

Plants Versus Animals: Do They Deal with Stress in Different Ways?¹

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SYNOPSIS. Both plants and animals respond to stress by using adaptations that help them evade, tolerate, or recover from stress. In a synthetic paper A. D. Bradshaw (1972) noted that basic biological differences between plants and animals will have diverse evolutionary consequences, including those influencing how they deal with stress. For instance, Bradshaw argued that animals, because they have relatively well-developed sensory and locomotor capacities, can often use behavior and movement to evade or ameliorate environmental stresses. In contrast, he predicted that plants will have to emphasize increased physiological tolerance or phenotypic plasticity, and also that plants should suffer stronger selection and show more marked differentiation along environmental gradients. Here we briefly review the importance of behavior in mitigating stress, the behavioral capacities of animals and plants, and examples of plant responses that are functionally similar to behaviors of animals. Next, we try to test some of Bradshaw's predictions. Unfortunately, critical data often proved non-comparable: plant and animal biologists often study different stressors (e.g., water *versus* heat) and measure different traits (photosynthesis *versus* locomotion). Nevertheless, we were able to test some of Bradshaw's predictions and some related ones of our own. As Bradshaw predicted, the phenology of plants is more responsive to climate shifts than is that of animals and the micro-distributions of non-mobile, intertidal invertebrates ("plant" equivalents) are more sensitive to temperature than are those of mobile invertebrates. However, mortality selection is actually weaker for plants than for animals. We hope that our review not only redraws attention to some fascinating issues Bradshaw raised, but also encourages additional tests of his predictions. Such tests should be informative.

INTRODUCTION

Perhaps then zoologists might look at plants, and botanists look at animals, and we may find that evolution in some animals is like that in plants, and evolution in some plants like that in animals, particularly when their properties overlap.

A. D. Bradshaw (1972, p. 25)

Environmental changes influence the performance and fitness of organisms. Some environmental changes are beneficial, but most will be stressful (Fisher, 1958). To ameliorate stressful changes, organisms can adopt three general and non-exclusive mechanisms (Larcher *et al.*, 1973, p. 231). First, they can evade or reduce the stress by using *behavior* (e.g., changing habitats or temporal activity patterns) or dormancy. Second, they can evolve greater *resistance* to stress (via increased tolerance, greater plasticity, reduced sensitivity). Third, if actually damaged, they can activate *recovery* mechanisms (e.g., regeneration of damaged tissues, cellular stress responses).

Animals and plants use all three strategies, but are thought to differ in which of these strategies they emphasize. In particular, animals often rely on behavior as their first line of defense against environmental challenges (Bartholomew, 1964). Such behavioral adjustments can sometimes completely mitigate a challenge, thus obviating the need to activate alternative anti-stress responses. However, plants cannot run away from a stress and are thus more likely to emphasize dormancy, stress-resistance, or stress-recovery mechanisms (see below).

In 1972 A. D. Bradshaw published a seminal paper "Some of the evolutionary consequences of being a plant." Noting that plants are relatively immobile and have fewer behavioral options than do animals, Bradshaw proposed that plants should tolerate a broader range of environmental conditions, show greater phenotypic plasticity, and experience stronger selection in nature. Subsequently, other botanists have extended Bradshaw's theme (Harper, 1977; Levin, 1978; Niklas, 1992). Moreover, as Bradshaw noted (1972, p. 26), some of his predictions can be readily applied to comparisons involving sessile (*i.e.*, "plant-like") *versus* mobile animals.

Here we have three general goals. First, we briefly review how and why behavior is a useful way to deal with environmental stress. Second, we evaluate whether plants are really as immobile as sometimes assumed. Third, we review some of Bradshaw's predictions and try to evaluate their validity.

