m, \( U_{167,136} = 10551, P = 0.27 \)). The sex difference was more prominent in low-density years (during medium-density years, males moved a median of 14 m, and females 16.5 m, \( U_{82,85} = 3791, P = 0.31 \); during low-density years, males moved 0 m, and females 24.5 m, \( U_{60,76} = 2862.5, P = 0.01 \)).

**MO dispersal distances**

Knowledge of the mother’s location indicates that most juveniles breed on or adjacent to their natal home ranges, as previously reported, but that median dispersal distances have been substantially underestimated. One hundred twelve of the 306 known-maternity juveniles survived to breed the following March, and 107 of these did so within their deme of origin. Based on MO distances, 22 offspring (21%) bred in their mother’s primary mound and 50 (47%) bred close enough to be in secondary mounds owned by their mothers (based on FCB distances, the numbers would have been 47% and 76%, respectively). Considering both dispersers and nondispersers, median MO distances were nearly three times as long as FCB distances (35 m vs. 12 m). During this study, females lived on average 26 m from their nearest adult neighbours, indicating that the average kangaroo rat dispersed approximately one nearest-neighbour distance between birth and first breeding.

The distribution of MO distances is density-dependent, with lower maximum dispersal distances and more individuals remaining in their natal mounds in years of greater density (Fig. 3). Similar numbers of male and female juveniles inherited their mothers’ primary residences: 13/55 males (24%) vs. 9/57 females (16%) (\( P = 0.21 \), Fisher test), and this result appeared to be independent of density. However, when juveniles did disperse, median MO distances were longer for females (77.5 m) than for males (40 m, \( U_{41,44} = 1169, P = 0.02 \)). This pattern was particularly clear in years of low density (median MO distance for females that did disperse = 85 m, males = 26 m, \( U_{15,15} = 163.5, P = 0.03 \)).

**Timing of juvenile movements**

The majority of juveniles remain at their mother’s primary residence until they reach a mass of approximately 70 g, corresponding to an age of about 60 days (Fig. 4). Above this age, juvenile departures from the mother’s mound (and to a lesser extent additional movements by juveniles that have already left) produce a rapid increase in median distance moved that asymptotes around the time that juveniles reach 110 g (age ∼160 days). Individual variation is, however, considerable.

Influences of sex and density on the timing of juvenile movements become clearer if we examine distance moved with respect to season rather than age. First examining departures from the natal mound: the percentage of trapped juveniles that were still using their mothers’ primary mound gradually dropped from March (53%) to May (43%) to August (34%). At no point did we detect a significant difference between high- and low-density years (0.29 < \( P < 0.62 \), Fisher tests). However, sex did influence the timing of departures: in May and August, a significantly lower proportion of daughters were still using their mothers’ primary mound (22% of sons, 53% of daughters, \( P < 0.001 \), Fisher test). By August, enough sons had dispersed to erase this difference. The tendency for daughters to leave their mothers’ primary mound earlier than sons was particularly strong in low-density years.

Focusing only on those juveniles that did leave their mothers’ mound, we found that median distances from the mothers’ mounds were similar in March, May and August, suggesting that most juveniles move once, then settle. Median distances moved were longer in low-density years, but never significantly so (0.12 < \( P < 0.96 \), \( U \)-tests). During low-density years, median distances moved by females were significantly greater than those of males in all three censuses (0.02 < \( P < 0.03 \), \( U \)-tests). These results suggest that the sex differences seen in natal-breeding site dispersal distances, reported above, develop shortly after emigration from the natal mound.
Interdeme dispersal

Genetic parentage information also provided information on interdeme dispersal. In our sample of 112 juveniles, five bred in demes other than the one they were first captured in, and maternal genotypes confirmed all five as cases of interdeme dispersal. Maternal genotyping detected an additional case of precapture interdeme dispersal: a juvenile first captured in the SSW deme was incompatible with all adult females there, and was assigned by cervus to a female in the adjacent deme. Four out of the six interdeme dispersers were females, and maximum MO distance (including the distance moved after our first capture) was 664 m.

