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# BRIEF COMMUNICATIONS

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## FLUCTUATING POPULATION SIZE AND THE RATIO OF EFFECTIVE TO CENSUS POPULATION SIZE

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The effective size of a population ( $N_e$ ) quantifies the rate at which genetic diversity is eroded by genetic drift (i.e.,  $1/2N_e$  per generation), a fundamental process of evolutionary change. Genetic diversity and its rate of decay have been linked with key components of population fitness (Allendorf and Leary 1987; Ralls et al. 1988; Briscoe et al. 1992; Newman and Pilson 1997; but see Britten 1996).  $N_e$  is thus a central parameter both in studies aimed at understanding evolution (Falconer and Mackay 1996) and in the field of conservation genetics (Lande and Barrowclough 1987; Nunney and Campbell 1993; Nunney and Elam 1994). Unfortunately, accounting for all factors that influence  $N_e$  is notoriously difficult (reviewed by Caballero 1994). This difficulty is apparently responsible for significant disagreement between theoretical (Nunney 1993) and observed values of the ratio,  $N_e/N$  (Frankham 1995).

Here we investigate whether this disagreement can be reconciled by incorporating the effect of a factor long known to reduce  $N_e$ , namely temporal fluctuations in population size (FPS; Wright 1938). More specifically, we consider the extent to which  $N_e/N$  is depressed by FPS over the range of fluctuations observed in wild animal populations. In addition, we present a method for predicting  $N_e/N$  from a standard measure of population variability, and we discuss the implications of this theoretical relationship.

Several factors affect the effective size of a population: fluctuations in size, variance in fecundity, sex ratio, and the degree to which generations overlap (Crow and Kimura 1970). One difficulty in estimating  $N_e$  is that no single formula simultaneously accounts for all these factors. This difficulty would be largely inconsequential if the ratio  $N_e/N$  were known to fall consistently within a narrow range. Estimating  $N_e$  would be trivial because  $N$  is often relatively easily estimated. Theoretical and empirical studies have searched for such a range of  $N_e/N$ .

Theoretical studies have explored the plausible range of  $N_e/N$  through analysis of a reparameterized version of Hill's (1972) expression for  $N_e$  (Nunney 1991, 1993, 1996). This reparameterization provides several advantages.  $N_e$  is expressed in parameters that are biologically interpretable, and for which typical ranges are known. In addition, the parameters can be estimated from data commonly available from *single-season* studies of real populations (Nunney and Elam 1994). Through thorough numerical exploration of the pa-

rameter space, these studies led to the conclusion that  $N_e/N$  is usually close to 0.5 and only rarely outside the range 0.25–0.75 (Nunney 1991, 1993, 1996; hereafter, referred to as the theoretical expectation.)

In contrast with this theoretical expectation, a review of 192 empirical estimates (based on a variety of demographic and genetic methods) revealed that  $N_e/N$  was usually less than 0.5 (Frankham 1995; hereafter, referred to as empirical estimates.) In fact, approximately one-third of the  $N_e/N$  estimates were less than 0.25, and a subset of these estimates (37 from animal taxa) accounting for all factors that influence  $N_e$  had an average  $N_e/N$  of 0.15 (median = 0.08). By contrast, a subset of estimates (27 from animal taxa) accounting for all factors except FPS had an average  $N_e/N$  of 0.38 (median = 0.38). The discrepancy between theoretical expectation and empirical estimates may thus be largely attributable to the fact that the theoretical expectation is based on the assumption of constant  $N$ . The theoretical expectation may provide a reasonable estimate of the short-term  $N_e/N$ , but the longer-term ratio may often be less than 0.25, owing to the effect of FPS.

A long-term estimate of  $N_e$  that accounts for FPS is obtained by transforming a series of short-term effective sizes (Wright 1938; see also Crow and Kimura 1970; Lande and Barrowclough 1987):

$$N_e = \frac{1}{2} \left[ 1 - \left\{ \prod_{t=1}^q \left( 1 - \frac{1}{2N_{e,t}} \right) \right\}^{1/q} \right], \quad (1)$$

where  $N_{e,t}$  is the short-term effective size in generation  $t$  and  $q$  is the total number of generations. This transformation assumes populations have discrete (nonoverlapping) generations. Unfortunately, no existing formula accounts for overlapping generations, and the consequences of violating this assumption are not well understood (Nunney and Elam 1994; Nunney 1996). This transformation also assumes, perhaps unrealistically, independence between FPS and other factors influencing  $N_{e,t}$ .

