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13. Supported by NIH grants CA-29537 and AM-28149 and a grant from the Milheim Foundation. Synthetic TGF-α was kindly provided by J. Tam.

10 September 1984; accepted 15 March 1985

Selection for Increased Safety Factors of Biological Structures as Environmental Unpredictability Increases

Abstract. *Theory predicts that selection should increase the ratio of the performance of a biological structure or system to the requirements placed upon it (that is, its safety factor) as conditions become increasingly unpredictable. Although conventional safety factors are rarely measurable, an alternative, truncation safety factor (the ratio of mean strength to maximum possible load), can be measured quantitatively for certain load-bearing structures. For intertidal limpet shells subject to prying forces, truncation safety factor was found to increase with increased variability in shell strength, thus providing direct support for the theory.*

Most biological structures, from the cellular to organ system level, have evolved in environments that are, to a greater or lesser degree, unpredictable. In particular, using load-bearing structures as an example, one would expect lifetime maximum loads on such structures to vary in an unpredictable fashion. Through environmental effects on development and aging, the strength of these structures should also vary unpredictably. Therefore, selection for the strength of a structure, relative to the maximum load it must bear, should be sensitive not only to the average maximum load likely to be encountered, but also to variability in the strength of the structure or the maximum load on the structure, or both (*1*). One measure of relative strength is "safety factor"—that is, the ratio of mean strength to mean lifetime maximum load (*2*).

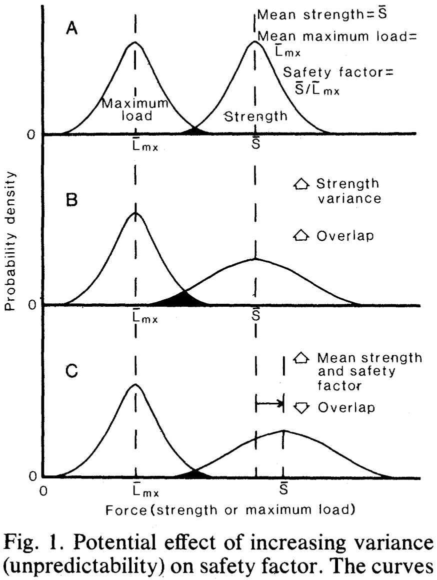

Fig. 1. Potential effect of increasing variance (unpredictability) on safety factor. The curves illustrate, for a given load-bearing, biological structure, the distribution of structural strengths and lifetime maximum loads for individuals within a single population as strength variance is increased. Increasing maximum load variance would have an analogous effect.

Figure 1A illustrates, for a hypothetical load-bearing structure, the mean force required to break the structure ($\bar{S}$) and the mean maximum force that structure experiences during its lifetime ($\bar{L}_{mx}$), where these means are calculated for a population of individuals; safety factor equals $\bar{S}/\bar{L}_{mx}$. Since individual structures in the population will not all break at the same force (S), there will be a variance in S. Also, since individual structures will not all experience the same lifetime maximum load (L_{mx}), there will be a variance in L_{mx}. If the distribution of L_{mx} is described by function f and the distribution of S is described by function g, then the probability (PF) that an individual structure, chosen at random from the population, will fail sometime during its lifetime is

$$PF = \int_0^\infty g(x) \int_x^\infty f(y)dydx$$

(relative magnitudes of PF are depicted as shaded overlap regions in Fig. 1). If such a failure is deleterious, selection should act to minimize PF by increasing $\bar{S}$ when it is not possible to reduce $\bar{L}_{mx}$ or either variance. However, if there is a cost to strengthening the structure, PF may not be reduced to zero. If the variance in S or L_{mx} is increased without changing the means, the overlap, and thus PF, will increase (Fig. 1B). Consequently, selection should act to increase the safety factor by increasing $\bar{S}$ to bring PF back down to a suitably low value (Fig. 1C). Therefore, more variable systems should experience selection for greater safety factors—that is, greater relative strengths (*3*).