Paternal genotyping also detected several additional cases of interdeme movement. For two juveniles, cervus was unable to find a mother, excluded all candidate fathers in the deme where the juvenile was first trapped, but assigned a father in an adjacent deme. These might represent additional cases of precapture interdeme dispersal, but they might also result from long-distance forays by the male into the deme where we captured the juvenile, and mating with a female we were unable to genotype.

As an additional test of our ability to detect interdeme movement, we searched for parents of 72 animals first trapped as adults (and presumed to be 1 year old). We were able to identify one or both parents for 47 of these; the mother was from an adjacent population in one case, the father in two cases, and in one case cervus located both parents, living 38 m apart but 251 m from the offspring.

Discussion

The retroactive assignment of juveniles to their natal location using parentage is a potentially powerful approach in the study of dispersal. In Dipodomys spectabilis, parentage assignment shows that a nontrivial number of animals moved from their birth site prior to capture. This reveals a source of error present in trapping data even in a system chosen to ensure that animals can be readily located throughout life, and in which mark–recapture analyses confirm that we detect > 95% of all cases of dispersal by tagged animals (Skvarla et al. 2004).

Many previous conclusions regarding patterns of dispersal in D. spectabilis are qualitatively confirmed by the inclusion of precapture dispersal information. For example, our re-analysis confirms that banner-tailed kangaroo rats are highly philopatric, most individuals of both sexes breeding either in or adjacent to their natal home range (Jones 1987, 1988). Genetic data provide quantitative support for the inference of Jones (1984) that most juveniles remain in their natal mound well after they become independent.

On the other hand, using MO rather than FCB distances in dispersal analyses improves both accuracy (in the sense that our previous dispersal distance estimates were biased) and precision (in the sense that we can determine more exactly dispersal’s temporal pattern and the impact of sex and population density). In this species, previously published FCB data overestimated the proportion of animals that breed in the natal mound, underestimated median natal-breeding site distances and even failed to detect some cases of movement between demes. Before parentage assignment made it possible to infer the location of the mother’s mound, it was difficult to distinguish impacts of sex and density on juveniles’ decisions to leave their mothers’ mounds, from their impacts on the distances juveniles travelled after departure.

Our finding that MO dispersal distances are shorter at higher population densities replicates the pattern previously reported for FCB distances (Jones 1988), but makes it clearer that the pattern is primarily driven by the behaviour of females. Jones et al. (1988) reported that female FCB distances were more strongly influenced by density than those of males, but the effect was not large enough to produce a detectable sex bias. Knowledge of birth locations allows us to detect a female bias in dispersal distance at low (but not medium or high) density; sex and density interact to influence dispersal in at least two ways. First, the timing of departure from the natal den is earlier in low-density years; both males and females are more likely to remain in their mothers’ mound in August in years of greater habitat

Fig. 4 Distances moved from the mother’s primary mound as a function of juvenile weight; line indicates median. The data include all juveniles, including those that never left their presumed natal mound, except for seven that dispersed between demes. Recall that the mean distance between nearest adult neighbours is 26 m, and the maximum distance between a female’s primary mound and her secondary mounds is 30 m. Based on data from a sample of juveniles of known birth date (Waser, unpublished), age = [(weight – 7.9) * 60]/(148.6 – weight).
found less structure than anticipated from short FCB sharing analyses (Keane et al. 2001; Matthysen 2005). In banner-tailed kangaroo rats, mound construction is a prolonged affair, but reconstructing a mound left vacant by the death of another individual is much quicker. Dispersers rarely construct new mounds, preferentially reconstructing a vacant mound even if it has been abandoned for many years; if they do not find a mound, they die (Best 1972; Jones 1984; Waser, unpublished). McCarthy (1997) showed analytically that under such circumstances, dispersal distances should decrease as the ratio of juveniles to openings increases, because at higher densities, individuals that attempt dispersal are only likely to succeed if they find an opening immediately.

