SOCIAL SUBDIVISION INFLUENCES EFFECTIVE POPULATION SIZE IN THE COLONIAL-BREEDING BLACK-TAILED PRAIRIE DOG

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Using a long-term study of black-tailed prairie dogs (*Cynomys ludovicianus*), we asked whether subdivision of a subpopulation (colony) into social breeding groups (coteries) influenced gene dynamics. We measured gene dynamics with common statistical tools, *F*-statistics and effective population size (N_e), but at a finer scale to account for coteries. We used 2 methods of estimating the gene dynamics of subgroups, and determined if these methods produced similar results that were congruent with an empirical measure of the observed effective population size (N_{eO}). Modified *F*-statistics were estimated from pre- and postdispersal data from pedigrees and allozymes. Both indicated significant genetic substructuring of the colony subpopulation into coterie breeding groups. The rate of inbreeding of individuals relative to the coterie lineage indicated lower than expected inbreeding at the coterie level. Inbreeding of individuals relative to the colony was consistent with random mating. Asymptotic effective size estimates varied substantially. Chesser's method produced estimates of 77 (range 69–90, pedigree) and 86 (range 70–111, allozyme) individuals consistent with the N_{eO} of 76 and previous empirical estimates of the instantaneous asymptotic effective size from pedigrees (92.9). Nunney's method produced much lower estimates of approximately one-half the N_{eO}. Social subdivisions of the colony into coteries clearly influenced gene dynamics. Only the Chesser method accounted for genetic structure introduced by genealogy, both from polygynous mating and matrilines of philopatric females. This may prove important when estimating the rate of loss of genetic variation in highly social mammals.

Key words: breeding groups, colony, *Cynomys ludovicianus*, effective population size, *F*-statistics, gene dynamics, inbreeding, matrilines, philopatry, polygyny

The genetic properties of populations can be strongly influenced by population subdivision. Wright (1969) envisioned this in a geographical framework, where the complete population (metapopulation) was broken into smaller "island" subpopulations. Within the subpopulations, individuals mate randomly, but mating is nonrandom in the total population. Thus, the genetic properties of both the subpopulations and population are strongly influenced by the degree of dispersal among the islands. If dispersal is low, then subpopulations become genetically different from each other. If dispersal is high, then subpopulations remain genetically similar. Chesser (1991a, 1991b) noted that such subdivision could occur in social, cooperatively breeding species, where breeding groups act in the same way as subpopulations, but at a finer spatial scale. Several mammalian species exhibit social breeding groups, coupled with male polygyny and female philopatry (Dobson 1998; Emlen 1997; Hayes 2000; Nievergelt et al. 2002). Dispersal among breeding groups should affect the gene dynamics of social mammals, perhaps in a similar manner to dispersal among subpopulations (Sugg et al. 1996). Thus, there are potentially several hierarchical levels of population subdivision that influence the gene dynamics of the larger metapopulation.

Wright (1969) described the gene dynamics of a subdivided population with *F*-statistics. F_{ST}, the degree of genetic differentiation among subpopulations, reflects the genetic correlation among individuals within a subpopulation, relative to the

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average genetic correlation among individuals in the overall population. F_{IS} indicates deviation in the rate of inbreeding of individuals from an expectation of random mating within the subpopulation. F_{IT} likewise indicates deviation in the rate of inbreeding from random mating, but relative to the entire population. Thus, F-statistics reveal much of the dynamics of genetic variation, especially with respect to inbreeding. However, F-statistics do not directly indicate how rapidly genetic variation is lost from a population.

To estimate the rate of loss of genetic variation, Wright (1938) developed the idea of a genetically effective population size (N_e). The effective size of a population is a theoretical construct that describes the rate of loss of neutral genetic variation in an observed population (Wang and Caballero 1999). N_e can be thought of as an unbiased estimator of the actual gene dynamics of an observed population, which takes into account all of the differences between observed and ideal populations, such as fixed and equal numbers of males and females that mate randomly, without any mutation, selection, or dispersal (Caballero 1994). In an ideal population, mating between relatives occurs even if mating is random and the population is large. As a result, genetic variation is inevitably reduced. One estimate of N_e is to calculate the rate of change in the inbreeding coefficient, F: $N_e = 1/2\Delta F$ (Wright 1969). ΔF is the change in the inbreeding coefficient between parents and offspring, relative to the remaining genetic variation. Inbreeding N_e approximates how rapidly genetic variation is lost in a population, and over time it converges with variance N_e (an estimate of N_e that reflects gene-frequency drift—Crow and Denniston 1988) at the asymptotic N_e value (Wang and Caballero 1999). We focused on comparing asymptotic N_e, deviations from an ideal population, and their effects on the maintenance of genetic variation.

