

Female-biased dispersal in the monogamous mammal *Crocidura russula*: evidence from field data and microsatellite patterns

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SUMMARY

We investigated dispersal patterns in the monogamous *Crocidura russula*, based both on direct field observations (mark-recapture data) and on genetic analyses (microsatellite loci). Natal dispersal was found to be low. Most juveniles settled within their natal territory or one immediately adjacent. Migration rate was estimated to two individuals per year and per population. The correlation between genetic and geographical distances over a 16 km transect implies that migration occurs over short ranges. Natal dispersal was restricted to first-litter juveniles weaned in early May; this result suggests a direct dependence of dispersal on reproductive opportunities. Natal dispersal was highly female biased, a pattern unusual among mammals. Its association with monogamy provides support for the resource-competition model of dispersal. Our results demonstrate that a state-biased dispersal can be directly inferred from microsatellite genotype distributions, which opens new perspectives for empirical studies in this area.

1. INTRODUCTION

Natal dispersal is the permanent movement an individual makes from its birth site to the place where it reproduces – or would have reproduced had it survived and found a mate (Howard 1960; Endler 1977). Natal dispersal is often sex-biased, one sex usually remaining more philopatric than the other (Greenwood 1980). Which sex disperses more, however, varies among taxonomic groups. Although hotly debated in the past two decades, the reasons for this variability remain an area of major controversy (Dobson 1982; Johnson & Gaines 1990; Stenseth & Lidicker 1992; Wolff 1993, 1994). Dispersal presents both costs (e.g. the mortality risk of travelling in suboptimal or unknown habitats) and benefits (e.g. in terms of inbreeding avoidance or colonization opportunities), and therefore should be optimized by natural selection. That the optimum differs among sexes suggests asymmetries in costs and/or benefits. Three main asymmetries have been suggested to account for this bias. All three turn out to attribute a key role to mating systems.

(1) The ‘resource-competition hypothesis’ (Greenwood 1980, 1983) builds on the benefits brought by philopatry (and familiarity with natal area) in terms of ability to exploit local resources. In polygynous species, such benefits are more valued by females, as they are mainly responsible for defending the breeding territory and rearing the young. Females, therefore, are under

stronger selective pressure than males to remain philopatric. In monogamous species, by contrast, males not only help rear the young, but they also may need to acquire and defend sufficient resources to attract a female. Males, therefore, should be more philopatric, being the sex which benefits the most from familiarity with birth site. This hypothesis therefore predicts a male-biased dispersal in polygynous species, and a female-biased dispersal in monogamous species.

(2) The ‘local mate competition hypothesis’ (Dobson 1982) builds on the observation that philopatry induces competition for mates among kin, which bears both direct and indirect fitness costs (Hamilton 1972). The sex with the highest reproductive potential should suffer more from competition, and so should disperse more. This hypothesis therefore predicts that, in polygynous species, males should be the dispersing sex, while no difference in dispersal among sexes is expected in monogamous species.

(3) The ‘inbreeding hypothesis’ (Wolff 1993, 1994) holds that philopatry puts an animal at the risk of inbreeding with close kin, more specifically of mating with its opposite-sex parent. The sex at greatest risk should thus disperse. In polygynous species only mothers live in close contact with their progeny, so that daughters may safely remain philopatric, while sons should emigrate. By contrast, this asymmetry does not exist in monogamous species, so that no dispersal bias is expected.

One obvious problem with these models lies in the convergence of their predictions. All three predict a

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male-biased dispersion in polygynous species. In monogamous species, however, only the resource-competition model predicts a female bias. This last prediction (and thereby Greenwood's model) receives some support from the comparison of dispersal patterns and mating systems among birds and mammals. Broadly speaking, mammals, which are usually polygynous, often display a male-biased dispersal (Dobson 1982) as all three models predict. But birds, which are often monogamous, usually display a female-biased dispersal (Greenwood & Harvey 1982), as only the resource-competition model predicts. Since phylogeny is here an obvious confounding variable, a stronger test of the models would require comparisons within taxonomic groups. Within mammals, Dobson (1982) did find an effect of mating system on dispersal patterns, but this did not appear female-biased in monogamous species. This last result, however, relied on a small sample size, due to the paucity of data available on monogamous mammals.

