

of each of the nine measurements on the separation of the species on the two axes are shown in Fig. 3B.

The spatial relationships between the groups of large and small statoliths of *L. forbesi*, *L. vulgaris* and the European fossil are very similar despite the fact that the fossil statoliths are smallest. This may suggest that the fossil species grew to a smaller adult than the living species. These fossils are approximately the same size as statoliths from *L. forbesi* and *L. vulgaris* individuals, with dorsal mantle lengths of 8.3–15.8 cm (Fig. 2). As the size of statoliths in the Loliginidae is closely correlated with the dorsal mantle length of the animals⁵ it is likely that the fossil statoliths came from animals having mantle lengths of approximately 8–16 cm.

When the scores for all individual statoliths were plotted on the first two axes there was no overlap between *L. forbesi* and any of the fossils, whereas the larger *L. vulgaris* overlapped with the larger European fossils. The smaller *L. vulgaris* overlapped with *Loligo barkeri* and *Loligo stillmani* and the smaller European fossils overlapped with all three American fossils.

Thus, although differences between the species are rather too subtle to make identification possible between individual statoliths of *L. forbesi* and *L. vulgaris* or *L. vulgaris* and the large European fossils, discriminant analysis shows that there is a definite trend in form from the American fossils through the

European Miocene fossil and *L. vulgaris* to *L. forbesi* (Fig. 3). Although the difference between the two size groups of the European fossil shown in Fig. 3 is probably a function of size, it might indicate a difference in species, because they come from different sites whose fauna show some differences. For example, the fish otoliths assemblage of Paillon, in which the smallest statoliths were found, differs from that of Jean Tic in having no mesopelagic representatives and in having many genera which are restricted today to the Indian Ocean. In addition, the association of Jean Tic contains some typical species recorded only from younger strata (ref. 6 and unpublished data). Such features are due to the difference in depth of deposition, but also reflect slight differences in age.

These data show that *L. vulgaris* or a closely similar species lived in European seas during the early Miocene. These seas were rather shallow (~30 m; the deepest parts, the canyon in which the Marls of Saubrigues were deposited, certainly did not exceed 300 m) and the climatic conditions were similar to those on the Atlantic coast of southern Morocco today.

Thus, the form of the statolith has remained virtually unchanged during a period of 20 Myr.

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Best shape for nature reserves

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The ideas of classical island biogeography¹ have been used^{2–6} to derive rules for the optimal design strategy for nature reserves. For example, Diamond³ states that, given limited (financial) resources, it is better to purchase a few large reserves rather than many small ones of equal total area; and that reserves should be as close to one another as possible. The validity of some of these rules has, however, been questioned^{7–10}; for example it has recently been shown^{9,10} that several small reserves may contain more species than a single one of equivalent area. These rules have nevertheless been accepted uncritically by others, including the IUCN¹¹. Here, I examine Diamond's rule³ that reserves should be as round as possible and conclude that in certain circumstances the optimal shape may be other than circular. There is no *a priori* reason for believing that these circumstances are unrealistic, and I know of no observational evidence to suggest whether they are found in nature or not. I also reason that the rule that reserves should be as close to each other as possible is inconsistent with the statement that they should be circular.

According to the tenets of island biogeography, the number of species inhabiting islands or isolated habitat patches (such as many nature reserves) is governed by the rates of extinction and immigration¹; when these balance each other on average, the number of species is in equilibrium. If the extinction rate is higher than that of immigration, the island is supersaturated and the number of species will decline or 'relax' towards equilibrium. The rate of relaxation or net loss of species can be reduced by decreasing the rate of extinction or by increasing that of immigration and the purpose of Diamond's rules is to achieve both of these. For example, he states³ that a large reserve is preferred to a smaller one because, amongst other things, it will have a lower extinction rate; and that reserves should be "as close to each other as possible . . . to increase the immigration rates between reserves".

If immigration into nature reserves is indeed an important factor maintaining the total number of species, then it is questionable whether reserves should preferably be circular as this requirement implies the reduction of extinctions without reference to any simultaneous effects on immigration rate. To many dispersing organisms the apparent size of an island, and therefore the probability of colonization, must be more a reflection of the island's linear dimensions perpendicular to the direction of travel, that is the apparent width and height, rather than the area (J. L. Harper, personal communication). Therefore, immigration rate will depend on shape, not just area, whether the organisms are dispersed by voluntary or involuntary means. Thus, whereas departure from circularity may adversely affect extinction rate, this may be ameliorated by an increase in the immigrant population. The optimal shape for a reserve will depend on the balance between these two factors.

