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Testing demographic models of effective population size

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Due to practical difficulties in obtaining direct genetic estimates of effective sizes, conservation biologists have to rely on so-called 'demographic models' which combine life-history and mating-system parameters with *F*-statistics in order to produce indirect estimates of effective sizes. However, for the same practical reasons that prevent direct genetic estimates, the accuracy of demographic models is difficult to evaluate. Here we use individual-based, genetically explicit computer simulations in order to investigate the accuracy of two such demographic models aimed at investigating the hierarchical structure of populations. We show that, by and large, these models provide good estimates under a wide range of mating systems and dispersal patterns. However, one of the models should be avoided whenever the focal species' breeding system approaches monogamy with no sex bias in dispersal or when a substructure within social groups is suspected because effective sizes may then be strongly overestimated. The timing during the life cycle at which *F*-statistics are evaluated is also of crucial importance and attention should be paid to it when designing field sampling since different demographic models assume different timings. Our study shows that individual-based, genetically explicit models provide a promising way of evaluating the accuracy of demographic models of effective size and delineate their field of applicability.

Keywords: *F*-statistics; individual-based models; life history; mating system; sex-specific dispersal

1. INTRODUCTION

The amount of genetic diversity that natural populations can maintain in the face of isolation or fragmentation is a central issue in conservation biology. Extinction probabilities may depend on it in at least two ways. First, low genetic diversity decreases the potential of populations for responding adaptively to environmental changes (Nunney & Campbell 1993). Second, low genetic diversity leads to inbreeding depression, which may significantly increase extinction risks (Saccheri *et al.* 1998). Conservation biologists thus need conceptual tools in order to delineate the ability of populations to resist genetic drift and operational ways of measuring it.

The concept of effective population size (N_e) was developed by Wright (1931) in order to quantify a population's responsiveness to genetic drift. It represents the size of an 'ideal' population that would respond to random processes in the same way as the observed population. Ideal features include panmixis, non-overlapping generations and a Poisson distribution of fecundities. In principle, effective population sizes might be estimated directly from molecular markers. If mutation rates were known, N_e could be inferred from either the observed heterozygosity (Wright 1931) or from allele numbers (Chakraborty & Neel 1989). However, mutation rates normally remain inaccessible, best bets usually ranging over two orders of magnitude (e.g. Jarne & Lagoda 1996). Alternatively, variation in allele frequencies over time could be used, assuming this to be due to random drift only (Waples 1989). However, in practice problems of sampling variance, migration events and spatial heterogeneity introduce such a noise in the estimate that confidence intervals frequently range from a few individuals to slightly more than infinity (e.g. Turner *et al.* 1999).

The way out of this dilemma consists of using an indirect approach through so-called 'demographic models'. These provide estimates of effective sizes on the basis of life-history and mating-system parameters (e.g. fecundity, mortality, generation overlap, dispersal rate and polygyny level), either alone (e.g. Hill 1972; Nunney 1993; Nunney & Elam 1994) or in combination with robust and readily estimated genetic parameters such as the *F*-statistic (Wright 1921, 1951; Nei 1973). However, these models have to rely on simplifying assumptions, which presumably introduce biases, the consequences of which are difficult to delineate. Testing the accuracy of demographic models is not an easy task for the same practical reasons mentioned above that make genetic measures out of reach, thereby precluding access to 'exact' values of effective sizes to which demographic estimates could be compared.

In the present paper, we want to suggest that computer simulations offer a powerful alternative. We propose an individual-based, genetically explicit approach to evaluating the accuracy of two demographic models of effective size, namely those of Chesser *et al.* (1993) and Nunney (1999), which are aimed at investigating the hierarchical and social structure of populations under a range of dispersal patterns and mating systems. We thereby show that individual-based models offer a promising way of validating these important tools of conservation biology and delineate their limits of applicability.

2. MATERIAL AND METHODS

(a) *Simulations*

We used a slightly modified version of EASYPOP 1.6.1 (Balloux 1999), an individual-based software that is designed to simulate the changes in the genotypic composition of populations subjected

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to different evolutionary forces (mutation, migration and genetic drift). Populations are structured in a number of local groups that are connected through a dispersal rate that may be sex specific. The model organism is annual, with a sex-specific juvenile dispersal. Each individual is characterized by two alleles at each of a number of independent loci. Every generation, females are chosen randomly with replacement for reproduction, which results in a Poisson distribution of fecundities. As the population is maintained stable, females produce two offspring on average. Males contribute to reproduction according to a predefined mating system (see below). Each offspring randomly inherits one allele from each parent at each locus, except for mutational events. These occur at some fixed rate and according to a chosen model (KAM, stepwise, etc). Offspring are then attributed to one of the existing groups with a probability depending on the predefined dispersal rate and pattern (island, stepping stone, etc). After a number of generations, the equilibrium genotypic distributions are monitored, from which a series of statistics can be evaluated (allele numbers and frequencies, *F*-statistics, etc.). Further details can be found at http://www.unil.ch/izea/research.html#softs.