This paucity of data prompted us to investigate dispersal patterns in the greater white-toothed shrew (*Crocidura russula*), which has been shown to have a monogamous mating system (Cantoni & Vogel 1989). In this article we present direct evidence, from field mark and recapture data, that dispersal is female-biased in this species, thus adding support to Greenwood's resource-competition hypothesis. Second, and more importantly, we also demonstrate, from the study of microsatellite patterns, that this bias in dispersal can be directly inferred from the analysis of genotypic distributions. This last result opens important perspectives for new empirical studies of state-biased dispersal.

2. MATERIAL AND METHODS

(a) Study species

Crocidura russula is a medium-sized (11–14 g), monogamous shrew, with an annual life cycle (Jeanmaire-Besançon 1986; Cantoni & Vogel 1989). Common in southwestern Europe, *C. russula* is anthropophilic in the northern part of its range (Genoud & Hausser 1979). Pairs defend territories (about 100 m²) in which they rear up to three (–four) litters, of two to nine offspring each (Jeanmaire-Besançon 1988). Natal dispersal is observed immediately after weaning (Cantoni & Vogel 1989).

(b) Field methods

We followed populations from three gardens (about 2000 m² each) near Lausanne (Switzerland) over 2 years (1993–94) by trapping animals every other week: 50–80 Longworth traps per study area, baited with *Tenebrio molitor* larvae, were settled for 30 h, including a 12-h prebaiting period and an 18-h trapping session (checked every 2–3 h). As all individuals caught were captured twice or more per trapping session (with no gender difference) we estimate the trappability to be very close to 100% for both sexes. Breeding adults were individually marked by toe clipping before the start of the reproductive season. In addition, females were marked with a low-activity (100 µCi) radioactive (¹⁸²Ta) ear tag (0.1 g), and followed for 24 h with a Geiger-Müller

counter (details in Ricci & Vogel 1984) in order to locate their nest. Pregnancy and parturition time were determined by weighing females (weight increases up to 18–22 g during the 30 d of pregnancy, then drops back to 13–14 g at parturition). All offspring from their three (–four) consecutive litters were similarly marked before weaning (which occurs 20 d after parturition), and their dispersal/disappearance patterns were recorded. Two weeks after weaning, 120 traps were dispatched for 30 h (same design as above) in an area of 150 m radius around the study sites to detect the possible settlement of locally-born juveniles. All immigrants that settled within the study areas during reproductive seasons were similarly marked.

(c) Microsatellite data

Genetic analyses were performed in 1993–94 on 74 first-litter juveniles from the three populations above, including nine immigrants. These analyses were extended in autumn 1995 to a further sample of 142 individuals from 15 populations (7–12 per population) along a 16 km N-S transect west of Lausanne. DNA was extracted from cut-off toes using standard procedures (Sambrook *et al.* 1989) and rediluted in 100 µl water. The individuals were typed on either four (1993–94) or eight (1995) microsatellite loci specifically designed for *C. russula* (Favre & Balloux 1996). PCR amplifications were carried out in 10 µl reaction volumes overlaid with 20 µl oil. The following conditions were used for all loci: 5 ng genomic DNA, 0.7 µM dNTP, 1.5 mM MgCl₂, 1 µM primers, 0.3 µCi ³³P and 0.25 U Taq polymerase. Thermal profiles started with an initial denaturation at 94 °C for 2 min, followed by 35 cycles consisting of: 45 s denaturation at 94 °C; 45 s annealing at 55 °C; 1 min polymerization at 72 °C. The last polymerization step was extended to 7 min. End products were run on standard polyacrylamide denaturing sequencing gels, together with both a size marker and the end product of a sequencing reaction to determine allele length.