Equation (1) is closely approximated by the harmonic mean (Wright 1938):

$$N_e \cong q / \sum_{t=1}^q (N_{e,t})^{-1}, \quad (2)$$

provided the terms of order  $(N_{e,t})^{-2}$  are small (Crow and Kimura 1970) and the time scale is short (Lande and Bar-

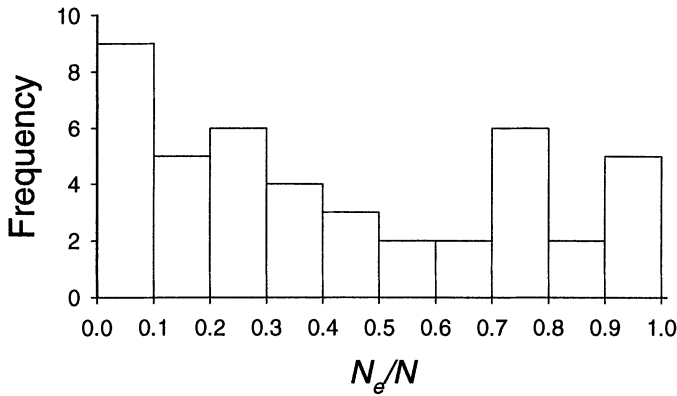


FIG. 1. Frequency distribution of theoretical values of  $N_e/N$  for populations assumed to be ideal except for fluctuations in size. The distribution represents 44 values of  $N_e/N$ , where  $N_e$  is calculated as the harmonic mean of a series of seasonal  $N_e$  values, and seasonal  $N_e$  is assumed to be equal to the census size.

rowclough 1987; see also Motro and Thomson 1982). The utility of this approach for estimating  $N_e$  has been broadly confirmed by simulation modeling (Motro and Thompson 1982).

An estimate of long-term  $N_e$  that accounts for the effect of FPS may be obtained using a two-step procedure. The first step is to calculate a series of short-term (or seasonal) estimates of  $N_e$  (following Nunney and Elam 1994). The second step is to calculate the harmonic mean of that series (eq. [2]). In many cases, however, only a single short-term estimate of  $N_{e,t}$  will be readily obtainable. In such cases, a short-term estimate of  $N_e/N$  can be calculated as  $N_{e,t}/X_t$ , where  $X_t$  is the population count for generation  $t$ . If a series of census records is also available, then an estimate of long-term  $N_e$  can be obtained by multiplying  $N_{e,t}/X_t$  by the harmonic mean of  $X_t$  values, thereby adjusting for the effect of FPS (Nunney and Elam 1994; Nunney 1996). An important assumption of this latter approach is that the short-term ratio is independent of population size. This assumption is known to be violated to some degree (e.g., Pray et al. 1996; see also Hedrick and Gilpin 1997), but the estimate is likely to be robust provided the dependence is weak.

Here we use this general approach to evaluate the effect of FPS on  $N_e/N$ . We use annual census records for 44 animal populations (23 mammalian, five avian, and 16 invertebrate species), each censused for at least 18 consecutive years. The time series are described elsewhere (Turchin and Taylor 1992; Dennis et al. 1991; Vucetich et al. 1997). Our data collection was based simply on availability of population time series in the literature. Assuming the time series are representative, we use these data to evaluate the depression of  $N_e/N$  by FPS over the range of fluctuations observed in wild animal populations. To perform this evaluation, we initially treat the 44 populations as if they were ideal in all respects except FPS. We thereby evaluate the hypothetical influence of FPS on  $N_e/N$  in the absence of other influences. In this initial evaluation, we unrealistically assume: (1) that  $N_{e,t}$ , the seasonal effective population size, is equal to  $X_t$ , the population count at time  $t$ ; and (2) that all 44 populations had a generation time of one year. The numerator of  $N_e/N$  is estimated by applying