To investigate this quantitatively, define the dimensionless parameter R by¹²

$$R = \frac{P}{2(\pi A)^{1/2}}$$

where p is the island perimeter and A its area. R is a simple measure of shape; for any given area A , R may vary from unity for a circular shape to infinity for an infinitely long and narrow one. R is 1.1 for a square and 5.7 for a hedge 100 m long by 1 m wide; the greater the departure from circularity, the greater is R .

Assuming that the effects of shape act independently of other influences, such as area and isolation, the average extinction and immigration rates, E and I , may be approximated by^{1,4,13}

$$E = SVf(R)$$

$$I = (P - S)Ug(R)$$

where $f(R)$ and $g(R)$ are functions describing the effects of shape on E and I , S is the number of species present on the island at the given time, P is the total number of species in the species pool available for colonization, and V and U express the effects of other factors such as area, isolation, habitat diversity and such. To simplify the analysis, I ask: what value of R maximizes the equilibrium number of species, S_0 ? An alternative but qualitatively similar question would have been: what

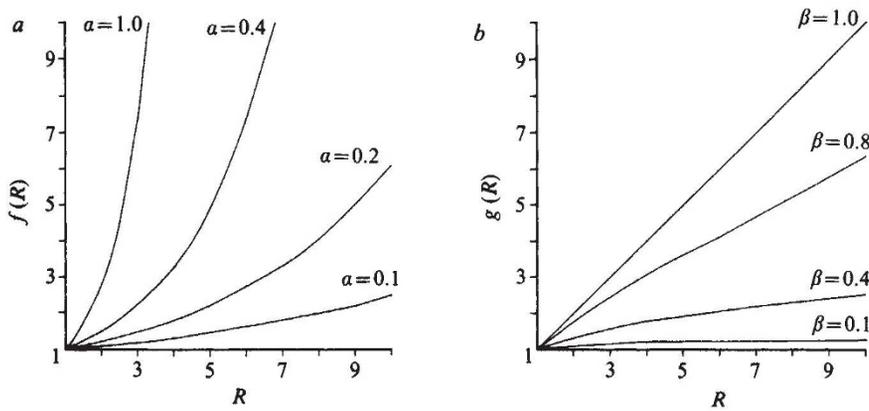


Fig. 1 a, Variation of $f(R) = C^{\alpha(R-1)}$ with α . b, Variation of $g(R) = R^{\beta}$ with β .

value of R minimizes the net extinction rate, $E - I$? At equilibrium, $I = E$, so that

$$S_0 = \frac{PUg(R)}{Vf(R) + Ug(R)}$$

and this is maximum at constant U and V when

$$f(R) \frac{\partial g(R)}{\partial R} = g(R) \frac{\partial f(R)}{\partial R} \quad (1)$$

I now ask what values $f(R)$ and $g(R)$ may reasonably be expected to take. It might be expected that the influence of shape on E is relatively slight when R is low (nearly circular reserves), but becomes severe at large R so that $f(R)$ would vary with R as shown in Fig. 1a. On the other hand, $g(R)$ might rise roughly linearly with R (which is proportional to perimeter length p) or level off towards some asymptotic value, as shown in Fig. 1b. Examples of functions with these general shapes, normalized to $f(1) = g(1) = 1$, are:

$$f(R) = \exp(\alpha(R-1)) \text{ with } \alpha \geq 0$$

$$g(R) = R^{\beta} \text{ with } 0 \leq \beta \leq 1$$

Substituting these functions in equation (1), the value of R which yields the highest value of S_0 is given by

$$R = \frac{\beta}{\alpha} \quad (2)$$

(It is easily verified that this represents a maximum rather than minimum in S_0 .) As $R \geq 1$, equation (2) only has a solution when $\alpha \leq \beta$.