(d) Statistical treatment

Genetic diversity per population was calculated as the average over *n* loci of expected heterozygosity,

$$\frac{1}{n} \sum_k^n (1 - \sum_i p_{i,k}^2),$$

where *p_{i,k}* is the frequency of allele *i* at locus *k* (Weir 1990). Genetic differentiation between pairs of populations was computed as pairwise *F_{ST}* (Goudet 1995), and the overall genetic differentiation among populations as Weir & Cockerham's (1984) estimator of *F_{ST}* (Goudet 1995). From this overall *F_{ST}* value, the number of migrants (*Nm*) under island-model assumptions was estimated using Wright's (1943) equation:

$$Nm = \frac{1 - F_{ST}}{4F_{ST}}, \quad (1)$$

where *N* is the effective population size and *m* the migration rate. Ninety-five per cent CI of *F_{ST}* were obtained through bootstrapping over loci (Goudet 1995). Ninety-five per cent CI of *Nm* were obtained by applying equation (1) to the *F_{ST}* CI.

An assignment index (Paetkau *et al.* 1995) was computed for each individual. The assignment index (*AI*) of individual

k sampled in population l is the probability that its genotype occurred by chance in population l , given allelic frequencies in this population (frequencies calculated including the focal individual). Formally, the probabilities of this individual's genotype at each locus (i.e. p_{il}^2 if homozygous, $2p_{il}p_{jl}$ if heterozygous, where p_{il} and p_{jl} are frequencies of alleles i and j in population l) were multiplied over loci. Since we were not interested in population effects (which may arise simply from differences in genetic diversity), AI values were corrected (AI_c) by subtracting population means after log-transform. It follows that AI_c values average zero for each population, and that negative values characterize individuals with a lower probability than average to be born locally.

3. RESULTS

(a) Field data

Over the 2 years of the study, a total of 44 breeding adults, 287 locally-born juveniles, and 14 immigrants were marked. This last figure corresponds to an immigration rate of 2.33 (± 0.33 SE) individuals per year and per population. Among the 287 locally-born juveniles, 141 disappeared for unknown reasons (table 1), in which mortality certainly played a major role (cats exert a strong predation on juvenile shrews in these suburban populations). The 146 remaining settled either within the study areas (145 individuals), or in the immediate surroundings (one 1993 female). Among these, philopatry was high: 138 juveniles (i.e. 95%) settled either within their natal territory or in one immediately adjacent, and are considered philopatric (Φ). Only eight individuals (5%) settled in non-adjacent territories (that is, in territories a distance of more than one home range away from their birth place), and are considered to be emigrants (E, table 1).

Settlement patterns varied with season: all the eight emigrants recorded were first-litter juveniles, weaned in early May (table 1). This pattern was tested by a generalized linear model for contingency tables (Baker

et al. 1985). The null model included dispersal status (Φ vs E), sex, litter, and sex-by-litter interaction. The decrease in deviance following addition of the interaction term litter number by dispersal status, tested by likelihood ratio (Baker et al. 1985) was highly significant ($p < 0.0001$). Similarly, all of the 14 immigrants (I) were juveniles, as was evident from their weight (9–10 g) and coloration, and all from first litters, as implied by their arrival dates (table 1). This pattern also differs highly significantly from random ($p < 0.001$, χ^2 test). Dispersal, therefore, defined here as settlement in any territory farther than one home range from the natal one, was only observed in first-litter juveniles, weaned in early May (table 1, a); neither emigration (E) nor immigration (I) were observed later in the season (table 1, b and c).

Settlement patterns were strongly sex-dependent (table 1): all emigrants were females ($p < 0.0001$; Fisher's exact test on the contingency table sex by dispersing-status), as were 13 out of the 14 immigrants ($p < 0.0001$; binomial test).

(b) Microsatellite data

Both the 1993–94 and the 1995 samples displayed a high genetic diversity per population (average over loci 0.706 and 0.813 respectively). Interpopulation comparisons from the 1995 sample revealed an important genetic differentiation (F_{ST} over the eight loci = 0.135 (0.114–0.153 95% CI), $p < 0.0002$, tested by generating 5000 random permutations of genotypes among samples; Goudet 1995). This F_{ST} value would correspond to 1.51 (1.38–1.94 95% CI) migrants per year and per population under the island model of dispersal (equation 1). Genetic differentiation correlated with geographic distances ($r = 0.43$, $p < 0.005$, Mantel test), which implies a significant isolation by distance (Slatkin 1993).