Testing this prediction requires a consistent measure of relative strength—that is, a measure (with statistically fixed points such as $\bar{S}$ and $\bar{L}_{mx}$ used to define a safety factor) of the relative positions of the two curves illustrated in Fig. 1A. The mean and variance of strength are readily obtained for many structures by measuring the force required to break several test specimens from the population of interest. The mean and variance of lifetime maximum load, however, are usually difficult to measure under natural conditions because of the heterogeneous environment of forces that most load-bearing structures experience. For example, $\bar{L}_{mx}$ for a given segment of an adult zebra femur would be a complex function of several variables including the adult lifetime probabilities of a wide range of accelerations, decelerations, cruising speeds, falls, and collisions with predators and conspecifics. Biewener (*4*) has shown that a nonrigorous choice of $\bar{L}_{mx}$ can lead to the perhaps unreasonable conclusion that the limb bones of

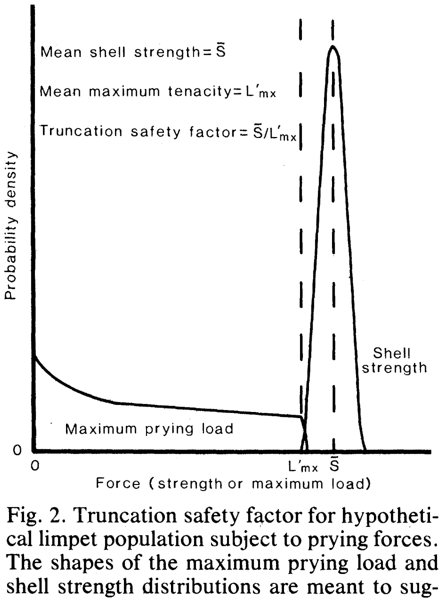

Fig. 2. Truncation safety factor for hypothetical limpet population subject to prying forces. The shapes of the maximum prying load and shell strength distributions are meant to suggest that (i) maximum load variance is likely to be greater than strength variance because of the heterogeneity of the intertidal environment, (ii) many limpets probably live to reproduce and then die without ever having experienced a prying load, and (iii) maximum tenacity determines the right-hand truncation of the maximum load curve.

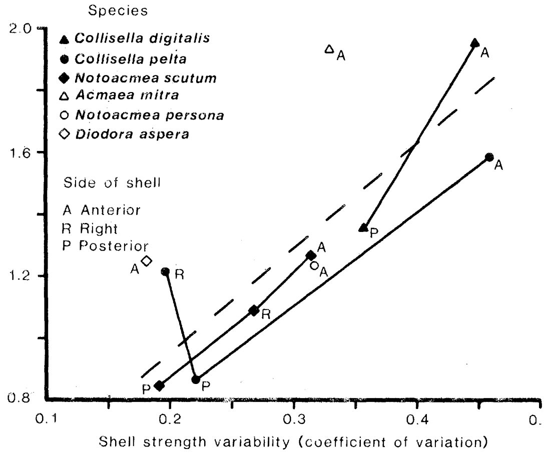

Fig. 3. Truncation safety factor (*TSF*) versus strength variability for limpet shells. The dashed line [reduced major axis (*13*) calculated for all species and shell sides combined, $r = 0.7407$, $P = 0.009$] illustrates the statistically significant average increase of *TSF* with increasing variability in shell strength. Solid lines connect the points for within-species comparisons of the different sides of the shell: *N. scutum*, $r = 0.9987$, $P = 0.032$; *C. pelta*, $r = 0.8270$, $P = 0.380$; *C. digitalis*, $t = 1.648$, d.f. $= 31$, $P = 0.109$, two-tailed *t* test for the difference between the natural log of anterior *TSF* and the natural log of posterior *TSF* (*14*).

small mammals and birds have much greater safety factors than those of large mammals.

