Population genetics meets behavioral ecology

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Populations are often composed of more than just randomly mating subpopulations – many organisms form social groups with distinct patterns of mating and dispersal. Such patterns have received much attention in behavioral ecology, yet theories of population genetics rarely take social structures into account. Consequently, population geneticists often report high levels of apparent inbreeding and concomitantly low effective sizes, even for species that avoid mating between close kin. Recently, a view of gene dynamics has been introduced that takes dispersal and social structure into account. Accounting for social structure in population genetics leads to a different perspective on how genetic variation is partitioned and the rate at which genic diversity is lost in natural populations – a view that is more consistent with observed behaviors for the minimization of inbreeding.

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Sewall Wright showed that genetic variation (i.e. heterozygosity) can be partitioned into components that reflect population structure[1,2]. The basic model breaks genetic diversity into three components: variation within individuals (H_I); expected variation among individuals in the same subpopulation (H_S); and total variance (H_T) (Ref. 1). These components can be used to partition variation into the fixation indices. Fixation indices describe (1) the proportion of variation within individuals relative to that expected in subpopulations (F_{IS}), and the population (F_{IT}), and (2) the proportion of variation in subpopulations relative to total variance (F_{ST})[1–4].

Wright's method of describing genetic variance is useful for understanding inbreeding and differentiation among population units. Positive F_{IS} and F_{IT} values indicate that individuals in subpopulations or the population, respectively, are more inbred than they would have been had they mated at random. Wright showed that apportionment of variation is related to the rate at which genetic variation is lost[1,5]. The rate at which genetic variation is lost is inversely proportional to the effective population size (N_e).

As the theory of population genetics developed, behavioral ecologists and population biologists were studying many aspects of populations in detail, such as dispersal, breeding tactics and social structure[6–11]. In many species, most individuals of one sex disperse while the other sex is philopatric[12,13]. Patterns of mating other than random mating were found to be quite common[14]. Many organisms exhibit social organizations that give some individuals an advantage in obtaining mates[8,9]. Thus, assumptions of random mating and equal dispersal of the sexes are often unjustified. Two fundamentally different views of how populations are structured have developed: the classical 'subpopulation' of genetics and the 'social structure' view of behavioral ecology (Fig. 1). The classical view envisions organisms mating randomly within subpopulations. In the social structure view, the classical 'subpopulations' are composed of breeding groups with behaviors that determine mating tactics. While this difference may seem trivial, one must recognize that maintenance of genetic variation in the classical models results largely from differentiation among subpopulations and rates of inbreeding. Structure that results from breeding groups provides an additional means by which populations can maintain genetic variation, and by which behaviors may minimize inbreeding.

Social structure is often inferred from the fixation indices (see Box 1) based on sampling that ignores social structure. However, social structures affect the apportionment and loss of genetic variation. Therefore, the very patterns sought by geneticists are hidden by ignoring this aspect of structure. Here, we discuss the theory of gene dynamics in socially structured populations, and explain how the fixation indices and effective sizes can be estimated.