The assignment index of individuals sampled in 1993–94 (all first-litter juveniles) was strongly affected by their dispersing status: the nine immigrants analysed had significantly lower AI_c values than the 65 locally-born juveniles (-2.70 ± 0.90 vs 0.38 ± 0.17 (SE); $p < 0.002$, Mann-Whitney U -test). The 42 females also had lower AI_c values than the 32 males when immigrants (all females) were included in the data set (-0.56 ± 0.33 vs 0.76 ± 0.18 (SE); $p < 0.01$, Mann-Whitney U -test), but not after their removal ($p > 0.05$, Mann-Whitney U -test). Thus, the difference in AI_c among sexes was due to the female bias in dispersal. This last result implies that such a bias can be directly inferred from sex differences in AI_c distributions.

The 1995 sample was also characterized by a strong sex difference in AI_c . The 64 females had, on average, lower values than the 76 males (-1.27 ± 0.46 vs 1.04 ± 0.23 (SE), $p < 0.002$, Mann-Whitney U -test; figure 1). Their distribution also displayed a higher variance (13.59 vs 4.12, $p < 0.01$, maximum F -ratio test), with an important left skew (or possibly a second mode; figure 1) consisting of individuals with a low probability of being born locally. The single most plausible interpretation of this pattern is that females

Table 1. Number, origin and fate of the juveniles marked, as a function of sex and litter number

| | M | † | Φ | E | I |
|-----|--------|----|--------|----|---|
| (a) | male | 37 | 10 | 27 | 0 |
| | female | 38 | 26 | 4 | 8 |
| (b) | male | 51 | 31 | 20 | 0 |
| | female | 41 | 16 | 25 | 0 |
| (c) | male | 62 | 29 | 33 | 0 |
| | female | 58 | 29 | 29 | 0 |

(a) Corresponds to the first litter, weaned in early May, (b) corresponds to the second litter, weaned in June, (c) corresponds to the third and fourth litters combined, weaned July–August. Data summed over two seasons and three sites. Among the juveniles born locally (M), some disappeared (†), some settled in their natal territory or one immediately adjacent (these are considered philopatric, Φ), and some emigrated (E) towards non-adjacent territories. Several immigrants (I, all weaners, as evident from their weight and coloration) also settled in the study areas. All dispersal (i.e. both E and I) was restricted to first-litter juveniles. Among them, dispersal was sex-dependent: both immigration and emigration were female biased.

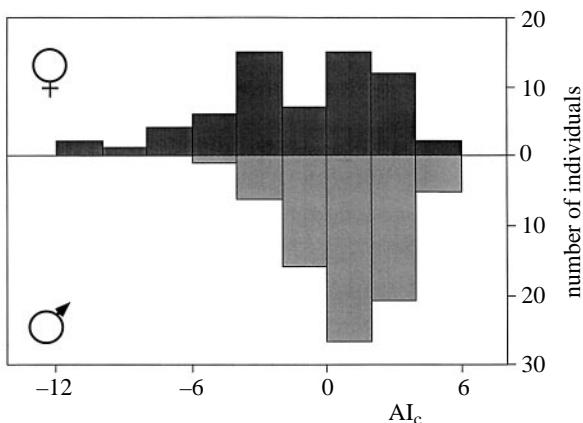


Figure 1. Frequency distributions of the corrected assignment index (AI_c) for 64 females (dark bars above axis) and 76 males (light bars below axis) sampled from 15 populations near Lausanne. AI_c values differed among sexes, females having on average negative values, and males positive values. This implies that immigration was female biased in the populations studied. This bias is also reflected in the larger variance of the female distribution, and in its possible bimodality which, suggests the existence of two distinct classes (immigrants vs locally born individuals).

were the dispersing sex in these populations, too. A very crude estimate of the number of migrant females can be obtained by subtracting from the left-hand side of female distribution the number expected under the assumption of similarity with male distribution. The right-hand side (positive AI_c values) comprises 29 females for 53 males, i.e. a 0.547 ratio. This ratio predicts about 12.5 females with negative AI_c values (since 23 males have such values), which makes a 22.5 difference with the number observed (35 females). This rough estimate of 22.5 putative immigrants in 15 populations corresponds to a migration rate of 1.5 individuals per year and per population.

