

CRISIS INBREEDING: RAPID EVOLUTION IN LARGE, ECOLOGICALLY INTACT POPULATIONS?

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Received 27 January 1988, 13 June 1988

ABSTRACT: A mechanism which changes an outbreeding bias into an inbreeding bias during a stress-producing survival crisis in a large population of animals should mean a distinct evolutionary advantage to the population and, ultimately, to the individual. Adverse changes in sperm production for the male during a time of stress could lead to the situation where only inbreeders would reproduce at all. Some plants do have mechanisms which cause them to switch from outbreeding to inbreeding when changes in the environment make such a switch beneficial. Theoretical studies, experimental work, paleontological findings, and several hypotheses, published statements, predictions, etc., are cited, all of which either support the idea of "crisis inbreeding" or are linked to or indicative of the phenomenon. A chemosensory mechanism which could cause such a shift in inbreeding bias for some animal species is discussed. Other possible mechanisms are also outlined. They would cause a large, outbreeding population to switch to inbreeding during the earlier stages of a prolonged crisis. That way, spells of rapid evolution in that large (safe) population should occur during crisis times, and sympatric speciation would become possible. Additional information is provided in Addendums A through F, to supplement information outlined in brief in the main text.

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Introduction

Investigators have, in recent years, gathered information which confirmed that there was a tendency in many species to avoid inbreeding (e.g., Packer, 1979; Pusey, 1980; Hoogland, 1982; Sherman and Holmes, 1985; Berger and Cunningham, 1987; Hanby and Bygott, 1987). It is generally presumed that, for this type of species, extensive inbreeding would only occur in the case of a small population.

Unfortunately, the problems with a small, isolated population are numerous (see Addendum A). Deleterious traits from the inbreeding itself are far more likely to show up in such a small population than advantageous traits for survival in an adverse new environment, and inbreeding depression should generally add to an already high probability of extinction. In addition, the level of stress in any environment which has decimated a population down to a few individuals is likely to be high enough to stop all reproduction (cf. Section 3 in this paper; also Mann, 1964; DeLong, 1967). And where closely related individuals impact one another's reproductive capabilities as negatively as Hanby and Bygott (1987) detailed for the lion, any small group of individuals which must inbreed or perish, would probably be doomed.

If, instead of delaying the inbreeding until that bottleneck where the population is so extremely vulnerable, the individuals should switch to inbreeding during the earlier stages of any adverse change in the environment (i.e., when the population is still large and reproductively fertile and ecologically intact), the population's chances of survival should be vastly improved. There would be thousands of inbreeding demes, instead of just one vulnerable one, in such a large population of predominantly inbreeding individuals. Even if deleterious traits should show up in the vast majority of those demes, there would be enough genetic variability in that population to produce at least one deme (or a few demes) with

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Evolutionary Theory 8: 365-395 (April, 1989)

The editors thank D. Charlesworth, A. Pusey, and W.M. Shields for help in evaluating this paper.

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individuals having advantageous traits for the emerging new environment. Any demes that are lost because of deleterious traits, as well as the inbreeding depression which would cause most demes to reproduce at lower rates, would help to ease the pressure on that population (where the changing environment probably resulted in an insufficient share of the remaining resources for every individual). This should make survival easier for the newly advantaged individuals.

In other words, deleterious traits and inbreeding depression would indirectly help to increase the chances of the advantaged individuals to make it through the environmental crisis. And because the inbreeding per se would make possible that burst of rapid evolution, which would lead to the appearance of the advantageous traits for the emerging new environment (and thus a selective advantage over the outbreeders which might fail to evolve rapidly enough at that appropriate yet safe time), the survivors which make it through the crisis would actually do so because of their ability to switch to inbreeding while the inevitable need to evolve rapidly could be accomplished at minimum risk for the successful-to-be demes.

Those demes with their tendency for early inbreeding would then end up leaving more offspring (i.e., in the long term) than all those individuals in other populations where the tendency is to continue to outbreed until the disadvantages of inbreeding (Maynard Smith, 1978; Hoogland, 1982; Ralls and Ballou, 1982) become so disproportionately large for a small population that extinction becomes virtually inevitable. (See also Fisher, 1949.) Then the mechanism which would cause most of the individuals in the successful population to switch from outbreeding to inbreeding during the earlier and much safer part of the environmental crisis should make it through into the next species/variety with those survivors despite the inbreeding depression which might have placed them at an apparent disadvantage for a while -- i.e., in the short term only, but not in the long term.

However, it might not be necessary to rely only on group-selection arguments to explain a mechanism that exists at the level of the individual. It will be argued in Section 3 of this paper that there is also a selective advantage for the individual in turning from outbreeding to inbreeding during a stress-producing crisis.

Scope of Study

The primary purpose of this study was to gather sufficient facts to alert evolutionists to the possibility that mechanisms for "crisis inbreeding" may exist in some animal species, and perhaps even in a majority of species.

However, the topic of crisis inbreeding extends beyond the existence of mechanisms which cause individuals to reverse their inbreeding avoidance at certain times. It should even make possible a spell of rapid evolution in a large, ecologically intact population such as one that has grown to the point of saturating its habitat. The prolonged stress from the individuals' search/competition for limited resources might trigger the inbreeding.

Such a tendency of the individuals to inbreed whenever an adversely changing environment causes them (say) nutritional stress beyond the depletion of the fat reserves they have built up, would enable most large, safe populations to evolve rapidly and exactly "on cue" every time there is a stressful crisis which makes rapid evolution essential if extinction (because of infertility of the stressed individuals, etc.) is to be avoided.

The long-term selective advantage which the eventual survivors would enjoy as part of such a population with the ability to alter its rate of evolution in almost perfect synchrony with the rates of change in the environment, has to be significant. The probability for appropriate changes of form, to suit the new environment, would not rest so heavily on the remote likelihood that a chance mutation would produce a (rare) advantageous new trait for the emerging new environment in time to avert disaster. Instead, this already existing possibility

of useful new mutations would be supplemented by the prompt access to many thousands (even millions) of recessive mutations which had accumulated in any large, outbreeding population, and which the inbreeding would help to express in the phenotypes. Then even rapid, successful change to a totally different form becomes possible in a drastically changing environment -- such as when a meteorite impact or volcanic eruption should blanket out the sunshine for months on end. Centuries of outbreeding with its slow evolution (or stasis) would be interspersed with spells of rapid evolution (in a matter of generations) to adapt to severe upheavals in an environment with a precariously balanced climate that has the potential to change rapidly enough to cause long periods of unusual drought, etc.

Any such large population of inbreeding demes would increase the possibilities for both anagenesis and cladogenesis. For instance, the greater success of the newly advantaged individuals in the emerging new environment should cause their level of stress to decrease sufficiently to return them to outbreeding with other advantaged demes, and thus to new combinations. An ecologically intact population would make that outbreeding between the various newly advantaged demes possible, and would help to make rapid (even substantial) evolution possible for that population as a unit. On the other hand, the continued inbreeding in an environment which continues to change in a stress-producing way might cause two or more demes to evolve into totally different directions which would either take them into new habitats or cause them to exploit different resources in the same geographic region (such as a lake). And in a population which is existing so close to the carrying capacity for its habitat that some individuals would be compelled to forage near the more stressful periphery of the habitat (where resources are likely to be more sparsely distributed than elsewhere), one or more of these peripheral demes, which should be inbreeding because of their stress, could end up evolving away from the original population. They would be able to do so without first having to run the risk of venturing out to the point of (say) geographic isolation in their parental form, or of being threatened by all the sudden dangers of inbreeding and a chance-dependent direction of evolution after accidental isolation. (See Addendum B.)

The scenarios which have been touched on briefly above, give some idea of the vast field for research which would be opened up by the topic of crisis inbreeding. However, the present study intends to limit itself to alerting evolutionists by means of evidence and arguments from existing literature, to the possibility that crisis inbreeding might exist in the wild.

To further help accomplish this, some possible mechanisms which could induce the individuals in a large population to switch to close inbreeding, will be proposed.

These references to published evidence, arguments, and proposals will be presented as follows:

Section 1: Summary of favorable conditions for rapid change.

Section 2: Brief evidence that individuals tend to avoid intraspecific competition, thus making the abnormal stress of increased competition during crisis times a suitable trigger for crisis inbreeding.

Sections 3 - 8: Evidence and arguments in support of crisis inbreeding.

Sections 9 & 10: Possible crisis-inbreeding mechanisms.

Sections 11 & 12: Discussion and Conclusion.

The chemosensory mechanism that will be proposed in Section 9 may well apply to most species where the individuals detect and distinguish one another olfactorily, or even to species which rely on waterborne tastes to accomplish this; but it should not apply to species that have to rely on visual or auditory cues. And for species in an environment which is not subject to rapid or drastic change (e.g., the open ocean) crisis-inbreeding mechanisms for rapid evolution may never have evolved because there might never have been any significant advantage in having them. Only species that might have a need for rates of evolution in excess of those made possible by their "conservative" genotypes (see Addendum C) would benefit from

crisis-inbreeding mechanisms.

As for species which normally inbreed, increased phenotypic variance (and thus the potential for more rapid evolution than usual) should come with a similar switch to outbreeding. Whatever the direction of the switch, the evolutionary advantage would be the same: the "instantaneous" potential for more rapid evolution than usual.

For those readers who need further information to help them assess whether inbreeding in normally outbreeding species is not just for small populations, Addendums A through F will be added at the end of this paper.

1. Conditions for Rapid Evolution

Wright (1945), in discussing "the conditions most favorable for rapid evolution" stressed that "conditions are enormously more favorable in a population which may be large but which is subdivided into many small local populations almost but not quite completely isolated from each other" because such a population "carries the maximum amount of potential variability." Bush et al. (1977) mention "widespread acceptance [of the] hypothesis regarding the evolutionary importance of demes" and list, among other things, "small demes maintained by social structuring" as situations where rapid speciation may result.

A large, ecologically intact population in which the individuals have switched from outbreeding to inbreeding during a time of crisis would not only satisfy all these conditions for rapid evolution, but would also have access to a vast storehouse of recessive mutations which had accumulated virtually undisturbed during the long period of outbreeding which preceded the spell of inbreeding.