Estimates of N_e can be informatively compared to the census size (N_T) of the population for which it was calculated, to examine the loss of genetic variation (Nunney and Campbell 1993; Schwartz et al. 1999). If N_e is smaller than N_T, then genetic variation is being lost more rapidly from the real population than is expected. This should be common because adult sex ratios are seldom unity (Wright 1969), N_T varies over time (Frankham 1995), and nonrandom mating is common (Jennions and Petrie 1997). Nunney (1996) and Vucetich et al. (1997) have suggested that N_e is usually about half of N_T, and Frankham (1995) argued that N_e is often much smaller than this, reflecting highly elevated rates of the loss of genetic variation due to fluctuations in N_T. On the other hand, population subdivision due to social breeding groups can increase estimates of N_e to N_T (Chesser et al. 1996; Dobson et al. 2000a, 2004; Sugg et al. 1996). Although population subdivision of diploid organisms often leads to a decrease in N_e (Whitlock and Barton 1997), subdividing a population into breeding groups of several philopatric females with a single unrelated male as a common mate results in minimal variance lost in the paternal genetic contribution to offspring. Under these conditions, N_e can exceed N_T (Wang and Caballero 1999).

Currently there are 2 approaches for estimating the N_e and gene dynamics of subpopulations that are further subdivided by social groups. Based on the genetic correlation approach of Cockerham (1973), Chesser (1991a, 1991b) estimated F-statistics for subpopulations that are further divided into social "breeding groups," where F_{LS} is the degree of genetic differentiation among breeding groups within a subpopulation, F_{IL} is the deviation in the rate of inbreeding of individuals from what would be expected if there were random mating within a breeding group, and F_{IS} is the deviation in the rate of inbreeding from that expected under random mating, relative to the subpopulation. Chesser's approach has been extended to estimating N_e (Chesser et al. 1993), including under conditions such as multiple paternity and uniparental inheritance (Chesser and Baker 1996; Sugg and Chesser 1994).

In the 2nd approach, Nunney (1999) used more traditional estimates of F-statistics (Nei 1987) to estimate N_e for a subpopulation divided into groups of arbitrary size and number. This approach reduces N_e from N_T when distributions of successful matings do not follow a Poisson distribution, and where variances in male, female, and group reproductive success can be measured. In both approaches, the level of population structure due to mating within social breeding groups can be incorporated.

Basset et al. (2001) used computer simulations to test Chesser's and Nunney's models of the gene dynamics within subdivided subpopulations and found that Chesser's approach was inappropriate in monogamous species without sex-biased dispersal. Nunney's approach was more generally applicable, but requires knowledge of difficult-to-measure population parameters such as lifetime reproductive variance for both sexes and knowledge of whether population regulation occurs at the level of local breeding groups or the whole subpopulation. In their analysis, Basset et al. (2001) assumed the former. Furthermore, the 2 approaches differ in the data used to estimate gene dynamics. In Chesser's approach, gene dynamics may be estimated for the offspring generation, before dispersal from the natal breeding groups (e.g., Dobson et al. 2004). In Nunney's approach, gene dynamics are estimated for the parental generation, after dispersal. To compare these approaches, Basset et al. (2001) made several simplifying assumptions, to determine the most general formula applicable to a range of species.

The purpose of our study was to apply these 2 approaches to a typical mammalian species with a polygynous mating system and strongly male-biased dispersal. We applied each method to black-tailed prairie dogs (*Cynomys ludovicianus*), which is one of the best-studied species of small mammal (Hoogland 1995, 2006). We incorporated data from both pedigrees and allozyme alleles, using both models of gene dynamics. We avoided the simplified expressions of Basset et al. (2001), and applied our extensive data to the more accurate formulae used in the 2 approaches (Sugg and Chesser 1994: equation 21; Nunney 1999: equation 14). Our basic question was whether these 2 approaches would yield similar estimates of gene dynamics, particularly N_e. The question of whether social breeding groups lead to significant genetic substructure within a subdivided population is controversial and has only been examined in a few studies (see reviews by Dobson 2007; Dobson and

Zinner 2003; Ross 2001). Thus, our ultimate goal was to evaluate whether the gene dynamics of colonial black-tailed prairie dogs were influenced by subdivision into social breeding groups.

