Breeding System and Genetic Variance in the Monogamous, Semi-Social Shrew, Crocidura russula

Francois Balloux, Jerome Goudet, Nicolas Perrin

Evolution, Volume 52, Issue 4 (Aug., 1998), 1230-1235.

Stable URL:
http://links.jstor.org/sici?sici=0014-3820%28199808%2952%3C1230%3ABSAGVI%3E2.0.CO%3B2-5

Evolution, 52(4), 1998, pp. 1230–1235

BREEDING SYSTEM AND GENETIC VARIANCE IN THE MONOGAMOUS, SEMI-SOCIAL SHREW, *CROCIDURA RUSSULA*

FRANÇOIS BALLOUX, JÉRÔME GOUDET, AND NICOLAS PERRIN[1]
Institut de Zoologie et d'Ecologie Animale, Université de Lausanne, CH-1015 Lausanne, Switzerland
[1]*E-mail: Nicolas.Perrin@izea.unil.ch*

Abstract.—The population-genetic consequences of monogamy and male philopatry (a rare breeding system in mammals) were investigated using microsatellite markers in the semisocial and anthropophilic shrew *Crocidura russula*. A hierarchical sampling design over a 16-km geographical transect revealed a large genetic diversity ($h = 0.813$) with significant differentiation among subpopulations ($F_{ST} = 5–6\%$), which suggests an exchange of 4.4 migrants per generation. Demic effective-size estimates were very high, due both to this limited gene inflow and to the inner structure of subpopulations. These were made of 13–20 smaller units (breeding groups), comprising an estimate of four breeding pairs each. Members of the same breeding groups displayed significant coancestries ($F_{LS} = 9–10\%$), which was essentially due to strong male kinship: syntopic males were on average related at the half-sib level. Female dispersal among breeding groups was not complete ($\sim 39\%$), and insufficient to prevent inbreeding. From our results, the breeding strategy of *C. russula* seems less efficient than classical mammalian systems (polygyny and male dispersal) in disentangling coancestry from inbreeding, but more so in retaining genetic variance.

Key words.—Breeding systems, *Crocidura russula*, dispersal, genetic structure, microsatellites, shrews.

Received April 11, 1997. Accepted March 30, 1998.

Following the pioneering work of Wright (1921), population geneticists have developed important conceptual and statistical tools to investigate the apportionment and dynamics of genetic variance in structured populations (Cockerham 1969, 1973; Nei 1973; Cockerham and Weir 1993). Among other effects, structure increases genetic drift within demes (subpopulations), thus allowing wider exploration of adaptive landscapes (Wright 1977). The potential for adaptation is thereby enhanced, a key element in Wright's shifting balance theory. Demic differentiation also increases the variance effective size of populations (a measure of their ability to retain genetic diversity; Gliddon and Goudet 1995), unless it is counter-balanced by the extinction-colonization processes that may characterize metapopulation dynamics (Whitlock and Barton 1997).

Within Wright's original framework, drift and effective size, as well as the measurements of the apportionment of genetic variance encompassed in the *F*-statistics (Wright 1921, 1951; Nei 1973), strongly depend on a single population parameter, the number of migrants between demes. This parameter in particular is the main determinant of inbreeding (gene correlations within individuals) and coancestry (gene correlations among individuals from the same deme). Both are lowered by migration. Conversely, coancestry (and therefore relatedness) cannot accrue within demes without a concomitant increase in inbreeding.

This may seem problematic in the context of social evolution. Social structures, which are based on cooperation and reciprocity, are expected to be facilitated by relatedness (Hamilton 1972), and indeed appear strongly dependent on kinship structures (Trivers 1985). Thus, the potential benefits accruing from cooperation should select for low dispersal and thereby close kinship. However, because low dispersal also leads to inbreeding, and more specifically to inbreeding depression, it should be counter-selected. It follows that a constraint linking coancestry and inbreeding might prevent the building of kinship structures and thereby constitute a major negative force on the evolution of sociality.

The point must be made, however, that Wright's approach was primarily designed to investigate gene flow at a geographic scale. Accordingly, it relied on simplifying assumptions (in particular with respect to the randomness of mating and dispersal patterns among panmictic demes; Slatkin 1985, 1993) that might be realistic at one scale, but not necessarily at the local scale at which social behavior matters. Indeed, the subpopulations of social species, far from being random-mating entities, are often structured into social units (e.g., breeding groups, coteries, lineages). Dispersal and mating strategies among such units rarely meet assumptions of randomness over ecological time scales. Mammalian breeding systems, for instance, are usually characterized by a male-biased dispersal associated with polygyny (Greenwood 1980, 1983). Such deviations from assumptions may result in critical discrepancies from the predictions of classical models. A sex-biased dispersal, for instance, may significantly disentangle the dynamics of inbreeding from that of coancestry (Sugg et al. 1996), thereby removing the above-mentioned obstacle to the evolution of sociality. In addition, structure within subpopulations provides a further means of maintaining genetic variation (between breeding groups).