We made some progress towards the first two goals,

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but have had limited success with the third. Quantitative tests of Bradshaw's predictions proved difficult to implement, not merely because the relevant literatures are huge and scattered, but mainly because the studies often proved *non-comparable*. The problem here is simply that plant and animal biologists often measure different traits and different environmental variables. Nevertheless, the issues raised by Bradshaw (1972) are fascinating, relevant, and deserving of additional testing. We hope that our paper will acquaint animal biologists with Bradshaw's paper. Although frequently cited by botanists, it has not (to our knowledge) been cited by a zoologist.

ON THE UTILITY OF BEHAVIOR

Regulatory behavior (by which we mean the capacities to sense the environment and to respond with movement) can be an effective way of dealing with changing environments. For example, such behavior can help an organism control its physiological vulnerability to *abiotic* factors by reducing the odds that it encounters stressful or lethal conditions (Bartholomew, 1964; Stevenson, 1985) and by increasing the proportion of time that it spends at physiologically optimal conditions (Huey *et al.*, 1989).

Behavioral evasion can also influence the outcome of *biotic* interactions (Helfman, 1986). Consider a frog being stalked by a heron. The frog can use its senses to detect the predator at a distance and then take evasive action. In contrast, consider a pumpkin that is in the path of a migrating elephant. The inevitable happens: the pumpkin is transmuted into a squash.

The ability to detect and evade biotic and abiotic threats is often—but not always—adaptive on balance. Movement expends energy and can attract predators (Roth, 1986), and increased movement capacity may evolve only at the sacrifice of reproductive effort (Chai and Srygley, 1990). In any case, high mobility is not inevitably the *sine qua non* of evolution. Sloths and barnacles are derived from mobile ancestors, implying that selection sometimes favors reduced mobility of animals (*i.e.*, becoming more plant like).

ARE PLANTS STATIONARY?

I shall publish in a month or two a book on the "Movements of Plants." I will send you a copy, but I fear it is much too special for anyone but a physiological botanist to care about. I have long thought that old men, like myself, ought to write only on confined & easy subjects.

Charles Darwin, Oct. 7, 1888
(unpublished letter to Ernst Krause)

Bradshaw (1972, p. 25) noted that some plants are animal like and that some animals are plant like. Nevertheless, he (1972, p. 26) generalized that animals are mobile and that plants are stationary: "So a plant cannot move from one environment into another in the course of its lifetime, in the way that an animal may traverse numerous different environments in the course

of a day." This generalization is obviously valid, but what strikes us (as zoologists looking at plants) is that some plant responses do involve physical movement and are remarkably animal-like in effect, though not in scale.

Let us continue with the theme of behavioral thermoregulation. Stevenson (1985) showed that many animals gain considerable control over body temperature by using movement to select habitats that differ in operative temperatures (Huey, 1991), to restrict activity to times with suitable temperatures (Porter and Tracy, 1983), or to orient to heat sources and sinks (Heath, 1965). (Nevertheless, not all animals that have such regulatory capacities always use them in nature [Feder *et al.*, 1996; but see Jones *et al.*, 1987].)

What about plants? Are they passive to changes in the thermal environment? In fact, some plants have responses that achieve much the same ends as the overt locomotor adjustments of animals. As Bazzaz (1991) noted, some plants can effectively "select habitats" by *growing* towards some desirable resource or away from an environmental stressor. Some plants use the ratio of red:far-red wavelengths of light, which depends on the degree of shading, as a cue of the presence of other plants in the immediate environment; and they can adjust their growth accordingly and adaptively (Dudley and Schmitt, 1995). Neotropical stilt palms (*Socratea exorrhiza*) are reported (Leopold *et al.*, 2000) to move on their stilts towards light gaps: alas, this is apparently a tropical myth (A. Henderson, personal communication).

Climbing and clonal plants can literally crawl across the environment, selecting habitats much like animals. In fact, such movements are sometimes called "foraging" (Bazzaz, 1991; Harper, 1986; Ray, 1992). Remarkably, connected ramets living in different habitats can even share nutrients and water (Pitekla and Ashmun, 1985; Salzman, 1985).