2. Harmony, not Competition

The literature abounds with evidence, arguments and hypotheses which indicate that individuals usually try to avoid direct competition and/or confrontation with conspecifics. Some of the ways are:

- Mutualism, nepotism and/or altruism (Kurland, 1980; Kareem and Barnard, 1982; Hoogland, 1983; Sherman and Holmes, 1985).
- Dominance hierarchies established by means of a single confrontation, often without an actual fight (Maynard Smith and Price, 1973; Maynard Smith, 1974; Cowan, 1979).
- Avoidance behavior rather than aggression, as per the Social Cohesion Hypothesis by Bekoff (1977).
- Indirectly, by regulation of a population at well below the environmental carrying capacity (Wynne-Edwards, 1962; Rowe et al., 1964; Christian et al., 1965).
- Individuals curtail their own evolutionary fitness by, for instance, withdrawing from social interaction when intraspecific harmony is threatened (cf. Holst, 1985; Rogers, 1986).
- Individuals use actions, sensory cues, etc., on a continual basis to signal to other individuals whether they should stay away or are welcome to approach (West et al., 1962; Archer, 1968; Evans and Goy, 1968; Doty, 1974).

In any species where the avoidance of intraspecific competition has such a high priority, it should cause considerable stress to the individual when a changing environment or overpopulation causes an essential resource to decrease to the point where the individuals must compete intensely for that resource. This prolonged stress with its increasing wariness of conspecifics would then be the ideal trigger for a crisis-inbreeding mechanism, because it would only trigger that mechanism when the changing environment makes rapid evolution essential, and when the costs of migration are most likely to exceed the costs of inbreeding (see Section 5). It should also cause the bias to shift toward inbreeding at more or less the time when the prolonged stress would make it impossible for outbreeders to reproduce at all,

while the inbreeders would still be able to reproduce (see Section 3).

3. Selective Advantage for the INDIVIDUAL in Crisis Inbreeding

If the individual's level of stress should trigger the crisis-inbreeding mechanism near that point of the crisis where the costs of emigration begin to exceed the costs of inbreeding (Section 5), the crisis inbreeding (i.e., at that time of prolonged stress only) has to confer a selective advantage at the level of the individual. However, there appears to be an even more definite evolutionary advantage for the individual in inbreeding during times of prolonged stress.

For instance, MacLeod and Gold (1951) did semen analyses for 2000 men, and found that the fertile half had a mean sperm count of (107 ± 74) million/ml, whereas the infertile half had a mean sperm count of (90 ± 76) million/ml.

In a more recent study by Hammitt et al. (1988), the fertile men which served as controls had a mean sperm count of (96.3 ± 48.3) million sperm per ml. From the same publication, for 226 men attending an infertility clinic, the mean sperm count was determined to be (81.6 ± 3.5) million/ml by Keel and Webster (1988).

Data like this indicate that, for the average man, a reduction of only about 15% in sperm count might well be disastrous.

Similarly, a relatively small decline in the motility of the man's sperm, or the velocity with which they move on their way to the ovum, or the percentage of them that have adequate morphology, etc., could make the difference between fertility and infertility (cf. Keel and Webster, 1988).

The position appears to be a potentially precarious one.

Moreover, on March 21, 1988, PBS stations from New York broadcast a NOVA program called "The Miracle of Life" which stated that only a tiny group of about fifty (50) sperm out of a total of 200 million sperm made it to the woman's ovum. (See also Mann, 1964, p. 67.)

This gives an idea how extremely successful the female's immune defenses are against a male's sperm during sexual reproduction. And according to the U.S. News and World Report of October 5, 1987, there are now data available which indicate that in the case of about 10% of all married couples the woman's immune system consistently destroys all of the husband's sperm before they can reach her ovum. This estimate appears reasonable in the light of the "somewhere between 5% and 30% of men and women with apparently unexplained infertility" which Jones (1987) links to "evidence of antibodies to sperm."

In other words, laboratory workers may have been way off the mark during animal experiments when they interpreted the presence of millions of sperm after copulation, or the sight of tubules in the cauda epididymides, or any other evidence of spermatogenesis, as proof that the male was fertile. And even if a male is fertile with one female, it does not necessarily mean he would be fertile with another female.

The reason for this is that tissue-specific substances become part of the spermatozoa while in the male's body. Whether this is accomplished through histocompatibility (HLA) antigens being expressed on epididymal sperm or by HLA molecules from the seminal plasma being passively absorbed onto sperm, or in some other way, is not relevant here. The fact is that the female's "genital tract, particularly the uterus, is well endowed with immunologically competent cells [which] phagocytose spermatozoa and process their antigens for recognition by the host's immune defences" (Jones, 1987). The resulting onslaught from antisperm antibodies (cf. Jones, 1987) and other immune defenses in the woman's body is going to make the journey to the ovum hazardous in the extreme for the sperm.

The most important aspect of male fertility is, therefore, that tiny number of sperm which can survive the female's immune defenses. And to ensure that some sperm will reach the ovum, the average male has to have a certain sperm count of vigorous, morphologically adequate sperm. But when the male becomes more and more

nutritionally stressed, less and less energy can be spared for spermatogenesis, and less and less nutrients become available for the sperm themselves. The result may be a lower sperm count and/or less vigorous sperm and/or a higher percentage of sperm which have not been formed properly. Then none of the male's sperm would make it to the female's ovum despite the fact that there might still be many, many millions of sperm in the ejaculation.

Consider also an experiment described on page 333 of Mann (1964), which led him to conclude that just "4 weeks on a deficient diet" can reduce "the content of fructose and citric acid in the accessory glands [of rats] to a castrate level." (See also pages 335-337.) And on page 20 of Mann and Lutwak-Mann (1981) it is stated that, "As in man, a common early sign of underfeeding in animals is a decline in . . . testosterone [levels] resulting from diminished endocrine activity of the Leydig cells." Also, on page 21, that "spermatogenesis seems to be particularly sensitive [to] folic acid deficiency," and that symptoms associated with "reduction of spermatogenic activity are also typical of animals suffering from vitamin A deficiency."

The list does not end there. Zinc, proteins, fatty acids -- they all affect male reproductive function.

Therefore, sperm production in the animal seems to be extremely sensitive to any of the various aspects of nutritional stress.

Furthermore, on page 330 of Mann and Lutwak-Mann (1981) there are graphs of sperm concentration and volume of ejaculate for a pair of identical (monozygous) twin pubescent bullcalves. The graphs show that semen volume was slightly more than halved for the one with half the calorie intake of the other one, and the sperm concentration per 100 ml was considerably less than 50% for the nutritionally stressed bullcalf.

If semen volume can run at less than 50% of the normal volume when the diet is 50% deficient in calories only, one can imagine how soon a diet deficient in all the essential nutrients would reduce a male's sperm count by something like just 15% or 20%. (See also Addendum D.)

In addition to the problems that can be caused by deficient nutrition, it is known that stress itself (see Selye, 1950, p.103) can have an adverse effect on a male's sperm production and/or sperm count (cf. Jequier and Crich, 1986, p.26; Christie, 1987; also the above-mentioned NOVA program). An instance of male infertility under social stress may well have been recorded by Southwick (1955). He found that, for mice under crowded conditions, the "birth rate fell from 1.79 to 0.81 young per adult female per month. Yet in November just as many females were ovulating and just as many males showed evidence of sperm production as in April, May, June and July."

As stated before, the presence of sperm does not necessarily mean a male is fertile. Southwick does suggest, among other things, that the decline in birth rate may have been caused by the males interfering with one another during copulation, but actual infertility by the males, while the females still ovulated as usual, cannot be ruled out. Social stress may have helped to lower the sperm production by that fraction which was enough to affect fertility. And some additional data in Addendum D seem to support this contention.

In other words, for the average male in the wild, with the average sperm count of average motility, average velocity, average morphology, etc., there would be a certain number of sperm making it to the average female's ova. But when the environment changes adversely, some essential resources are going to end up in short supply. The nutritional stress and/or social stress (because of increased competition for the limited resources) are going to result in lower sperm counts and/or less vigorous sperm, etc., and this will result in fewer sperm reaching the average female's ova.

If the environment continues to change in an adverse way, the animal's level of stress should increase more and more. Then fewer and fewer sperm are likely to make

it to the female's ova.

Sooner or later the male is going to reach that critical point where no more sperm will reach the ova of the average female in the population.

This might sound like imminent extinction. However, it need not be.

Jones (1987) states that "only a genetically selected minority [of spermatozoa] gain access to the Fallopian tube and that these are immunologically different from the residual majority." And with the growing awareness of such matters as the tissue specificity involved in the immunological regulation of fertility (cf. Takai et al., 1987) and the successful "use [of] spermatozoa as typing cells for the HLA-D determinants" (Halim and Festenstein, 1975), it is becoming clearer every day that more of a closely related male's sperm should normally make it to a female's ova -- the same way as a transplanted organ (such as a kidney) which has been donated by a closely related individual is usually more likely to survive someone's immune defenses than an organ donated by the average unrelated individual.

In other words, when a specific male's level of stress reaches that critical point where his sperm lack the density and/or vigor and/or morphology, etc., required to impregnate the majority of females in the population, the chances would be considerably greater that he would find a tissue-compatible female among those females that are closely related to him than among those that are unrelated to him. Then a greater proportion of his sperm should survive the immune defenses of that (closely related) female, and some of his sperm should still make it to her ova at that critical time when none of his sperm would be successful in the average, unrelated female.

In addition to these greater chances for survival of sperm in a closely related female because of tissue compatibility, "antigens [which] are individual-specific rather than cell-specific . . . also contribute to the antigenic profile of the spermatozoa" (Jones, 1980). This should mean that the sperm of a closely related tissue-compatible male should, because of greater genetic similarity with the female, have an even better chance of surviving in a specific female than the sperm of an unrelated tissue-compatible male. The closely related male should have the advantage on two fronts, not just on one front the way other tissue-compatible males would have. And there might even be genetically determined factors which make it easier for a sperm cell to penetrate the layers of unique protective cells around the ovum when the sperm and ovum share a greater genetic identity.

This means that any individual with a mechanism for turning an outbreeding bias into an inbreeding bias at that point where inbreeding is so very likely to become the best strategy would have a selective advantage over the individual which tries to avoid inbreeding at all times. And if the small (15%) difference between mean "fertile" and mean "infertile" sperm counts in man is an indication, this point of infertility during outbreeding should be reached fairly early by the average male during a nutritional crisis.

The lower the male's sperm parameters during normal times, the sooner the male would reach that critical point where inbreeding would be the best reproductive strategy. And for the males whose sperm parameters normally hover right on the brink of "infertility" during times of ample food, inbreeding would become the better strategy from the very start of the nutritional stress, close to the onset of the crisis.

Moreover, for every new generation of inbred offspring the greater genetic similarity of siblings should mean an even greater proportion of the male's sperm that would make it to the female's ova during inbreeding. That way, each inbreeding generation would be able to "tolerate" (from a reproductive point of view) a higher level of stress than the previous generation, because immunologic infertility would occur at a lower and lower sperm count (etc.) as the siblings become more and more genetically identical.