This problem sometimes can be avoided by using another statistically fixed point, L'_{mx} (Fig. 2), from the maximum load distribution that can be measured for several kinds of structures. This point, L'_{mx}, is the maximum possible force a structure can experience under natural conditions—that is, the right-hand edge or truncation of the maximum load distribution—and can be used to obtain an alternative measure of relative strength, truncation safety factor ($TSF = \bar{S}/L'_{mx}$). In general, more variable systems should also experience selection for greater *TSF*'s since, on average, greater *TSF*'s should be associated with greater safety factors. In particular, when the load distribution remains constant among the different structures being compared, $\bar{L}_{mx}/L'_{mx}$ will also remain constant, and *TSF* will, therefore, be a constant multiple of the true safety factor.

To test this prediction, I measured *TSF*'s and shell strength variances for single populations of six species of intertidal limpets from the northeastern Pacific Ocean, including five acmaeids (*Acmaea mitra*, *Collisella digitalis*, *C. pelta*, *Notoacmea persona*, *N. scutum*) and one fissurellid (*Diodora aspera*). The shells of these limpets are subjected to prying forces by predatory crabs (*5*) and birds (*6*). To find $\bar{S}$, I measured the prying force (shell strength) required to break various sides of wet shells from newly killed limpets (*7*). I could also measure L'_{mx} (*8*) since, in evolutionary terms, the maximum possible prying load that the edge of a limpet shell can experience equals the maximum force (maximum tenacity) required to detach the foot of a previously undisturbed, healthy limpet on a flat rock surface in the field. This is because after the foot is detached, the shell no longer affords any protection. Thus, *TSF*'s could be assigned to those species and sides of the shell measured where $\bar{S}$ was mean shell strength, and $\bar{L}_{mx}$ was mean maximum tenacity. Strength and maximum load distributions for a hypothetical intertidal limpet population whose shells are subjected to prying forces are illustrated in Fig. 2. Although the distributions illustrated in Figs. 1 and 2 are for the simplified case of a single structural size class, I actually measured shell strength and maximum tenacity for limpets of several sizes and used analysis of covariance to calculate *TSF*'s and shell strength variances from adjusted means and residual variances (*9*).

Shell strength is strongly affected by shell thickness as well as by cracks and irregularities in the shell (*10*). These variables are, in turn, affected by several environmental factors such as infection by endolithic organisms, shell erosion, previous shell damage, and the particular microhabitats available to a limpet as it grows. For the most part, these environmental factors should be unpredictable to individuals and, consequently, the shell strength of any given individual would most likely also be unpredictable, resulting in the observed variability in shell strength. For example, *C. digitalis* is particularly susceptible to infection by the endolithic fungus *Pharcidia balani* (*11*) and also exhibits great variability in shell strength (Fig. 3).

The use of *TSF* assumes that the shape of the maximum load distribution is independent of strength variance. This assumption is likely to be true for all the following comparisons since the shape of the maximum load distribution is presumably a function of limpet and predator distributions, whereas strength variance is presumably an independent function of environmental effects on shell development and aging. Differently shaped maximum load distributions, as well as selective pressures other than prying forces, which could independently affect shell strength as measured here, would tend to increase the noise (variance) about the expected average increase of *TSF* due to increased variability in shell strength. This noise should be reduced when the overlapping portions of the maximum load distributions are of approximately the same shape among the different structures or species being compared and when differences in selective pressures other than prying forces are minimal. These latter conditions are most likely to hold when comparing different sides of the shell within a single population.

I estimated single-population *TSF*'s for the anterior, posterior, and right sides of *C. pelta* and *N. scutum* and for the anterior and posterior sides of *C. digitalis* where each side of the shell had its own characteristic shell strength variance. The causes for the within-population differences in strength variance between the different sides of the shell are not known; one possibility is that these differences are due to interactions of shell asymmetry and environmental factors that weaken the shell. In any case, these differences exist, and the results (points connected by solid lines in Fig. 3) suggest a within-population increase in *TSF* with increasing variability in shell strength, although this trend was significant for only *N. scutum*. Since the individuals of five of the six species came from populations along the same 50-m stretch of shore and since all six species were exposed to the same suite of predators, the shapes of the overlapping portions of the maximum load distributions, as well as selective pressures other than prying forces, may also be similar for interspecific comparisons. For all species and sides of the shell combined (all points in Fig. 3), *TSF* increased significantly with increasing variability in shell strength. Thus, the relation holds even across four genera and two superfamilies of gastropods.