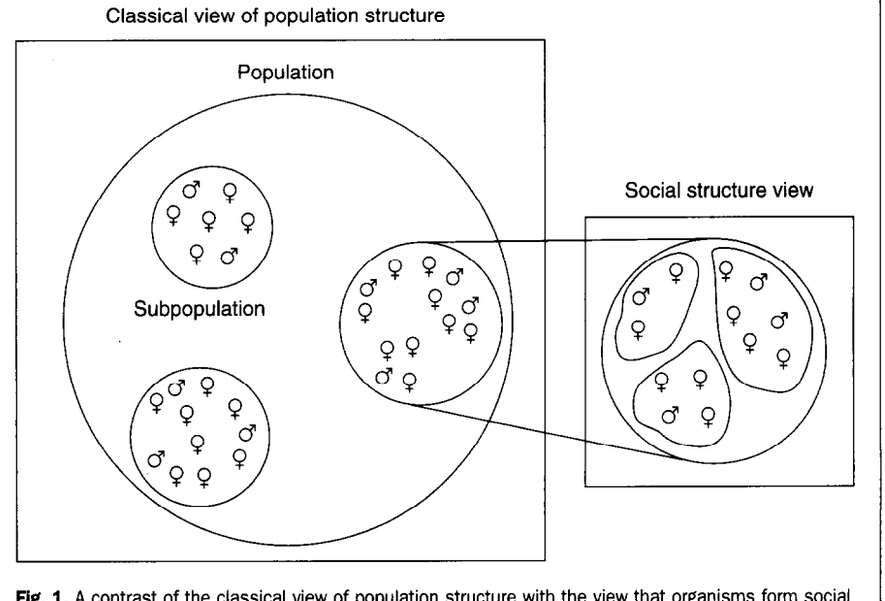

Fig. 1. A contrast of the classical view of population structure with the view that organisms form social affiliations. The classical view takes the approach that subpopulations comprise males and females that mate at random. Conversely, much of the ecological literature suggests that local subpopulations often consist of mating pairs or polygynous groups that prevent complete admixture of genes among the groups. These breeding groups violate some of the assumptions of the classical models and can lead to deviations from Hardy–Weinberg expectations. The breeding group models of population genetics have relaxed these assumptions.

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Accounting for social structure

There have been several attempts to extend the classical models to relax the restrictive assumptions identified by ecologists[15–18]. Here, we concentrate on an approach that explicitly takes social structure into account. The breeding group models describe how sex-specific dispersal rates and mating tactics directly influence gene dynamics[15,16,19,20]. This is accomplished by a series of mathematical equations that describe how genes are passed among individuals within and among social groups. A major difference between breeding group models and other models that address nonrandom mating is the recognition that coancestry may develop more rapidly than inbreeding within social groups. Coancestry is a measure of the kinship of individuals, and, in the absence of inbreeding, it is half the coefficient of relatedness (r) (Ref. 21). These models account for the impact of coancestry on the inbreeding coefficient and the total genetic variation in subsequent generations, thereby integrating changes in genetic diversity at each level[19–21]. Therefore, the models describe the mechanisms by which genetic variation will change because of a particular social structure.

The conceptual importance of coancestry has been recognized for some time, but its application to population genetics has been limited. The average inbreeding coefficient of offspring from a mating is the coancestry of their parents[22]. The idea that coancestry develops within social groups through mechanisms other than inbreeding is fundamentally different from classical theories. In social systems, however, coancestry is maintained primarily by relationships among adults of the philopatric sex. Thus, high values of coancestry can be maintained in the absence of inbreeding[23].

Box 1. Gene correlations and fixation indices

Gene correlations can be estimated from genic data at each level of structure. There are two types of gene correlations, those within individuals (F) and those between individuals (for example, θ, α) (Refs 15,16, 19,20). The table below provides the correlation coefficients within and between individuals for a single locus with two alleles.

Genotype		Correlation coefficient		
Individual 1	Individual 2	Within individual 1	Within individual 2	Between individuals
AA	BB	1	1	0
AA	AB	1	0	0.5
AA	AA	1	1	1
AB	BB	0	1	0.5
AB	AB	0	0	1
BB	BB	1	1	1

Wright developed measures of genetic variation that are related to the gene correlations: heterozygosity within individuals (H_I); expected heterozygosity within subpopulations ($\bar{H}_S$); and expected heterozygosity of the total population (H_T) (Ref. 1). The gene correlations and heterozygosity estimates are related by:

$$H_I = 1 - F$$

$$\bar{H}_S = 1 - \theta$$

$$H_T = 1 - \alpha$$

Both Wright[1] and Chesser[15,16] give formulae that describe how genetic variation is apportioned among the various levels existing in a structured population. These descriptions of the partitioned variance are termed the fixation indices, and one can show that they are identical in expectation:

$$F_{IS} = \frac{\bar{H}_S - H_I}{\bar{H}_S} = \frac{(1-\theta)-(1-F)}{1-\theta} = \frac{F-\theta}{1-\theta}$$

$$F_{IT} = \frac{H_T - H_I}{H_T} = \frac{(1-\alpha)-(1-F)}{1-\alpha} = \frac{F-\alpha}{1-\alpha}$$

$$F_{ST} = \frac{H_T - \bar{H}_S}{H_T} = \frac{(1-\alpha)-(1-\theta)}{1-\alpha} = \frac{\theta-\alpha}{1-\alpha}$$