Dispersal should have predictable effects on gene dynamics and predispersal and postdispersal estimates of F-statistics and N_e. For example, after dispersal of individuals from a coterie, the degree of genetic differentiation among coteries (F_{LS}) should decline. However, because dispersal is strongly male-biased (Hoogland 1995), F_{LS} should remain positive and significant. Further, we expected that dispersal would have little influence on F_{IS}. At the colony level, given strong sex-biased dispersal, inbreeding should be similar under either predispersal or postdispersal estimates and also should be near 0, reflecting random mating within the colony. Given these 2 expectations, F_{IL} is predicted to be strongly negative, because $(1 - F_{IS}) = (1 - F_{LS})(1 - F_{IL})$ (Wright 1978). Finally, because we applied methods appropriate for calculating N_e from pre- and postdispersal estimates of F-statistics, we expected congruent values of N_e relative to observed effective population size (N_{eO}) from the 2 models.

We also examined the relation N_e/N_T. This important metric has been extended to management consideration in conservation genetics (e.g., Nunney and Elam 1994), and it is highly variable depending on deviations from an ideal population and on how N_T is defined (Frankham 1995). We have eliminated some of this variation by greatly restricting our measure of N_T only to individuals known to have successfully contributed to the annual gene pool. Thus, we consider our measure of N_T to be an empirical measure of N_e (N_{eO}) for our study colony and use it to compare model-based estimates of N_e.

MATERIALS AND METHODS

Field methods.—Black-tailed prairie dogs were studied from 1975 to 1989 at Wind Cave National Park, Hot Springs, Custer County, South Dakota (Hoogland 1995). All research was conducted in a humane manner and met guidelines approved by the American Society of Mammalogists (Gannon et al. 2007) and the Institutional Animal Care and Use Committees at Princeton University and the University of Maryland according to permits held by JLH. The Rankin Ridge study colony and our methods have been previously described (Dobson et al. 2004; Hoogland 1995).

Demography.—In spring, the number of adult and yearling prairie dogs in the colony averaged 123 ($n = 14$ years, range 92–143 prairie dogs) based on the study of Hoogland (1995). The annual average number of juveniles weaned in the colony was 88 (range 41–133) across an average of 20 coteries (range 15–26). Coteries consisted of 1 or 2 adult males, 2–4 adult females that were invariably close relatives, and their young and yearling offspring. Prairie dogs usually begin breeding at 2 years of age, but some yearling females occasionally bred. The mating season occurred in February and March, with 1st emergence of young above ground and subsequent weaning in May and June, 76 days postmating.

Both pedigree and allozyme estimates of F-statistics and N_e have been calculated in previous publications for this study

population (Dobson et al. 1998; Dobson and Zinner 2003; Sugg et al. 1996). In the present study, we restricted the time period to 10 years (1979–1988) and the data to adults with offspring surviving to adulthood in order to determine N_{eO} and allow a comparison of the 2 methods. Unlike our previous studies, we included all the allozyme loci available. Thus, the patterns of gene dynamics that we present are similar to those in previous reports, but the specific estimates vary slightly. In addition, the allozyme-based F-statistics were calculated using Goudet's FSTAT software (Goudet 1995).

Pedigree estimates.—The coancestry between any pair i, j of individuals was calculated using previously described methods (Dobson et al. 2004) and equation 1 from Chesser (1991a, 1991b):

$$\theta_{i,j} = \frac{1}{4}(\theta_{S_iS_j} + \theta_{S_iD_j} + \theta_{S_jD_i} + \theta_{D_iD_j}), \qquad (1)$$

where subscripts S and D denote sire and dam, respectively, for the ith and jth individuals. This expression describes the way in which coancestry accumulates over the generations. The concestry of an individual to itself is $\theta_{i,i} = (1 + F_i)/2$. The inbreeding coefficient of a progeny is equal to the coancestry of its parents:

$$F_i = \theta_{S_iD_i}. \qquad (2)$$

The average inbreeding coefficient in the population was determined over all individuals in the census population (N_T) for a given year, and was calculated as:

$$\overline{F} = \frac{1}{N_T}\sum_{i=1}^{N_T} F_i. \qquad (3)$$

The weighted average coancestry within coteries each year was determined by the summed pairwise coancestries from the pedigree for individual coteries, divided by the number of pairs (dyads) in the ith coterie $[N_i(N_i - 1)]/2$, averaged among the number of coteries (s) in the population (c.f., Chesser 1991a, 1991b):

$$\overline{\theta} = \frac{1}{s}\sum_{i=1}^{s}\frac{2}{N_i(N_i - 1)}\sum_{j=1}^{N_i-1}\sum_{k=j+1}^{N_i}\theta_{i,j,k}. \qquad (4)$$