To some extent, plants may target dispersal of progeny toward favorable habitats (Bazzaz, 1991). Of course, fruits and seeds of many plants are adapted for dispersal by animals: in most cases, such dispersal is undoubtedly haphazard. However, seed dispersal by some ants (Kalisz *et al.*, 1999), and perhaps also mistletoe seeds by birds, is not.

Plants can orient their leaves and flowers towards or away from the sun (Stanton and Galen, 1989), in ways functionally similar the orientation movements of animals (Heath, 1965; Stevenson, 1985). Ehleringer and Forseth (1980) showed that the leaves of many plants change their orientation during the day, maintaining a perpendicular orientation to the sun's rays, and thereby enhance photosynthesis (rather than modulate body temperature as in lizards). However, water stressed plants reposition their leaves to a vertical orientation (Ehleringer and Forseth, 1980), reducing heat gain and thus conserving water. Solar tracking by flowers of alpine buttercups (*Ranunculus*) provides a heat reward to insect pollinators as well as to increase seed set (Stanton and Galen, 1989).

Charles Darwin (see quote above) and his son Francis wrote a book on movement of plants (Darwin and Darwin, 1880) and included a chapter on “sleeping” in plants. The leaves of many plants droop at night, and this had long been interpreted as a way of conserving energy. Darwin suspected that such “sleeping” postures actually had a thermoregulatory function: a leaf held horizontal and exposed to the clear night sky would lose heat by radiation and potentially suffer frost damage. To test this hypothesis, the Darwins put out plants at night, allowing some leaves to “sleep,” but holding others horizontal. Leaves allowed to sleep had much lower frost damage than did leaves held horizontal. In *Oxalis actosella*, for example, 92% of the leaves that were “sleepers” survived a cold night, whereas only 37% of the “non-sleepers” survived ($P = 0.003$, by a Fisher exact test, of course). Although competing explanations for the phenomena have been offered (Bunning, 1967), our point is that leaves can move, in ways that are functionally similar to the orientation movements of many animals.

Some plants even shift the solar orientation of chloroplasts within their leaves, even when the leaves do not move. Duckweed is a small-leaf plant that is aquatic, with the leaves held horizontally on the water surface. The chloroplasts are oriented perpendicularly to the light in dim light, thereby maximizing uptake of light; but in bright light, which is potentially damaging, the chloroplasts rotate so that they are parallel to the light, thereby minimizing light exposure. The sensory mechanism underlying such remarkable chloroplast movement has recently been described in *Ara-bidopsis* (Kagawa *et al.*, 2001).

Finally, even though they themselves are relatively sessile, plants can take advantage of an animal’s mobility. Plants of course routinely manipulate animal movement for pollination and dispersal, but some plants even manipulate animal movement for self-defense (Kessler and Baldwin, 2001). When attacked by herbivorous spider mites, lima beans secrete volatile compounds that attract predatory mites, which then attack the herbivorous mites, thus providing an “indirect defense” for the plant (Dicke, 1999). Further, some plants (sundews, Venus flytrap, pitcher plants) trap mobile animals (Hart, 1990).

We have highlighted only a few examples of plant movements (Hart, 1990). We are not claiming that plants can match the sensory and locomotor capacities of animals, and we wish to avoid the semantic debate of whether plant movements should be called “behavior.” What does matter here is that some plants movements achieve many of the same functional ends as those of animals. Plants may not move as far or as quickly as animals, but some are hardly immobile. Mobility differences are often a matter of scale.

DO PLANTS AND ANIMALS DEAL WITH STRESS IN DIFFERENT WAYS?

Given that plants are relatively stationary and thus forced to experience environmental pressures, Brad-

shaw (1972) made several predictions as to ways plants and animals should differ in their ecology and evolution. We focus on the subset of his predictions relating to environmental tolerance, and we’ve added a few predictions that are philosophically consistent with his perspective.