The identical representations for the fixation indices show that if genes were sampled using the social structure view of population structure, then, applying Wright's methods, one would obtain similar estimates for the fixation indices as provided by the breeding group model. However, most studies do not treat breeding groups as subpopulations and $\bar{H}_S$ does not equal $1-\theta$.

Gene correlations

One of the most useful concepts to arise from a social structure view of populations is the recognition of gene correlations as estimators of genetic diversity. Coancestry is simply the correlation of genes between individuals within the same group. Values are averaged over all loci and over all possible pairs of individuals in a group. Correlations can also be determined between genes within an individual or among all individuals in a population (Box 1). There is a direct relationship between gene correlations and estimates of genetic variation; specifically, one minus the correlation ($1-\rho$) equals the variance[3,4]. Chesser also showed that one can estimate the fixation indices with the gene correlations[15,16]. In a simple three-level hierarchy there are three gene correlations: within individuals (F), coancestry (θ), and the intergroup correlation (α). With gene correlations one can also estimate the rate of loss of variation ($2N_e^{-1}$) because as correlations increase, variation necessarily decreases[19,20].

Hierarchical effective sizes

There are separate effective sizes for each level of structure in a population[19,20]. This notion is contrary to classical approaches, where biologists have concentrated only on the inbreeding and variance effective sizes[1,22]. Because genetic variation can be lost within groups and among groups, it is reasonable to estimate effective sizes for these levels as well. One need not limit correlations to a single collection of breeding groups; there may be collections of subpopulations and populations. Each of these levels will have a separate gene correlation, and hence each is a level at which genetic variation can be lost.

Loss of genetic variation at one level indicates a change in apportionment of variation among levels, causing fixation indices to change over time. When individuals mate with close relatives in a breeding group, both coancestry and inbreeding will increase in the next generation[19,20,22]. However, breeding groups diverge as they approach fixation for alternate genes, and there will be more variation partitioned among them[23]. Thus, the process of inbreeding alone does not necessarily eliminate genetic variation in the population, it reapportions variation among the levels. The avenue for unrecoverable loss of variation is the highest level of structure, and it results from finite size and the resulting genetic drift. From this conclusion, one may infer that the effective size of the highest level is the most important. However, when organisms have constant tactics for breeding, dispersal and mating, all effective sizes converge on a common value[19,20]. Thus, populations that start with unrelated individuals go through two distinct phases of gene dynamics (Fig. 2). A transitional