The need to understand the evolution of breeding and social systems has recently prompted the development of a "social-structure" view of population genetics. Designed to account for species-specific peculiarities in dispersal and mating strategies, this view explicitly acknowledges the breeding-group level as a distinct sublevel in hierarchical studies, and one of crucial importance (Chesser 1991a,b; Chesser et al. 1993a,b; Sugg and Chesser 1994; Sugg et al. 1996).

Applications of this approach to a typical mammalian breeding system (the black-tailed prairie dog *Cynomys ludovicianus*, a social species displaying polygyny and nearly complete male dispersal) showed this combination of features

boosted coancestry within breeding groups (up to 16%) while keeping inbreeding at a negligible level (1%; Sugg et al. 1996). Social structuring, furthermore, turned out to be surprisingly efficient in retaining genetic variance, because the effective size of subpopulations (colonies) exceeded the number of breeders, despite polygyny and high male dispersal. Thus, typical mammalian breeding systems (polygny and male dispersal) apparently allow the building of significant coancestry at very local scales, without inflicting much inbreeding costs and excessive loss of genetic variance.

In the present paper, we apply this social-structure approach to an atypical mammal. The greater white-toothed shrew (*Crocidura russula*) is monogamous (Cantoni and Vogel 1989) with female-biased dispersal (Favre et al. 1997). This combination of features, while common in birds (Greenwood and Harvey 1982), occurs very rarely in mammals (Dobson 1982). In addition, *C. russula* displays a semisocial structure: Individuals living in close proximity use communal nests in winter when resting or entering torpor (Cantoni and Vogel 1989). The peculiarities of this shrew's breeding system prompted us to investigate its genetic correlates.

A first aim of the present paper is to explore the consequences of this system in terms of the maintenance and apportionment of genetic variance and to test the theoretical expectation (Chesser et al. 1993b) that monogamy and female dispersal should be less efficient than typical mammalian breeding systems in building up kinship structures. In order to do so, we perform a hierarchical analysis of genetic patterns at different spatial scales, focusing on the possible existence of breeding units (operationally defined as genetic structures below the subpopulation level). We investigate whether coancestry levels that are high enough to facilitate social evolution can evolve locally despite monogamy and whether female dispersal is sufficient to prevent local inbreeding. Also, we investigate how this shrew's particular breeding structure affects the effective size of its subpopulations and thereby their ability to retain genetic variance.

The second aim of this paper is to explore the possibility of inferring the actual values of breeding-structure parameters from genetic data. Indeed, the social-structure view of population genetics was developed to predict genetic structure and effective sizes from social and behavioral data. But the logical argument can be turned around, with genetic data used to investigate breeding structures. We therefore perform numerical simulations (because no explicit analytical solution is feasible) to estimate the values of demographic parameters that best fit our genetic data. The question under scrutiny here is: How useful can genetic markers be as indirect tools for investigating breeding and social structures?

Materials and Methods

Study Species

Crocidura russula is a medium-sized shrew (11–14 g) with a widespread distribution in southwestern Europe. In the northern part of its range (including western Switzerland, where our study was conducted), *C. russula* depends on temperate and insect-rich locations (such as garden composts) for winter survival (Genoud and Hausser 1979). Populations are therefore geographically discontinuous, with most subpopulations being found in the close proximity of human habitations.

The species is monogamous (Cantoni and Vogel 1989) and has an annual life cycle (Jeanmaire-Besançon 1986). Pairs defend territories (about 100 m^2) in which they rear up to three to four litters of two to nine offspring each (Jeanmaire-Besançon 1988). Juvenile dispersal is mostly restricted to female weanlings from first litters (Favre et al. 1997).

Sampling Design and Genetic Markers

A hierarchical sampling was performed in autumn 1995, that is, after juvenile dispersal had occurred. Five villages (hereafter subpopulation level, *s*), were chosen along a 16-km line transect west of Lausanne (Switzerland), from Prévérenges (6°32′E 46°31′N) to Eclépens-Gare (6°33′E 46°39′N). In each village, three gardens were sampled 200 m apart from each other (hereafter breeding-group or lineage level, *L*). Seven to 12 individuals were captured per garden (Longworth traps baited with *Tenebrio molitor* larvae), which sum up to a total of 142 individuals (64 females, 76 males, and two individuals whose sex could not be determined). DNA was extracted from clipped toes using standard procedures (Sambrook et al. 1989). Genotypes were typed at eight microsatellite loci specifically designed for *C. russula*, using the procedure described in Favre and Balloux (1997).