Prediction: plants have broader tolerance ranges than do animals

Frequent exposure to extreme environments may select for enhanced tolerance capacity (Hoffmann and Parsons, 1991). Accordingly, plants should tolerate broader ranges of environmental conditions than would animals, simply because plants won’t be able to evade a stressor.

This prediction is testable in two ways. First, the premise that plants experience wider ranges of conditions could be tested by determining whether, for example, plants have actually experience more variable “body” temperatures over time than do sympatric ectothermal animals. Unfortunately, such data have never been gathered systematically at any locality. Doing so will be difficult because some individual plants will show much greater “regional heterothermy” (*i.e.*, the temperature differences between different parts of the plant) than do animals (see fig. 4.7 in Körner, 1999), making it relatively hard to characterize *the* temperature of a plant.

Second, data on actual tolerance ranges (*i.e.*, the range between upper and lower lethal temperatures) of plants and of animals could be compared directly, ideally for organisms studied at the same sites. Implementing this test proved frustrating. Much of the literature on vertebrate ectotherms measures “critical thermal limits” (temperatures at which the righting response is lost), which have no direct equivalents in the plant literature. Lethal temperatures are commonly measured in both groups, but would have to be standardized for exposure time and acclimation condition. Supercooling points are also measured in some plants and animals (Lee *et al.*, 1995; Levitt, 1980), but often in quite different ways (R. E. Lee, personal communication). So one would have to validate (study by study) that the techniques and end-points being used were comparable. Moreover, any meaningful analysis would need to compare tolerance temperatures of multiple stages of plants *versus* animals, as tolerance can be strongly stage dependent, on species collected from the same area or habitat.

Given these and other complications, we made only a cursory search of the literature. Consistent with Bradshaw’s reasoning, some plants (especially seeds) are extraordinarily cold tolerant (see table 3.1 in Levitt, 1972) relative to insects (table 5.7 in Withers, 1992) and reptiles (table 1 in Heatwole, 1976). Similarly, some plants (especially seeds) are extraordinarily heat tolerant (table 11.2 in Levitt, 1972) even relative to desert reptiles (Heatwole, 1976). However, whether plants generally have broader tolerance ranges than do

sympatric animals remains to be quantified systematically.

Prediction: plants should emphasize biochemical adaptations more than do animals

Bradshaw (1972) did not discuss specific physiological mechanisms. However, if plants have evolved greater physiological tolerance than animals (above), then their enhanced tolerance should be evident at the biochemical level.

Organisms that experience a wide range of body temperatures may possess eurythermal enzymes, which operate efficiently over a wide range of temperatures (Somero, 1995). An enzyme's thermotolerance is often assessed by measuring the thermal sensitivity of its K_m value (Patterson and Graham, 1987; Somero *et al.*, 1996; Teeri, 1980), which is the concentration of substrate needed for an enzyme to operate at half maximal velocity. Unfortunately, we know of no direct comparisons of the thermal sensitivity of K_m values of plants *versus* animals.

An organism's thermal tolerance could also be increased by evolving multiple variants of a given enzyme, or isozymes, each with a different thermal optimum (Baldwin and Hochachka, 1970; Hochachka and Somero, 1984; Lin and Somero, 1995). Few animals use isozymes, perhaps because of the genetic constraints of diploidy (Hochachka and Somero, 1984; Somero, 1995). Interestingly, many plants are polyploids (Ramsey and Schemske, 1998) and might therefore be more likely to evolve thermally distinct isozymes. However, whether plants commonly use isozymes to cope with wide thermal ranges is unclear (Lutova, 1995; Teeri, 1980), though some plants have isozymes that fluctuate in quantity with seasonal changes (Hausladen and Alscher, 1994).