(b) *Genetic effective size*

Our genetic approach follows from a simple mutation-drift model (Fisher 1930; Wright 1931). At equilibrium, the loss of genetic variance due to drift (random sampling of alleles with replacement) is exactly offset by the gain resulting from new mutations. Assuming these occur at rate μ and follow an infinite-allele model (IAM), the equilibrium heterozygosity of an ideal population of size N can be approximated as $H_T = 4N\mu/(4N\mu + 1)$ (Hartl & Clark 1989). The equilibrium effective size of a population may thus be written

$$\mathcal{N}_e = \frac{H_T}{4\mu(1 - H_T)}, \qquad (1)$$

where H_T is the expected heterozygosity at the population level. Equation (1) provides the reference effective size to which both demographic estimations will be compared.

(c) *Chesser* et al.*'s (1993) model*

Chesser *et al.* (1993) considered a finite-island model made of g groups connected by different male (d_m) and female (d_f) juvenile dispersal. The n females in each group show average fecundity k with variance σ_k^2. The mating system is accounted for by a parameter ϕ that expresses the probability that two females from the same group are fertilized by the same male (ϕ ranges from zero under complete monogamy to 1 under complete polygyny). These authors first wrote down the transition matrix describing the dynamics of gene correlations within individuals (F), between individuals within groups (θ) and between individuals from different groups (α) as functions of the several parameters delineated above. Then the effective sizes associated with the accruing of gene correlations within individuals ($\mathcal{N}_{eI} = (1-F_t)/2(F_{t+1}-F_t)$) and between groups ($\mathcal{N}_{e\alpha} = (1-\alpha_t)/2(\alpha_{t+1}-\alpha_t)$) were calculated. Depending on initial conditions, these effective sizes may differ over a few generations. For example, starting from a situation of maximal diversity (all correlations set to zero), inbreeding (F) first increases more rapidly than coancestry between groups (α), so that $\mathcal{N}_{e\alpha}$ first exceeds $\mathcal{N}_{eI}$. However, both estimates eventually converge with time as the overall rate of loss of genetic variance reaches a steady state. Thus, equating the two expressions for $\mathcal{N}_{eI}$ and $\mathcal{N}_{e\alpha}$ provides the equilibrium effective size. This can be approximated by (Chesser *et al.* 1993, eq. (48))

$$\mathcal{N}_e \approx \frac{4g - 3F_{IT} - 1}{6(F_{ST} - F_{IT})} \qquad (2)$$

where $F_{ST} = (\theta-\alpha)/(1-\alpha)$ is the proportion of genetic variance in the system due to differentiation between groups and $F_{IT} = (F-\alpha)/(1-\alpha)$ is the heterozygote deficit at the population level.

Two important points are to be made regarding Chesser *et al.*'s (1993) model. First, breeding groups (subpopulations) are explicitly defined as the lowest hierarchical level of genetic structure, so that local inbreeding ($F_{IS} = (F-\theta)/(1-\theta)$) cannot be positive. Second, gene correlations and *F*-statistics are calculated before dispersal so that F_{IS} may actually become strongly negative: dispersal and the ensuing reproduction between mates from different origins induces an excess of heterozygotes among offspring within a group (and the more so if dispersal is sex biased and the system polygynous). Homozygosity (F) is thereby smaller than predicted from Hardy–Weinberg equilibrium given local gene frequencies (θ), which results in a negative F_{IS}. As the several *F*-statistics are linked by the relationship $(1-F_{IT}) = (1-F_{IS})(1-F_{ST})$, a negative F_{IS} implies that F_{ST} exceeds F_{IT}, hence inducing positive $\mathcal{N}_e$ values in equation (2). The within-group inbreeding must in fact be negative in order to obtain positive effective sizes and only vanishes when the effective size tends to infinity.