The results support the proposal that the relative strength of load-bearing biological structures should increase as the variability of the system increases. The use of *TSF* should allow further testing in several other kinds of load-bearing structures such as (i) the stipes of those intertidal macrophytes where the maximum possible force on the stipe is determined by the strength of attachment to the substrate or (ii) those tendons and apodemes where the maximum possible force on the tendon or apodeme is determined by maximum muscular contraction.

The use of safety factor and *TSF* described above can be generalized beyond load-bearing structures to make predictions about the relative performance of a much wider array of biological structures and systems by redefining safety factor as the ratio of average realized performance ($\bar{S}$) to average required performance ($\bar{L}_{\mathrm{mx}}$) where, again, these averages are calculated for a population of individuals. For instance, one would predict that the average maximum hormonal output of a given type of endocrine gland would be greater, relative to the average threshold output required during stressful conditions, for populations whose maximum hormonal outputs or threshold requirements (or both) are more unpredictable. An analogous prediction would be that the average nectar output of a given flower type would be greater, relative to the zero variance output required to attract pollinators away from another population, for populations whose nectar outputs are more unpredictable. There is already empirical evidence that bumblebee foraging decisions could provide the selective pressures required for this prediction (*12*).

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7. A force (measured in newtons) was applied, with a Monsanto (type W) tensometer, in a dorsal direction perpendicular to the plane of the aperture by a steel hook of circular cross section (1.16 mm in diameter) inserted under the edge of the shell to mimic the prying action of a rounded crab appendage; the breaking force did not differ significantly in pairwise comparisons among hooks ranging in diameter from 0.67 to 2.64 mm (smallest $P > 0.15$, $n = 7 - 20$; analysis of covariance).
8. Spring scales were used to load (force measured in newtons) the edge of the shell in a manner identical to and on the same sides as the breaking force measurements. Limpets from Lime Kiln Lighthouse (all except *N. persona*) and False Bay (*N. persona*) on San Juan Island, Washington, were used both for strength and tenacity measurements.
9. Model 1 analysis of covariance was used to calculate *TSF* and shell strength variance (data were transformed to natural logarithms). For each species and side of the shell, I calculated regression equations for breaking force as a function of foot area ($n = 7 - 20$) and maximum tenacity as a function of foot area ($n = 8 - 23$). All breaking force–maximum tenacity regression pairs were parallel (no statistically significant differences between the regression coefficients of each pair; smallest $P > 0.05$). Hence, the *TSF*'s were essentially constant over the size ranges tested. Therefore, $TSF = \exp(\ln \bar{S} - \ln L'_{\mathrm{mx}})$ where $\ln \bar{S}$ was the adjusted mean of the breaking force regression and $\ln L'_{\mathrm{mx}}$ was the adjusted mean of the maximum tenacity regression for each species and side of the shell. Shell strength variance equaled the residual variance (*MSe*) of the breaking force versus foot area regressions. The *MSe*'s are reported as coefficients of variation (*CV*) where $CV = [\exp(MSe) - 1]^{0.5}$ [P. N. Chalmer, *J. Zool. (London)* **191**, 241 (1980); R. C. Lewontin, *Syst. Zool.* **15**, 141 (1966); S. Wright, *Evolution and the Genetics of Populations* (Univ. of Chicago Press, Chicago, 1968), vol. 1].
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14. For each point in Fig. 3, ln *TSF* ± 1 standard error, and *CV* ± 1 standard error: *C. digitalis* A, 0.67 ± 0.147, 0.45 ± 0.108; *C. digitalis* P, 0.30 ± 0.161, 0.36 ± 0.100; *C. pelta* A, 0.46 ± 0.125, 0.46 ± 0.117; *C. pelta* R, 0.20 ± 0.128, 0.20 ± 0.051; *C. pelta* P, −0.15 ± 0.093, 0.22 ± 0.062; *N. scutum* A, 0.23 ± 0.086, 0.31 ± 0.054; *N. scutum* R, 0.08 ± 0.137, 0.27 ± 0.072; *N. scutum* P, −0.17 ± 0.102, 0.19 ± 0.050; *A. mitra* A, 0.66 ± 0.121, 0.33 ± 0.077; *N. persona* A, 0.21 ± 0.128, 0.31 ± 0.086; *D. aspera* A, 0.22 ± 0.134, 0.18 ± 0.047; A, R, P as for Fig. 3.
15. I thank R. McN. Alexander, A. A. Biewener, G. M. Branch, J. D. Currey, D. H. Kelker, M. LaBarbera, A. R. Palmer, C. Strobeck for their suggestions and the use of equipment, and two anonymous reviewers for comments. I also thank the staff and biomechanics group at the University of Washington's Friday Harbor Laboratories for providing research space and facilities. Funding was provided by a Killam predoctoral fellowship to R.B.L., NSERC operating grant A7245 to A. R. Palmer, and the Department of Zoology, University of Alberta.