This means that continued inbreeding in successive generations during an intensifying environmental crisis would result in a continued reproductive advantage

for the crisis inbreeders -- an advantage the persistent outbreeders cannot possibly have if they wait right until a very small population (likely to be at the worst part of the crisis) before they yield to the need to inbreed. The continued inbreeding would actually ease the inbreeders ever deeper into the crisis while protecting them against infertility from their mounting stress.

Therefore, inbreeding should be the best strategy during a time of nutritional stress. But during a time of ample food and/or low social stress, the opposite would be true. The greater proportion of sperm surviving the female's immune system during inbreeding should mean a greater possibility that inadequate sperm cells might make it to the ova, and such a risk could contribute toward inbreeding depression. Then outbreeding would be the better strategy under normal circumstances.

The result is that outbreeders should produce more offspring during times of abundant food and/or low competitive stress, but after a certain time of prolonged nutritional and/or other stress, the outbreeders would no longer be able to produce any offspring, while the inbreeders would still produce some offspring for a definite period. Then outbreeding should be the better strategy during good times, but inbreeding should be the better strategy during harsh times.

Some of the evolutionary significant factors in such an inbreeding strategy during stressful times should be:

- Continued inbreeding is likely to become the only successful strategy if the environment continues to change so drastically that it keeps the individuals under continued stress for generation after generation (cf. the Red Queen Hypothesis, Van Valen, 1973), and this should result in a greater likelihood that the genes associated with advantageous new traits for the changing environment would become fixed in the deme where they had been expressed.
- Such a situation of inbreeding as the only reproductively successful strategy available in stressed demes would reduce the chances that the ancestral genome might find its way back into the demes which are in the process of drifting away from the ancestral form while the crisis lasts. This would help along the speciation process.

The precarious interaction between a female's immune system and a male's sperm might well be one of the earliest mechanisms for initiating true reproductive isolation between a male and female whose genotypes have diverged beyond a crucial point of similarity, and this could make continued inbreeding essential in any deme where enough distinctly different traits for the new environment have emerged during the initial inbreeding. Outbreeding with ancestral types might then produce no offspring, and any individual with a willingness to mate with the new phenotype instead (matching its own) would have a clear-cut evolutionary advantage.

4. "Crisis Inbreeding" in Plants

Strong evidence for mechanisms which change outbreeding to inbreeding during harsh times comes from plants.

Ford (1964) devotes an entire chapter of his book to the heterostyle-homostyle system in plants, and discusses the primrose at length. Among the statements he makes are the following:

- "The less perfectly a plant or animal may be fitted to the conditions of its life, the greater the chances that from an outburst of variability something worthwhile may be selected" (p.224).
- "It is natural therefore that we should sometimes encounter the means of transition from outbreeding to inbreeding and the reverse and find it attained in diverse ways. It is achieved for example in those Cilioporah which are capable both of binary fission and conjugation and it will especially be noticed that the latter, or sexual mechanism, is resorted to only when the conditions deteriorate. A similar principle is at work in the heterostyle-homostyle

device, one which can favour a relatively greater degree of outcrossing or selfing as circumstances dictate" (pp.224-5; italics mine).

- "marginal populations of normally heterostyled plants are frequently homostyled" (p.225).
- "Yet it must be remembered that the countryside of southern England . . . has been much modified by changing forestry practice . . . It is not surprising therefore that within this region a few areas should be found in which the primrose, with its delicate heterostyle-homostyle adjustment, should be selected for a high degree of inbreeding rather than the normal outbreeding" (p.225).
- "We may remark also that it would seem to be in the highest degree likely that a mechanism which alters the reproductive system from outbreeding to selfing is powerfully controlled by selection to adjust the plant to those situations where diversity or relative stability of the genetic material is respectively advantageous" (p.227).
- "It is clear that the heterostyle-homostyle mechanism provides a means for adjusting the mating system from a relatively great amount of outbreeding to a relatively great amount of inbreeding" (p.230).

Everything Ford said about the advantages of the heterostyle-homostyle system in plants, could have been said about crisis inbreeding in animals.

5. Theoretical Considerations

Bengtsson (1978) posited that there might be a selective advantage in the willingness to inbreed when the chances of dying during emigration from the natal territory were great, and since those chances of dying increase considerably when an essential resource like food reduces to the point of critical shortage where acceptance of immigrants into other social hierarchies is extremely unlikely (cf. Gaines and McClenaghan, 1980) it follows that there has to be some selective advantage in any increased tendency to remain close to the natal area during a time of food shortage. This should mean reduced dispersal and greater inbreeding (Shields, 1982a, 1982b, 1983; Moore and Ali, 1984; Rowley et al., 1986; Grosberg, 1987) during times of food shortage when dispersal is likely to be more costly than inbreeding, and a mechanism that actually encourages such inbreeding during any time of prolonged nutritional stress would do its part to prevent emigration.

The advantages of staying near the natal area during a time of intense competition for food are not just limited to the avoidance of mortality from emigration. Familiarity with the natal region should ensure greater efficiency in foraging activities, defense of the territory, predator avoidance, etc. (Shields, 1983; Moore and Ali, 1984). This should make for a highly essential conservation of energy at a time when replenishment of that energy does not come easily, and there should be yet a further selective advantage in a tendency toward philopatry -- and thus increased inbreeding -- during every time of severe food shortage.

The natural inclination among animals may well be to leave the natal territory when there is a food shortage and to search elsewhere for food. However, Gaines and McClenaghan (1980) pointed out that the evidence for this was not always statistically significant. (See also DeLong, 1967; Hanby and Bygott, 1987.)

Whatever the truth, if the individuals in a population should suddenly show a bias in favor of inbreeding during such a time of nutritional stress when dispersal is so likely to be fatal, the chances reduce significantly that they would leave the natal territory. Then a mechanism for crisis inbreeding would help to confer an overall selective advantage to the individuals, because it would still leave them with a tendency to disperse during times of sufficient food, but to remain at the natal territory during harsh times.

The mechanism for this might not be strong enough to stop dispersal altogether during the harsh times. Then field observations may well show that there still is some dispersal, but if the high mortality for the dispersers results in an overall

reduction of the population, the chances for survival of the inbreeders which remain at home would be improved accordingly, and the selective advantage would still remain with the inbreeders -- more so than before. And there is evidence in the literature that dispersal might actually decrease in some species when competition for resources become high. (See Section 6.)

Whatever the complexities of dispersal in nature (cf. Van Valen, 1971; Harcourt, 1978), theoretical considerations do indicate that there should be a clear selective advantage in a tendency to switch from outbreeding to inbreeding during times of intense competition and low energy levels at which no energy can be spared for emigration, or when it would be much more difficult than usual to enter and successfully breed in another social hierarchy.

For instance, if

m = probability of dying during migration,

i = fraction of the inbreeder's offspring that will die or fail to reproduce as a result of inbreeding depression, and

f expresses the degree of consanguinity between the mating partners,

then Bengtsson's (1978) general relation for comparing the selective values of two reproductive strategies, namely

$$(1 - m)[1 - i(1 + 2f)]$$

reduces down to a simple relation of

$$m > (3/2)i$$

when the comparison is made between outbreeding on the one side where $i = f = 0$, and an inbreeding situation on the other side where $m = 0$ and $f = 0.25$ for the coefficient of consanguinity between sibs in an outbred population.

This simplified relation then provides the value of " m " above which the inbreeding would enjoy a selective advantage over the outbreeding.

In this same vein Packer's (1979) relation of

$$i > \frac{fm}{1 + f}$$

gives an idea of the point above which outbreeding should be favored over inbreeding by a female. This can be rearranged to read:

$$m > \frac{(1 + f)i}{f}$$

for the condition where inbreeding would be favored.

Chesser and Ryman (1986) allow for the history of inbreeding by the inclusion of the inbreeding coefficient (F) of the progeny, and an accumulation rate, c , for inbreeding depression. They arrive at various expressions for various situations, such as for sib-mating versus outbreeding, where F^* is the inbreeding coefficient of offspring produced by full-sib mating, and get

$$m > \frac{F(4 - c - 7cF) + cF^*(3 + 5F)}{2(1 + F)}$$

They conclude that "sib-mating may also be advantageous if the initial F is low and the cost of migration is relatively high."

In other words, when it becomes ever more dangerous to emigrate from the natal area, such as during a time of increasing nutritional stress, an ever greater degree of inbreeding can be tolerated without loss of the selective advantage. Then

natural selection must favor individuals with a mechanism that automatically switches the bias against inbreeding into a bias in favor of inbreeding at the point where the individual's nutritional stress makes migration from the natal area too hazardous to attempt.

It will be the bias in favor of inbreeding, rather than any knowledge of dangers from emigration, that will provide the individual with the incentive to stay in the natal area. In this way the crisis-inbreeding mechanism will confer a selective advantage at the level of the individual.

6. Experimental Work

Some evidence for possible crisis inbreeding comes from experimental work by Band and Ives (1961). They do mention that there had indeed been an "increase in inbreeding" among the Drosophila melanogaster of South Amherst when "the former relatively stable environment has shifted to instability."

For the study itself, flies were collected for one week at a time in 11 different years, and the "frequency of recessive lethal chromosomes" for every sample of flies was plotted against the temperature range for the week prior to the collection of flies.

In 4 of the 11 years (1947, 1948, 1953 and 1958) the investigators took two samples, usually in two successive months, and tested them. They made no attempt in their study to plot the lethal frequency in that second sample of the year against the temperatures which the flies in the first sample experienced. However, when their data are used to check that specific correlation, a remarkably consistent relationship emerges between the mean temperature (for the week prior to collection of the first sample) and the lethal frequency in the second sample (containing many offspring from flies in the first sample) -- see Fig. 1.