Similarly, the average correlation of gene frequencies among groups (α) was calculated from the mean coancestry of all individuals in different coteries:

$$\overline{\alpha} = \frac{\sum_{i=1}^{s-1}\sum_{j=1}^{N_i}\sum_{k=i+1}^{s}\sum_{m=1}^{N_k}\theta_{j,m}}{\sum_{i=1}^{s-1}\sum_{k=i+1}^{s}N_iN_k}. \qquad (5)$$

From these equations, we estimated N_e under the methods developed by Chesser et al. (1993) and Sugg and Chesser (1994). For this, we examined only the offspring in each year, because a pedigree analysis at the level of offspring produces an accurate estimate of N_e (Haig and Ballou 2002; Spielman et al. 1977) encompassing predispersal gene dynamics (sensu Basset et al. 2001). We calculated annual time-specific fixation indices (F-statistics) using the average values from equations

3,4, and 5 substituted into the following equations to determine F_{IL}, F_{IS}, and F_{LS}, where subscript "I" indicates the individual, "L" the coterie breeding group (usually a lineage), and "S" the colony subpopulation (Chesser et al. 1993; Cockerham 1973):

$$F_{IL} = \frac{F - \theta}{1 - \theta} \rightarrow F_{IS} = \frac{F - \alpha}{1 - \alpha} \rightarrow F_{LS} = \frac{\theta - \alpha}{1 - \alpha}. \quad (6)$$

From 1979 to 1988, we used these annual F-statistics to estimate N_e (Chesser et al. 1993; Sugg and Chesser 1994):

$$N_e = \frac{1}{2F_{LS}\left[\frac{d_m + d_f - d_m d_f}{2s} + \frac{(kn - 1)(d_m + d_f)}{4(kns - 1)}\right]}. \quad (7)$$

These estimates are for the asymptotic effective size under specific conditions of F, θ, and α that prevail at a given time, and thus may vary slightly from year to year. Annual estimates of N_e were averaged using the harmonic mean (Wright 1969). The variables d_m and d_f are the dispersal rates among coteries for males (1.00) and females (0.02), respectively (Dobson et al. 1997), s is the average number of coteries in the colony (20.2 ± 1.2 SE, $N = 10$ years), and n is the average number of breeding females per coterie (2.64 ± 0.07 SE, $N = 10$ years). Lastly, k is the average lifetime reproductive success of adult females (1.97 ± 0.15 SE, $N = 118$ females). In this approach, reproductive success of males and variation in reproductive success underlie F_{LS}, which was estimated from θ and α for each year (see equation 6), and calculated from the actual pedigree in the population. We calculated N_e using equation 7 from data restricted to marked individuals with a known birth and death date that lived ≥ 2 years and had offspring ≥ 2 years of age. Equation 7 is only appropriate for populations of stable demography and size and that do not exhibit extreme inbreeding (Chesser 1998; Chesser and Baker 1996), which was the case for our colony (Dobson et al. 1997; Hoogland 1992).

To estimate N_e via Nunney (1999), we substituted average annual values from equations 3, 4, and 5 from 1979 to 1988 into equation 6, but included only adult prairie dogs (≥ 2 years old); thus estimating postdispersal F-statistics:

$$N_e = \left[4r(1 - r)N_T\left(1 + \frac{V_s F_{LS}}{g - 1}\right)\right]$$

$$\div \left[\left(\left\{1 - F_{IL} + 8(1 - r)[r^2 + (1 - r)^2]F_{IL}\right.\right.\right.$$

$$+ 2r(I'_{ki} + xI_{ks})(1 + 3F_{IL})$$

$$+ [(1 - r)I_m(1 + xI_{ks}) + (1 - 2r)xI_{ks}](1 + 7F_{IL})$$

$$\times (1 - F_{LS}) + 4r(1 - r)V_s\left[\frac{2gN_s F_{LS}}{(g - 1)}\right]\right\}\right)\right]. \quad (8)$$

We included only individuals older than yearlings, because yearlings rarely bred and were a small fraction of the population (Hoogland 1995). In this model, the number of groups (g) can be defined at any level of population structure. We chose to define g as coteries, which is the same value as s in equation 7. In addition, we calculated r, the proportion of males in the colony subpopulation (0.33 ± 0.02 SE, $N = 10$ years) and N_s, the number of adults in a coterie (3.95 ± 0.16 SE,