Equation (2) receives the following interpretation with respect to the effect of dispersal. With panmixis, the population-level inbreeding coefficient vanishes ($F_{IT} = 0$), while F_{ST} is positive, being measured before dispersal. The effective size is then close to the census size. An increase in philopatry enhances F_{IT} more than F_{ST}, which reduces the difference between them and thereby increases $\mathcal{N}_e$. The latter tends to infinity when these two *F*-coefficients equalize, which only occurs when gene flow stops completely. Similarly, the effect of mating systems receives the interpretation that an increase in polygyny (ϕ) increases F_{ST} (differentiation between groups), while F_{IT} remains largely unchanged, thereby resulting in a decrease in the effective size.

(d) *Nunney's (1999) model*

In contrast, in Nunney's (1999) model the hierarchical position of groups is totally arbitrary so that these may be substructured, resulting in positive F_{IS} values. Furthermore, the *F*-statistics are not equivalent to those used in Chesser *et al.*'s (1993) model, being evaluated after dispersal. This further enhances F_{IS} and decreases F_{ST} relative to Chesser *et al.*'s (1993) timing of measurement (F_{IT} obviously remains the same, being unaffected by the spatial location of individuals). Other differences from Chesser *et al.*'s (1993) model include an explicit account of the sex ratio (r) and of differential group productivity. The distribution of female fecundities may differ from a Poisson distribution due to either individual differences in female quality within groups or to differences between groups stemming, for example, from patch quality. A parameter x allows modulation of local population regulation: x ranges from zero (all regulation is local, which annihilates any difference in patch productivity) to 1 (regulation only occurs at the global population level) (some patches thus contribute more genes than others, which is bound to lower effective sizes).

Under the simplified assumptions implemented in our computer simulations (an even sex ratio, a Poisson distribution

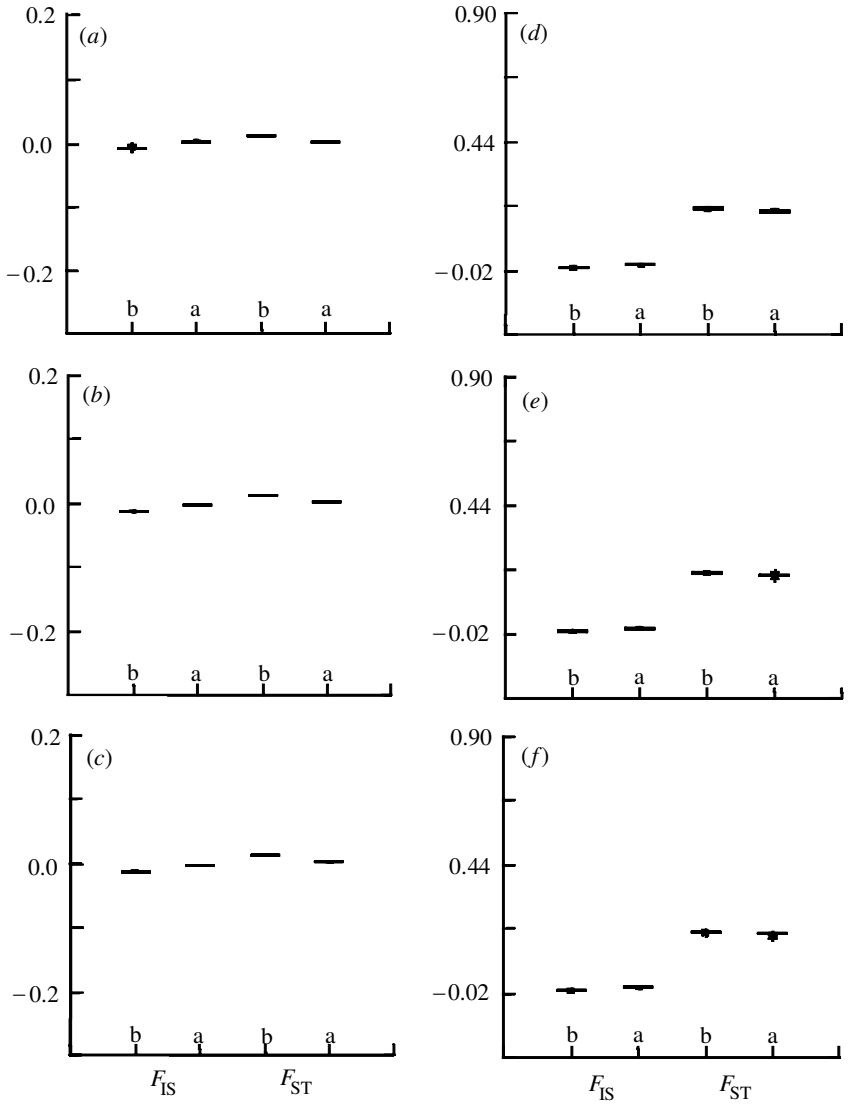

Figure 1. F_{IS} and F_{ST} values under monogamy measured (*a*) after and (*b*) before dispersal. The six graphs (*a–f*) refer to the six dispersal scenarios envisaged (see § 2). F_{IS} and F_{ST} always diverge more before than after dispersal. Under high-dispersal scenarios (left column), both values vanish or nearly so when measured after dispersal, while under low dispersal (right column) F_{ST} takes large and positive values.