Genetic-Variance Analyses

Genetic diversity, *h*, was estimated as the average over loci of expected heterozygosity (Nei 1973). The structure at the metapopulation level was calculated as F_{ST}, that is, the proportion of total variance accounted for by differences among villages. Coancestry within putative breeding groups (gardens) was measured as F_{LS}, that is, the proportion of variance within subpopulations due to the differentiation among gardens. The possible existence of a substructure below our putative breeding groups was investigated by looking at F_{IL}, a measure of heterozygote deficit (relative to Hardy-Weinberg expectations) within gardens. Inbreeding was estimated as F_{IS}, that is, the excess in homozygotes at the subpopulation level. The relatedness within breeding groups (gardens) relative to their subpopulation (village) was measured on the basis of the above *F*-statistics as (Queller and Goodnight 1989):

$$r_{LS} = \frac{2F_{LS}}{1 + F_{IS}}. \quad (1)$$

All *F*-statistics were computed using the program FSTAT VI.2 (Goudet 1995) and the Nested procedure of SAS (SAS Institute 1989). Both procedures use the unbiased estimators of Weir (1996).

Breeding Structure and Effective Sizes

Let us denote *F*, θ and α as the gene correlations within individuals, breeding groups, and subpopulations, respectively. Chesser (1991b) provides the necessary recurrence equations to calculate the dynamics of these correlations as functions of the number of breeding groups per subpopulation (*s*), the number of females per group (*n*), the polygyny level

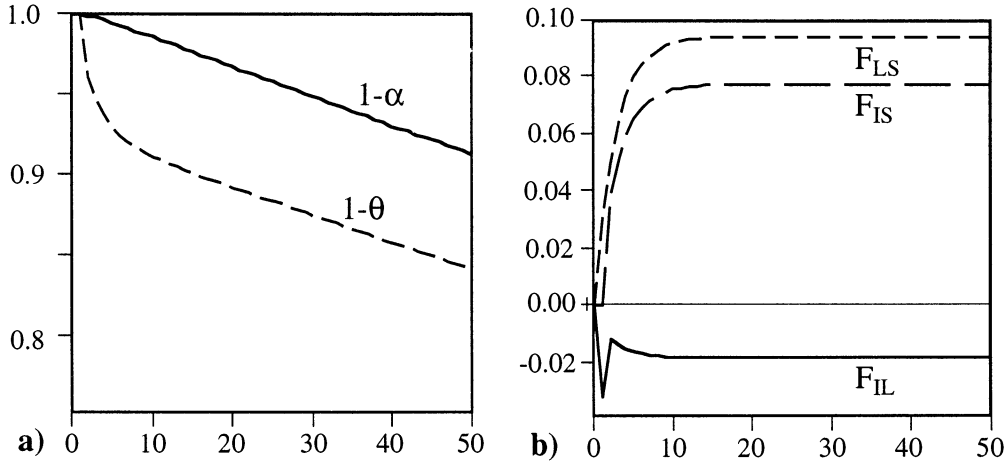

FIG. 1. Dynamics over 50 generations of (a) gene correlations within breeding groups (θ) and subpopulations (α); and (b) corresponding fixation indices. The breeding system exemplified is monogamous with complete male philopatry ($\phi = d_m = 0$). The other parameters were fixed to $n = 4$, $d_f = 0.39$, and $s = 15$. The initially strong decrease in genetic variance within breeding groups ($1 - \theta$) stems from the rapid building of kinship structures. The loss in variance then reaches an equilibrium rate, the value of which depends on effective population size. Fixation indices simultaneously reach equilibria, whose values depend on specific breeding-system parameters. In the simulation displayed, the equilibria were the same as the values observed in the field ($\hat{F}_{IL} = -0.018$, $\hat{F}_{LS} = 0.094$, and $\hat{F}_{IS} = 0.078$).

(ϕ), and the migration rate of males (d_m) and females (d_f). These correlations accrue with time (Fig. 1a), and do so faster when effective population sizes are low. Expectations for fixation indices are calculated from gene correlations as $F_{IL} =$

$$\frac{F - \theta}{1 - \theta}, \qquad F_{IS} = \frac{F - \alpha}{1 - \alpha}, \quad \text{and} \quad F_{LS} = \frac{\theta - \alpha}{1 - \alpha}.$$

These expectations quickly reach (i.e., after 5-10 generations) asymptotic values (Fig. 1b) that depend on the above-defined breeding parameters.