$N = 10$ years). The standardized variance in male reproductive success, I_m, was 0.72. The standardized variance in female reproductive success, I_k, was 0.69. The island component of the variance in female reproductive success, I_{ks}, was 1.96. The variable x describes the regulation of group reproductive productivity, from local regulation where each group is equally productive, to global regulation where groups can differ in productivity. From these last 2 values and for specific values of x, it was possible to estimate I_{ki} and I'_{ki}, the uncorrected and corrected individual components of the variance in female reproductive success, respectively:

$$I_k = I_{ki} + xI_{ks} = \frac{1}{k} + I'_{ki} + xI_{ks}. \quad (9)$$

The variable k is the mean net fecundity of females, and we used the same empirically estimated value as we did for Chesser's methods. The overall standardized variance in the productivity of islands, V_s, was calculated using these parameters and Nunney's (1999) equation:

$$V_S = x\left[\frac{I_{ki}}{N_S(1 - r)} + I_{ks}\right]. \quad (10)$$

Typically, population genetics models are based on the assumption that local regulation of group productivity is complete ($x = 0$), where all breeding groups produce the same number of migrants (Basset et al. 2001). From Nunney (1999), the value of x can vary from 0 to 1, and at the latter value population regulation is global and successful islands contribute many more migrants. We calculated N_e of the prairie dog population using this range of x values and annual estimates of N_e were harmonically averaged.

Allozyme and pedigree-based F-statistics.—Blood samples were collected from virtually all active prairie dogs in the colony and allozyme-based F-statistics were calculated as previously described (Dobson et al. 2004). Pedigree-based annual F-statistics were calculated from 1979 to 1988 for offspring via equations 6 and 7. This procedure produced predispersal estimates of N_e (Chesser et al. 1993; Sugg and Chesser 1994). To estimate N_e via Nunney (1999), we estimated F-statistics as above, but only for prairie dogs older than yearlings, and substituted these estimates into equation 8, producing postdispersal estimates of N_e. To evaluate each model we compared their estimates of N_e to N_{eO} for the prairie dog data set.

RESULTS

As expected, predispersal and postdispersal estimates of F-statistics were very different; however, both showed significant genetic differentiation among coteries (Table 1; reviewed by Dobson 2007). Before dispersal, F_{LS} was close to 0.17, the predicted value for mean relatedness of offspring within coteries (Dobson et al. 2000b). After dispersal, coteries exhibited a lower, but still significant level of genetic differentiation (about 0.04). Both before and after dispersal, significant negative values of F_{IL} likely reflected the nearly complete dispersal of yearling males from natal coteries (Dobson et al. 1998). Although some pre- and postdispersal values of F_{IS} had

TABLE 1.—The *F*-statistics for a colony of black-tailed prairie dogs. Individuals are labeled *I*, breeding groups (coteries) are labeled *L*, and the subpopulation (colony) is labeled *S*. Values are means of 10 years of annual sampling. Confidence intervals (*CI*s) are for the 10 annual values. Predispersal estimates were calculated for offspring in each year, and postdispersal estimates were calculated for prairie dogs ≥ 2 years of age in each year. Estimates were based on pedigrees and allozyme data.

|	F_{LS} ($\bar{X} \pm CI$)	F_{IL} ($\bar{X} \pm CI$)	F_{IS} ($\bar{X} \pm CI$)
Predispersal			
Pedigree	0.186 ± 0.034	-0.223 ± 0.053	0.000 ± 0.019
Allozyme	0.167 ± 0.053	-0.208 ± 0.168	0.080 ± 0.025
Postdispersal			
Pedigree	0.049 ± 0.009	-0.056 ± 0.010	-0.005 ± 0.002
Allozyme	0.032 ± 0.027	-0.059 ± 0.041	0.015 ± 0.013

confidence intervals indicating significant differences from 0, all values were low and close to 0.

The harmonic average N_{eO} was 76.2 (range 54–109, $n = 10$ years). Chesser's N_e (equation 7) using pedigree and predispersal data was slightly higher than N_{eO} (harmonic average = 77.0, range = 68.5–89.6; Fig. 1a). Chesser's N_e from allozyme data was 85.6 (range 69.7–110.7). The allozyme estimates were more variable relative to pedigree estimates.

