The application of fluctuating asymmetry in the monitoring of animal populations

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The maintenance of fitness levels is an important part of the management of animal populations. Unfortunately, measuring fitness and determining the relative contributions of genetic and environmental components to that fitness represent considerable problems for management. The simple and inexpensive method of measuring non directional asymmetry (fluctuating asymmetry) in bilateral morphological characters may provide a useful contribution to this problem. The relationship of levels of fluctuating asymmetry to fitness has been explored at considerable length in the scientific literature but this knowledge has yet to be used effectively by wildlife managers. We examine the potential of fluctuating asymmetry as a management tool and show by use of a case study of island and mainland populations of lizards, how it may be used as a comparative tool in which to determine populations that require management priority.

Key words: Fluctuating asymmetry, Fitness, Heterozygosity, Wildlife management.

INTRODUCTION

THE increasing rate of species extinctions makes it imperative that wildlife managers involved in conservation can identify species at risk, obtain information on the causes of their decline, and apply that knowledge in management programmes designed to stem and reverse the decline. Managing species at risk requires knowledge of the numerical responses of populations to environmental change, be it through habitat modification, climatic change, or new competitors, predators or pathogens. Environmental conditions can then be moderated or enhanced to achieve a desired increase in population numbers. While we may achieve short-term conservation objectives by manipulating the environment, it is unreasonable to expect that former human disturbances can be reversed or that future human disturbances can be halted. In the long term, if species are to survive, their populations must retain the genetic capacity to respond to environmental change. Therefore, wildlife managers should be concerned not only with maintaining animal species through the manipulation of population dynamics, but also with factors such as fecundity and vigour which affect the probability of persistence, or fitness, of a population.

To maintain fitness in natural populations, managers have two tasks. They must monitor changes in mean levels of fitness within the populations being managed and they must be able to identify the underlying causes of any observed changes in mean fitness. Measuring fitness *per se* is very difficult in natural populations because detailed and time consuming demographic studies over generations are required to estimate mean lifetime reproductive output or other fitness parameters. In most management situations, particularly those involving long lived species, such studies are expensive and impractical.

To identify the factors that underlie a change in fitness levels is also difficult because the level of fitness exhibited by an individual is a function of the interaction of its genotype and the environment (Hoffman and Parsons 1991). Individuals with genotypes that cope poorly with the prevailing environmental stresses are likely to exhibit lower levels of fitness than those with more robust (or better adapted) genotypes.

The genotype of an individual can affect the extent to which it can cope with environmental stress in two ways. First, inbreeding within a population will result in increased levels of homozygosity. Within a normally outbreeding population, such increased levels of homozygosity can cause inbreeding depression through the expression of deleterious recessive alleles or the disruption of coadapted gene complexes (Mather 1953). Second, heterozygosity may infer a fitness advantage through heterozygous superiority resulting from the inherent biochemical versatility of heterozygotes over homozygotes (Lerner 1954). Therefore, fitness levels in natural populations will be a reflection of the levels of inbreeding, heterozygosity and environmental stress experienced by individuals. The relative contribution of these factors will need to be assessed before correct management procedures can be applied.

Allozyme electrophoresis has been a favoured tool for measuring the genetic characteristics of animal populations (Nevo *et al.* 1984; Lande and Barrowclough 1987) and there are now several other convenient and useful molecular techniques

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available for use at the population level (Amos and Hoelzel 1992). However, results of genetic surveys of natural populations, whilst useful in many·ways, will not be sufficient to identify populations with genetic problems or to detect the impact of environmental stress on the population in question. This is because the relationship between genetic variation (as measured by mean levels of heterozygosity) and fitness is not a simple one (Allendorf and Leary 1986). It is quite possible for example, that a population that has gone through a severe bottleneck at some time in the past, has purged itself of a large component of its deleterious alleles and is no longer as susceptible to problems of inbreeding (e.g., Templeton and Read 1983). In such a situation, a genetic survey might register levels of variation that are very low (high homozygosity) but which may be having little influence on the mean fitness of the population unless overdominance is making a substantial contribution to fitness. To solve this dilemma, wildlife managers must look for additional approaches to monitoring natural populations that complement genetic analyses. In this paper, we explore the potential of a morphological approach using fluctuating asymmetry as an adjunct to molecular techniques for assessing the fitness of natural populations.