Lambin et al. (2001) have also reviewed evidence for birds and mammals suggesting that dispersal characteristics are more labile in the less dispersive sex. For example, among Townsend’s voles, Microtus townsendii, females are more likely than males to settle within the trapping grid they are born in, and females (but not males) settle closer to their birth site at high than at low density (Lambin 1994). Similarly in a number of mammalian carnivores, the proportion of females that emigrate responds more strongly to density than does the proportion of males (Waser 1996). On the other hand, Wauters et al. (2004) reported that immigration into forest patches by European red squirrels, Sciurus vulgaris, is density-dependent in males but not females. Our results are consistent with the possibility that those *D. spectabilis* females that do emigrate are either more selective than males in their choice of vacant mounds to settle in, or less capable of evicting competitors for those mounds. This hypothesis, in combination with the assumption that dispersers settle in the nearest mound they can successfully compete for or die, would predict that overwinter survival of dispersing females is higher in years of low density. Jones (1988) found this to be true in a nearby *D. spectabilis* population.

While median MO distance dispersed by banner-tailed kangaroo rats is very short, the fact that is approximately double that inferred from FCB distances goes a long way towards resolving the discrepancy between direct and indirect estimates of dispersal distance in this species. Previous spatial autocorrelation and minisatellite band-sharing analyses (Keane et al. 1991; Waser & Elliott 1991) found less structure than anticipated from short FCB distances, and an *F*_{ST}-based isolation-by-distance approach (Rousset 2000) implied that distance moved per generation was about twice as long as observed. Many authors (e.g. Koenig et al. 1996) have argued that observational studies of dispersal inherently produce downwardly biased estimates of dispersal distance because they cannot detect dispersal off the study site. Although this concern undoubtedly applies to many species, we have previously argued that it does not apply to *D. spectabilis*: the dimensions of our study site are nearly two orders of magnitude greater than the median dispersal distance. Instead, we have argued that ‘gamete dispersal’, in the form of forays by adults away from their residences to mate, may effectively move genes further than individuals (Winters & Waser 2003). The effect of pre-capture movements reported here is similar in magnitude to that previously inferred for gamete dispersal.

Undoubtedly, many ‘direct’ studies of dispersal accurately locate the site of origin of the study individuals by capturing them while still in the nest or den, or with the mother. Indeed, approaches related to this one have frequently been used in analyses of plant dispersal (e.g. Nason et al. 1996; Trappnell & Hamrick 2005). But sometimes, as in grid-trapping studies of small mammals, the birth site of a juvenile is inferred rather than located directly. Often, young individuals may be more difficult to capture than adults. Where mothers can be more reliably trapped and located around the time of parturition than juveniles can, parentage assignment provides a useful addition to the armamentarium for the study of animal dispersal.

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Peter Waser’s laboratory has used the banner-tailed kangaroo 
rat as a model system for the study of mammalian dispersal for 
more than 20 years. Joseph Busch is a graduate student using 
this species to ask questions about population genetics and mate 
choice. Andrew DeWoody is particularly interested in genetic 
studies of mate choice and his laboratory group studies an array 
of vertebrate taxa, including rodents, raptors, fish and salamanders.
Dear Author,

During the copy-editing of your paper, the following queries arose. Please respond to these by marking up your proofs with the necessary changes/additions. Please write your answers on the query sheet if there is insufficient space on the page proofs. Please write clearly and follow the conventions shown on the attached corrections sheet. If returning the proof by fax do not write too close to the paper’s edge. Please remember that illegible mark-ups may delay publication.

Many thanks for your assistance.

<table>
<thead>
<tr>
<th>No.</th>
<th>Query</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Please confirm if changing <em>roughly</em> to <em>approximately</em> is OK here, to make it clear that ‘about 150 recombinant clones were sequenced’ or does the sentence originally mean ‘the manner with which the 150 recombinant clones were sequenced was rough’. Please check.</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Please note that Morrissey et al. 2005 has been changed to Morrissey &amp; Wilson 2005 so that this citation matches the one in the list.</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Please note that Berry et al. 2004 has not been cited in the text.</td>
<td></td>
</tr>
</tbody>
</table>
## MARKED PROOF

**Please correct and return this set**

Please use the proof correction marks shown below for all alterations and corrections. If you wish to return your proof by fax you should ensure that all amendments are written clearly in dark ink and are made well within the page margins.