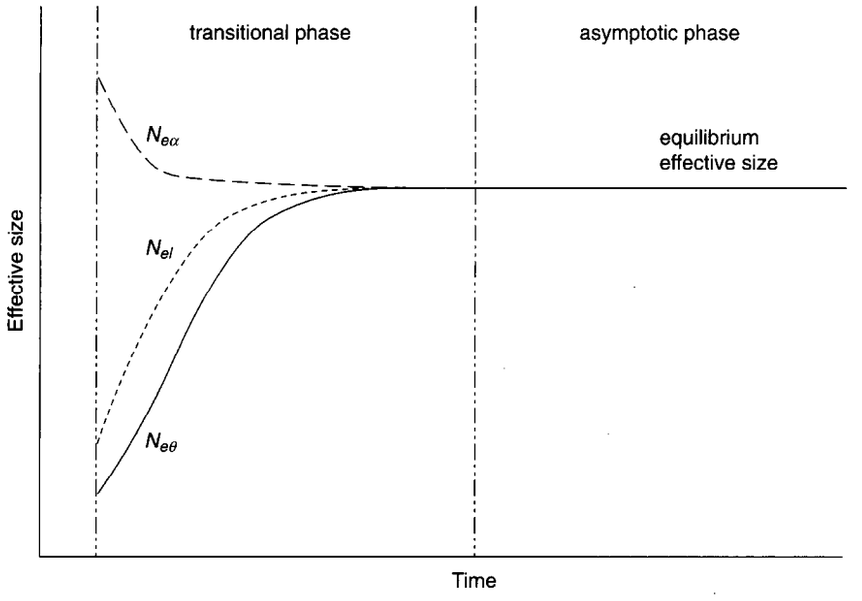

Fig. 2. There are distinct effective sizes of each level in a structured population. In this example, there is an effective size that corresponds to the variation within individuals (N_{el}), within breeding groups ($N_{e\theta}$), and within the total population ($N_{e\alpha}$). With time, the rate of loss of genetic variation at each of these levels becomes equal, and the effective sizes converge on a common, asymptotic value called the equilibrium effective size[19,20].

rate of loss occurs during which genetic variation in unrelated individuals is reapportioned among levels. The asymptotic rate occurs when genetic variation is lost at the same rate for each of the levels and the fixation indices become constant[15,16,19,20].

Regardless of whether demographic parameters are stable or fluctuate over time, one should recognize how genetic variation is preserved at each level. Rapidly increasing coancestry may indicate that genetic variation is being lost within social groups, but it also indicates differentiation, and cooperative behaviors that are tied to kinship can be promoted[24]. Conservation plans that call for mixing individuals of the philopatric sex would stem the loss of genetic variation at this level, but they would also reduce evolutionary payoffs from cooperative behaviors. Such a change may have dire consequences for the demographic stability of populations. This ramification of management plans based on translocations would not be evident if social structure was ignored when estimating loss of genetic variation.

Estimations from behavioral data

Often one does not have genic data, but with some commonly collected behavioral and demographic information one can still estimate some important genetic parameters. The breeding group models provide equations for the change in inbreeding (ΔF), coancestry ($\Delta\theta$) and intergroup correlation ($\Delta\alpha$), in terms of parameters such as number of males and females, dispersal rates and number of offspring produced. Applying estimates of parameters to transition equations will yield the rate at which gene correlations accrue. This information can be used to estimate the different effective sizes.

Box 2 summarizes the necessary parameters using data from Hoogland's book on black-tailed prairie dogs (*Cynomys ludovicianus*)[25]. The behavioral and population ecology of this population were studied intensively for 16 years. Although better estimates of these parameters are available from the original data, the values from the book are presented to demonstrate that even rough estimates give reasonable approximations of the gene dynamics. Prairie dogs live in social groups called coteries, and they have strongly male-biased dispersal. Changes in genetic variation can be estimated from transition equations (see Box 2), assuming that the individuals founding the population were unrelated. The assumption that founders are unrelated may seem restrictive at first; however, this only provides a starting point for the transition and does not affect the asymptotic values. The ultimate goal from behavioral data should be to determine the asymptotic values and not to ascertain current levels of genetic variation. Current levels of genetic variation can only be estimated with genic data from, for example, allozymes or DNA.

Complete transitions for fixation indices and effective sizes of prairie dogs

Box 2. Gene dynamics in prairie dogs

Previous papers have given the critical parameters necessary for determination of gene correlations in socially structured populations[15,16,19,20]. Because prairie dogs exhibit some potential for multiple paternity and females can mate with more than one male during their lifetimes, we use the breeding group model of Sugg and Chesser[20].