The conclusion is: if extinction rate is not too dependent on shape (α is small) but immigration rate has a relatively stronger dependence on shape (β is not small), then the optimal shape for a reserve to maximize the equilibrium number of species is not circular. If these conditions are not met (that is, $\alpha \geq \beta$), so that a long boundary length affects the extinction rate more than the immigration rate, then the optimal shape is circular.

The above conclusion does not depend qualitatively on either the exact forms of f and g which were used or the equilibrium state being achieved. In general, if I depends relatively strongly on shape and E relatively weakly at least at low R , then there is no *a priori* reason to believe that a circular reserve will lead to the greatest number of species being conserved. However, this result does depend on immigration contributing significantly to the maintenance of the total number of species.

There are several ways in which reserves may come into existence and this will influence whether immigration or extinction processes predominate. Perhaps the commonest mode of creation is the preservation of a remnant habitat patch while surrounding habitat is removed or degraded. However, reserves have also been created *de novo* by establishing habitats on a site where they had been destroyed or damaged. When existing habitat is being preserved, species extinctions are likely to dominate immigration if the reserve is either heavily supersaturated or has become relatively isolated. Supersaturation

may occur through at least two processes. If habitat is destroyed, mobile creatures may concentrate in remaining patches. Alternatively, if the 'area-per se' hypothesis is correct^{1,14,15} and the number of species increases with area because greater populations of each species cause a decrease in extinction probabilities, then if habitat area is suddenly reduced the site may be supersaturated for a time depending on the rate of relaxation. It is not known whether many reserves in Britain are supersaturated in this sense; Terborgh² and Diamond¹⁶ believe that supersaturation occurs on some tropical islands and that it takes thousands of years for the avian fauna to relax to equilibrium, but this time scale is questioned by Abele and Connor⁸.

Isolation of suitable habitat affects the ability of species to colonize. Many reserves in Britain are relatively remote from each other, reducing the probability of inter-reserve transfer. However, although species in need of conservation are often sedentary¹⁷⁻¹⁹ this is not the case for migratory animals or for some plants such as orchids and bryophytes (M. O. Hill, personal communication). Therefore there are cases where immigration is an important factor even when long established habitat is involved. Immigration must certainly be of primary significance when new habitat is created. Note that where immigration is not an important factor, there is no need to locate reserves as close to each other as possible because the possibility of inter-reserve transfer of 'desirable' species is slight. Therefore Diamond's rules concerned with reducing mutual isolation of reserves are inconsistent with his statement that reserves should be as circular as possible: the first assumes that immigration is important and the second that it is not.

Finally, reserve shape may also affect other factors not explicitly accounted for in the above analysis. In particular, as J. L. Harper (personal communication) has pointed out, soil diversity and other habitat heterogeneities might be greater in long, linear reserves than in circular ones, and this might increase the number of species.

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Habitat selection maintains a deleterious allele in a heterogeneous environment

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Little is known of how the large amount of genetic variation found in natural populations is maintained. Diversifying natural selection in a heterogeneous environment has great potential for promoting genetic polymorphism¹. If one allele is favoured in one microhabitat and the alternative allele in another (which may be separated from the first by space or time), the disruptive effects of selection can maintain both alleles in the population. The limiting conditions of niche size, selective intensity and gene flow which could in theory maintain polymorphism in this way have been widely discussed^{2,3}. This mechanism is much more effective in promoting genetic diversity if carriers of the alternative alleles are able to select the niche in which their fitness is greatest⁴. Here we explore the properties of a system in which two *Drosophila* eye colour alleles, known to show differences in fitness, are given the opportunity to select different microhabitats in a population cage. It seems that habitat selection in a heterogeneous environment can lead to the maintenance of polymorphism for an allele which is disadvantageous in either habitat when no opportunity for choice is available.

Eye colour mutants in *Drosophila* alter their carriers' response to light^{5,6}. Wild-type (red-eyed) flies are in general positively phototactic, but are repelled by very bright light⁷. Flies lacking red screening pigment in the eye are more sensitive to light and tend to choose habitats in which light intensity is lower⁸. Wild-type flies are effectively blind in dim light (which is blocked by their screening pigment) whereas white-eyed flies (which lack this pigment) move towards dim red light as it is within their preferred range of hue and intensity. They avoid the bright white light selected by the wild type. White-eyed *Drosophila melanogaster* are considerably less fit than the wild type in white light, and are rapidly eliminated from polymorphic populations in cages⁹.