We iterated (using Mathematica; Wolfram 1991) Chesser's transition equations for 20 generations, while assuming monogamy and male philopatry ($\phi = d_m = 0$). The other parameters (n, d_f, and s) were varied until the resulting asymptotic fixation indices matched observed values. However, because fixation indices are linked ($F_{IS} = F_{IL} + F_{LS} - F_{IL}F_{LS}$), they provide only two independent equations, which is insufficient to fully determine three parameters. Full determination could be achieved by taking account of the amount of variance found in subpopulations in addition to its relative proportion. We took advantage of the fact that subpopulation effective sizes (i.e., their ability to retain genetic variance) strongly depend on the number of breeding groups (Chesser et al. 1993a). Effective sizes were first calculated from the method of Chakraborty and Neel (1989; eq. 4) which is a generalization to q loci and s subpopulations of Ewens's (1972) sampling formula. Using maximum-likelihood functions, this method simultaneously estimates the effective sizes (N_e) of the subpopulations (with standard errors calculated over loci) and the mutation rate of the several loci, based on a priori information and/or assumptions about the geometric mean of this rate (here assumed to be $\bar{\mu} = 10^{-3}$; Jarne and Lagoda 1996). The average of the estimates for N_e was then substituted into equation (48) of Chesser et al. (1993a):

$$s \approx \frac{1}{4}[6N_e(F_{LS} - F_{IS}) + 3F_{IS} + 1] \qquad (2)$$

to obtain the associated s value.

Finally, the number of migrants ($N_e m$) among subpopulations under island-model assumptions was estimated as (Wright 1943):

$$N_e m \approx \frac{1}{4}\left(\frac{1}{F_{ST}} - 1\right). \qquad (3)$$

TABLE 1. Hierarchical fixation indices (F) and relatedness (r) calculated for pooled individuals and by sex. Tests were based on 5000 permutations (*** $P < 0.0002$). Because no global test could be performed on the F_{LS}, we tested instead the five subpopulations independently. After Bonferroni corrections (Rice 1989), the results remained extremely significant when all individuals were pooled (all $P < 0.0002$), significant to extremely so for males ($0.05 \geq P \geq 0.0002$), and not significant for females, except for one village ($P < 0.05$). r_{LS}-values were attributed the same significance as F_{LS}, the numerator in the ratio.

	F_{ST}	F_{LS}	F_{IL}	F_{IS}	r_{LS}
All	0.054***	0.094***	−0.018 ns	0.078***	0.174***
Males	0.054***	0.145**	−0.033 ns	0.117***	0.260**
Females	0.052***	0.025 ns	−0.009 ns	0.016 ns	0.049 ns

RESULTS

Genetic Variance and Relatedness

Microsatellite analyses revealed a large amount of polymorphism, with an average of 12.4 alleles per locus (effective number 5.35) and a genetic diversity of $h = 0.813$. A significant part of this overall variance was due to differences among subpopulations ($F_{ST} > 5\%$; Table 1) and a still larger part to coancestry within local groups ($F_{LS} > 9\%$, Table 1). No substructuring was observed within local groups: F_{IL} remained low and slightly negative (Table 1), as expected under random mating with separate sexes (Cockerham 1969). In