Nunney's N_e (equation 8) varied according to the level of local versus global population regulation (Fig. 1b). However, the field data were inconsistent with some of the potential levels of regulation. Variance-corrected individual female reproductive success (I'_{ki}) was only positive when *x* values were between 0 and 0.177, becoming negative at higher values of *x*. Negative components of variance in reproductive success seem unlikely to occur in nature. Nonetheless, we examined values of N_e for values of *x* between 0 and 0.4 (Fig. 1b), and found a decreasing function for estimates based on both the pedigree and allozyme data. We had no estimate of *x* from field data, but a value of 0.14 was consistent with the assumptions that N_e is typically one-half N_T and that measurements of bias and precision should be based on one-half N_e (Nunney 1996; Vucetich et al. 1997; Wang and Whitlock 2003). Remarkably, pedigree estimates of N_e (using $x = 0.14$) exhibited little variation, perhaps because the *F*-statistics also exhibited little variation (Fig. 1c; Table 1). N_e from the pedigree data was about one-half N_{eO} (harmonic mean = 38.4, range 37.4–39.2, $n = 10$ years). Average allozyme estimates of N_e were slightly more variable (39.5, range = 36.5–46.9, $n = 10$ years). When $x = 0$, the harmonic mean N_e was still lower than N_{eO} (pedigree estimate = 55.1, range 46.9–61.6; allozyme estimate = 54.4, range 35.4–147.0).

DISCUSSION

Our primary purpose was to answer the question of how coteries influence the genetic structure of the larger colony. Genetic differences among coteries were exhibited, as reflected by significant F_{LS} values, even when measured after the genetic homogenization caused by male dispersal. These genetic
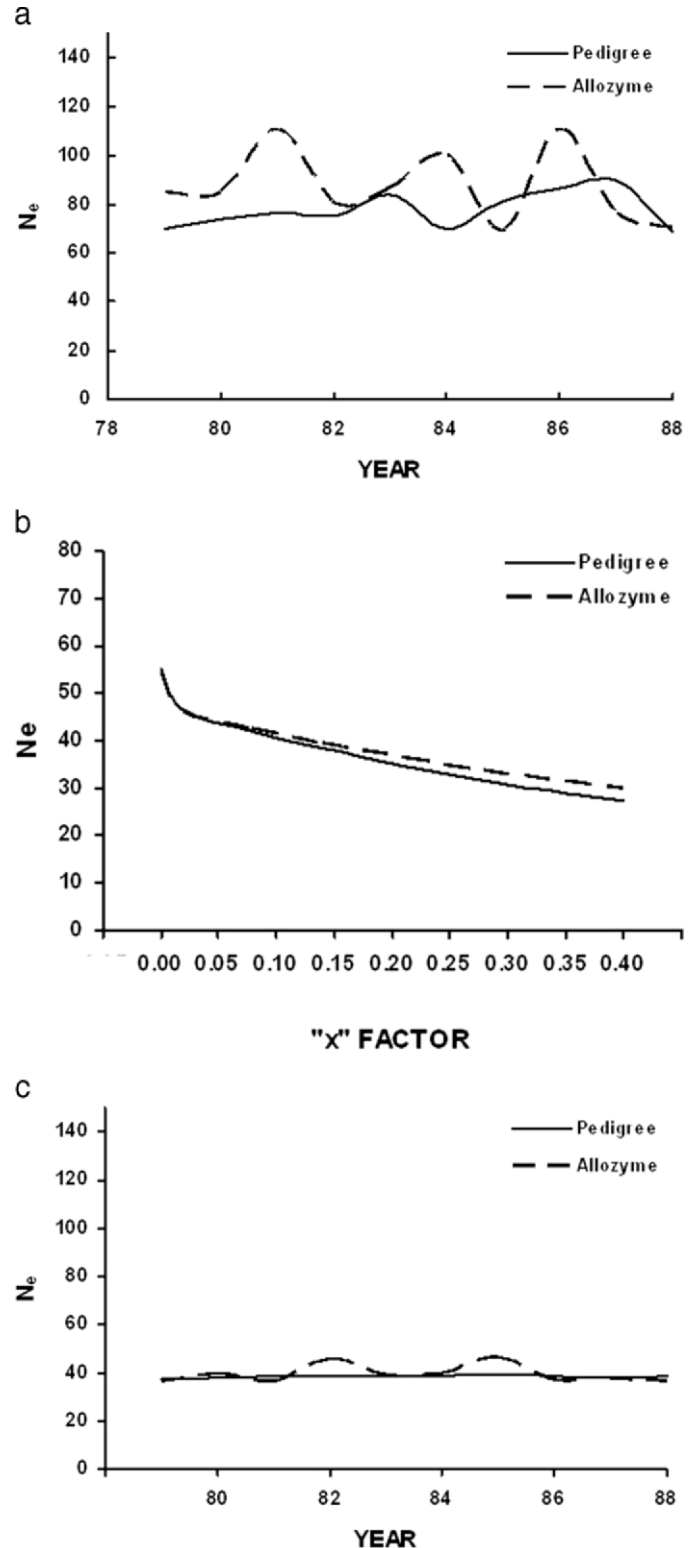
FIG. 1.—a) Annual estimates of effective population size (N_e) for a colony of black-tailed prairie dogs, using equation 21 of Sugg and Chesser (1994). b) Annual estimates of N_e for a colony of black-tailed prairie dogs, using equation 14 of Nunney (1999). The different values of *x* (the degree of local versus global regulation of colony productivity) produce different estimates. c) Annual estimates of N_e for a colony of black-tailed prairie dogs, using equation 14 of Nunney (1999). A value of $x = 0.14$ was used. Solid lines indicate estimates from gene correlations measured from pedigrees; dashed lines indicate estimates from allozyme data.