Drosophila simulans (unlike *D. melanogaster*) mates less well in reduced light¹⁰. It is therefore possible that, in dim red light, white-eyed *D. simulans* might have a mating advantage over the wild type, as this is within their perceptual range but below that of the wild type. There is thus the opportunity to design a system in which lights of different hue and intensity cause flies of different genotype at the eye colour locus to select, because of their phototactic behaviour, an environment in which they are relatively fit. We describe here an experiment on the role of habitat choice and diversifying selection in a patchy environment on eye colour polymorphism in *D. simulans*.

Experimental populations were founded in cages of volume 8,750 cm³ each of which was divided into two by a vertical partition having at its upper edge a 20 × 2-mm slit through which flies could pass freely. In the five white light controls, both halves of the cages were illuminated from above by a bright white light produced by three 80-W 'daylight' fluorescent tubes. The light in the five red light controls resulted from the attenuation of this by 10 thicknesses of red filter material to give a dim red light in

both sections of the cage. In the five experimental cages, one half was illuminated by the bright white and one half by the dim red light. Each population was founded with 120 homozygous fertilized females from a wild-type strain, and the same number of fertilized female homozygotes from a white-eyed strain. The founding generation of flies was phased in over 3 weeks to reduce later population fluctuations. Cages were kept at 22–25°C and contained 200 ml of cornmeal-agar-molasses medium, one-third of which was replaced each week. Samples were taken by scoring the offspring of four sampling vials introduced to each side of the cage at 3-week intervals.

Figure 1 shows the course of gene frequency change. The frequency of the *w* allele drops rapidly in both white light and red light control cages; by week 30 its mean frequency in the white light controls is 0.01 and in the red light controls 0.06. However, although this allele is deleterious in both environments when no habitat choice is available, in the heterogeneous environment of the experimental cages the polymorphism is maintained for at least 30 weeks; the mean frequency of *w* in the patchy cages after this period is 0.32. Habitat selection (which may lead to an apportionment of resources between flies of different genotype) is maintaining polymorphism for an allele which in a uniform environment is lost from the population.

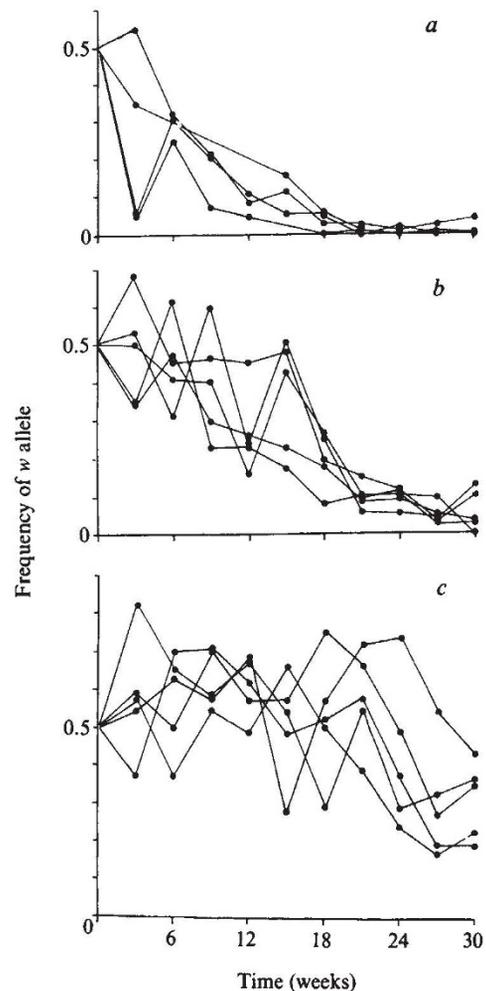


Fig. 1 Changes in the frequency of the *w* allele in *D. simulans* in: a, white light controls, b, red light controls and c, heterogeneous environments. One of the white light controls became extinct early in the experiment. Allele frequencies at this sex-linked locus were estimated using the weighted mean frequency in each sex. Although this does not provide an exact measure of allele frequency (as Hardy-Weinberg conditions do not hold) it is the most efficient estimate available.