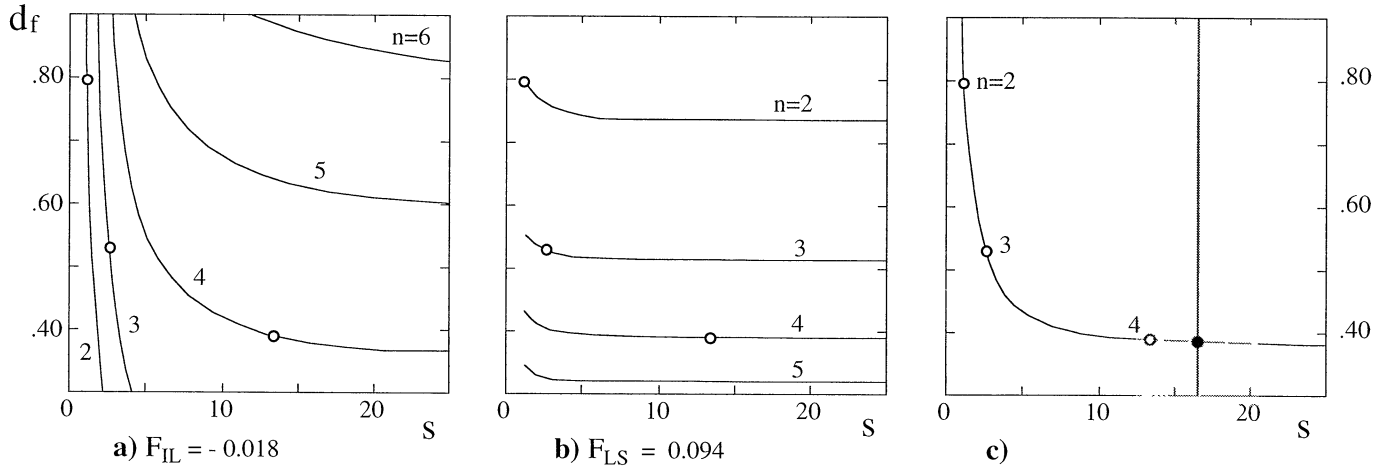

FIG. 2. (a) Surface solution in the three-dimensional parameter space to the constraint $\hat{F}_{IL} = -0.018$. For each of several n-values ($n = 2$ to 6), the solution is plotted as a function of d_f and s. Empty circles identify points that also meet the constraint on $\hat{F}_{LS}$ (i.e., where the n-isoclines meet the corresponding curves of Fig. 2b). (b) Surface solution to the constraint $\hat{F}_{LS} = 0.094$. For each of several n-values ($n = 2$ to 5), the solution is plotted as a function of d_f and s. $\hat{F}_{LS}$ turns out to depend mainly on the product $d_f n$, here close to 1.5. Empty circles identify points that also meet the constraint on $\hat{F}_{IL}$ (Fig. 2a). (c) Joint solution to the $\hat{F}_{IL} - \hat{F}_{LS}$ constraints. The shaded area corresponds to the estimate of s from effective population sizes ($s = 16.5 \pm 3.5$). The global solution (black circle) points to parameter values $n = 4$ and $d_f = 0.39$.

contrast, inbreeding was significant ($F_{IS} \sim 8\%$). Raw data (genotypes by location) are available at our website http://www.unil.ch/izea/.

Analysis by sex showed that, whereas males and females did not differ with respect to subpopulation differentiation (both F_{ST}-values $\sim 5\%$; Table 1), coancestry was much higher in males ($\sim 15\%$) than in females ($< 3\%$). This resulted in large sex differences in relatedness within local groups, with males being related at the half-sib level, that is, about five times more than females (26% vs. 5%).

Breeding Structure and Effective Sizes

From our computer simulations, F_{IL} turned out to depend mainly on s and n at small s-values and on n and d_f at large s-values (Fig. 2a). By contrast, F_{LS} was mainly dependent on the product $d_f n$ (number of females exchanged among groups per generation), with a slight effect of s at small s-values (Fig. 2b). Taken together, the two constraints on F_{IL} and F_{LS} determine a curve in the three-dimensional parameter space (Fig. 2c) that appears to greatly reduce the set of possible solutions. No solution exists for $n \geq 5$, because the corresponding isoclines never meet (Fig. 2a,b). Furthermore, solutions involving $n \leq 3$ are highly implausible because of the associated s-values ($s \leq 2.5$). This would imply less than three breeding groups and less than eight breeding pairs per subpopulation, which opposes direct observations. Thus, realistic solutions are restricted to a very small range of n ($3 < n < 5$) and d_f ($0.5 > d_f > 0.3$) values. By contrast, s varies enormously within this range (from 2.5 to infinity). As noted above, however, this last parameter can be better approximated from its effect on N_e.

The effective sizes of our five subpopulations, based on the approach by Chakraborty and Neel (1989) and assuming a 10^{-3} geometric mean for the mutation rate, ranged from 435 ± 74 (SE) to 833 ± 113. These estimates were consistent over loci, the highest mutation rate obtained (1.54×10^{-3}) was only twice as large as the lowest (0.74×10^{-3}). Introducing the average $N_e = 676 \pm 148$ (SD) into equation (2) leads to a number of breeding groups $s = 16.5 \pm 3.5$ (SD), a quite realistic range. Back into the parameter space, this s-value corresponds to a n very close to 4.0 and a migration rate $d_f = 0.39$. The corresponding flux among breeding groups amounts to $d_f n = 1.56$ females per generation.

Finally, the F_{ST}-value suggests a migration rate among subpopulations of 4.4 migrants per generation, assuming an island model of dispersal (eq. 3). Spread over 16.5 groups, this number implies that on average 0.27 immigrant from other subpopulations reach any given breeding group per generation.

DISCUSSION

The significant coancestries detected within gardens confirm the existence of genetic structure below the subpopulation level. Fixation indices pointed to very small groups, averaging four breeding pairs. As this figure approximates the number of breeders within one single garden (P. Vogel, pers. comm.), the territorial units of breeding groups may broadly match the surface of individual gardens.