25 June 1984; accepted 23 November 1984

Floral Mimicry Induced by Mummy-Berry Fungus Exploits Host's Pollinators as Vectors

Abstract. *Leaves and shoots of blueberries (*Vaccinium *spp.) and huckleberries (*Gaylussacia *sp.) when infected by ascospores of* Monilinia *spp. become ultraviolet-reflective and fragrant and secrete sugars at their lesions. Insects that normally pollinate these hosts are attracted to the discolored leaves, ingest the sugars, and transmit conidia to their flowers, resulting in sclerotia (mummy-berry) formation.*

Monilinia vaccinii-corymbosi (Sclerotiniaceae), an economically important discomycete fungus, blights leaves and vegetative and floral shoots and mummifies fruit of wild and cultivated blueberries (*Vaccinium* spp.; Ericaceae); crop yield losses may reach 85 percent in individual fields (*1*). This polytrophic, dimorphic fungus overwinters on moist soil as sclerotia in mummified berries (or mummy berries). Unfolding young leaves of the host are infected by windborne, sexual ascospores released from apothecia, which arise from the sclerotia in early spring; these leaves (blight or wilt stage) produce asexual conidia that are transferred by pollinating insects to the host's flowers where the ovaries become infected, producing seedless, inedible mummy berries (*1*).

Various polyphagous insects that casually feed on exudates or spores of fungal plant pathogens are well known to disperse spores randomly (*2*). Azalea flower spot, caused by *Ovulina azaleae* (Sclerotiniaceae), is transmitted by pollinators that accidentally contact spores (*3*). We describe the behavior and role of insect pollinators of blueberries and huckleberries (*Gaylussacia* sp.; Ericaceae) in transmitting mummy-berry diseases. The exploitative modification of pollinator behavior through induction of floral mimicry in infected leaves by a vector-dependent, host-specific plant pathogen appears to be unique.

We investigated the interrelationships among 22 species of pollinating insects (*4*), *Monilinia vaccinii-corymbosi*, an unnamed *Monilinia* sp. (*1*), and their respective hosts, *Vaccinium corymbosum*, *V. vacillans*, and *Gaylussacia baccata*, between 1976 and 1984 in Greenbelt, Maryland (*1*). These sympatric wild hosts grow as understory shrubs in moist soil in a mixed oak-pine forest; most of their flowering is completed within 10 days, before the tree canopy fully leafs out. They have pendant flowers with poricidal anthers that require insect pollination (Fig. 1A) for fertilization (*5*). The earliest symptom of infection by *Monilinia* is wilting of young leaves and shoots, followed within 24 hours by browning of the upper side of the drooping shoots, midribs, and lateral veins of leaves (Fig. 1, B and C). Discoloration, which may spread to engulf the entire leaf, ranges (in daylight) from grayish brown to deep brown and dark brown, often noticeably to strongly tinged with moderate violet (*6*); in *Gaylussacia*, the discoloration is dark to moderate olive with a slight violet sheen (*6*). A grayish mantle of conidia, conidiophores, and occasional hyphae appears on the surface of infected shoots, peduncles, petioles, and at the base