of fecundities and population maintained stable through local regulation), equation (14) in Nunney (1999) reduces to

$$N_e = \frac{2ng}{\left[1 + F_{IS} + I_m(1 + 7F_{IS})/2\right](1 - F_{ST})}, \qquad (3)$$

where I_m is the standardized variance (variance over squared mean) in male mating success. As can be seen from equation (3), the increased variance in male mating success induced by polygyny decreases the effective size. Dispersal also decreases N_e. Under complete philopatry F_{ST} tends to 1 and, therefore, the effective size tends to infinity. At the opposite end, free exchange between groups makes F_{ST} vanish so that the effective size equals the census size ($2ng$) devaluated by the effects of polygyny (I_m) and local inbreeding (F_{IS}).

It is worth noting that, in this second demographic model, F_{IS} decreases the effective size (the more so when male mating success is variable). This contrasts sharply with the preceding model, where F_{IS} increases the effective size. As already pointed out, the two models do not evaluate F_{IS} (heterozygote deficit within groups) at the same time during the life cycle and, thus, measure different quantities. In Nunney's (1999) model, F_{IS} measures inbreeding between close relatives within otherwise panmictic groups: 'this tends to reduce N_e because the reproductive success of individuals no longer translates into the success of two independent alleles per locus' (Nunney 1999, p. 2). This cannot be the case in Chesser *et al.*'s (1993) model, which requires the absence of a substructure. Being evaluated before dispersal, F_{IS} measures the heterozygosity deficit of offspring born in otherwise panmictic groups. It is more negative when groups are small, polygyny high and parents differ in origin. It thus correlates positively with philopatry, reaching its highest value (zero) when philopatry is complete (and the effective size infinite).

(e) *Simulations and statistical analyses*

The number of groups (g) was fixed at 200 in all simulations and their size to 50 individuals (with an even sex ratio so that $n = 25$). Ten loci were used, mutating randomly to any of the 999 possible allelic states at a rate of 10^{-3}. This high number