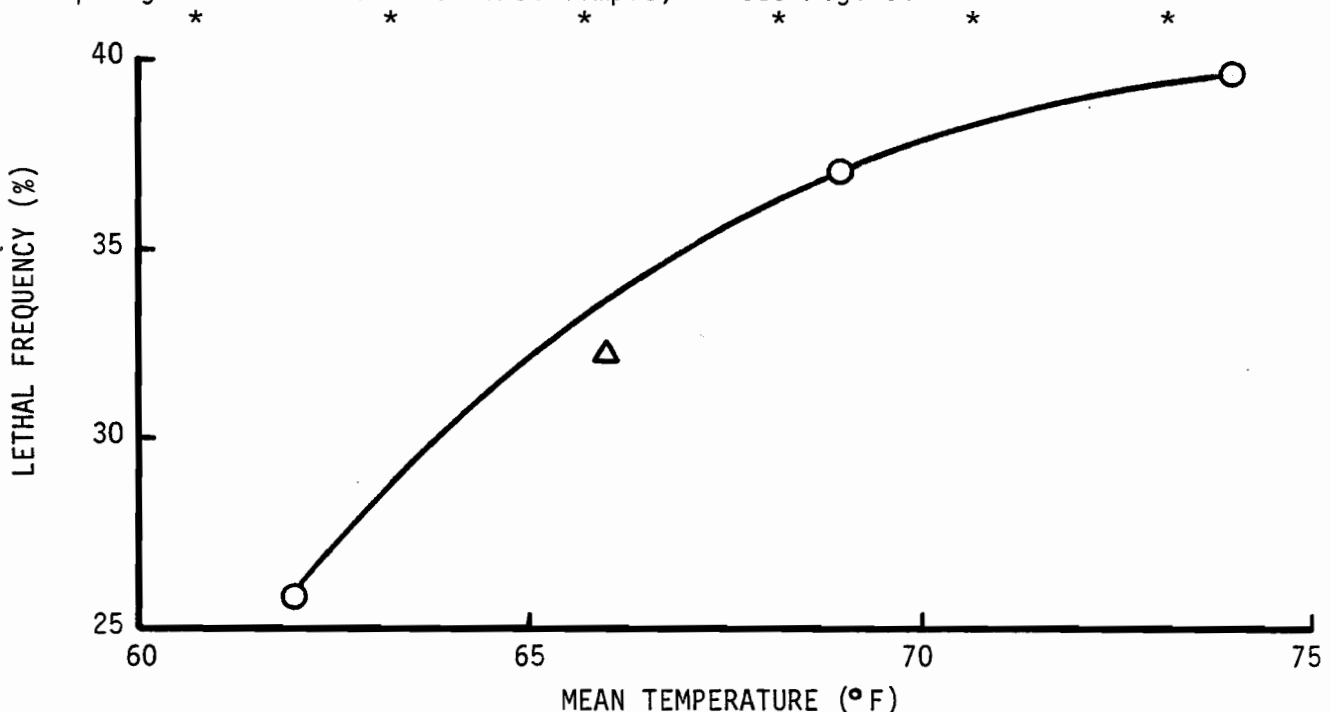


FIG. 1. Relationship between mean temperature and lethal frequency in a following generation of Drosophila melanogaster at South Amherst -- based on data from Band and Ives (1961).

○ = Mean temp. for one week in Sept.; lethal frequency in October.

Δ = Mean temp. for one week in June; lethal frequency in September.

* * * * *

From these results it would appear that the mating behavior of the one generation had been affected by the mean temperature of the environment at the time, and that this may have contributed toward the change in lethal frequency in the following generation of flies. It seems to be the most reasonable explanation how the temperature in one month could have affected the lethal frequency in another month, when most of the flies from that second month had not been around yet to experience that first month's temperature.

Ives (1954) in another study of lethal frequencies in *D. melanogaster*, which included the area at South Amherst, acknowledges a link between the lethal frequency and inbreeding when he associates "the frequency of lethal chromosomes . . . and the amount of allelism among the lethals" with "breeding units within populations." He also states that an elimination of lethals could be attributed "either to inbreeding or selection," and that one interpretation which "fits the data of the local [Amherst] area" is that there has been "an increase in the amount of inbreeding."

More evidence for possible crisis inbreeding comes from the house mouse.

Beauchamp et al. (1985) found that mice showed a preference for mating with unrelated individuals, and DeLong (1967) found that mice in their natural habitat did migrate readily into other populations. Yet there are numerous studies (e.g. Anderson, 1964; Petras, 1967; Reimer and Petras, 1967) which demonstrated that house mice will just as readily subdivide into small breeding units, and Petras (1967) stated: "If the population density is high, an immigrant is either killed or driven off." DeLong (1967) also observed that immigration into a mouse population with high density was much lower than immigration into adjacent populations with low densities.

This lower immigration rate into more crowded populations is to be expected. Similarly, one would expect greater emigration out of such a crowded population and into the less crowded populations nearby. However, DeLong (1967) found exactly the opposite, namely that "a far smaller portion of the [high density] RFS 4 population emigrated than that of other populations."

DeLong (1967) further stated that "increased dispersal between populations occurred primarily in late October and early November."

When his statistics for this period of increased dispersal were obtained by measurements on his graph for population densities and from his table of known immigrants into every population (based on new mice that had to be tagged, etc.), a surprisingly lopsided dispersal pattern emerged for the four populations occupying territories (average = 0.815 acres) that were adjacent to one another but separated by dirt roads (i.e., similar conditions of climate, predation, and vegetation for all four territories).

The results are shown in Tables 1 and 2.

TABLE 1. Population densities and known new immigrants per acre for four populations of mice -- based on statistics from DeLong (1967).

A = mice per acre at the start of the period.

B = new individuals tagged per acre during period.

Period	Pop'n RFS 3 (1.00 acre)		Pop'n RFS 4 (0.68 acre)		Pop'n RFS 5 (0.79 acre)		Pop'n RFS 6 (0.79 acre)	
	A	B	A	B	A	B	A	B
Oct. 14-27, 1963.	33	18	150 \pm 10	3	31	20	32 \pm 14	15
Oct. 28-Nov. 10.	15	21	108 \pm 9	15	11	20	21 \pm ?	35
Nov. 11-24, 1963.	25	10	112 \pm 10	1	20	18	30 \pm 20	49
Averages:	24.3	16.3 (67.1%)	123.3	6.3 (5.1%)	20.7	19.3 (93.5%)	27.7	33.0 (119.3%)

(SEE NOTES FOR TABLE 1 AT TOP OF NEXT PAGE)

TABLE 1 CONTINUED:

Note: (1) Standard errors have mostly been omitted from the tables because they were not always given by DeLong. Some SEs are given in Note (2) below as a guide. Other SEs (for population densities at three diverse stages for each population) were:

63 \pm 8; 38 \pm 15 and 11 \pm 10 for population RFS 3

240 \pm 15; 112 \pm 10 and 19 \pm 9 for population RFS 4

82 \pm 28; 39 \pm 14 and 11 \pm (no SE given) for RFS 5

183 \pm 31; 95 \pm 25 and 32 \pm 14 for population RFS 6.

- (2) Population densities at the end of the 6-week period (October 14 through November 25, 1963) were: 21 \pm 18 for RFS 3; 93 \pm 8 for RFS 4; 33 \pm (?) for RFS 5; and 58 \pm 19 for RFS 6.

* * * * *

TABLE 2. Estimated net loss of individuals per acre (from emigration and mortality) in four populations of mice -- based on statistics from DeLong (1967).

A = Maximum density of mice/acre [see Note (1) below]

B = Net loss per acre [see Note (1) below].

Period	Population RFS 3		Population RFS 4		Population RFS 5		Population RFS 6	
	A	B	A	B	A	B	A	B
Oct. 14-27, 1963.	51	36	153	45	51	40	47	26
Oct. 28-Nov. 10.	36	11	123	11	31	11	56	26
Nov. 11-24, 1963.	35	14	113	20	38	5	79	21
Averages:	40.7	20.3 (50.0%)	129.7	25.3 (19.5%)	40.0	18.7 (46.7%)	60.7	24.3 (40.1%)

Note: (1) The maximum number of mice per acre was taken as the density at the start of the period plus the number of known immigrants per acre during the period. The number should therefore give an idea of all the different mice that had been present in the territory (per acre) at some time during the period. The difference between that number and the number at the start of the next period represents the total number of mice that left per acre during the two-week period.

- (2) The net loss per acre includes mice that died but excludes new mice born. It should give some idea (for purposes of comparing the four populations) of mice that emigrated.

- (3) See notes at Table 1 for standard errors.

* * * * *

As can be seen from the tables, the average known immigration rate into the population with the highest densities throughout was only 5.1%, as against an average rate of 93.3% for the three populations with lower densities. Similarly, the estimated loss of individuals from population RFS 4 (owing to both emigration and mortality) was 19.5%, as against an average of 45.6% for populations RFS 3, RFS 5, and RFS 6.

From the statistics in the notes at Table 1 it is also clear that RFS 4 did not necessarily have a territory which prevented immigration or emigration. RFS 6 (the only one where the mice were being fed supplemental food as part of the experiment) reached population densities close to those at RFS 4, and the RFS 4 population did eventually decline to densities as low as those in the least dense populations. However, for those particular 6 weeks when dispersal was highest (probably because the growing season was reported to be from October until June in California, and food resources were likely to have been close to depleted by the end of October), migration in and out of RFS 4 was being resisted. And if it is borne in mind that

"42% of the males and 12% of the females [in RFS 4] evidenced fresh wounds in November, whereas no more than 5% of the individuals in other populations had fresh tail wounds at any time" (DeLong, 1967), a picture of intense competition for increasingly limited resources emerges at RFS 4.

DeLong also found that RFS 4 had the lowest mean body growth rate of all populations during October and November, and that the body growth rate remained well below 0.5% per week for RFS 4 throughout November, whereas it was between 1.5% and 2.0% for RFS 3 and RFS 5. This indicates that nutritional stress was highest at RFS 4. Therefore, when the nutritional crunch came in October, and mice started to migrate in and out of the other populations where the food was not as scarce as at RFS 4, the RFS 4 population appeared to have turned to protecting their limited food against immigrants and against one another (which could account for some of the high incidence of wounds). But instead of leaving this high-density population with its intense competition, less than half as many mice left per acre as from the other populations. In fact, more mice disappeared from RFS 6, where they were being fed supplemental food. Scarcity of food therefore discouraged emigration instead of encouraging it. And the lower emigration rate from RFS 4 would be even more remarkable if the higher nutritional stress had caused higher mortality rates than in the other populations, and thus even lower rates for mice that actually left RFS 4.

One possible explanation for this unexpected reluctance of the mice to emigrate out of such a high-density population could be an increased willingness to remain at home and to inbreed during harsh times. And if it were the individuals' reluctance to confront aggressive conspecifics on the way out of the population's territory, then that fear of confrontation may well be an incidental crisis-inbreeding mechanism which helps to keep individuals (and probably also littermates) confined to restricted ranges (with their greater chances of inbreeding) during times of high competition for limited resources. It would prevent that same unrestricted migration throughout the population's range as there would be in a more peacefully existing population with ample resources. (See also Holst, 1985; Rowley et al., 1986; also Section 8, 7th item.)

Therefore, the house mouse might even be one of the better known species where the normal reluctance to inbreed during good times can readily turn to a willingness to inbreed when the intraspecific competition for a scarce resource becomes intense.

7. Paleontological Findings

It might never be possible to prove crisis inbreeding from the study of fossils. However, Williamson (1981) found, during his study of mollusk fossils at the Turkana Basin in northern Kenya, all the indications one would expect in a population which had switched to crisis inbreeding.