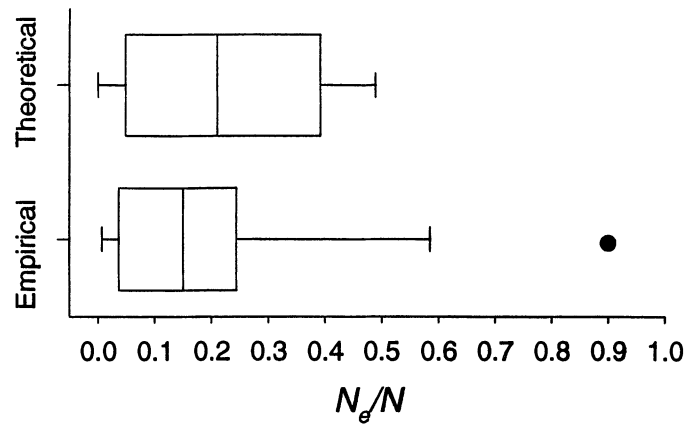


FIG. 2. Comparison of theoretical (this study) and empirical (Frankham 1995) distributions of  $N_e/N$ . The vertical line indicates the mean, the box the interquartile range, and the horizontal line the range (with one outlier; see fig. 1 in Frankham 1995). The empirical distribution represents 37 comprehensive  $N_e/N$  estimates (excluding plants); all but two of those values were less than 0.38. Comprehensive estimates are those attempting to account for all factors that influence  $N_e/N$ . The theoretical distribution represents 44 estimates of  $N_e/N$ , where  $N_e$  is estimated as the harmonic mean of a series of seasonal  $N_e$  values, and seasonal  $N_e$  is assumed to be equal to half the census size (Nunney 1991, 1993, 1996).

equation (2) to each series of  $N_{e,t}$  values, and the denominator is estimated as the arithmetic mean of  $X_t$ .

Figure 1 shows the hypothetical effect of natural FPS on the frequency distribution of the  $N_e/N$  estimates. The average  $N_e/N$  was 0.43, and values ranged from  $7.5 \times 10^{-4}$  to 0.98. ( $N_e/N$  was not significantly correlated with the length of the time series [slope =  $-0.0014$ ,  $r^2 = 0.018$ ,  $P = 0.39$ ].) We therefore conclude that natural levels of FPS, in the hypothetical absence of any other influence, are often sufficient to depress  $N_e/N$  to small values (36% of the estimates were less than 0.25).

In the above analysis, we assumed that the 44 populations were ideal in every respect except that they fluctuated in size across years. Here we attempt to account indirectly for all factors that influence  $N_e/N$  (i.e., FPS, variance in fecundity, sex ratio, and overlapping generations). To do so, we recalculate  $N_e/N$  by taking the harmonic mean of  $N_{e,t}$ , where we assume that  $N_{e,t} = X_t/2$  (Nunney 1991, 1993, 1996). These calculations yielded an average  $N_e/N$  of 0.21, a median of 0.18, and values ranging from  $3.8 \times 10^{-4}$  to 0.49. This distribution of theoretical values of  $N_e/N$  resembles the distribution of empirical estimates for various animal taxa (Fig. 2).

Although the harmonic mean may adequately adjust  $N_e$  for the influence of FPS (Wright 1938), other statistics quantify FPS more conveniently. Since the distribution of population size across time is highly skewed, population dynamics are appropriately measured and modeled following logarithmic transformation (e.g., Lewontin and Cohen 1969; Dennis et al. 1991 and references therein). The statistical properties and various ecological and evolutionary correlates of the standard deviation of the log-transformed population size,  $SD[\log(X)]$ , are well studied (reviewed by Pimm 1991; Gas-