differences are due to the matrilineal genealogies of coteries, even though coteries occasionally fission (Hoogland 1995; Manno et al. 2007). Considerable outbreeding occurs in prairie dog coteries, in part because of the avoidance of consanguineous mating (Hoogland 1992). This conclusion is supported by the significantly negative pre- and postdispersal estimates of F_{IL}. However, as the spatial scale is expanded to the colony and regional levels of sampling (indicated by F_{IS}, and F_{IX} values for higher levels of population structure) this value becomes close to 0 and then positive, because of the limits of the dispersal distance of individual prairie dogs (Dobson et al. 1997). This effect simply indicates that mating between individuals is more likely at local than regional spatial scales (Wright 1969).

We studied gene dynamics of black-tailed prairie dogs using 2 models incorporating the potential effects of coteries on the larger subpopulation or colony. Following earlier empirical work (reviewed by Dobson 2007) and a simulation study (Basset et al. 2001), we analyzed data gathered before dispersal for the Chesser approach and after dispersal for the Nunney approach. These 2 approaches do not necessarily differ in the way that F-statistics are calculated, but they differ in the way that F-statistics are applied to estimate N_e. In specific applications, they may also differ in the timing of population sampling (Dobson 2007). Chesser's approach uses the information contained in genetic correlations to estimate N_e, whereas Nunney's approach makes a number of adjustments to N_T for variations in male, female, and breeding-group reproduction, with adjustments for the genetic structure of the population through F-statistics. We found substantial differences in estimates of N_e using these 2 approaches; however, Basset et al. (2001) concluded that the 2 approaches produced very similar estimates for polygynous species with male-biased dispersal, such as prairie dogs,

This particular conclusion of the study by Basset et al. (2001) was predicated on simplifying assumptions that may be untenable for black-tailed prairie dogs. These assumptions include an equal adult sex ratio, a Poisson distribution of female reproductive success, a coterie size of 50, 200 coteries in a colony, and complete local regulation of breeding group productivity. Using these assumptions, Basset et al. (2001) reduced Nunney's (1999) estimate of N_e to a simplified formula (their equation 3). In addition, they also substituted an approximation of the full estimate of N_e (their equation 2) derived by Chesser et al. (1993). We used the more complete formulae of Nunney and Chesser in order to examine whether these methods produce similar estimates of N_e for a polygynous species where multiple paternity is uncommon (Hoogland and Foltz 1982), and co-occurs with strong male-biased dispersal (Hoogland 1995).

The pre- and postdispersal F-statistics were consistent with our expectations (Table 1). Predispersal F_{LS}, in Chesser's N_e, reflected the average degree of relatedness among coterie offspring, at a predicted value of one-sixth when inbreeding is low (Dobson et al. 2000b). Pedigree estimates of F_{LS} may have been slightly inflated by the occasional infanticide of complete litters. F_{IL} was strongly negative, as expected, because the nearly complete dispersal of males effectively distributes their genetic

contributions among the coteries (Hoogland 1995). This pattern indicates an inbreeding coefficient (F) that is lower than expected with random mating of offspring within coteries (Dobson et al. 1997, 1998). Finally, our F_{IS} values indicate that in the prairie dog colony, mating and dispersal patterns have produced an F-value that is consistent with random mating within the colony.

The postdispersal calculation of F_{LS}, in Nunney's N_e, was much lower than the predispersal value, reflecting the genetic homogenization that occurs when males disperse (Table 1). F_{LS} was still significant, however, reflecting the relatedness within matrilines of philopatric females (Dobson 2007). Estimated F_{IL} also was significant and negative, indicating that F was lower than expected and heterozygosity somewhat higher than expected, due at least in part to the avoidance of consanguineous mating (Hoogland 1992). F was much closer to what would be predicted from random mating within the overall colony, as reflected by F_{IS} values near 0. Thus, although pre- and postdispersal F-statistics were very different, they both indicated patterns of gene dynamics consistent with the mating, dispersal, and demography of black-tailed prairie dogs (Hoogland 1995).