For instance, he found a flurry of "speciation events at both the Suregei and Guomde levels" when "stunting of faunas immediately before the Suregei level and the small number of lineages in the Guomde may reflect stress at these levels." He also found "significant changes in phenotypic variance during this period."

However, the most significant aspect of the Turkana mollusks is that the rapid changes of form occurred in large populations with numbers estimated in the millions. This seems to confirm that rapid evolutionary change need not be restricted to population bottlenecks with small numbers where there would be a high inbreeding intensity even in a truly panmictic population (see Fig. 2); and the fact that the large mollusk populations appear to have been under stress every time when there were sudden increases in phenotypic variance, seems to indicate that the stress may have brought on widespread crisis inbreeding within those large populations.

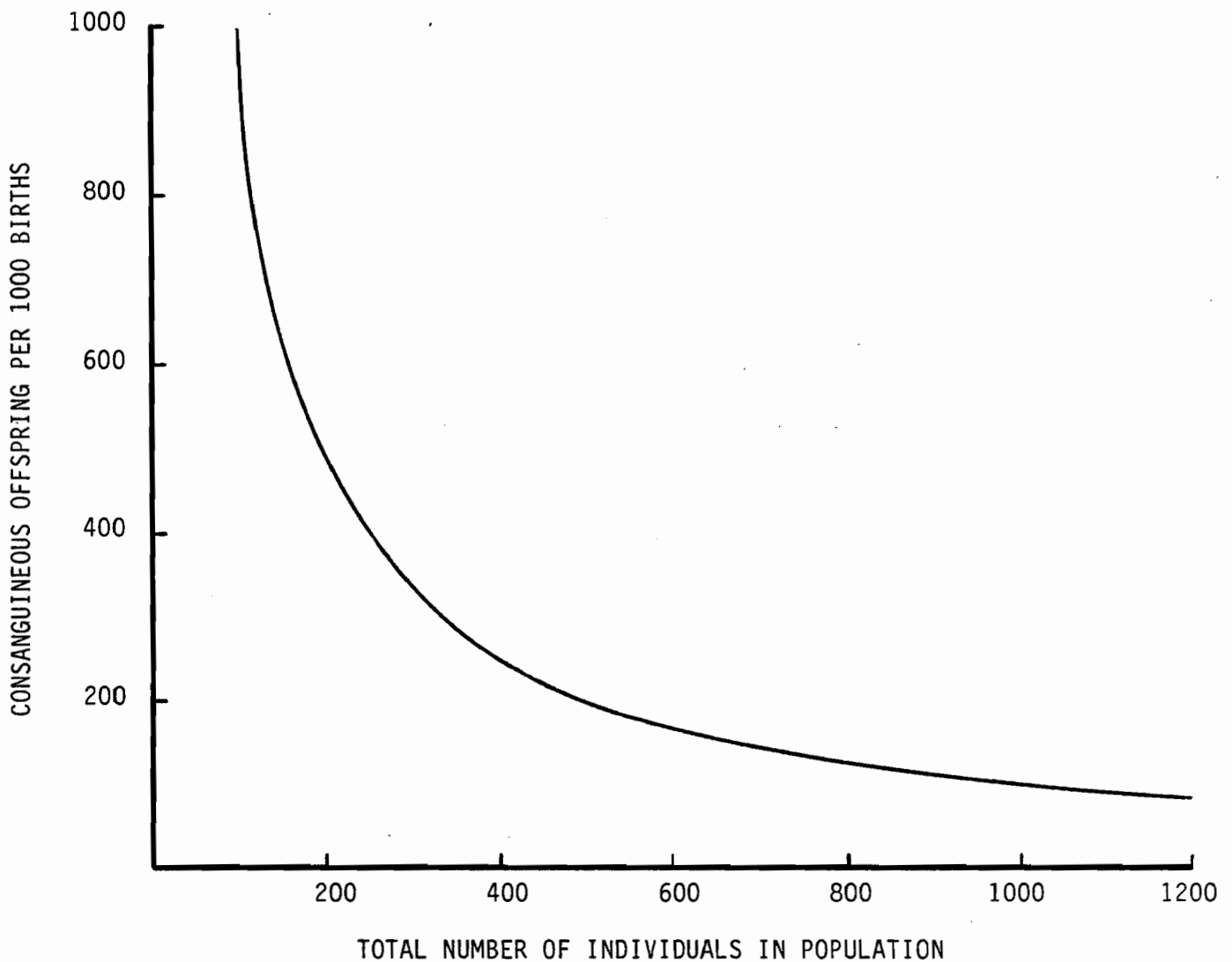


FIGURE 2. Inbreeding curve for 100 closely related individuals in a panmictic population.

* * * * *

8. Other Relevant Literature, Etc.

Some of the existing hypotheses, published statements, interpretations, etc., which appear to be indicative of crisis inbreeding, or somehow linked to the possibility of its existence, are:

- Mutualism between kin, as predicted by the theory of kin selection (Hamilton, 1964; Maynard Smith, 1964), should be more likely to change from non-interference mutualism (NIM) to interference mutualism (i.e., incurring some cost, such as exclusion from an essential resource, on other conspecifics) when an essential resource like food is suddenly in short supply. According to Wrangham (1982) "kin are more likely to be favored as partners in IM than in NIM." One would therefore expect to find a selective advantage in the tendency toward greater kin-oriented mutualism, and thus probably also greater chances of inbreeding, during a time of intense competition for an essential resource. Evidence for this kind of kin favoring in competitive situations has been observed by Cheney

- (1977) and Massey (1977), while Chesser and Ryman (1986) point out that "ameliorating effects of increased cooperative behavior . . . and potentially enhanced ability to utilize resources in short supply . . . may make inbreeding more tolerable in some situations."
- Barash (1974) concluded that fat storage was an important factor in dispersal, and Gaines and McClenaghan (1980) referred to unpublished data on yellow-bellied marmots which revealed that "dispersal of yearling males was delayed when yearlings were underweight and occurred early when they were heavy." DeLong (1967) also found a reluctance to emigrate in a mouse population where body growth rate was lower than in control populations. This appears to indicate that individuals in some species would be less inclined to disperse during harsh times when fat storage is likely to be inadequate for successful dispersal, and that should increase the chances for inbreeding during a time when food is in short supply.
 - The existence of reproduction-switching mechanisms in Ciliophora and plants like the primrose, where the switch to another form of reproduction usually takes place "when the conditions deteriorate" (Ford, 1964), bodes well for the possibility that similar mechanisms for coping with a crisis might exist in several animal species. (See Section 4.)
 - An increased tendency to switch from outbreeding to inbreeding in an environment where the increasing smoke pollution from industrial development has caused stress to the individuals in a species would result in the appearance of more recessive melanics than usual at a time when the melanic form is most needed. It makes sense that a mechanism which would improve the chances of survival for a species in that way (while the population is still large enough for the parents with the usual form to be taken by predators without the disastrous consequences this may have in a small population) should evolve sooner or later.
 - Shields (1982a, 1982b, 1983) argues strongly in favor of the hypothesis that there should be a correlation between inbreeding intensity and average degree of fecundity, and that the inbreeding intensity should be higher in the species with lower fecundity. It is also reasonable to assume that fecundity declines in the vast majority of nutritionally deprived populations (cf. DeLong, 1967; Bronson, 1974; Mann and Lutwak-Mann, 1981; Rogers, 1986). Then there could be a similar correlation between fecundity and frequency of inbreeding within the species/population if the tendency toward inbreeding increases as the individuals become more nutritionally stressed.
 - Ford (1964), in discussing a study of the butterfly Maniola jurtina, stated that there was "continued drought up to early July" in 1957, and in 1958 "abnormal" frequencies of the various types of the butterfly were noticed in one area, namely, "approximately equal numbers at 0 and 1 spots and substantially less at 2, while it was intermediate again in 1959." This abnormal shift in frequencies may have been caused by strong selection, but then one would have expected to be told that the "abnormal" frequencies were first observed during 1957, not during the following year. That justifies some conjecture that the stressful weather of 1957 might have caused some of the individuals to show a greater inclination to inbreed than usual, and that this may have given rise to more individuals with a low number of spots during 1958. Then a return to the more usual outbreeding could have caused a return to the more intermediate numbers of spots (which can reach 5) in 1959.
 - High population density is sometimes mentioned as a factor that facilitates emigration out of a population (e.g. Hanby and Bygott, 1987). That same high population density also, as a general rule, means that there is ample food around. Then it would encourage outbreeding if littermates disperse more readily during times when high population density (together with adequate nutrition) indicates ample food. However, the same mechanism which causes the individual to prefer inbreeding during the times of nutritional stress, and thus to avoid the all but certain death (or outbreeding infertility) that awaits it if

it attempts emigration during harsh times, could then also prevent that individual from emigrating (despite the high population density) when a growing population finally saturates its habitat and the high density is accompanied by nutritional stress (cf. DeLong, 1967). The rule should, in general, be that dispersal would increase as population density increases, but beyond that point where population density becomes so high that there is no longer sufficient food for every individual, the dispersal rates should fall off because insufficient body fat, fear of competitive confrontations with conspecifics, etc., should keep most individuals close to their birthplace. Then inbreeding would increase. And if a lack of sufficient energy for fights should cause individuals to shun other individuals altogether at this stage, signs of fighting might also show a decrease despite the continued wariness that had been brought on by the competition for the scarce resources.