These kinship structures essentially stemmed from coancestry among males. Syntopic males were on average related at the half-sib level ($r = 0.26$), which suggests a mixture of full brothers and cousins. These values are consistent with the mark-recapture findings of Favre et al. (1997), who showed that males are strongly philopatric and settle within either their parental home range or one immediately adjacent from the same garden.

The lower coancestry among syntopic females also corroborates the mark-recapture results (Favre et al. 1997) that females are the dispersing sex in this species. Our present estimate of exchange rate per generation (1.56 immigrants from the same subpopulation plus 0.27 from other subpop-

ulations) closely matches the direct estimate (Favre et al. 1997) of about two individuals per generation.

Inbreeding avoidance has often been invoked as a major determinant of dispersal (references in Johnson and Gaines 1990), and indeed the sex-biased dispersal of several social mammals appears quite efficient in preventing inbreeding (e.g., Frame et al. 1979; Packer and Pusey 1993; Smale et al. 1993; Sugg et al. 1996). Clutton-Brock (1989) suggested that female should be the dispersing sex whenever daughters incur a significant risk of mating with their father (e.g., when the residence time of males exceeds their daughters' age at maturation). It might be of significance therefore that only first-litter females migrate in *C. russula* (Favre et al. 1997), because only they reproduce during their year of birth. Females from later litters only reach maturity the following year, at which time their fathers will normally have died.

The point remains, however, that these philopatric females (which actually sum up to more than half of the total number) still incur a risk of inbreeding through mating with brothers or cousins. Such matings with close kin do not seem avoided, because our F_{IS}-values imply significant inbreeding. Furthermore, we found no significant heterozygote excess within local groups (F_{IL}), as would be expected under full migration by one sex (Chesser 1991a). Significant inbreeding is not uncommon among social mammals. Some species, such as the naked mole-rat (*Heterocephalus glaber*; Reeve et al. 1990) or the dwarf mongoose (*Helogale parvula*; Keane et al. 1996) show little sign of inbreeding avoidance or depression. This peculiarity might correlate with high ecological costs of dispersal. Whether dispersal is costly in *C. russula* and whether inbreeding is associated with any sort of fecundity depression remain open and relevant empirical questions.

Our estimate of 13–20 breeding groups per subpopulations seems quite realistic, given the size of the villages investigated, and matches reasonably well the number of suitable gardens (pers. obs.). This match confirms that the territories of breeding groups might broadly correspond to individual gardens. Our value also implies (because breeding units average four pairs) that subpopulations consist of about 50–80 breeding pairs.

This last figure, however, contrasts sharply with effective population sizes. From the method of Chakraborty and Neel (1989), we obtained a range of 435–833 individuals per village, that is, about five times higher than our estimate of actual breeder numbers. Although the underlying assumption of mutation-drift equilibrium could not be checked, we do not think these effective sizes to be overestimates. They might even be conservative, because a mutation rate of 10^{-3} lies in the upper range of published values (Jarne and Lagoda 1996).

Two reasons must be invoked to account for this discrepancy. The first one lies in the breeding structure itself. Very high effective sizes logically derive from Chesser et al.'s (1993a) equation (48) (our eq. 2), given the observed fixation indices and a realistic value for the number of breeding groups (ranging from 13 to 20). Sugg et al. (1996) already noticed that social structuring may dramatically boost effective population sizes. Their analysis of black-tailed prairie dogs showed that, despite polygyny, uneven sex ratio, highly variable reproductive success, and near complete male dispersal, effective population size nevertheless exceeded the number of breeders. The still larger discrepancy documented here may partly stem from the peculiarities of the breeding system under investigation. By securing a reasonably equal share of reproduction among males, monogamy greatly helps in maintaining diversity. The weakness of dispersal among breeding groups must also play a role. Not only are males extremely philopatric, but only a minority of females disperse (and not very far presumably; Favre et al. 1997). The resulting genetic differentiation among breeding groups creates important barriers to the loss of variance at the subpopulation level.

The second reason for our high estimates lies in the fact that our study system was not closed, which implies that some diversity was generated external to the subpopulations. F_{ST}-values point to an exchange rate of 4.4 individuals per year and per village, which is low enough to ensure a significant structure among subpopulations over a restricted spatial range (16 km), but sufficient to provide a regular inflow of variability. Indeed, although significant, the F_{ST}-values found here are still smaller than those found in mice, a similarly sized mammal, in which Dallas et al. (1998) report F_{ST}-values of 0.15–0.39 over comparable geographic distances (as well as much lower effective sizes, interestingly). It is unfortunately not possible with the data available to disentangle the effects of breeding structure, gene flow, and metapopulation dynamics on the enhancement of effective sizes. This casts some uncertainty on our estimate of s (the number of breeding units per subpopulation), but not on the other breeding parameters (n and d_f), which were mostly determined from the relative proportion of genetic variance rather than from the amount of it.