4. DISCUSSION

Dispersal appears to be low in *C. russula*. Both direct and indirect lines of evidence indicate a strong philopatry. First, the number of immigrants in the 1993–94 sample was small (14) relative to the juveniles that settled locally (146). This direct evidence is corroborated by the fact that 95% of the locally-born juveniles recaptured settled within their natal territory or one directly adjacent (this last figure, however, might overestimate real philopatry, since some of the juveniles that disappeared could have emigrated outside the study areas and surroundings). Second, the AI_c -values distribution also suggests a limited number of immigrants per population (figure 1). Third, the genetic analysis of the 1995 sample revealed both a large differentiation of populations over a few kilometers and a significant isolation by distance.

This last result allows us to reject the island model of dispersal (Slatkin 1993), which comes as no surprise. But, more importantly, it also suggests that the x -axis in figure 1 might reflect a dispersal distance: the farther left an individual is on this axis, the more different genetically should be its natal population, and so the

more distant its birth place. Or put otherwise: as genetic and geographic distances correlate, an immigrant will show more genetic peculiarities if its natal population is far away than if it is in close neighbourhood. Further investigations on this speculative point should properly examine the statistical properties of AI_c frequency distributions under various assumptions regarding migration rates and distances.

Although similar, our three estimates of migrant numbers diverge slightly. Mark-recapture data allowed us to recognize a total of 14 immigrants in the three populations over the 2 years of the study, which corresponds to a migration rate of 2.33 (± 0.33 SE) migrants per year and per population. The calculated F_{ST} value would correspond to a rate of 1.51 (1.38–1.94 95% CI) migrants per year and per population under the island model assumptions. Finally, the AI_c distribution data (figure 1) suggest a very close number of 1.5 migrants per year and per population. However, this last value is probably an underestimate, since sampling was not exhaustive. Similarly, the value provided through F_{ST} is certainly an underestimate. The observed isolation by distance implies that migrants are not randomized over populations, but originate preferentially from close populations, and therefore have a lower homogenizing effect than under the island model assumption. One should also be aware that these three approaches do not estimate strictly the same parameters. The direct approach measures the number of individuals that succeeded in reaching a target population. The AI_c approach, based on autumnal sampling, only accounts for immigrants still alive at this time. Finally, the F_{ST} value estimates effective migrants, i.e. those individuals that succeeded in reproducing locally. Thus, part of the discrepancy might stem from a higher mortality of immigrants, or more generally a failure to integrate their genes into the local pool. By and large, the effective migration rate should be situated somewhere between our extreme values, i.e. around two individuals per year and per population. Dispersal distances are certainly short, as the strong isolation by distance implies.

The syntopic and similarly-sized common shrew *Sorex araneus* seems to present a very close pattern as far as dispersal rate is concerned: juveniles generally do not disperse more than 30–60 m before reaching sexual maturity (Stockley *et al.* 1993), and those that disperse are usually individuals of relatively low competitive ability that are unlikely to breed (Hanski *et al.* 1991).

The seasonal bias in dispersal, observed in both immigrants and emigrants (table 1), suggests that natal dispersal has direct links to breeding opportunities. While first litter juveniles, weaned in early May, have enough time left to successfully mate and breed before winter, juveniles from subsequent litters must wait until the next year to reproduce (personal observation). Presumably, the main potential benefits of dispersal (prospects of immediate reproduction) decrease with season, and at some point are outweighed by costs (e.g. mortality risks). This scenario might be tested experimentally by manipulating breeding opportunities. In any case, this seasonal bias also suggests that dispersal is a highly plastic trait

that can be adjusted on a short scale according to local circumstances. This same sort of plasticity, as well as the predominant role of breeding opportunities on dispersal decisions, has also been observed in the recent and detailed studies by Komdeur on the mating system of the Seychelles warbler, *Acrocephalus sechellensis* (e.g. Komdeur 1994).