<table>
<thead>
<tr>
<th>Instruction to printer</th>
<th>Textual mark</th>
<th>Marginal mark</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leave unchanged</td>
<td>( \cdot \cdot \cdot ) under matter to remain</td>
<td></td>
</tr>
<tr>
<td>Insert in text the matter indicated in the margin</td>
<td>( \cdot ) through matter to be deleted</td>
<td></td>
</tr>
<tr>
<td>Delete</td>
<td>( \cdot ) through letter or ( \cdot ) through word</td>
<td></td>
</tr>
<tr>
<td>Delete and close up</td>
<td>( \cdot ) under matter to be deleted</td>
<td></td>
</tr>
<tr>
<td>Substitute character or substitute part of one or more word(s)</td>
<td>( \cdot ) under matter to be changed</td>
<td></td>
</tr>
<tr>
<td>Change to italics</td>
<td>( \cdot ) under matter to be changed</td>
<td></td>
</tr>
<tr>
<td>Change to capitals</td>
<td>( \cdot ) under matter to be changed</td>
<td></td>
</tr>
<tr>
<td>Change to small capitals</td>
<td>( \cdot ) under matter to be changed</td>
<td></td>
</tr>
<tr>
<td>Change to bold type</td>
<td>( \cdot ) under matter to be changed</td>
<td></td>
</tr>
<tr>
<td>Change to bold italic</td>
<td>( \cdot ) under matter to be changed</td>
<td></td>
</tr>
<tr>
<td>Change to lower case</td>
<td>( \cdot ) under matter to be changed</td>
<td></td>
</tr>
<tr>
<td>Change italic to upright type</td>
<td>(As above)</td>
<td></td>
</tr>
<tr>
<td>Insert ‘superior’ character</td>
<td>( \cdot ) through character or ( \cdot ) where required</td>
<td></td>
</tr>
<tr>
<td>Insert ‘inferior’ character</td>
<td>(As above)</td>
<td></td>
</tr>
<tr>
<td>Insert full stop</td>
<td>(As above)</td>
<td></td>
</tr>
<tr>
<td>Insert comma</td>
<td>(As above)</td>
<td></td>
</tr>
<tr>
<td>Insert single quotation marks</td>
<td>(As above)</td>
<td></td>
</tr>
<tr>
<td>Insert double quotation marks</td>
<td>(As above)</td>
<td></td>
</tr>
<tr>
<td>Insert hyphen</td>
<td>(As above)</td>
<td></td>
</tr>
<tr>
<td>Start new paragraph</td>
<td>(As above)</td>
<td></td>
</tr>
<tr>
<td>No new paragraph</td>
<td>(As above)</td>
<td></td>
</tr>
<tr>
<td>Transpose</td>
<td>(As above)</td>
<td></td>
</tr>
<tr>
<td>Close up</td>
<td>(As above)</td>
<td></td>
</tr>
<tr>
<td>Insert space between letters</td>
<td>(As above)</td>
<td></td>
</tr>
<tr>
<td>Insert space between words</td>
<td>(As above)</td>
<td></td>
</tr>
<tr>
<td>Reduce space between letters</td>
<td>(As above)</td>
<td></td>
</tr>
<tr>
<td>Reduce space between words</td>
<td>(As above)</td>
<td></td>
</tr>
</tbody>
</table>

- Stet
- New matter followed by
- New letter or new word
- \( \cdot \cdot \cdot \) under character
- \( \cdot \cdot \cdot \) over character e.g. \( \cdot \)
- \( \cdot \cdot \cdot \) and/or \( \cdot \cdot \cdot \)
- \( \cdot \cdot \cdot \) and/or \( \cdot \cdot \cdot \)
- \( \cdot \cdot \cdot \) linking \( \cdot \) letters
- \( \cdot \cdot \cdot \) between letters affected
- \( \cdot \cdot \cdot \) between words affected
- \( \cdot \cdot \cdot \) between letters affected
- \( \cdot \cdot \cdot \) between words affected

Please use the proof correction marks shown below for all alterations and corrections. If you wish to return your proof by fax you should ensure that all amendments are written clearly in dark ink and are made well within the page margins.