From our present results, the breeding system of *C. russula* consists of small units (about four monogamous breeding pairs) linked by a strong and essentially male coancestry. These units presumably consist of those individuals that aggregate in communal nests for overwintering, a point that awaits empirical investigation. Our expectation from evolutionary theories of the family (Emlen 1995) is that longer-term field studies will reveal male dynasties (patrilines) closely linked to favorable overwintering places. Because composts constitute such favorable places, individual gardens might indeed act as dynastic territories.

Our study supports the theoretical expectation (Chesser et al. 1993b) that the peculiar breeding system investigated (monogamy and female dispersal) is less efficient than typical mammalian systems (polygyny and male dispersal) in building up kinship structures. Although coancestry within breeding groups may reach 17–20% under polygyny (Chesser et al. 1993b), it did not exceed 10% in our case. Furthermore, this last value could only be reached because of the partial philopatry of the dispersing sex (female), that is, at the cost of some inbreeding. This system therefore does poorly when it comes to building kinship while avoiding inbreeding. However, it may prove very efficient in boosting effective sizes and retaining genetic variance within subpopulations. This last point deserves further examination.

Acknowledgments

This research was supported by the Swiss National Foundation, grants 3130-038762 to NP and 31-43443.95 to NP

and JG. The comments by two anonymous referees helped clarifying the presentation of our work. We dedicate this paper to P. Vogel, for his everlasting and infectious enthusiasm for shrews.

Literature Cited

Cantoni, D., and P. Vogel. 1989. Social organization and mating system of free ranging, greater white-toothed shrews, *Crocidura russula*. Anim. Behav. 38: 205–214.

Chakraborty, R., and J. V. Neel. 1989. Description and validation of a method for simultaneous estimation of effective population size and mutation rate from human population data. Proc. Nat. Acad. Sci. USA 86:9407–9411.

Chesser, R. K. 1991a. Gene diversity and female philopatry. Genetics 127:437–447.

———. 1991b. Influence of gene flow and breeding tactics on gene diversity within populations. Genetics 129:573–583.

Chesser, R. K., O. E. Rhodes, D. W. Sugg, and A. Schnabel. 1993a. Effective sizes for subdivided populations. Genetics 135: 1221–1232.

Chesser, R. K., D. W. Sugg, O. E. Rhodes, J. M. Novak, and M. H. Smith. 1993b. Evolution of mammalian social stucture. Acta Theriol. 38:163–174.

Clutton-Brock, T. H. 1989. Female transfer and inbreeding avoidance in social mammals. Nature 337:70–72.

Cockerham, C. C. 1969. Variance of gene frequencies. Evolution 23:72–84.

———. 1973. Analysis of gene frequencies. Genetics 74 :679–700.

Cockerham, C. C., and B. S. Weir. 1993. Estimation of gene-flow from *F*-statistics. Evolution. 47:855–863.

Dallas, J. F., F. Bonhomme, P. Boursot, J. Britton-Davidian, and V. Bauchau. 1998. Population genetic structure in a robertsonian race of house mice—evidence from microsatellite polymorphism. Heredity 80:70–77.

Dobson, F. S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. Anim. Behav. 30:1183–1192.

Emlen, S. T. 1995. An evolutionary theory of the family. Proc. Nat. Acad. Sci. USA 92:8092–8099.

Ewens, W. J. 1972. The sampling theory of selectively neutral alleles. Theoret. Popul. Biol. 3:87–112.

Favre, L., and F. Balloux. 1997. Characterization of microsatellite loci in the greater white-toothed shrew *Crocidura russula*. Mol. Ecol. 6:211–212.

Favre, L., F. Balloux, J. Goudet, and N. Perrin. 1997. Female-biased dispersal in the monogamous mammal *Crocidura russula*: evidence from field data and microsatellite patterns. Proc. R. Soc. Lond. B Biol. Sci. 264:127–132.

Frame, L. H., J. R. Malcolm, G. W. Frame, and H. van Lawick. 1979. Social organization of African wild dogs (*Lycaon pictus*) on the Serengeti plains, Tanzania, 1967–1978. Zeitschr. Tierpsychol. 50:225–249.

Genoud, M., and J. Hausser. 1979. Ecologie d'une population de *Crocidura russula* en milieu rural montagnard. Terre et Vie 33:539–554.