- Where individuals under stress, especially from the same sex, produce primer pheromones that impair the reproductive potential of other individuals around them, it is likely that those pheromones of the individual will be more similar to the pheromones of siblings than of unrelated individuals, and the individual should be so immune/habituated to its own quality of pheromones, that closely related individuals would not have quite the same suppressing effect on one another's endocrine systems as unrelated individuals would have (cf. Christian et al., 1965; Bruce, 1968; Yamazaki et al., 1980). This should provide some selective advantage to individuals with an inclination to associate with close kin during times of severe, reproduction-curtailling stress. And in any species where related individuals impact negatively on one another's reproductive capabilities, there would have to be a mechanism which reverses that effect during times of stress or other times when inbreeding is the best (or only) strategy, because no species can make it through a population bottleneck if related individuals continue to suppress one another's reproductive potential. The same mechanism which would help such a species through a bottleneck where inbreeding is inevitable, could easily come into operation during a time of crisis inbreeding.
- Dixon and Mackintosh (1971) noticed an increase in sexual behavior when there was a reduction in aggression among the mice in their experiments. It is virtually self-evident that the chances of copulation in most species will be greatly reduced if individuals interact agonistically. Even a female in estrus should be reluctant to approach a male which is threatening her with attack while protecting his access to limited food resources, and the female's sensory cues should not exert the normal pacifying effect on the male if those cues are accompanied by the nutritionally stressed female's own threat signals. Therefore, where intraspecific aggression increases during any time of intense competition for a limited resource (i.e., before the nutritional stress reaches the point where it turns the individuals lethargic with inanition), and where aggression between individuals decreases as the degree of relatedness increases (Kareem and Barnard, 1982; Linsenmair, 1985), the chances of full sexual interaction should, during any time of intense intraspecific competition, increase with the degree of relatedness. The threat signals which tend to discourage mating should be stronger when the individual is approached by an unrelated individual, and this could override the mating signals completely, whereas the threat signals toward the related individual would still be weak enough for the mating signals to prevail. (See also later.)
- Wool and Sverdlov (1976) did experiments on populations of the flour beetle, Tribolium castaneum, where they compared fitness parameters like "productivity," developmental period of offspring, and adult sterility in successive generations of inbreeding populations in various environments. They concluded that stronger selection against (disadvantaged) homozygotes in the variable environment

resulted in higher fitness for the inbred lines in the sub-optimal environment, and stated that "inbreeding populations should have a better chance of surviving for a long period if they live in an unstable and unpredictable environment," and that there was "higher fitness of the inbred lines in the variable, sub-optimal environment" as against those in the standard environment. In other words, inbreeding appeared to be a better strategy in that sub-optimal environment than in the environment where the population was not under the same stress. This seems to indicate that a bias in favor of inbreeding could be of greater evolutionary advantage to a population during harsh times than it would be during good times. If so, it becomes conceivable that inbreeding might continue this trend of becoming more and more advantageous as the environment becomes more and more stressful, and there may well be a certain point of stress where inbreeding may actually be more beneficial than outbreeding -- even at the level of the individual.

9. Chemosensory Discrimination?

Research work by Beauchamp et al. (1985) has shown just how accurately rodents can distinguish between the odors from two mice when there is reward or (by inference) punishment involved. The researchers point out that the H-2 type of a mouse is determined by "a string of genes with immunologic functions" (the Major Histocompatibility Complex, or MHC) where "the individual odor of an animal is in part determined," and these genes "might impart to each individual a characteristic scent." Some of the genes composing the MHC are extremely mutable, according to the above researchers, and their many alleles mean that "unrelated individual animals are extremely unlikely to have identical MHC types." In other words, unrelated individuals are also extremely unlikely to have the same individual odors. These odor differences can then be detected by the individual.

Between full siblings, on the other hand, the odor differences can usually be expected to be less (say half as much) than it is between unrelated individuals. And since it is virtually self-evident that the individual's own odor must not interfere with its ability to detect odors from outside, mechanisms like sensory adaptation and habituation have apparently evolved to ensure that the individual (in the wild where the detection of odors is important for survival) will not usually smell itself. Then it is not unreasonable to assume that the odor of an average sibling with a high proportion of identical odor-specifying genes will not be as distinct to the individual as the odor of an unrelated conspecific. This could lower the ability of the individual to detect the odor of an average sibling (two unrelated parents) to as much as half of its ability to detect the odor from an unrelated conspecific (cf. Whitten and Bronson, 1970; Segel et al., 1986). It should also be even lower for two siblings after a few generations of full-sib inbreeding -- because "genetically identical animals [probably] smell alike" (Beauchamp et al., 1985. See also Bruce, 1968; Greenberg, 1979; Yamazaki et al., 1980; Buckle and Greenberg, 1981; Linsenmair, 1985).

The outcome should be that, during times with plentiful resources, the overall array of sensory cues from an unrelated individual should make a greater impact on the perceiving individual than would the array of cues from a closely related individual, and this should cause the two unrelated individuals to be attracted more readily; but during harsh times when there are suddenly threat signals of an overriding magnitude (more likely in the case of unrelated individuals) present in that array of cues, or when the individual's perception of the normal array of cues from a conspecific has changed from receptiveness to wariness, those same two unrelated individuals should be more inclined to shun each other's more readily perceptible cues than would two closely related individuals (which had grown up together and had learned to ignore some of each other's threat signals during numerous "play" encounters). Unrelated individuals should then get together more

readily for mating during good times, but closely related individuals should be more willing to tolerate one another's presence under circumstances that could lead to mating during harsh times, especially where the intensity of the individual's threat signals toward the closely related individual is low enough to let the mating signals prevail, or where those many "play" encounters as juveniles or subadults had caused the two related individuals (or even others that had been raised together) to take each other's threat signals less seriously than the threat signals from unrelated individuals which had shown themselves more capable of harm than the "friends" from juvenile days had.

The extensive literature on alarm signals and other sensory cues that warn conspecifics to stay away from an area (Muller-Velten, 1966) or an individual (West et al., 1962; Evans and Goy, 1968; Doty, 1974), and the fact that some animals do indeed change from tolerating close physical contact to warning off all but certain related individuals when their level of stress changes (cf. Simpson, 1973; Mykytowycz, 1974) suggest that sensory discrimination and other changes in animal behavior could indeed cause outbreeding populations to switch to inbreeding at a critical point during a nutritional crisis. However, the literature (including the many studies on kin recognition) is as yet void of conclusive evidence that an individual's ability to distinguish kin from unrelated individuals can lead to inbreeding during a stress-producing crisis. This does not mean that a mechanism for crisis inbreeding does not exist; only that it may not have been recognized yet, because of investigators usually crediting "strong selection" for unusual frequency changes during stressful times.

10. Other Possible Crisis-Inbreeding Mechanisms

Bateson (1980) mentions four hypotheses that might help to explain why the Japanese quail appears to "prefer slightly novel members of the opposite sex." The hypotheses rely mainly on the fact that animals tend to associate other individuals with positive or negative experiences from the animal's own past, and that these associations can then influence the individual's choice (i.e., sight and sound included) of a sex partner.

As an example, the "punishment hypothesis" is stated in these words: "Numerous competitions for food and other resources in early development mean that individuals encountered during that period are associated with punishment and therefore have become slightly aversive."

If a resource crisis in a population should extend this aversion-causing competition to include all the members of the population, it is likely that all of them would become equally aversive to the individual. Then a closely related individual would almost certainly enjoy an advantage over unrelated individuals by virtue of the theoretically predicted (Hamilton, 1964; Maynard Smith, 1964) and subsequently verified (Kurland, 1980; Hoogland, 1983) tendency of individuals to be more mutualistically inclined toward kin. And if the tendency to be less aggressive toward more closely related individuals (Kareem and Barnard, 1982; Linsenmair, 1985) causes the animal in the presence of an unrelated individual to sooner reach that critical "no-more-mating" point (i.e., where the intensity of the signals for sexual activity is finally counterbalanced by the increasing intensity of the stressed animal's threat signals) than it would in the presence of a closely related individual, the frequency of inbreeding should show an increase during any time of competitive stress -- even in a large, ecologically intact population.

Another mechanism which could result in increased inbreeding in a large, intact population is the mechanism for fear of confrontation that was mentioned in Section 6. (See also Section 2.) Such a mechanism, which would usually have its origins in the individual's fear of pain (an essential evolutionary mechanism for obvious reasons), would make the individual more reluctant to leave its natal area when the risk of pain-inflicting confrontations with conspecifics increases during a time

when competition for essential resources becomes more intense than usual. Then closely related individuals, which seem less likely to attack and hurt one another (Kareem and Barnard, 1982; Linsenmair, 1985), should become confined to the same or adjacent "territories" during a time of overpopulation, and littermates would be more likely to be forced into close inbreeding at that specific time of crisis.

Other crisis-inbreeding mechanisms may be linked to the animal's metabolism, so that the lack of fat in the body during times of nutritional stress may stop the individual from emigrating (see Section 8, second item, as well as Barash [1974]; Gaines and McClenaghan [1980]). This should increase inbreeding.

In the case of insects like moths, "changes in reproductive behavior which are due to crowding" and the observed changes in "the pattern of emergence of the adults from the cocoons" (Cotter, 1963) could cause an increase in inbreeding. (See Addendum E.) And since a maximally crowded situation would mean that some females would be forced to deposit their eggs in more unfavorable parts of the habitat than they would otherwise, some eggs might hatch sooner than usual (e.g. ones exposed to more sun) and others might hatch later than usual (e.g. ones in colder locations than average). Then the closely related individuals from these eggs might also emerge sooner or later than the rest of the population, which could also mean sooner or later metamorphoses and sooner or later emergence from the cocoons -- i.e., they would have to mate with one another because the other (unrelated) moths would not be available to them at the time when they emerge and have to start mating. And in an adversely changing environment there should be an increase in unfavorable areas within the usual habitat -- where all individuals used to emerge from the eggs and, therefore, the cocoons at approximately the same time. Now they would emerge at different times, and inbreeding should increase. It would be a suitable crisis-inbreeding mechanism in species where competition for food resources is not a factor during the mating stage. However, the nutritional stress of the (say) caterpillars could conceivably remain with the individual through all its stages of development, and might cause discrimination in the way the moth finally perceives the pheromones from related and unrelated individuals.

As for plants, one way to switch from one form of fertilization to another when the environment makes such a switch desirable, is by means of the mechanism described on page 228 of Ford (1964), namely, "the opportunities for homostyle crossing are greatest when the stigma is relatively high and the anthers dehisce late. Both these variables, position of the stigma and the time when the pollen is shed, are controlled partly by polygenes but partly by the environment. Thus it comes about that the amount of such cross-fertilization varies from year to year."

If natural selection in the past could have selected in favor of a mechanism which cause the reproductive system in certain populations to change when a change in the environment makes such a switch advantageous to some individuals (and thus to their population/species in the long term), it can be expected that natural selection would have selected in favor of crisis inbreeding in certain animal species as well -- i.e., where a shift toward inbreeding during an environmental crisis would almost certainly mean greater chances of survival for some animals, and thus for their population/species as well.

Mechanisms which will help the fortunate individuals (those that will eventually survive the crisis) respond more rapidly and effectively to a whole spectrum of possible changes in the environment (including drastic changes), should increase the chances of "survival" for a phylogenetic lineage so much that natural selection would have to favor all individuals with that mechanism in the long term.

11. Discussion

All of Wright's (1945) most favorable conditions for rapid evolution would exist in a large, ecologically intact population where unstressed individuals tend to outbreed with other unstressed individuals, whereas stressed individuals turn to

crisis inbreeding within their specific demes -- i.e., threat signals etc. discouraging members of other demes from mating with members of demes still under stress. Such a barrier to mating with individuals from the (stressed) ancestral population would then prevent the ancestral genome from re-establishing itself in those newly advantaged demes and thus pushing the expressed "recessives" back into the recessive state in future offspring -- unless the environment should return to the ancestral environment, in which case the ancestral types would no longer be under stress, and would return to outbreeding.