FLUCTUATING ASYMMETRY

Lerner (1954) first proposed that heterozygosity is important in determining the degree of developmental homeostasis exhibited by an individual. He suggested that individuals that are more heterozygous are better buffered against environmental perturbations during development than those that have lower levels of heterozygosity. Developmental stability can be considered a major component of fitness and the measurement of developmental stability within populations can therefore, potentially at least, provide valuable information on the levels of fitness within animal populations.

One character that has been used as a convenient measure of developmental stability is fluctuating asymmetry (Mather 1953; Van Valen 1962). Fluctuating asymmetry is the degree of random difference between left and right sides of bilateral structures. Since both sides of an organism have the same genotype, the differences between the left and right sides of bilateral characters measure the ability of its genotype to buffer environmental perturbations during development. Fluctuating asymmetry arises through the interaction of environmental stress during development and the genetic capacity of the individual to cope with the stress.

A wide range of both metric and meristic characters have been used to measure fluctuating asymmetry in inter and intra population studies of many organisms. Characters used include cranial characters in Pocket Gophers (Patterson and Patton 1990), large cats (Wayne *et al.* 1986) and Rhesus macaques (McGrath *et al.* 1983), teeth (Bailit *et al.* 1970; Greene 1984) and palm ridge counts (Soulé and Couzin-Roudy 1982) in humans, scale counts and measurements in lizards (Soulé 1967, 1979; Jackson 1973; Sarre and Dearn 1991) and fish (Leary *et al.* 1985; Quattro and Vrijenhoek 1989), wing length (Brückner 1976), wing vein length and number of hamuli (Clarke *et al.* 1992) in honey bees and wing length in butterflies (Mason *et al.* 1976).

Fluctuating asymmetry has been correlated with average levels of protein heterozygosity (Brückner 1976; Soulé, 1979; Vrijenhoek and Lerman 1982; Biémont 1983; Leary, Allendorf and Knudsen 1985; Leary *et al.* 1985; Quattro and Vrijenhoek 1989) either as population averages or at the level of the individual, though some studies have failed to show a correlation (e.g., Jackson 1973; Bradley 1980; Patterson and Patton 1990). Increased levels of fluctuating asymmetry have also been observed in populations that are experiencing inbreeding (Clarke *et al.* 1986; Quattro and Vrijenhoek 1989) or subjected to environmental stress (Valentine *et al.* 1973; Pankakoski *et al.* 1992). As a consequence it has been suggested (Wayne *et al.* 1986a; Leary and Allendorf 1989; Parsons 1990) that fluctuating asymmetry may have merit as an indicator of inbreeding and stress in captive bred and natural populations. As such, fluctuating asymmetry may represent a useful tool for examining the effect of the interaction of genetic and environmental factors on fitness levels in faunal populations that are being managed for conservation purposes.

SLEEPY LIZARDS ON ISLANDS — A CASE HISTORY

An example of one way in which fluctuating asymmetry (in conjunction with an electrophoretic survey) may be used to rank natural populations for management, is provided by a recent study of populations of a lizard (Sarre *et al.* 1990; Sarre and Dearn 1991). In this study, seven island and three adjacent mainland populations of a large, common and long-lived lizard *(Trachydosaurus rugosus)* were examined for variation in mean levels of both heterozygosity and fluctuating asymmetry. *T. rugosus* is not currently endangered, but its distribution was fragmented by rising sea levels 8 000 to 10 000 years before the present, leaving several insular populations in addition to the mainland populations. Such a situation is analogous to many species that are now restricted to habitat fragments by human activities and for which scarce conservation funds must be allocated wisely. The islands range in size from 8 ha to 20 400 ha with populations on the two smallest islands consisting of approximately 50 individuals each (Sarre *et al.* 1990).

Heterozygosity was assessed by examining genetic variation at 16 protein loci of which seven were polymorphic. Departures from Hardy-Weinberg equilibrium occurred in some loci from several populations but there were no populations with consistent departures from Hardy-Weinberg equilibrium across all loci (see Sarre *et al.* 1990 for more detail). Mean per cent heterozygosity levels were high in all populations (ranging from 10.5 to 16.8; direct count) but were not significantly different from each other ($F = 0.12$, $P > 0.1$, one-way ANOVA after an arcsine transformation; Fig. 1a). However, there was a trend towards reduced allelic diversity in the island populations (Mean no. alleles per locus: Island = 1.33; Mainland = 1.6; Fig. 1b) resulting from the loss of alleles that were rare in the mainland populations. In contrast to the electrophoretic study, levels of fluctuating asymmetry in three meristic, bilateral characters varied significantly among the nine populations. When the three characters are combined using a rank sum procedure to form a single estimate of population asymmetry (Soulé 1967), four island populations stand out as having distinctly higher levels of fluctuating asymmetry (Fig. 2) than all others.