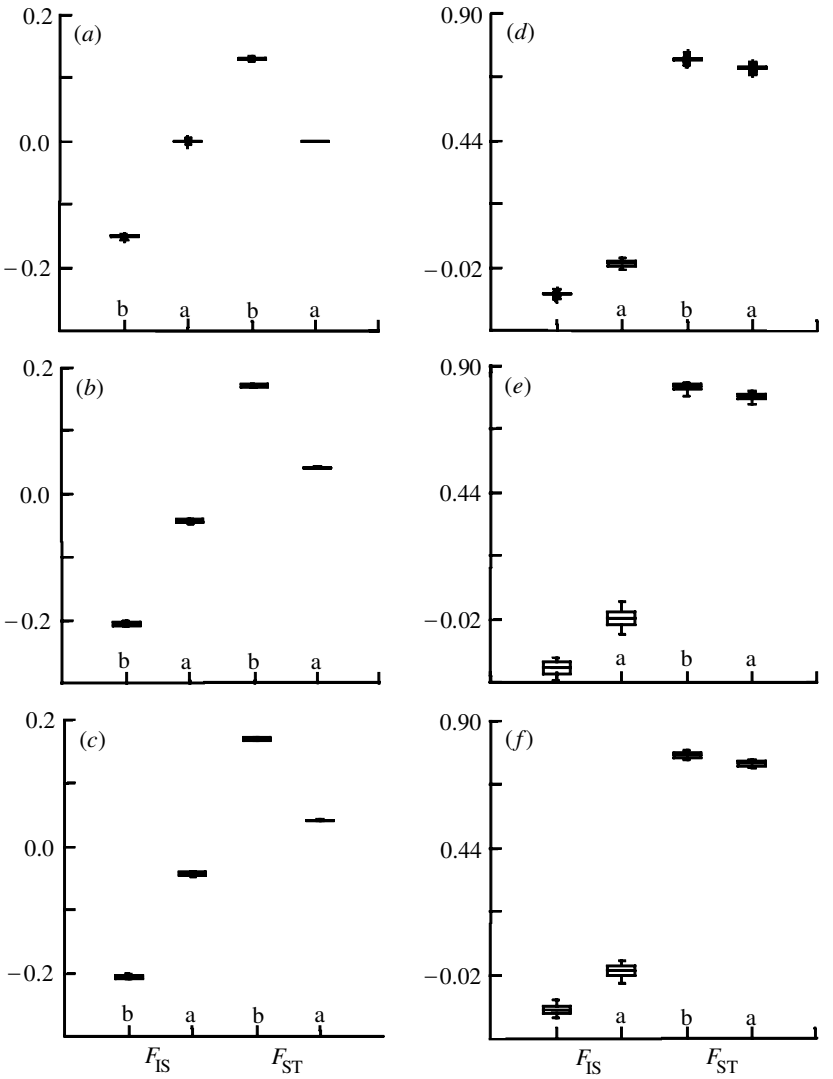

Figure 2. F_{IS} and F_{ST} values under polygyny measured (*a*) after and (*b*) before dispersal. The six graphs (*a–f*) refer to the six dispersal scenarios envisaged (see § 2). The values taken before and after dispersal diverge more compared to figure 1and F_{IS} also differs more from F_{ST}, in particular when measured before dispersal.

allowed homoplasy (probability of obtaining two alleles identical by state through different mutational events) to be kept small enough such that the IAM (an assumption of our genetic model) was approximated very closely (see below).

The following six dispersal regimes were investigated. Note that the total amount of dispersal is identical in scenarios (ii) and (iii) as well as in scenarios (iv)–(vi). Only the sex specificity of dispersal differs.

(i) Panmixia: $d_f = d_m = (g-1)/g = 0.995$.
(ii) Complete female dispersal and complete male philopatry: $d_f = 1$ and $d_m = 0$.
(iii) Complete female philopatry and complete male dispersal: $d_f = 0$ and $d_m = 1$.
(iv) Low female dispersal and complete male philopatry: $d_f = 0.04$ and $d_m = 0$.
(v) Complete female philopatry and low male dispersal: $d_f = 0$ and $d_m = 0.04$.
(vi) Low dispersal of both sexes: $d_f = d_m = 0.02$.

In addition, two contrasting mating systems were tested for every dispersal scenario.

(i) Complete monogamy where each male has access to one and only one female, i.e. $\phi = I_m = 0$.
(ii) Complete polygyny where one male monopolizes all females within his group, i.e. $\phi = 1$ and $I_m = n-1$.

Each of these 12 scenarios (two mating systems × six dispersal patterns) was replicated 20 times. Every simulation was run for 2000 generations, which turned out to be enough for reaching equilibrium. Multilocus genotypes were then analysed at generation 2000, both before and after dispersal, using the program FSTAT 2.8 (Goudet 1995) (http://www.unil.ch/izea/research.html#softs). We calculated the number of alleles in each group, the corrected heterozygosities (H_T) according to Nei & Chesser (1983) and the *F*-statistics according to Weir & Cockerham (1984). From these data, effective sizes were calculated for each replicate following the three models shown in equations (1)–(3). The effective sizes obtained through the two demographic models were tested against those provided by the genetic model using Wilcoxon signed-ranks tests. The same test was used in order to compare allele numbers and effective sizes under monogamy and polygyny as well as *F*-statistics before and after dispersal.