Data from Hoogland's book[25] on a colony of black-tailed prairie dogs (*Cynomys ludovicianus*) indicated that there were 1.33 males (m) and 2.72 females (n) per coterie. The entire colony averaged 21 coteries (s) over the period of the study. The average number (l) of mates that females have over their lifetimes was 3.56, and during her life each female produces 2.14 offspring (k) that survive to reproduce themselves, and the variance in that quantity (σ_k^2) was 5.20. The average number (p) of progeny in a single coterie sired by a single male was obtained by dividing k by l (= 0.60). Since it was impossible to estimate the variance in this quantity from the data in the book, we assume that this variable had a Poisson distribution ($\sigma_p^2 = p$) and hence a variance of 0.60. The most difficult quantities to estimate are the mean (b) and the variance (σ_b^2) in the number of females mated by males that produce successful offspring. These estimates were obtained from unpublished data ($b = 1.57$; $\sigma_b^2 = 0.58$). Finally, male dispersal (d_m) is nearly complete and female dispersal (d_f) is nearly absent, so we assigned values of 0.95 and 0.05, respectively, to these parameters.

These critical parameters can be used to estimate the breeding parameters: degree of polygyny (ϕ_m), probability that two offspring of a given mother were sired by the same male (ϕ_w), and the probability that two offspring in a coterie share the same mother (ϕ_f). The expressions for these breeding parameters are as follows:

$$\phi_m = \frac{m\left[\sigma_b^2 + b(b-1)\right]}{ln(n-1)} = \frac{1.33\left[0.58 + 1.57(0.57)\right]}{3.65 \cdot 2.72(1.72)} = 0.12$$

$$\phi_w = \frac{\sigma_p^2 + p(p-1)}{p(k-1)} = \frac{0.6 + 0.6(-0.4)}{0.6(1.14)} = 0.53$$

$$\phi_f = \frac{\sigma_k^2 + k(k-1)}{k(kn-1)} = \frac{5.2 + 2.14(1.14)}{2.14(4.82)} = 0.74$$

With these additional parameters, one can use transition equations provided in Sugg and Chesser[20] to determine how gene correlations, fixation indices and effective sizes will change over time. With prairie dogs as an example, the fixation indices (see Fig. 3a) and effective sizes (see Fig. 3b) asymptote in only a few generations.