Gliddon, C. J., and J. Goudet. 1995. The genetic structure of metapopulations and conservation biology. Pp. 107–114 *in* V. Loeschke, J. Toniuk, and S. Jain, eds. Conservation genetics. Birkhäuser Verlag, Basel, Switzerland.

Goudet, J. 1995. Fstat V1.2. A computer program to calculate *F*-statistics. J. Hered. 86:485–486.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. 28:1140–1162.

———. 1983. Mating systems and the evolutionary consequences of dispersal. Pp. 116–131 *in* I. R. Swingland and P. J. Greenwood, eds. The ecology of animal movement. Clarendon, Oxford.

Greenwood, P. J., and P. H. Harvey. 1982. Natal and breeding dispersal in birds. Annu. Rev. Ecol. Syst. 13:1–21.

Hamilton, W. D. 1972. Altruism and related phenomena, mainly in social insects. Annu. Rev. Ecol. Syst. 3:193–232.

Jarne, Ph., and P. J. L. Lagoda. 1996. Microsatellites, from molecules to populations and back. Trends Ecol. Evol. 11:424–429.

Jeanmaire-Besançon, F. 1986. Estimation de l'âge et de la longévité chez *Crocidura russula*. Acta Oecol. 7:355–366.

———. 1988. Sexual maturity of *Crocidura russula*. Acta Theriol. 33:477–485.

Johnson, M. L., and M. Gaines. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annu. Rev. Ecol. Syst. 21:449–480.

Keane, B., S. R. Creel, and P. M. Waser. 1996. No evidence of inbreeding avoidance or inbreeding depression in a social carnivore. Behav. Ecol. 7:480–489.

Nei, M. 1973. Analysis of gene diversity in subdivided populations. Proc. Nat. Acad. Sci. USA 70:3321–3323.

Packer, C., and A. Pusey. 1993. Dispersal, kinship, and inbreeding in African lions. Pp. 375–391 *in* N. W. Thornhill, ed. The natural history of inbreeding and outbreeding. Univ. of Chicago Press, Chicago.

Queller, D. C., and K. F. Goodnight. 1989. Estimating relatedness using genetic markers. Evolution 43:258–275.

Reeve, H. K., D. F. Westneat, W. A. Noon, P. W. Sherman, and C. F. Aquadro. 1990. DNA "fingerprinting" reveals high levels of inbreeding in colonies of the eusocial naked mole-rat. Proc. Nat. Acad. Sci. USA 87:2498–2500.

Rice, W. R. 1989. Analysing tables of statistical tests. Evolution 43:223–225.

Sambrook, J., E. F. Fritsch, and T. Maniatis. 1989 Molecular cloning: a laboratory manual. 2d ed. Cold Spring Harbor Laboratory Press, New York.

SAS Institute. 1989. SAS/STAT user's guide. Vers. 6. Vol. 1. SAS Institute Inc., Cary, NC.

Slatkin, M. 1985. Gene flow in natural populations. Annu. Rev. Ecol. Syst. 16:393–430.

———. 1993. Isolation by distance in equilibrium and non-equilibrium populations. Evolution 47:264–279.

Smale, L., L. Frank, and K. E. Holekamp. 1993. Ontogeny of dominance in free-living spotted hyaenas: juvenile rank relationships with adult females and immigrant males. Anim. Behav. 46:467–477.

Sugg, D. W., and R. K. Chesser. 1994. Effective population sizes with multiple paternity. Genetics 137:1147–1155.

Sugg, D. W., R. K. Chesser, F. S. Dobson, and J. L. Hoogland. 1996. Population genetics meets behavioral ecology. Trends Ecol. Evol. 11:338–342.

Trivers, R. 1985. Social evolution. Benjamin/Cummings Publishing Company, Menlo Park, CA.

Weir, B. S. 1996. Genetic data analysis. II. Sinauer, Sunderland, MA.

Whitlock, A. C., and N. H. Barton. 1997. The effective size of a subdivided population. Genetics 146:427–441.

Wright, S. 1921. Systems of mating. Genetics 6:111–178.

———. 1943. Isolation by distance. Genetics 28:114–138.

———. 1951. The genetical structure of populations. Ann. Eugen. 15:323–354.

———. 1977. Evolution and the genetic of populations. Vol. 3. Experimental results and evolutionary deductions. Univ. of Chicago Press, Chicago.

Wolfram, S. 1991. Mathematica. A system for doing mathematics by computer. 2d ed. Addison-Wesley Publishing Company, Inc., Redwood City, CA.

Corresponding Editor: J. Neigel