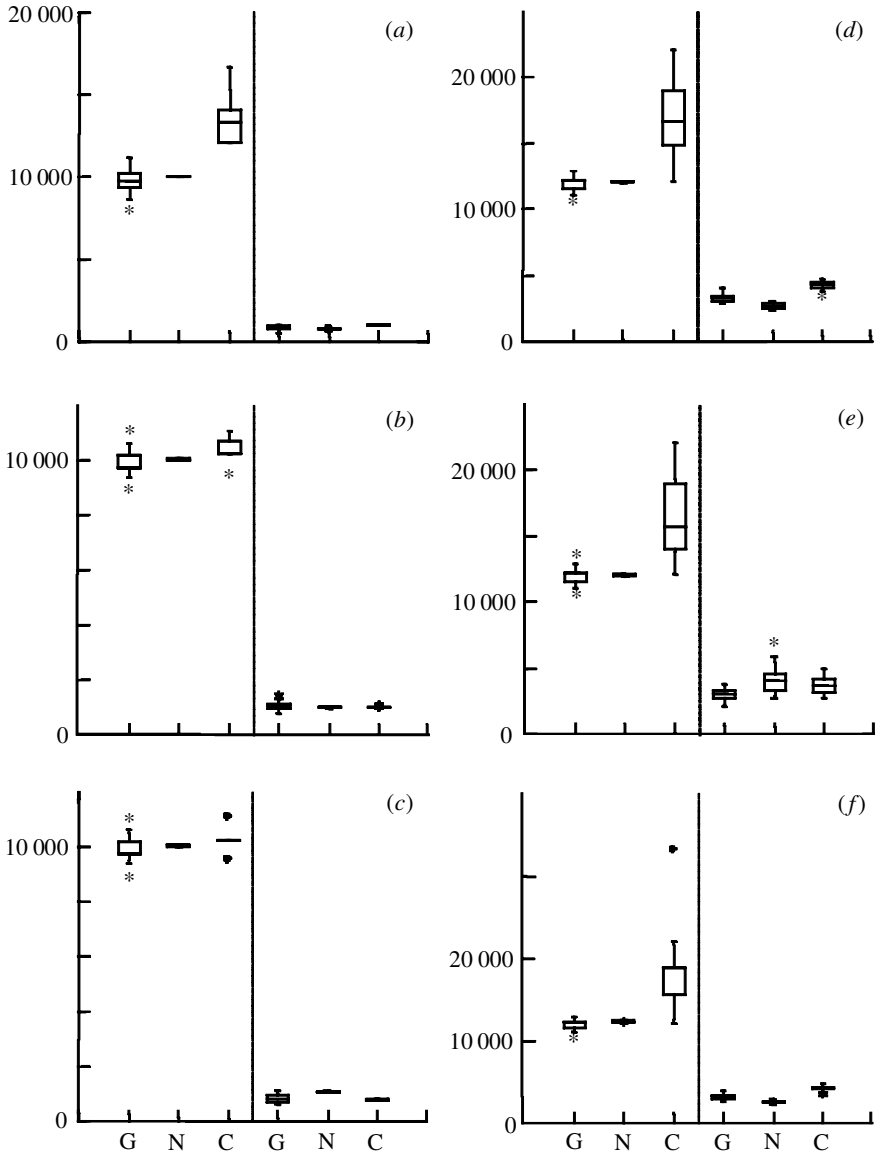

Figure 3. Effective sizes under the 12 scenarios explored (six dispersal regimes × two mating systems) for the three models investigated (G, genetic; N, Nunney (1999); C, Chesser *et al.* (1993)). The six graphs (*a–f*) refer to the six dispersal regimes envisaged (see § 2). The left panel on each of them shows the results for monogamy and the right panel the results for polygyny. Demographic models by and large produce good estimates of genetic effective sizes, except for Chesser *et al.*'s (1993) model under monogamy (left panel on each graph) when the sexes show similar dispersal (*a* and *d–f*).

3. RESULTS

(a) *Allele numbers and F-statistics*

The allele number at equilibrium was mainly dependent on mating system, being always much smaller under polygyny than under monogamy ($p < 0.001$ in all cases). The largest value under polygyny was 75.5 ± 1.7 (s.d.), which was obtained with dispersal values of $d_f = 0.04$ and $d_m = 0$, while the smallest value under monogamy was 226.0 ± 4.0 (s.d.), which was obtained with dispersal values of $d_f = 0$ and $d_m = 1$. This is less than one-quarter of the number available (999 possible allelic states) and, thus, is unlikely to induce significant discrepancies from IAM assumptions (as otherwise confirmed by the fit of genetic effective sizes to theoretical expectations) (see below).

As expected, the timing of gene sampling during the life cycle had large effects on F_{IS} and F_{ST} (figures 1 and 2), whereas no significant difference was ever seen for F_{IT}. The F_{ST} values were always higher before dispersal than after ($p < 0.001$ in all cases), while the F_{IS} values were always lower before dispersal than after ($p < 0.001$ in all cases). Polygyny and high dispersal tended to amplify these differences, while polygyny and low dispersal amplified the differences between F_{IS} and F_{ST}.

(b) *Genetic effective sizes*

The simulation results are all provided as box plots in figure 3. The genetic approach based on equilibrium heterozygosity and mutation rate (equation (1)) provided effective sizes under panmixia (figure 3*a*) that did not differ significantly from theoretical expectations. This expectation corresponds to the census size under complete monogamy ($2ng = 10\,000$) because all individuals contribute to reproduction. Under complete polygyny, the expectation is $4ng/(n+1) = 770$ (Wright 1938) because all

females but only one male per group reproduce. The fact that genetic effective sizes under panmixia did not differ significantly from the theoretical expectations of the IAM confirms the suggestion that the bias introduced by the limited number of possible allelic states (999) was negligible.