On occasion organisms (mobile or not) are exposed to stressful or damaging temperatures, and plants and animals synthesize special proteins that stabilize cells at such temperatures (Feder and Hofmann, 1999). These proteins have quite diverse functions (*e.g.*, stabilization of protein structure, alteration of membrane fluidity, and prevention of cellular ice formation). Many such proteins, particularly "heat shock" proteins, have been well studied in plants and animals (Boston *et al.*, 1996; Feder, 1999; Feder and Hofmann, 1999; Never *et al.*, 1996; Patterson and Graham, 1987; Sabehat *et al.*, 1998; Somero, 1995). However, whether plants have relatively heightened stress responses (*e.g.*, faster or stronger synthesis of stabilizing proteins; see Coleman *et al.*, 1995) has not yet been determined. Suggestively, however, the temperature that induces the synthesis of heat shock proteins (Buckley *et al.*, 2001; Roberts *et al.*, 1997; Tomanek and Somero, 1999) is lower for intertidal mussels (sessile) than that for sympatric snails (mobile) held under similar conditions.

Prediction: plants are more plastic than are animals

Organisms can adjust to environmental variation by altering their phenotypes (Schlichting and Pigliucci,

TABLE 1. Number of citations (Biosis, 1991 to fall 2000) that use combinations of key words ("phenotypic plasticity" + plant or animals + one of several environmental variables).*

| Taxon | Environmental variable | | | |
|--------|------------------------|-------|------|-------|
| | Temperature | Light | Soil | Water |
| Plant | 52 | 42 | 44 | 40 |
| Animal | 140 | 7 | 4 | 9 |

* We made no attempt to validate citation hits.

1998), a phenomenon that is called phenotypic plasticity (or "acclimation," when reversible). Plasticity is often assumed to be an adaptation, though some studies are contradictory (Huey *et al.*, 1999; Leroi *et al.*, 1994; Sultan and Bazzaz, 1993). In a classic paper, Bradshaw (1965) called attention to the general importance of plasticity. Then in his 1972 paper, he predicted that plants should have evolved relatively high levels of plasticity. In addition, the modular structure and less targeted vegetative morphology of plants enable them to have much greater morphological plasticity than could typical animals (Bazzaz, 1991; Sultan, 1987).

To test Bradshaw's (1972) prediction, we decided to use a useful index of Levins (1969) to quantify plasticity (see also Kingsolver and Huey, 1998). For example, the slope of the regression of lethal temperature on acclimation temperature quantifies the plasticity of the thermal acclimation response. However, when we tried to compile data on plasticity from literature, we ran into problems. First, and most importantly, plant and animal biologists often study different environmental variables. This became conspicuous when we conducted a citation search (Table 1) on "phenotypic plasticity" plus (plant or animal) plus one environmental variable (temperature, water, soil, or light): the vast majority of the animal studies dealt with temperature, whereas plant studies more commonly dealt with water, nutrients, or light (Sultan, 2001). Second, plant and animal biologists often measure very different traits (*e.g.*, photosynthesis *versus* running speed). Third, animal biologists typically acclimate animals to fixed temperature regimes, whereas plant biologists usually use cycling acclimation regimes. This may trace to Went's (1957) classic studies, showing that plants grow better on cycling regimes.

Despite these technical concerns, comparable data surely exist in the literature, but finding and compiling these data will require a cautious search. So a rigorous test of Bradshaw's plasticity hypothesis remains an open opportunity.

Prediction: plants show stronger inducible defenses than do animals

Inducible defenses are a special case of phenotypic plasticity made directly in response to cues from biotic agents such as predators, herbivores, or predators (Tollrian and Harvell, 1999); and they are assumed to provide at least partial protection following attack.