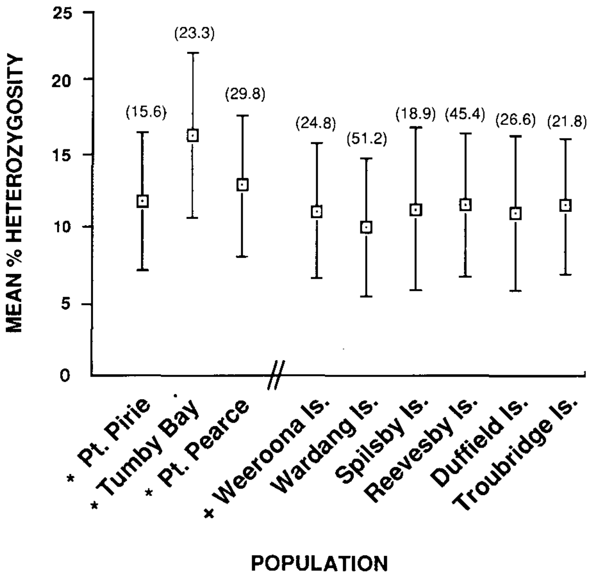

Fig. 1a. Mean levels of heterozygosity (with standard error bars) in island and mainland populations of the sleepy lizard. Mean sample sizes are in parentheses. * = mainland; island area (ha's): Duffield, Troubridge = 8, Weeroona = 210, Reevesby = 358, Spilsby = 425, Wardang = 20 400. ⁺Weeroona is connected to the mainland by mangrove swamp.

The incongruence observed between the levels of developmental stability and heterozygosity among the populations, suggested that forces were acting on several populations in a way that was not being detected by electrophoresis. In such a situation three explanations are possible. First, variation at the protein level may not be sufficiently sensitive to detect genetic changes

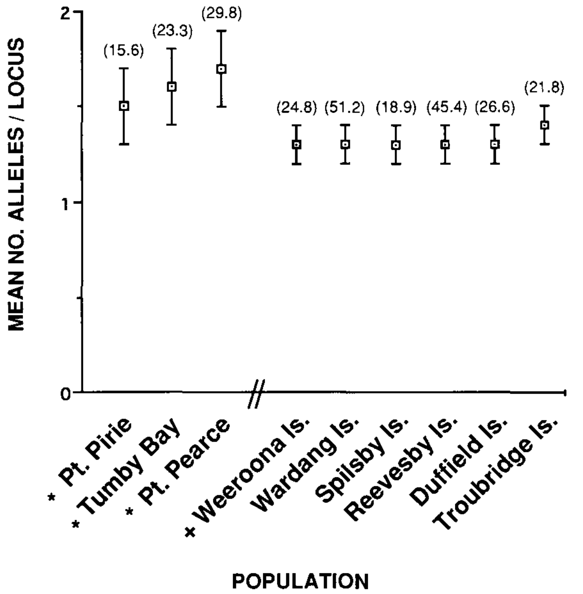

Fig. 1b. Mean number of alleles per locus (with standard error bars) in island and mainland populations of the sleepy lizard. Mean sample sizes are in parentheses.