The difference between monogamy and polygyny remained large and highly significant ($p < 0.001$) under all dispersal regimes, but to different extents. Under high dispersal by one sex and complete philopatry by the other (figure 3*b*,*c*), genetic estimates of the effective size did not differ significantly from those reached under panmixia. However, at low dispersal (figure 3*d*–*f*), N_e increased to *ca.* 12 000 under monogamy and to *ca.* 3000 under polygyny, independent of which sex dispersed. The negative effect of polygyny on the effective size thus appears much less marked when dispersal is low: polygyny depressed N_e by a factor of only 4 when the dispersal rate averaged 0.02, whereas this factor exceeded 12 under panmixia.

(c) *Demographic effective sizes*

The effective sizes predicted by the demographic models showed the same qualitative patterns with respect to the effect of mating system and dispersal. Quantitatively, Chesser *et al.*'s (1993) approach (equation (2)) provides values that are in very good agreement with genetic estimates under polygyny as well as under monogamy as long as dispersal is strongly sex biased (figure 3*b*,*c*). However, this model tends to overestimate the effective size under monogamy as soon as the sexes show similar dispersal rates (figure 3*a*,*d*–*f*). The standard deviations in this case also appeared to be very high. In contrast, the effective sizes obtained through Nunney's (1999) model (equation (3)) are overall extremely consistent with the genetic model, independent of mating system and dispersal pattern. The standard deviations also appeared to be extremely small, being actually smaller than those of the genetic model in every case but one.

4. DISCUSSION

Any factor increasing the variance in individual reproductive success (e.g. polygyny, a biased sex ratio and differential female fecundity) decreases the population effective size (Wright 1938). Under complete polygyny, a single male per group transmits his genes to the next generation. This is bound to increase the variance in individual reproductive success drastically (and the more so when groups are large). In our simulations, polygyny divided effective sizes by a factor ranging from four to 12, depending on the dispersal rate (figure 3). That polygyny is less effective in depressing the effective size at low dispersal was actually not unexpected. As dispersal decreases, groups become genetically homogeneous, which reduces the consequences of the variance in male mating success. Males within a group are strongly related, so the genes of non-reproducing males are not entirely lost (Whitlock & Barton 1997; Nunney 1999).

The effect of population structure stemming from group living and philopatry can also be interpreted in terms of variance in individual reproductive success. The isolation of groups and their local regulation prevents this variance being randomly distributed between individuals within the whole population. Drift cannot therefore freely eliminate genetic variance on a global population scale. At the very limit (i.e. under complete philopatry) all groups fix different alleles, so that the population maintains a residual diversity out of reach of genetic drift indefinitely. Its effective size is therefore infinite.

Qualitatively both demographic models behaved in good accordance with these expected effects of mating systems and dispersal patterns. However, quantitatively they showed contrasting behaviours. While Nunney's (1999) model consistently displayed remarkably accurate estimates of the genetic effective size (and usually with very low standard deviations), Chesser *et al.*'s (1993) model only did as well under polygyny and/or sex-biased dispersal. It is worth noting that this situation actually corresponds to the social systems of many mammals, for which this model was developed (e.g. Sugg *et al.* 1996; Dobson *et al.* 1997). Discrepancies appeared under monogamy when the sex bias in dispersal was low. In this case, the model tended to overestimate the effective size and the standard deviations were very large. Technically, this problem stems from the way this model deals with a local heterozygote deficit (F_{IS}). Both polygyny and sex biases in dispersal produce a strongly negative pre-dispersal F_{IS}. In contrast, under monogamy and unbiased dispersal, F_{IS} is only slightly negative. In such a case, the sampling variance is likely to provide measures of F_{IS} very close to zero, which boosts the effective size close to infinity (equation (2)). From this follows both the overestimate and the large standard deviations noticed.

That Chesser *et al.*'s (1993) model requires a single demographic parameter (g) in addition to the F-statistics (equation (2)) while Nunney's (1999) model requires three of them (g, n and I_m) (equation (3)) is definitely a serious advantage in terms of practical evaluation. However, for some applications conservation biologists may be more interested in the ratio of the effective size to census size ($N_e/2ng$) rather than the effective size *per se*. This ratio is readily estimated from Nunney's (1999) equation with the use of a single parameter (I_m) in addition to the F-statistics, while Chesser *et al.*'s (1993) formulation does not allow an explicit expression for it.