Bradshaw (1972) did not specifically discuss inducible defenses, but subsequent workers (Harvell, 1990) have proposed that inducible defenses might be especially favored in sessile and in clonal (or modular) organisms such as plants or colonial invertebrates, which are unable to run away from predators. Although many of the initial examples of inducible defenses came from studies of sessile organisms (Harvell, 1990), inducible defenses are increasingly detected in mobile and in non-clonal organisms (Relyea, 2001; Tollrian and Harvell, 1999). Moreover, immune responses, which are a class of inducible defenses (Frost, 1999), are well developed in vertebrates, which are neither sessile nor clonal. In any case, it is not obvious how to compare the magnitude of different kinds of inducible defense.

Prediction: selection should be stronger on plants than on animals

Because plants don't move through several habitats during their lifetimes but instead are chronically exposed to a single one, they experience the world as more "coarse-grained" (*sensu* Levins, 1968) than do animals. As a result, Bradshaw (1972, p. 26) predicted that selection should be relatively strong on plants. Indeed, many of the classic examples of strong selection in nature involve plants (Bradshaw, 1972).

To quantify the force of directional selection on a quantitative trait, we use the standardized selection gradient (Lande and Arnold, 1983), which is the partial regression coefficient (linear) of relative fitness on a trait score (in units of standard deviations). Kingsolver *et al.* (2001) have recently compiled estimates of these " β coefficients" (<http://www.bio.unc.edu/faculty/kingsolver/lab/>).

Analyzing this data set, we partitioned β s (absolute values) for morphological traits of plants, vertebrates, *versus* invertebrates; and we've done separate analysis for studies that measured *mortality* (viability) selection from those that measured *non-mortality* aspects of selection (*e.g.*, fecundity, fertility, or mating success).

Contrary to Bradshaw's prediction, plants do not in fact show stronger non-mortality selection gradients on morphological traits than do animals (Savage test, $P = 0.29$). In fact, no trend in this direction is even evident (Fig. 1a). Note, however, that plants show much weaker mortality selection gradients than do animals ($P < 0.001$, Fig. 1b).

Why do the data contradict Bradshaw's prediction? Perhaps the plant data are somewhat misrepresentative. Mortality selection on plants is probably strongest at the seed and seedling stages (D. Schemske, personal communication), yet most plant studies to date are on "adult" plants. For example, none of the available estimates of mortality selection involves seed mortality, and at least 2/3 of the estimates involve mortality selection after establishment.

SPATIAL DISTRIBUTIONS

When confronted by a stress, a mobile organism can seek refuge in physically benign microhabitats or

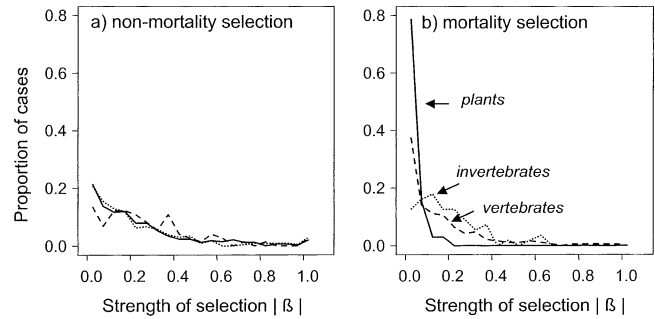


FIG. 1. Strength of directional selection on morphological traits of various taxa. (a) The proportion of estimates of non-mortality selection on plants (solid line, $n = 344$ estimates), vertebrates (dashed line, $n = 234$), and insects (dotted line, $n = 308$) as a function of the absolute standardized selection gradient ($|\beta|$). (b) The proportion of estimates of mortality selection on plants ($n = 33$), vertebrates ($n = 189$), and invertebrates ($n = 56$) as a function of $|\beta|$.

abandon the area entirely. Plants and sessile animals do not enjoy this luxury (though some use dormancy or seed banks) and may suffer widespread mortality from a single stressful event (Bowers, 1982; Tsuchiya, 1983). All else being equal, sessile species may thus have relatively restricted distributions along a stress gradient. Intertidal organisms provide a test of this expectation.