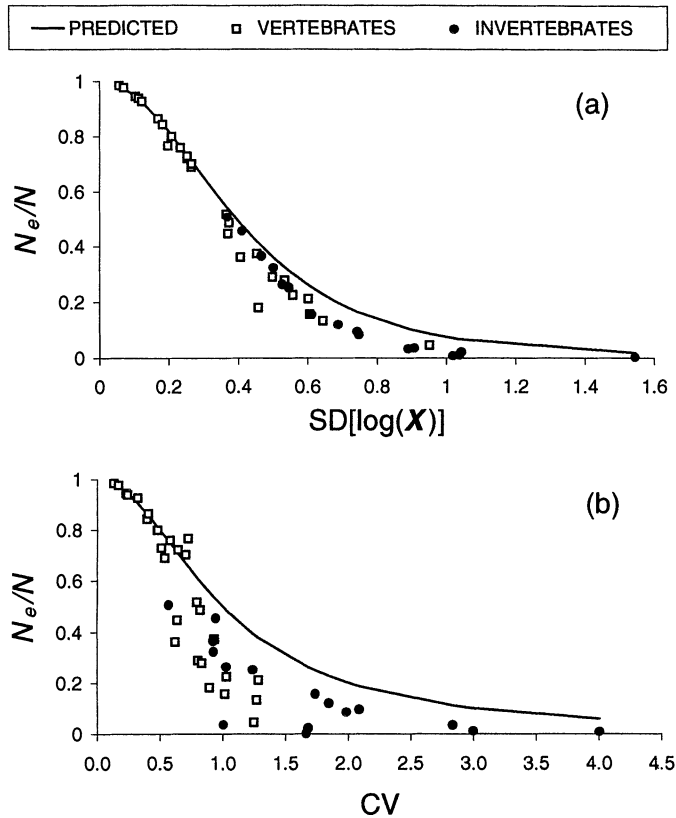


FIG. 3. The relationship between  $N_e/N$  and population variability measured as (a) the standard deviation of the log-transformed population size,  $SD[\log(X)]$ , and (b) the coefficient of variation of population size,  $CV$ . The curves are defined by equations (3) and (4), and the symbols show estimates for 44 animal populations (see Fig. 2 legend). This relationship assumes that populations are ideal in all respects except for fluctuations in size (i.e.,  $N_{e,t} = X_t$ ). Under the assumption that  $N_{e,t} = X_t/2$ , the y-axis would be rescaled such that  $N_e/N$  would range from 0 to 0.5 rather than 0 to 1.0.

ton and McArdle 1994). Consequently,  $SD[\log(X)]$  is useful for modeling the effect of FPS on  $N_e$ .

If a population fluctuates in size but is otherwise ideal, the relationship between FPS and  $N_e/N$  may be expressed in terms of  $SD[\log(X)]$ :

$$N_e/N = [1 + (\text{Var}[\ln(X)]/2)]^{-2} = \left[1 + \frac{[\ln(10)(SD[\log(X)])]^2}{2}\right]^{-2}, \quad (3)$$

where  $\text{Var}[\ln(X)]$  is the variance of the log-transformed population size (Fig. 3a). Equation (3) can be derived by approximating equation (1) with a pair of Taylor series expansions around the geometric mean. The first series approximates  $[1 - 1/(2X)]$  (i.e., the rate of genetic drift) and the second series approximates the arithmetic mean,  $N$ . This expression holds provided the third and higher moments of the distribution of  $\log(X)$  are small relative to the variance.

Another standard measure of population variability is the coefficient of variation of population size ( $CV$ ). Previous attempts to account for the effect of FPS on  $N_e/N$  relied on this measure (e.g., Lacy and Clark 1989; see also Harris and Allendorf 1989):

$$N_e/N = (1 + CV^2)^{-1}. \quad (4)$$

However,  $N_e$  estimators based on the  $CV$  may often perform relatively poorly (Fig. 3b) because the  $CV$  is less sensitive than  $SD[\log(X)]$  to variation in population size due to bottlenecks (Williamson 1984; Pimm 1991).

The relationship expressed in equation (3) has several implications. Assuming that the range of  $SD[\log(X)]$  in our sample typifies that observed in nature (see fig. 3.1 in Pimm 1991), our results (Fig. 2) may approximate the true distribution of  $N_e/N$ . Although estimating  $SD[\log(X)]$  is nontrivial (Gaston and McArdle 1994) and estimates may be inflated due to sampling error in population counts, equation (3) may be a valuable foundation for further investigations of the consequences of FPS for population genetics. In addition, correlates of  $SD[\log(X)]$  may serve as useful predictors of  $N_e/N$ . For example, vertebrate populations had significantly larger  $N_e/N$  values than did invertebrate populations (Fig. 3; Mann-Whitney  $U$ -test:  $P < 0.001$ ), reflecting the fact that vertebrates had smaller values of  $SD[\log(X)]$  than did invertebrates ( $P < 0.001$ ). Analysis of larger datasets may reveal additional taxonomic patterns in  $N_e/N$ , as suggested by previous work (Frankham 1995; Waite and Parker 1996).