Furthermore, Chesser *et al.*'s (1993) model also assumes the absence of a substructure within groups, which must be checked independently from biological observations. F-statistics *per se* may not be sufficient: if F_{IS} turns out to be positive then some substructure obviously exists so Chesser *et al.*'s (1993) model cannot be used. However, a negative F_{IS} does not imply the absence of a substructure. This may be small enough that it does not outweigh the effect of sex-biased dispersal. The resulting F_{IS} would be only slightly negative which, as a result, would strongly overestimate the effective size. In contrast, the hierarchical position of the group is arbitrary in Nunney's (1999) model, so that no independent biological information is required.

The timing of sampling is very important for both models. From our results (not presented here), Chesser *et al.*'s (1993) model usually produced negative effective sizes if post-dispersal F-statistics were used due to positive F_{IS} values. Similarly, Nunney's (1999) model produced negative or aberrant values under polygyny

when pre-dispersal *F*-statistics were used because of negative F_{IS} values. Field biologists should keep this important point in mind when collecting data and design their sampling according to which model they plan to implement. As for the choice of model, our simulations clearly show that Nunney's (1999) model should be preferred over Chesser *et al.*'s (1993) model whenever the focal species' breeding system approaches monogamy with no sex bias in dispersal or if some substructure within groups is suspected.

Overall, our study also clearly shows that a simulation approach relying on individual-based, genetically explicit models provides a promising way of evaluating the accuracy of demographic models of effective size and delineating their field of applicability.

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REFERENCES

Balloux, F. 1999 *EASYPOP, a software for population genetic simulation*. Lausanne, Switzerland: University of Lausanne.

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

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

Dobson, F. S., Chesser, R. K., Hoogland, J. L., Sugg, D. W. & Foltz, D. W. 1997 Do black-tailed prairie dogs minimize inbreeding? *Evolution* **51**, 970–978.

Fisher, R. A. 1930 *The genetical theory of natural selection*. Oxford, UK: Clarendon Press.

Goudet, J. 1995 FSTAT: a computer program to calculate *F*-statistics. *J. Hered.* **86**, 485–486.

Hartl, D. L. & Clark, A. G. 1989 *Principles of population genetics*. Sunderland, MA: Sinauer Associates.

Hill, W. G. 1972 Effective size of populations with overlapping generations. *Theor. Popul. Biol.* **3**, 278–289.

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

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

Nei, M. & Chesser, R. K. 1983 Estimation of fixation indices and gene diversities. *Annls Hum. Genet.* **47**, 253–259.

Nunney, L. 1993 The influence of mating system and overlapping generations on effective population size. *Evolution* **47**, 1329–1341.

Nunney, L. 1999 The effective size of a hierarchically structured population. *Evolution* **53**, 1–10.

Nunney, L. K. & Campbell, A. 1993 Assessing viable population size: demography meets population genetics. *Trends Ecol. Evol.* **8**, 234–239.

Nunney, L. & Elam, D. R. 1994 Estimating the effective population size of conserved populations. *Conserv. Biol.* **8**, 175–184.

Saccheri, I., Kuussaari, M., Kankare, M., Vikman, P., Fortelius, W. & Hanski, I. 1998 Inbreeding and extinction in a butterfly metapopulation. *Nature* **392**, 491–494.

Sugg, D. W., Chesser, R. K., Dobson, F. S. & Hoogland, J. L. 1996 Population genetics meets behavioral ecology. *Trends Ecol. Evol.* **11**, 338–340.

Turner, T. F., Richardson, L. R. & Gold, J. R. 1999 Temporal genetic variation of mitochondrial DNA and the female effective population size of red drum (*Sciaenops ocellatus*) in the northern Gulf of Mexico. *Mol. Ecol.* **8**, 1223–1229.

Waples, R. S. 1989 A generalized approach for estimating effective population size from temporal changes in allele frequency. *Genetics* **121**, 379–391.

Weir, B. S. & Cockerham, C. C. 1984 Estimating *F*-statistics for the analysis of population structure. *Evolution* **38**, 1358–1370.

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

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

Wright, S. 1931 Evolution in Mendelian populations. *Genetics* **16**, 97–159.

Wright, S. 1938 Size of population and breeding structure in relation to evolution. *Science* **87**, 430–431.

Wright, S. 1951 The genetical structure of populations. *Annls Eugenics* **15**, 323–354.

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