A spell of crisis inbreeding which segments a large, outbreeding population into numerous inbreeding demes may well be nature's most effective response to stressful situations. It could occur in the early stages of a survival crisis -- even before there has been any loss of genetic variability through elimination of individuals, or a disastrous loss of fertility. It should also have a vast reservoir of recessive mutations available to it, which had accumulated during all the outbreeding, and which a normally inbreeding population (social structuring) would not have available. The sudden "outburst of variability" (Ford, 1964) in such a large crisis-inbreeding population should be considerable. Then crisis inbreeding would be an excellent mechanism for dealing with a crisis at the best possible time -- before extinction even threatens, as for small populations.

If such a phenomenon of crisis inbreeding should occur in the wild, then the following would be true:

- The individuals in sexually reproducing animal species which normally display a bias against inbreeding during times of plentiful resources and low competition among conspecifics should show a decreased bias against inbreeding, and even a distinct bias in favor of inbreeding, during times when conspecific competition for a scarce resource is intense.
- Mechanisms which cause unrelated individuals to shun one another more readily than do related individuals during times of intense competition should help to create a higher inbreeding intensity than usual in a population of unchanged size when there is intense competition among conspecifics for a scarce resource. Such mechanisms may include sensory discrimination mechanisms which cause an individual to discriminate more readily or less readily against closely related individuals whose more similar and/or familiar cues are not (because of sensory adaptation, habituation, etc.) as clearly detectable or as promptly heeded as the cues from an unrelated individual.

Crisis inbreeding would most likely occur in the case of some individuals and/or strains before others because of differential stress levels. This could then provide every deme with its last opportunity to either evolve rapidly into an advantaged new form for the new environment, or to make way for other demes at a time when the elimination of all unsuccessful demes would help to make survival for the successful ones so much easier.

It is hoped that this search which was made of the literature, in an attempt to find the type of evidence for crisis inbreeding which would alert evolutionists to the reasonable possibility that the phenomenon might exist, will suggest new directions of experimentation to researchers. For instance the loss of genetic variability in the case of a large-to-small population bottleneck, peripheral isolate, small founder group, etc., makes it questionable whether substantial evolution is all that likely in such small populations. Since crisis inbreeding would even occur in very large populations (with their vast genetic potential for substantial evolution) the existence of crisis inbreeding should clarify many aspects of the large vs. small population issue. And if the segmentation into demes should be distinct enough during crisis inbreeding to keep some demes reproductively "isolated" from the other demes for successive generations, speciation while sharing the same habitat would be possible. That should throw some light on the sympatric/allopatric issue. And spells of rapid, substantial evolution in large populations could explain "punctuated" evolution.

12. Conclusion

The phenomenon of crisis inbreeding has such a strong theoretical base that it would not be surprising to find it occurring in some form in the wild whenever there is a stress-producing crisis with intense intraspecific competition.

ADDENDUM A: DISADVANTAGES OF THE SMALL OR ECOLOGICALLY FRAGMENTED POPULATION.

The strongest argument in favor of crisis inbreeding in large populations is that virtually every problem one may have with it, applies to a much greater degree to inbreeding in a small population. The chances that inbreeding in a small population will ever be safer than inbreeding in a large population are remote. Similarly, the chances that inbreeding in a small population will ever create the same potential for rapid, successful evolution as crisis inbreeding in a large population, are also remote.

It would, therefore, seem highly likely that selection should favor populations where the individuals have crisis-inbreeding mechanisms (for inbreeding in large populations) rather than mechanisms which cause avoidance of inbreeding right up until that vulnerable small population. After all, selection should favor mechanisms which make survival more certain, and a mechanism for inbreeding in a large population definitely makes survival of the population more certain than mechanisms which prevent inbreeding until the small (vulnerable) population.

Even in the small population a crisis-inbreeding mechanism should provide a distinct selective advantage, because the individual that actually prefers inbreeding at that (probably stressful) time when inbreeding is essential for survival of the lineage, would have a selective advantage over the individual that tries to avoid the inbreeding and wastes its energy searching for an unrelated mating partner.

However, for those readers who still doubt, the arguments against small populations will be expanded below.

As mentioned in the Introduction, some of the drawbacks of inevitable inbreeding in small populations such as founder groups, peripheral isolates, and narrow (large-to-small) population bottlenecks are:

- Deleterious traits from the inbreeding could well eradicate the whole population.
- Inbreeding depression would be a handicap instead of the help it would be in a large population saturating its habitat, etc.

However, the greatest disadvantage of a small population may well be that the stress of eking out an existence in a strange new environment (to which the few individuals in a small, isolated population are not yet adapted) would be high enough to cause total infertility in one or both the sexes -- especially if the environment differs significantly from the ancestral environment. That is likely to be the case for:

- the last few survivors of a population that had been decimated by an adversely changing environment, or
- a few individuals which by chance became so separated from the original population that they are ecologically isolated from those ancestral types they share so many traits with.

As an example of how rapidly fertility can be terminated by nutritional stress, DeLong (1967) found during his studies on house mice in the field in California that "breeding slackens and usually stops by the end of November." It begins again sometime between February and May. However, when some mice were provided with supplemental food throughout the winter they continued to breed throughout the winter despite the weather conditions and despite the fact that mice in control populations (where there was no supplemental food) still failed to breed for the winter.

If it is not nutritional stress that would cause the individuals to become infertile, other stress (see Section 3) would be likely to cause infertility. Even the stress of being totally isolated from the familiar old habitat or from the sense of "security" (e.g. herding) which individuals often seem to experience in a large population, might be enough to cause infertility. And Selye (1950, p. 103) states that reproduction is one of the very first functions that suffers when animals are under general stress.

Other problems for a small population, especially if it inhabits a relatively small territory, are given by Ford (1964, p. 355). Some of these are:

- vulnerability to severe weather (storms, etc.)
- likelihood of straying beyond the periphery for safe return to the population, such as is likely in a small population of insects.

Even a large diversified new terrain could be problematic to individuals in a small population, because of the risk of becoming separated in their search for suitable food, or when their state of stress causes them to emit "stay-away" cues which might readily be heeded if there are no heavy concentrations of other conspecifics with more distinct cues restricting the separation.

With all these factors counting against a small, isolated population, it is no wonder that Ford (1964) states that the disadvantages of a small population "will often be reflected in increasing mortality." That, at a time when the population is already so small that further mortalities would be disastrous!

The large, ecologically intact population where the individuals turn to inbreeding at such an early stage that closely related individuals would still be able to produce offspring (see Section 3), should have none of these problems. Even deleterious traits in the majority of the demes, and inbreeding depression in all demes, would be factors that would make survival easier for the eventual prevailers.

Furthermore, in subdivided populations where shrinking resources have caused small populations to become ecologically isolated in (say) valleys with foodless stretches between them, there would be some drawbacks. The isolated populations would initially (near the start of the crisis) be large enough to still permit outbreeding in a species with mechanisms for avoiding inbreeding at all times. Only when the population fragments have shrunk down to very small groups of closely related individuals would there be worthwhile inbreeding. By then most of the potential variability of the large population would have been lost with the individuals that could not survive -- without ever being expressed in the population through close inbreeding. And the last few survivors would probably be under severe stress if the environment had changed so adversely that it decimated all the conspecifics around them -- hence infertility.

Any individuals which keep preferring unrelated sexual partners until that point where inbreeding becomes inevitable, would likely retain their instinct to avoid inbreeding even then, and this would reduce the chances for successful reproduction more than for individuals with a crisis-inbreeding mechanism that makes them willing to turn to inbreeding during crisis times.

Furthermore, the isolated little groups in an ecologically fragmented population would not be able to get to the other groups for outbreeding and new combinations, and would therefore not have the same potential for rapid, substantial evolution as an ecologically intact population of crisis-inbreeding individuals.

Finally, no small population, whether of the bottleneck type or the fragmented type, can help a population which has grown to the point of saturating its habitat. For such a population crisis inbreeding would be the best means of evolving rapidly out of the crisis, if the danger of depleting all food resources suddenly (before the next season's crop) is to be avoided.

As for populations where social structuring usually causes heavy inbreeding, they are not relevant here unless they happen to be in the inbreeding part of a crisis situation. Suffice it to say that such a population of persistent inbreeders during good times would not have available to it (because of high homozygosity) the

vast variability of a large, outbreeding population which suddenly turns to extensive inbreeding.

With a large, ecologically intact population having all these evolutionary advantages over the other types of populations, it seems likely that mechanisms for crisis inbreeding may have evolved by now.

ADDENDUM B: CRISIS INBREEDING AND THE PERIPHERAL "ISOLATE."

Crisis inbreeding in a large, ecologically intact population would make it possible for several demes, which had been edged out by overpopulation to the periphery of their normal habitat (an area likely to be harsh and stressful), to evolve into various new varieties from out of which an advantaged new form (for that new habitat beyond the periphery of the old habitat) is likely to emerge sooner or later. Then the new form should already have one or more adaptations for a selective advantage in the new habitat. This would still leave them under stress in the old habitat, and they should still refuse to outbreed and pass the the new traits back into the parental population. Instead, they would find themselves with some unique trait (or traits) which would enable them to extend their range into a new habitat. It would not only make migration into that previously inhospitable habitat more likely without competition from the parental species, but should also make survival and further adaptation in that habitat a great deal more certain than for a group of individuals which had accidentally become isolated or had made its way into the new habitat on the strength of traits that would be likely to exist in other individuals in the parental population as well.

Such an opportunity to develop unique new traits which would make migration into the adjacent habitat so much easier, should improve the chances of the "ousted" deme to remain reproductively isolated in that adjacent habitat. There would be no ancestral types which, because of their having acquired the advantageous traits for the adjacent habitat before the break had occurred, would be passing back and forth between the two habitats. The previously inaccessible habitat would now still be inaccessible, except to that one deme for whom the inbreeding had made a unique new advantageous trait (and thus continued survival) possible. And because the individuals in this new deme would not be subject to the same intraspecific competition in that new habitat as they had been subject to in the old habitat, they would not have much incentive to return to the old habitat. That way, a clear reproductive break can be accomplished without the need for geographic isolation, and a potential new species can branch off to evolve away from the ancestral species while the latter remains virtually unchanged.

The dangers of chance isolations, as well as the possibility of genetic "contamination" from the ancestral genotype, would be eliminated without having to risk a precarious trek across (say) geographic barriers. Even birds and insects with flight, which are not so easily isolated geographically, would be able to become reproductively isolated from other populations.

Moreover, crisis inbreeding would provide an explanation for finding two distinct species with common origins existing in the same habitat -- without having to resort to arguments that part of the population must have gone off to evolve sexual isolation elsewhere before returning to the old habitat.

ADDENDUM C: THE "ALTRUISTIC" INBREEDER.