The accuracy of the harmonic-mean estimator of long-term  $N_e$  may be compromised when generations are overlapping rather than discrete (see above). If generations are overlapping, as was true for some of the 44 populations in our sample, the harmonic mean may underestimate long-term  $N_e$  (but see Felsenstein 1971). Such underestimation is possible when the harmonic mean is applied to the number of breeding adults; reproductively mature individuals failing to breed during a particular year may be excluded from that year's count, even though they might have reproduced in past years and may still reproduce in subsequent years (see Nunney and Elam 1994). Similarly, the harmonic mean may yield a biased estimate of  $N_e$  when applied to the total population size (juveniles and adults), since the contribution of juveniles to the gene pool depends on their survival to reproductive maturity (see eq. [22] in Nunney 1993). Interpretation of  $N_e/N$  values also depends on the operational meaning of the denominator. Ideally,  $N$  should represent the average number of potentially reproductive individuals (Nunney and Elam 1994). In our analysis,  $N$  represents variously the arithmetic average number of reproductive adults, all adults (reproductive and post-reproductive), or all adults and juveniles combined (total census size). These considerations are important, but they do not diminish our main conclusion that FPS in real animal populations can depress  $N_e/N$  to very low values. Indeed, the lowest estimates of  $N_e/N$  corresponded to the highest levels of population variability (Fig. 3a), which are typically associated with populations that have discrete generations (Pimm 1991).

Two additional considerations for proper estimation of long-term  $N_e$  deserve attention. First, where temporal trends in  $N$  are evident, recent values of  $N$  may be appropriate for estimating the denominator of  $N_e/N$ . Second, because the variance in population size tends to increase the longer a population is observed (Lawton 1988; Pimm and Redfearn 1988; Ariño and Pimm 1995), demographic estimates of  $N_e/N$

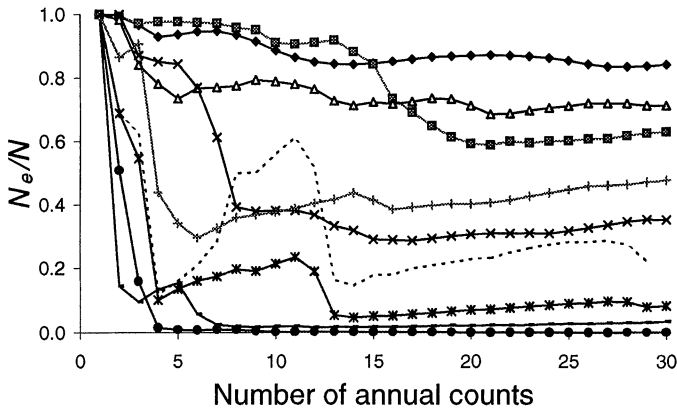


FIG. 4. The relationship between  $N_e/N$  estimates (for animal populations) and the number of consecutive annual counts included in the estimate. Each trajectory was constructed by calculating  $N_e/N$  based on one count ( $X_t$ ), then two counts ( $X_t, X_{t-1}$ ), and so on, up to 30 counts  $X_t, X_{t-1}, \dots, X_{t-29}$ . For ease of visualization, only nine such 30-year time series are presented. (Note that one time series [dotted line] was only 29 years long.) These examples typify the range of behavior for all time series in the dataset.  $N_e/N$  tended to decrease the longer the population was observed. However, in some populations,  $N_e/N$  calculated after just a few years was similar to that calculated after 30 years.

$N$  accounting for FPS tend to decrease the longer a population is observed (Fig. 4). The variance in population size may eventually reach an asymptote, but this is unlikely to happen within the short time frames over which populations are typically observed (Murdoch 1994; Ariño and Pimm 1995). That longer time series lead to lower estimates of  $N_e/N$  suggests that our 44 estimates may be inflated. Conversely,  $N_e/N$  values predicted from  $SD[\log(X)]$  appear to be too high in the tail region (Fig. 3a). This latter tendency may reflect the fact that equation (3) does not include higher-order terms. The influence of such terms would tend to increase as  $SD[\log(X)]$  increases. Despite these limitations, equation (3) may provide adequate estimates of  $N_e$  for the purpose of modeling the rate of genetic drift.