Finally, the strong female bias in post-natal dispersal, first revealed by direct evidence through marking of immigrants and emigrants (table 1), was confirmed by indirect evidence stemming from the use of microsatellite markers (figure 1). The relevance of the assignment index in this context is justified by our analysis of the 1993–94 sample: the significant difference in AI_c values among sexes was shown to be due to the presence of immigrants in the pool, and disappeared once these were removed from the comparison. These results imply that a sex-biased dispersal can be inferred from the AI_c values only. Application of AI_c to our 1995 sample confirmed that females were the dispersing sex in these populations, too, as implied by the lower mean and higher variance of their distribution. A possible bimodality of female distribution might even suggest a bimodality in dispersal patterns. This point however remains highly speculative and deserves further empirical and simulation work.

Thus, one main result arising from our study is that dispersal is heavily female-biased in *C. russula*, a pattern unusual among mammals. Only three mammalian species, out of 69, for which Dobson (1982) sampled relevant information (i.e. less than 5%) displayed such a bias. Its association with monogamy, while common in birds, is rare in mammals. Dobson (1982) cites but a single species from his data set, namely the wild dog *Lycaon pictus* (Frame & Frame 1976), that presents both characteristics. Since then, Ribble (1992) found the same association in the rodent *Peromyscus californicus*. Even though other detailed studies on yet poorly-known species will presumably extend the range, this pattern is bound to remain exotic in mammals. In this respect, the common shrew *Sorex araneus* is more classically ‘mammalian’, both in its breeding system (polygyny without pair bonds) and dispersal patterns (no female bias; Hanski *et al.* 1991).

This association provides some support for Greenwood’s (1980) resource-competition hypothesis, in so far as his hypothesis is the only one that predicts a female-biased dispersal in monogamous species. However, the point remains that Greenwood’s prediction also relies on the auxiliary assumption that males benefit more than females from philopatry. This might be the case if male *C. russula* do indeed play the major role in defending winter and/or breeding territories. This point is still unknown, and therefore deserves further empirical investigations. In any case, Greenwood’s model should not be directly extended to monogamous mammals without specific information on the precise role played by males in the pair’s reproductive effort.

A second main result lies in our demonstration that indirect evidence can be used to investigate migration patterns. Indeed, our data unambiguously show that

owing to the high polymorphism of microsatellite markers, biases in dispersal can be directly inferred from genotypic distributions, thus sparing the time-consuming work of following up individuals in the field. Combined with the possible use of non-invasive techniques for DNA extraction (e.g. Taberlet & Bouvet 1994), this last result opens important perspectives for further empirical work in the controversial area of state-biased dispersal.

This work was supported by the Swiss National Science Foundation (grants 31–38762.93 to N.P. and 31–43443.95 to J.G. and N.P.). The Institute of Zoology and Animal Ecology at Lausanne University provided all the necessary logistic support. We thank warmly S. Bolli, N. Mahboub and P. Vogel for their welcome help in the field.