If the ultimate evolutionary advantage went to the (surviving) individual that produced most offspring, every species would be evolving toward superfecundity with its short-term selective advantage for the individual but its long-term risk of one day suddenly depleting all the food resources before the next season's crop is due.

In other words, number of offspring should not always be the criterion for the evolutionary advantage. A "conservative" genotype which resists change by forcing

the great majority of new genetic mutations into the recessive state, and thus keeping the species in reasonable equilibrium with its prey until a changing environment (with its accompanying resource crisis) results in increased inbreeding and a "genetic revolution" of homozygously expressed recessives, may well be more important than producing many offspring (cf. Mayr, 1982).

It is obviously better to produce few offspring which survive a resource crisis rather than to produce many offspring which will all perish during that crisis.

Mechanisms for crisis inbreeding could easily have escaped the scrutiny of natural selection if they formed part of distinctly advantageous traits like chemosensory detection of other individuals, aversion of pain, threat signals, etc. And if the crisis inbreeding then also helped some populations to make it through crisis situations, whereas populations without any crisis-inbreeding mechanisms became extinct because they failed to evolve fast enough or to reduce their numbers sufficiently during the crisis to ward off mass starvation, those crisis-inbreeding mechanisms would undoubtedly have made it through those crises with the survivors that did manage to evolve rapidly enough, whereas the tendency to keep favoring outbreeding throughout a crisis would have gone extinct with all those populations where the individuals failed to evolve rapidly enough.

Those many demes which perish because of such a tendency of the individuals to turn to inbreeding after a certain period of prolonged stress should be of no consequence to natural selection. Only the traits which give the survivors a long-term selective advantage over individuals without those traits should be of consequence. The fate of all the losers would be an "altruistic fate," just as the nonreproducing sacrifice of the selectively "disadvantaged" worker bee would make more likely the survival of the reproductively successful few in that population.

After all, the survival of a population depends on those individuals that will eventually survive, not on those that will be eliminated. If crisis inbreeding should help those successful individuals to acquire advantageous traits that ensure their survival, it would not matter what the inbreeding does to all the other individuals. And if the inbreeding helps the survivors evolve more rapidly and adapt better to the new environment than it would have done otherwise, the mechanism for crisis inbreeding should be favored.

ADDENDUM D: IMPORTANCE OF MALE FERTILITY

The estrous cycle of female mice appears to be especially sensitive to stress. This has apparently led many investigators to accept that the females are the first to become infertile if there is stress in a population. However, the recent strides that have been made by researchers in immunological infertility appear to indicate that male spermatogenesis may be the crucial factor in sexual reproduction (see Section 3).

Unfortunately, semen analyses are relatively expensive and time-consuming. It is easier and cheaper to look for signs of estrus in the female. Those "parameters" are already known. No sign of estrus means a high likelihood of infertility. But to try to establish reliable sperm parameters for male infertility in any species would be a formidable task.

This has not even been accomplished for the human male yet. However, as stated in Section 3, there appears to be just a relatively small gap between fertile and infertile sperm counts for the average male in our species. Natural selection apparently did not select in favor of a grossly wasteful process of spermatogenesis. Only enough sperm to overcome the average female's immune defenses (with some relatively small proportion as "surplus" to ensure success for the average male with the majority of females) should be what one would expect from a selection process that should always favor an optimum situation rather than an overly successful one that requires excessive energy to maintain.

The presence of millions of sperm simply should not be interpreted as fertility

in the male. Eighty million perfectly healthy sperm (or whatever equivalent applies to a specific species) might still mean that none of them would make it past the female's immune defenses. That crucial extra million might make the difference between fertility and infertility -- not the vast bulk of sperm which is required to shift the odds closer to that critical threshold beyond which the male first achieves reproductive success.

There are some data available which indicate that male fertility is probably at greater risk than female fertility during a crisis. For instance, Rowe et al. (1964) found that the fertility of equal proportions of males and females of house mice was affected by crowding in corn ricks. However, the males were judged to be fertile if an autopsy revealed they had "tubules in the cauda epididymidis visible to the naked eye." This may well have resulted in an overwhelming proportion of males being classified fertile when they were not really fertile.

An interesting aspect of that study by Rowe et al. (1964) was that, for males weighing over 7.6 grams, 66.7% in the two least crowded corn ricks were found to be "fertile," but only 46.9% of the males in the two most crowded ricks were "fertile." For males over 12.6 grams, there were 86.3% "fertile" in the two least crowded populations, as against 69.3% in the two most crowded populations. One can imagine the male infertility if nutritional stress was also a factor.

Another interesting study with mice was done by Zamiri (1978). He found that changes in the estrous cycles of nutritionally stressed females only started to differ from those in the adequately fed control group when their food intake was reduced by more than 30%. When the food intake was reduced by an additional 15% (to 55% of normal intake) the mean estrous cycle length increased to 15.0 ± 1.7 days as against 8.9 ± 0.5 days in the control group.

If this is compared with the approximately 50% lower sperm counts which Mann and Lutwak-Mann (1981, p. 330) documented for a bullcalf on a diet of 50% of the calories of its monozygous twin, and if the 15% difference between mean fertile and mean infertile sperm counts in human males is any indication of the situation in other species, one might be justified to postulate that the average male in an animal species would no longer be fertile with the vast majority of conspecific females by the time the estrous cycle of the average female has only doubled in length. And, as explained in Section 3, for the males whose sperm counts normally hover right on the brink of "infertility" during times of ample food (particularly any males who have some sperm being hampered by autospem antibodies, etc. [Hammit et al., 1988]), outbreeding infertility would occur long before the average female's cycle is affected in any way.

In other words, the average male should become "infertile" long before the average female would stop estrus altogether.

Such a prediction might still be speculative deduction at this stage, and it might take years before a thorough study of male fertility parameters can be completed for an animal species, but there are already some studies which suggest that the male of the species is sensitive enough to nutritional and/or social stress to account for most of the decrease or cessation of breeding which has been observed in nutritionally stressed populations.

For instance, Laszczka et al. (1969) found that the total number of spermatozoa collected during depletion tests at 60-day intervals (i.e., each day for six successive days) decreased as follows for two bulls in an underfeeding experiment:

Months of underfeeding:	2	4	6	8	10	12
4½-year-old bull ($\times 10^9$):	34.8	28.3	23.2	12.6	--	--
3-year-old bull ($\times 10^9$):	71.5	66.5	30.1	24.6	9.2	X

The control animal for the 4½-year-old bull continued to deliver an average of 53.4×10^9 sperm throughout, even at the 10th and 12th months. The 3-year-old control increased its total sperm count by 88.2% between the 2nd and 10th months --

no test having been done after 12 months.

Similarly, the other sperm parameters (such as percentage of living spermatozoa, changes in morphology, survival time, etc.) showed some negative changes for the nutritionally stressed bulls. Fructose levels decreased by 34% and 73% for the older and younger bulls respectively between the 2nd and 8th months, whereas it increased by 68% and 13% respectively for the two controls. (See also Meacham et al., 1963.)

Finally, McClure (1966) showed that "Fasting both males and females [mice] significantly reduced the littering rate," then went on to conclude that nutritional stress in female mice reduced "fertility without markedly affecting the manifestation of oestrus" (*italics mine*).

Could the females not have been fertile, as their manifestation of estrus had indicated?

ADDENDUM E: COINCIDENCES IN THE LABORATORY

It is not always advisable to cite from cases of inbreeding in confined, relatively small laboratory populations -- especially if there had been no control population or if the investigators had managed to come up with seemingly sound explanations for their results. However, there are times when the investigators' remarks border, presumably by coincidence, on the remarks of someone who had witnessed crisis inbreeding.

For instance, Cotter's (1963) experiments with moths resulted in gene-frequency changes "at a rate greater than that expected." He states that the difference may indicate a lack of information about "behavioral adaptations of both male and female in the maximally crowded population situations. These may take on importance in those changes in reproductive behavior which are due to crowding." An "increase of the variance (S^2) about the mean emergence time, and the reduced over-all efficiency of the male in mating behavior" were also noted. These were attributed to "pleiotropic manifestations of the a allele." However, it was pointed out by Cotter that "the data have indicated some preferential mating of a/a males with a/a females."

An interesting aspect of the above study was that the homozygous a allele substitution changed "the pattern of emergence of the adults from the cocoons, thereby affecting the composition of the mating population." This led Cotter to state that the difference between expected and actual rates of change in gene frequency was "still greater if the disparity in emergence behavior is of any selective value for the mutant allele."

As stated in Section 10, such a change in the pattern of emergence of the adults may well constitute a crisis-inbreeding mechanism. It would increase the chances that the most genetically similar adults would end up mating during this time of severe crowding.

ADDENDUM F: IDEALIZED NATURAL SCENARIO

One might expect the ideal scenario for crisis inbreeding to be as follows:

During good times the overall array of cues from the individual tends to welcome conspecifics. The individual can detect cues from an unrelated individual more readily than cues from a closely related individual, and is likely to be attracted more readily by the mating cues of an unrelated individual -- hence a bias in favor of outbreeding.

During harsh times the individuals are involved in an intensified competition with conspecifics. Their array of cues is now likely to contain some stress-induced threat signals warning off other conspecifics, or the individuals have now learned to become wary of the normal cues emitted by conspecifics. They will tend to shun the cues from conspecifics. This way the individual should continue to wander

around and to avoid every area where it can detect the cues of a conspecific. But when it approaches a closely related individual it cannot detect the cues (or familiarity makes it less inclined to heed the cues) as readily or from as far away as the cues of an unrelated individual. This causes the individual to wander close enough to its relative to detect the mating cues -- which usually contain some elements that are different for the two sexes, and therefore not subject to quite the same habituation effects, etc., as most other genetically determined cues. This now creates a bias in favor of inbreeding.

The result should be:

- (a) greater outbreeding during good times of adequate adaptation when genetic mutations should ideally accumulate among recessive genes instead of continually modifying the adequately adapted phenotypes, and
- (b) greater inbreeding during harsh times so that the increased phenotypic variance from expressed recessives would occur "on cue" when most needed, and would increase the potential for evolving rapidly and successfully into a new optimal phenotype for the new environment.

Any advantaged new phenotypes for the changed environment would then be under reduced stress and should return to outbreeding, thus creating the potential for new genetic combinations, etc.

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Every male in a population will sooner or later reach that point during a crisis where he will no longer be able to fertilize the majority of conspecific females, and where he will be much more likely to fertilize a closely related female than an unrelated female. At that point inbreeding will be the better strategy for that male, and probably also for the closely related female. In the ideal scenario, the majority of males will show an inbreeding bias before they reach that point of outbreeding infertility.

ACKNOWLEDGMENTS

I wish to thank H. Goosen and S. Kadama for their help, and the referees for their comments.

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