In summary, we have shown that a single factor, fluctuation in population size, is sufficient to produce very small values of  $N_e/N$  in animal populations (Fig. 1). Additional factors tend to depress  $N_e/N$  even further (Fig. 2). When all factors are taken into account, the theoretical and empirical distributions of  $N_e/N$  are broadly overlapping (Fig. 2). However, further study is warranted because a roughly twofold difference remains between the medians of the theoretical (0.08) and empirical distributions (0.18). In addition, we suggest that the theoretical relationship between  $SD[\log(X)]$  and  $N_e/N$  (eq. [3]) provides a basis for predicting the rate of genetic drift as influenced by population dynamics, ecological variables, and life-history traits. Finally, our findings have practical implications for estimating  $N_e$ . In particular, we emphasize the importance of adequately accounting for the effect of fluctuations in population size on demographic estimates of long-term  $N_e$ . Long time series may often be necessary to obtain accurate estimates (Fig. 4), but it is premature to recommend how many censuses will typically be required. Clearly, though, estimates based on data collected during a single year will typically be inadequate. Such es-

timates may grossly overestimate long-term  $N_e$  (Fig. 4), thereby grossly underestimating the rate of genetic drift and perhaps overestimating the probability of population persistence (Newman and Pilson 1997).

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#### LITERATURE CITED

- ALLENDORF, F. W., AND R. F. LEARY. 1987. Heterozygosity and fitness in natural populations of animals. Pp. 57–76 in M. E. Soulé, ed. *Conservation biology*. Sinauer, Sunderland, MA.
- ARIÑO, A., AND S. L. PIMM. 1995. The nature of population extremes. *Evol. Ecol.* 9:429–443.
- BRISCOE, D. A., J. M. MALPICA, A. ROBERTSON, G. J. SMITH, R. FRANKHAM, R. G. BANKS, AND J. S. F. BARKER. 1992. Rapid loss of genetic variation in large captive populations of *Drosophila* flies: implications for the genetic management of captive populations. *Cons. Biol.* 6:416–425.
- BRITTEN, H. B. 1996. Meta-analyses of the association between multilocus heterozygosity and fitness. *Evolution* 50:2158–2164.
- CABALLERO, A. 1994. Developments in the prediction of effective population size. *Heredity* 73:657–679.
- CROW, J. F., AND M. KIMURA. 1970. *An introduction to population genetics theory*. Harper and Row, New York.
- DENNIS, B., P. L. MUNHOLLAND, AND J. M. SCOTT. 1991. Estimation of growth and extinction parameters for endangered species. *Ecol. Monogr.* 61:115–142.
- FALCONER, D. S., AND T. F. C. MACKAY. 1996. *Introduction to quantitative genetics*. 4th ed. Longman, New York.
- FELSENSTEIN, J. 1971. Inbreeding and variance effective numbers in populations with overlapping generations. *Genetics* 68:581–597.
- FRANKHAM, R. 1995. Effective population size/adult population size in wildlife: a review. *Genet. Res.* 66:95–107.
- GASTON, K. J., AND B. H. MCARDLE. 1994. The temporal variability of animal abundances: measures, methods, and patterns. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 345:335–358.
- HARRIS, R. B., AND F. W. ALLENDORF. 1989. Genetically effective population size of large mammals: an assessment of estimators. *Cons. Biol.* 3:181–191.
- HEDRICK, P. W., AND M. E. GILPIN. 1997. Genetic effective size of a metapopulation. Pp. 165–181 in I. A. Hanski and M. E. Gilpin, eds. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, New York.
- HILL, W. G. 1972. Effective size of populations with overlapping generations. *Theor. Popul. Biol.* 3:278–289.
- LACY, R. C., AND T. W. CLARK. 1989. Genetic variability in black-footed ferret populations: past, present, and future. Pp. 83–103 in U. S. Seal, E. T. Thorne, M. A. Bogan, and S. H. Anderson, eds. *Conservation biology and the black-footed ferret*. Yale Univ. Press, New Haven, CT.
- LANDE, R., AND G. F. BARROWCLOUGH. 1987. Effective population size, genetic variation and their use in population management. Pages 87–123 in M. E. Soulé, ed. *Viable populations for conservation*. Cambridge Univ. Press, New York.
- LAWTON, J. H. 1988. More times means more variation. *Nature* 334:563.