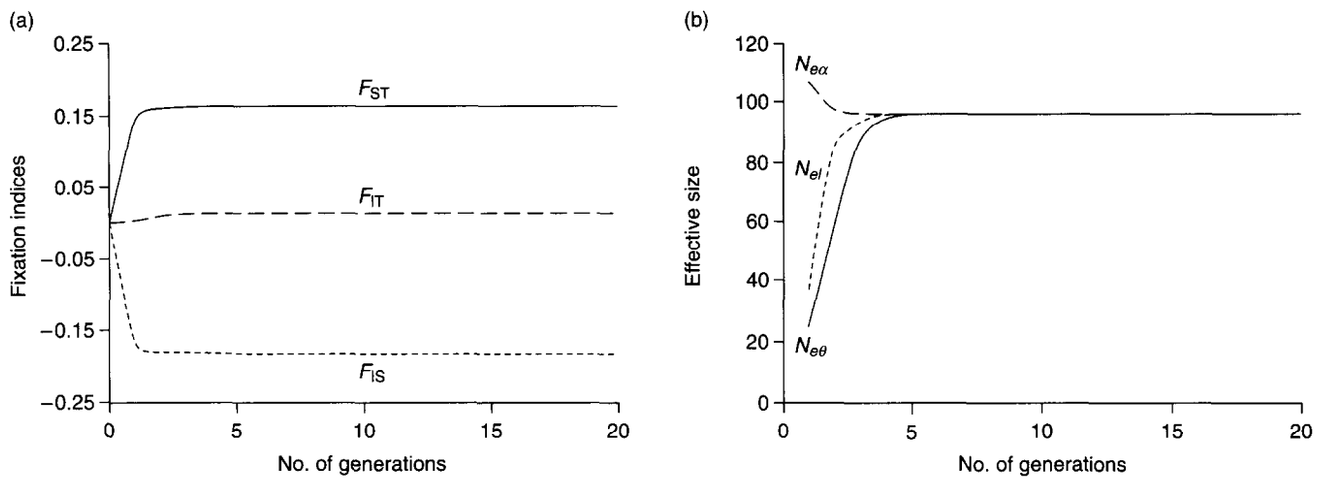

Fig. 3. (a) Genetic variation in a black-tailed prairie dog (*Cynomys ludovicianus*) colony is apportioned among the levels of population structure. The variation within individuals relative to the variation within coteries is given by F_{IS}. The variation within individuals relative to the total variation in the colony is given by F_{IT}. The variation within coteries relative to the total variation is given by F_{ST}. Theory predicts that F_{IS} should be negative if there is no artificial mixing of individuals that represent distinct, randomly mating groups[27,28]. Additionally, the accumulation of substantial differentiation among breeding groups, as indicated by high values for F_{ST}, is important for the evolution of cooperative behaviors within groups[24]. (b) As the variation is reapportioned among the levels of organization in the colony, the effective sizes associated with each converge on an equilibrium size of 94.8, which is greater than the actual number of breeding individuals estimated from behavioral observations. (N parameters as for Fig. 2.)

are presented in Fig. 3. Assuming that the critical parameters used represent long-term averages, the colony should have reached an equilibrium rate of loss of genetic variation in about nine generations. The asymptotic F_{ST} (differentiation among coteries) is 0.16, F_{IT} (inbreeding relative to the colony) is 0.01, and F_{IS} (inbreeding relative to the average coterie) is −0.18. Coteries have diverged genetically because of the matrilocal lines that dominate their social system, and F_{IT} is low because of male dispersal. The negative F_{IS} is an important result for two reasons. Ecologically, it indicates that inbreeding is being minimized by the mating system and dispersal pattern, which leads to the avoidance of mating among close kin[26].

On the genetic side, one expects a positive F_{IS} if randomly mating subpopulations are mixed, a concept called the Wahlund effect[4,15,16,27,28]. Wahlund effects can result from the natural joining of previously isolated populations, and it can be unintentionally produced by combining samples from distinct demes. In prairie dogs, breeding groups represent the natural subdivisions where mating occurs, not the colonies. Unfortunately, F_{IS} values that are significantly less than zero are rare in the literature[29–31]. This is because samples are usually taken from subpopulations of social organisms that mix breeding groups. Traditional measures of F_{IS} are conceptually similar to F_{IT} in the breeding group models. A study of prairie dogs that included Hoogland's colony estimated F_{IS} to be −0.023, which was not significantly different from zero[32]. In fact, this estimate of F_{IS} is very similar to our estimate of F_{IT}; both are essentially zero. Recognition of the breeding groups when sampling avoids the unintentional Wahlund effect.

An asymptotic effective size of 95 for this population indicates the maintenance of considerable genetic variation. Maintenance of variation comes despite the potential for increased coancestry within groups resulting from female philopatry. The asymptotic effective size is greater than the average number of adults (85). This result shows that the colony is losing genetic variation more slowly than if mating was random. More classical estimates of effective size include Wright's for uneven sex ratios, and Crow and Denniston's for variance in reproductive success[1,26]; these models yield estimates for N_e that are 75 and 50, respectively. Thus, classical models dramatically overestimate the rate of loss of genetic variation by underestimating the effective population size. Estimates