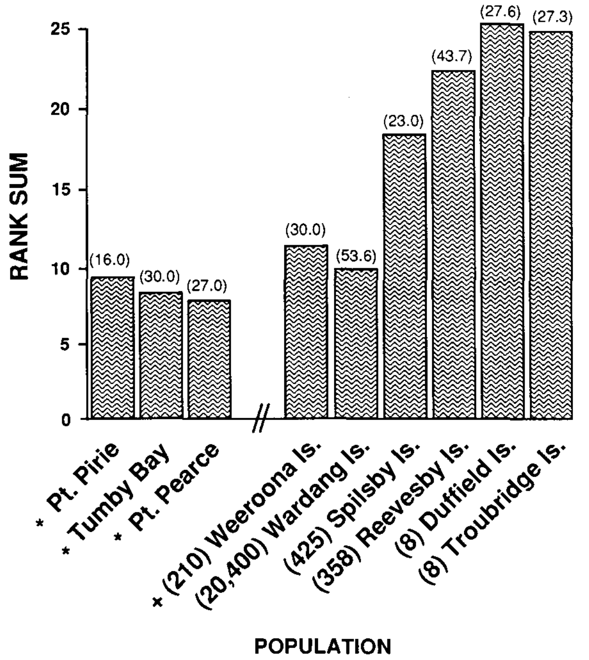

Fig. 2. The sum of the ranks of mean levels of fluctuating asymmetry in three meristic characters of island and mainland populations of the sleepy lizard. Levels of FA were calculated using the formula $\Sigma(L-R)^2/N$ where L = Left hand count; R = Right hand count; N = sample size. Rank sum was calculated by ranking the populations in order of their levels of fluctuating asymmetry for all three characters and then summing the rankings for each population. Island area (in hectares) is given in parentheses beside each island name. Mean sample sizes are in parentheses above the histograms.

occurring in some of the populations. If this is the case, findings based solely on the electrophoretic data have not identified potential genetic problems. Second, environmental stresses may be affecting developmental stability in some of the populations regardless of the level of genotypic variation within those populations. Third, the high levels of fluctuating asymmetry observed in some populations may be the result of genetic disruption caused by a major selection event (e.g., Clarke and McKenzie 1987) so that the populations are in the process of adapting to that selection event. There is no evidence that this is the case for the lizard populations described in this paper but, in any case, conservation management would still demand that the selective agent be identified. The important point is that although the analyses described in the above study do not enable the relative influence of environmental and genetic factors on developmental stability to be accurately apportioned, they do make it possible to identify the populations that are under stress. Thus, for management purposes, the populations that require conservation effort can be identified. These populations can then form the focus for future research and management.

To identify the causes of the high levels of fluctuating asymmetry within populations it will often be necessary to undertake detailed and extensive research. One approach may involve the use of more sensitive and elaborate (but more expensive and time consuming) genetic techniques. Techniques such as those involving mitochondrial or nuclear DNA can be used to establish the likelihood that a genetic phenomenon, such as inbreeding or reduced heterozygosity, is causing the high levels of fluctuating asymmetry. Poor or insufficient diet, lack of suitable habitat, disease, pollution and other environmental stresses may cause an increase in the level of fluctuating asymmetry within a population. These factors will need to be examined using field and laboratory experiments (Glotôv 1992) if the major cause of the high fluctuating asymmetry is to be identified and action taken to alleviate the problem. The role of fluctuating asymmetry in this process is to identify the populations that are under the greatest stress so that the available research and management resources can be targeted for maximum effect.

CONCLUSION

It has previously been suggested that fluctuating asymmetry may have an important role in conservation biology (Leary and Allendorf 1989). This view is supported by a study on three stocks of the endangered Sonoran Topminnow (Quattro and Vrijenhoek 1989) in which fluctuating asymmetry was used as one of four traits to test the prediction that genetic diversity is associated with enhanced fitness. The study showed that one particular stock (the most heterozygous stock) was the best choice to use for reintroductions because under laboratory conditions it was consistently fitter than the other two stocks. The results of the present study on island populations of the sleepy lizard suggest another way in which fluctuating asymmetry can be used in the management of animal populations: as an indicator of which populations should receive management priority.

Despite the extensive and established literature pertaining to fluctuating asymmetry and studies of fitness, fluctuating asymmetry has not been widely adopted by wildlife managers as a management tool. We feel that as an inexpensive and relatively simple technique, this lack of recognition needs to be redressed. Although our current understanding of the relationship between fluctuating asymmetry and fitness does not warrant conclusions to be drawn about the conservation status of populations from fluctuating asymmetry alone, a "first look" with fluctuating asymmetry could indicate whether further investigation involving direct analysis of genetic variation and ecological factors should be carried out.

In some populations, the genetic/developmental processes underlying fluctuating asymmetry may in themselves be a cause of population decline. Alternatively, changes in fluctuating asymmetry may simply be correlated with genetic/developmental changes caused by extrinsic factors. In either case, the observation of high levels of fluctuating asymmetry in a population is likely to be indicative of a fitness related problem which can then be identified and addressed.

The full utility of fluctuating asymmetry as a measure of fitness in natural populations is yet to be adequately explored. In particular, the sensitivity of fluctuating asymmetry to genetic and environmental changes requires further research involving the long-term monitoring of selected wildlife populations. However, with so much of our biota at risk, conservation biologists must explore ways of studying the processes involved in extinction rather than being forced to simply document extinctions as they occur. Only in this way can we hope to devise strategies to manage our remaining wildlife.

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