- LEWONTIN, R. C., AND D. COHEN. 1969. On population growth in a randomly varying environment. *Proc. Nat. Acad. Sci. USA* 62: 1056–1060.
- MOTRO, U., AND G. THOMSON. 1982. On heterozygosity and effective size of populations subject to size change. *Evolution* 36: 1059–1066.
- MURDOCH, W. M. 1994. Population regulation in theory and practice. *Ecology* 75:271–287.
- NEWMAN, D., AND D. PILSON. 1997. Increased probability of extinction due to decreased genetic effective population size: experimental populations of *Clarkia pulchella*. *Evolution* 51:354–362.
- NUNNEY, L. 1991. The influence of age structure and fecundity on effective population size. *Proc. R. Soc. Lond. B Biol. Sci.* 246: 71–76.
- . 1993. The influence of mating system and overlapping generations on effective population size. *Evolution* 47:1329–1341.
- . 1996. The influence of variation in female fecundity on effective population size. *Biol. J. Linn. Soc.* 59:411–425.
- NUNNEY, L., AND K. A. CAMPBELL. 1993. Assessing minimum viable population size: demography meets population genetics. *Trends Ecol. Evol.* 8:234–239.
- NUNNEY, L., AND D. R. ELAM. 1994. Estimating the effective population size of conserved populations. *Conserv. Biol.* 8:175–184.
- PIMM, S. L. 1991. *The balance of nature?* Univ. of Chicago Press, Chicago.
- PIMM, S. L., AND A. REDFEARN. 1988. The variability of animal populations. *Nature* 334:613–614.
- PRAY, L. A., C. J. GOODNIGHT, L. STEVENS, J. M. SCHWARTZ, AND G. YAN. 1996. The effect of population size on effective population size: an empirical study in the red flour beetle *Tribolium castaneum*. *Genet. Res.* 68:151–155.
- RALLS, K. J. D. BALLOU, AND A. TEMPLETON. 1988. Estimates of lethal equivalents and the cost of inbreeding in mammals. *Conserv. Biol.* 2:185–193.
- TURCHIN, P., AND A. D. TAYLOR. 1992. Complex dynamics in ecological time series. *Ecology* 73:289–305.
- VUCETICH, J. A., R. O. PETERSON, AND T. A. WAITE. 1997. Effects of social structure and prey dynamics on extinction risk in gray wolves. *Conserv. Biol.* 11:957–965.
- WAITE, T. A., AND P. G. PARKER. 1996. Dimensionless life histories and effective population size. *Conserv. Biol.* 10:1456–1462.
- WILLIAMSON, M. H. 1984. The measurement of population variability. *Ecol. Entomol.* 9:239–241.
- WRIGHT, S. 1938. Size of a population and breeding structure in relation to evolution. *Science* 87:430–431.

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### THE GENETIC BASIS OF DEVELOPMENTAL STABILITY. III. HAPLO-DIPLOIDY: ARE MALES MORE UNSTABLE THAN FEMALES?

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*Key words*—Coadaptation, developmental stability, fluctuating asymmetry, haplo-diploidy, heterozygosity.

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Previous studies using the haplo-diploid honey bee, *Apis mellifera*, consistently revealed that haploid males were developmentally more unstable than their diploid female counterparts. To test the generality of this phenomenon, the level of developmental stability, as measured by fluctuating asymmetry, was examined in both haploid and diploid individuals of a number of species from within the Hymenoptera and Thysanoptera. Despite males being more asymmetric than females for some characters, the phenomenon is neither consistent within or across species.

Developmental stability (the ability of an organism to buffer development against genetic or environmental perturbation) has been argued to be genetically controlled by genome-wide characteristics such as the level of genomic heterozygosity or genomic coadaptation (Clarke 1993). However, neither the heterozygosity nor coadaptation models adequately explain all the observed results in developmental stability studies, and alternative genetic models are under investigation (Emlen et al. 1993; Clarke 1995). Relationships between heterozygosity, coadaptation and developmental stability are inconsistent among characters within and among taxa (Palmer and Strobeck 1986). Unfortunately, much of the research to

date has treated the two hypotheses as mutually exclusive, with data being used in attempts to discriminate between the two alternatives.

To date, nearly all developmental stability studies have concentrated on diploid organisms. A problem of using diploids in an attempt to differentiate between heterozygosity and gene coadaptation models is that the two phenomena are not independent, and under most model systems it is impossible to manipulate one without concomitant changes in the other (Mather 1973; Clarke et al. 1992). The influence of ploidy on developmental stability has previously been examined in a number of systems. In general polyploid individuals have been shown to be developmentally more stable than diploids in both fish (Leary et al. 1985; Scheerer et al. 1987) and weevils (Mesaros et al. 1994). As polyploid individuals typically have greater levels of genomic heterozygosity than diploids, these results have been used to support the hypothesized relationship between heterozygosity and developmental stability. Aneuploid individuals have been shown to have decreased developmental stability and increased incidence of gross developmental abnormalities compared with normal individuals in humans (Shapiro 1992), fish