REFERENCES

- Baker, R. J., Clarke, M. R. B. & Melder, J. A. 1985 *The GLIM system – release 3.77* Oxford: NAG.
- Cantoni, D. & Vogel, P. 1989 Social organization and mating system of free ranging, greater white-toothed shrews, *Crocidura russula*. *Anim. Behav.* **38**, 205–214.
- Dobson, F. S. 1982 Competition for mates and predominant juvenile male dispersal in mammals. *Anim. Behav.* **30**, 1183–1192.
- Endler, J. 1977 *Geographic variation, speciation, and clines*. Princeton: Princeton University Press.
- Favre, L. & Balloux, F. 1996 Characterization of microsatellite loci in greater white-toothed shrews, *Crocidura russula*. *Mol. Ecol.* (In the press.)
- Frame, L. H. & Frame, G. W. 1976 Female African wild dogs emigrate. *Nature, Lond.* **263**, 227–229.
- Genoud, M. & Hausser, J. 1979 Ecologie d’une population de *Crocidura russula* en milieu rural montagnard. *Terre Vie* **33**, 539–554.
- Goudet, J. 1995 FSTAT V1.2. A computer program to calculate *F* statistics. *J. Heredity* **86**, 485–486.
- Greenwood, P. J. 1980 Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* **28**, 1140–1162.
- Greenwood, P. J. 1983 Mating systems and the evolutionary consequences of dispersal. In *The ecology of animal movement* (ed. I. R. Swingland & P. J. Greenwood), pp. 116–131. Oxford: Clarendon Press.
- Greenwood, P. J. & Harvey, P. H. 1982 Natal and breeding dispersal in birds. *A. Rev. Ecol. Syst.* **13**, 1–21.
- Hamilton, W. D. 1972 Altruism and related phenomena, mainly in social insects. *A. Rev. Ecol. Syst.* **3**, 193–232.
- Hanski, I., Peltonen, A. & Kaski, L. 1991 Natal dispersal and social dominance in the common shrew. *Oikos* **62**, 48–57.
- Howard, W. E. 1960 Innate and environmental dispersal of individual vertebrates. *Am. Midl. Nat.* **63**, 152–161.
- Jeanmaire-Besançon, F. 1986 Estimation de l’âge et de la longévité chez *Crocidura russula*. *Acta Oecol.* **7**, 355–366.
- Jeanmaire-Besançon, F. 1988 Sexual maturity of *Crocidura russula*. *Acta Theriol.* **33**, 477–485.
- Johnson, M. L. & Gaines, M. S. 1990 Evolution of dispersal: Theoretical models and empirical tests using birds and mammals. *A. Rev. Ecol. Syst.* **21**, 449–480.
- Komdeur, J. 1994 The effect of kinship on helping in the cooperative breeding Seychelles warbler (*Acrocephalus sechellensis*). *Proc. R. Soc. Lond. B* **256**, 47–52.
- Paetkau, D., Calvert, W., Stirling, I. & Strobeck, C. 1995 Microsatellite analysis of population structure in Canadian polar bears. *Molec. Ecol.* **4**, 347–354.

- Ribble, D. O. 1992 Dispersal in a monogamous rodent, *Peromyscus californicus*. *Ecology* **73**, 859–866.
- Ricci, J.-C. & Vogel, P. 1984 Nouvelle méthode d'étude en nature des relations spatiales et sociales chez *Crocidura russula*. *Mammalia* **48**, 281–286.
- Sambrook, J., Fritsch, E. F. & Maniatis, T. 1989 *Molecular cloning: a laboratory manual*, 2nd edn. New York: Cold Spring Harbor Laboratory Press.
- Slatkin, M. 1993 Isolation by distance in equilibrium and non-equilibrium populations. *Evolution* **47**, 264–279.
- Stenseth, N. C. & Lidicker, W. Z. 1992 *Animal dispersal: small mammals as models*. London: Chapman & Hall.
- Stockley, P., Searle, J. B., Macdonald, D. W. & Jones, C. S. 1993 Female multiple mating behaviour in the common shrew as a strategy to reduce inbreeding. *Proc. R. Soc. Lond. B* **254**, 173–179.
- Taberlet, P. & Bouvet, J. 1994 Mitochondrial DNA polymorphism, phylogeography, and conservation genetics of the brown bear *Ursus arctos* in Europe. *Proc. R. Soc. Lond. B* **255**, 195–200.
- Weir, B. S. 1990 *Genetic data analysis*. Sunderland (Mass.): Sinauer Associates.
- Weir, B. S. & Cockerham, C. C. 1984 Estimating *F* statistics for the analysis of population structure. *Evolution* **43**, 1358–1370.
- Wolff, J. O. 1993 What is the role of adults in mammalian juvenile dispersal? *Oikos* **68**, 173–176.
- Wolff, J. O. 1994 More on juvenile dispersal in mammals. *Oikos* **71**, 349–352.
- Wright, S. 1943 Isolation by distance. *Genetics* **28**, 114–138.

Received 13 June 1996; accepted 22 July 1996