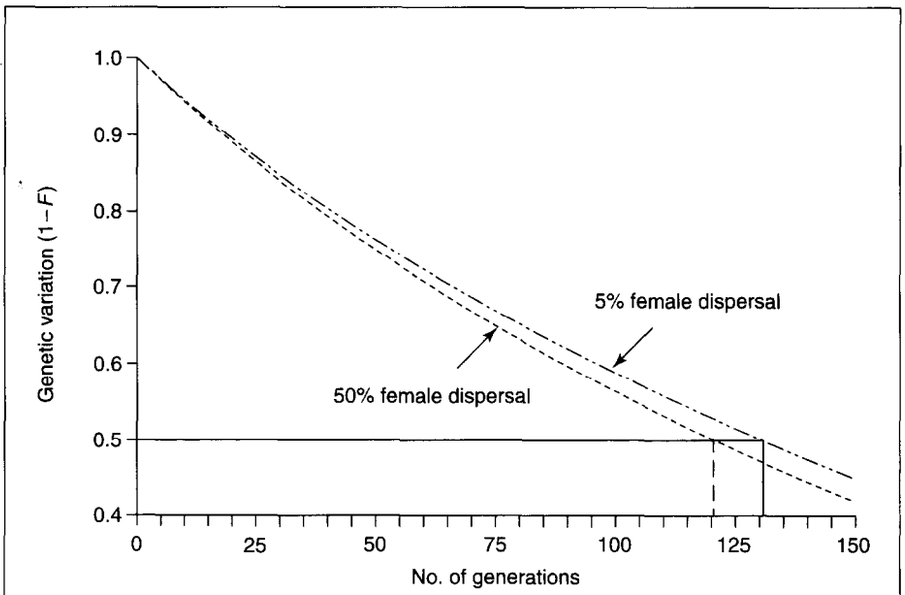

Fig. 4. Time-to-loss of half the genetic variation ($1 - F$) within individuals for two scenarios involving prairie dogs. Increasing the dispersal rate of the normally philopatric females decreases the time it takes to lose a given amount of genetic variation. These scenarios show that conservation strategies that ignore social structure may not have the desired effects. The breeding group models provide the means for biologists to predict the outcomes of particular strategies for socially structured populations.

from pedigrees, allozyme data and the entire behaviorial data set result in very similar estimates of effective size (86, 91 and 93, respectively; unpublished). These estimates are consistent with the value using parameters from Hoogland's book[25].

The results from prairie dogs have implications for both population genetics and behavioral ecology. From the genetics standpoint, one must be careful not to make erroneous interpretations about breeding structure from the fixation indices when samples combine social units. From the behavioral standpoint, the breeding group models offer the means by which to study the effects of mating systems on the loss of genetic variation and the development of coancestry. Such an approach may aid explanations of why organisms form cohesive groups at the apparent risk of inbreeding.

Conservation considerations

The most important aspect of these models for conservation biologists is that they show how social organizations are important for the maintenance of genetic variation. Beliefs that the effective size is much smaller than census number, as often stated in the literature[33,34], overgeneralize a complex problem. The breeding group models provide the opportunity to examine which aspects of an organism's biology influence the maintenance of genetic variation. Through such examinations, conservation biologists can devise better plans for the maintenance of genetic variation for particular species, and perhaps increase the probability that small populations will retain evolutionary potential. One can use the models to predict the time it takes individuals in a population to lose half their genetic variation ($1-F$) under different scenarios. In Fig. 4, the same data for prairie dogs are compared to a situation where female dispersal rate is increased to 50%. This scenario is likened to an attempt to avoid inbreeding in small groups that may be maintained in a breeding program. Increasing female dispersal actually increases the rate of inbreeding slightly, but more importantly, it decreases the half-time for loss of genetic variation by 11 generations. The reason this strategy does not have the desired effect is that the mating system is more efficient at minimizing inbreeding when females are philopatric and males disperse. This result is consistent with behavioral observations that kin recognition in this species is limited to individuals present in a coterie when an individual emerges from the natal burrow. It is these aspects of social biology, which have a profound influence on the gene dynamics, that are often ignored by conservation biology.

Conclusion

Breeding groups are an important component of population structure, yet they are often ignored when geneticists study populations. Because population structure impacts genetic diversity, rather than the reverse, sampling regimes and theoretical models should recognize social structures if they are accurately to predict gene dynamics. Breeding group models have been developed to bridge the gap between what ecologists observe and what population geneticists recognize as important aspects of gene diversity. These models show why sampling subpopulations without accounting for social subdivisions leads to higher than expected levels of homozygosity. The combined use of genetic data and behavioral information will give much better insight into past, present and future dynamics of genetic variation. Such an approach will provide useful information for understanding how social systems are maintained and how genetic variation is preserved.

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