However, our estimates of N_e present a less consistent picture. Chesser's method (Chesser et al. 1993; Sugg and Chesser 1994) produced estimates of N_e from pedigree and allozyme data (Dobson et al. 2004) that were slightly higher than N_{eO}. This may be due to nonindependent offspring mortality resulting from infanticide of complete litters. However, our inclusion of only adult (≥ 2 years of age) offspring should minimize this effect (Rockwell and Barrowclough 1995). Nunney's (1999) method produced estimates that depend in part on his "x" factor that describes the regulation of reproductive productivity. Methods of estimating x have not been described, so we conservatively applied a range of values. The resulting estimates of N_e were much lower than N_{eO} (Fig. 1b). A moderate value of $x = 0.14$ yielded estimates of N_e that were approximately one-half N_{eO} (Fig. 1c), consistent with previous assumptions (Nunney 1996; Nunney and Elam 1994; Vucetich et al. 1997).

Based on our results, the outcomes of these 2 approaches differ greatly. Consequently, the conclusion of Basset et al. (2001) that these methods should yield similar estimates for polygynous species with strongly male-biased dispersal may need modification. Our results may differ due to assumptions of an equal adult sex ratio (averaging about one-third male—Hoogland 1995) or more importantly a Poisson distribution of reproductive success ($\bar{X} = 2.00$, variance $= 1.44$—Dobson et al. 1997; see also Rockwell and Barrowclough 1995). Basset et al. (2001) attempted to assess which of these 2 methods is more generally applicable, and thus examined a variety of mating and dispersal patterns. It is perhaps not surprising that a more-detailed study of a single species with a single mating system and dispersal pattern, based on fewer simplifying assumptions, would produce a modified conclusion.

Because the Chesser and Nunney methods differ, it is reasonable to ask which was more appropriate for black-tailed prairie dogs. Chesser's method accounts for the matrilineal and genealogical structure of the population, and incorporates parameters that reflect population substructure and dispersal patterns. This N_e estimate is consistent with our N_{eO} value and

previous estimates of the instantaneous asymptotic N_e for this study population (92.9 from empirical calculation based on the pedigree—Dobson et al. 2004). Our estimate of N_e based on Nunney's (1999) model is inconsistent with these values. In addition, Nunney's method does not specifically incorporate information about genealogy, but requires more detail regarding reproductive variation, including variance components for males, females, and coteries. In particular, the variance in male reproductive success may be difficult to obtain for most species, as it was for *C. ludovicianus* (Foltz and Hoogland 1983). Nunney's method does not include specific estimates of dispersal rates, but perhaps the ''*x*'' factor, *F*-statistics, and variance components of reproductive success incorporate this information. Thus, the question of appropriate method may depend on the importance of explicitly incorporating information about genealogical structure into N_e, or whether it is sufficient for this information to be tacitly included within the different components of reproductive variance.

Two lines of evidence suggest that genealogical structure should be explicitly accounted when calculating N_e for species with polygynous, matrilineal breeding groups. First, genealogical structure often produces significant genetic differentiation among breeding groups. This genetic differentiation occurred for 2 reasons: because offspring in the breeding group are likely to have the same father and because of the genetic structure caused by female philopatry (Chesser 1991a, 1991b). Under these breeding and dispersal conditions, genetic variation is lost slowly, because alleles lost in 1 breeding group are likely represented in other breeding groups (Chesser et al. 1996). The 2nd line of evidence is that using different methods, 2 studies of polygynous primates with matrilineal philopatry (red howler monkeys [*Alouatta* seniculus—Pope 1998] and a Navaho [*Homo sapiens*] community [Long et al. 1998]) also resulted in estimates of N_e at or slightly above N_T. For these reasons, we believe that Chesser's method likely produced a more accurate estimate of N_e for the prairie dogs.

Values of N_e near N_T are surprising, because polygyny is expected to reduce N_e as a result of fewer males breeding and as a result of population fluctuations (reviewed by Frankham 1995; Parker and Waite 1997). Also, N_e typically declines with greater variance in individual or breeding group reproductive success (Wang and Caballero 1999). Further theoretical investigations of the importance of genealogical history and matrilines to N_e are sorely needed, as are sensitivity studies of the parameters and assumptions of the Chesser and Nunney models (Tallmon et al. 2004). The gene dynamics of species with social breeding groups have not been broadly studied (reviewed by Dobson 2007; Storz 1999), and the importance of genealogy to gene dynamics should ultimately be determined from studies of species that exhibit genetic structure due to breeding groups.

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