Intertidal organisms face severe stresses (heat, desiccation) when exposed to the air during low tide (Helmut, 1998 and references therein). The highest tolerable position in the intertidal is largely determined by an organism's ability to survive prolonged periods of emersion (Newell, 1979; Stillman and Somero, 1996). The upper limits of intertidal organisms vary predictably with between-site patterns of physical stress (Leigh *et al.*, 1987; Lewis, 1986; Wethey, 1984). For example, on foggy coasts with heavy wave action, intertidal species can survive above the actual limit of tidal excursion. However, on sunny, wave-protected shores, they survive only at lower shore levels where aerial exposure is minimal (see also Lewis, 1964).

The inverse relationship between upper distributional limits and magnitude of physical stress (*e.g.*, substrate temperature) should be relatively strong for sessile intertidal species. In contrast, upper limits of mobile species should be weakly related to between-site patterns of substrate temperature as these species can retreat down-shore or into crevices.

To test this prediction, one of us (Harley, 2001) contrasted the upper intertidal limits of several species of algae, sessile invertebrates, and mobile invertebrates at six localities ranging from the foggy, wave exposed outer coast of Washington to the sunny, protected shores of Puget Sound. Maximum rock temperatures in the mid-intertidal range from 26°C on the outer coast to over 41°C in Puget Sound. Consistent with expectation, upper limits are strongly negatively related to maximum rock temperatures for algae and sessile invertebrates, but only weakly related to maximum temperatures for mobile species. (Fig. 2). The upper

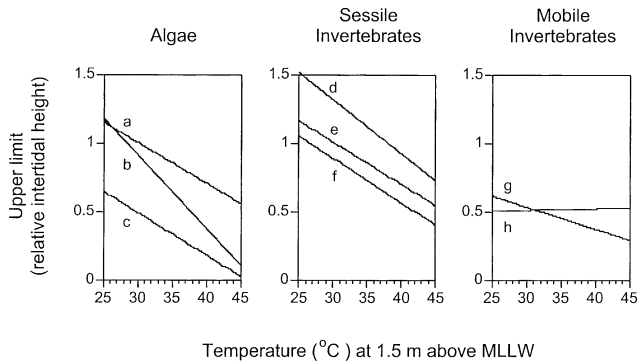


FIG. 2. Regression lines for the relationship between mid-intertidal rock temperatures and the upper limits of representative algae, sessile invertebrates, and mobile invertebrates. Both algae and sessile invertebrates display sharp decreases in upper limits with increasing thermal stress, whereas mobile invertebrates do not. Rock temperatures were measured at a standard 1.5 m above mean lower low water (MLLW) with ibutton temperature loggers (Dallas Semiconductor). Species' upper limits were determined using surveyors equipment. Relative intertidal height is scaled from zero (MLLW) to one (mean higher high water, MHHW) based on predicted tidal curves. The species shown are the algae *Fucus gardneri* (a), *Halosaccion glandiforme* (b), and *Hedophyllum sessile* (c), barnacles *Balanus glandula* (d) and *Semibalanus cariosus* (e), mussel *Mytilus californianus* (f), chiton *Katharina tunicata* (g), and sea star *Pisaster ochraceus* (h).

distributional limits of sessile species were significantly more sensitive to physical stress than were those of the mobile species (Table 2).

PATTERNS THROUGH TIME

The phenology of annual events can change in response to shifts in climate. If plants are more plastic than animals, then plant phenology should be relatively sensitive to inter-annual variability in climate.

We test this prediction by re-analyzing a remarkable, multi-century dataset of phenologies (*e.g.*, time of bud burst for plants, of nest building for birds) recorded in southeastern England (Sparks and Carey, 1995). Two patterns are evident. First, the timing of phenological events of plants was much more closely tied to between-year climatic variability than was that of animals (Fig. 3a, $P \ll 0.001$, compiled from table 4 in Sparks and Carey, 1995). The R^2 for stepwise regression models of timing on climate was 0.71 ± 0.09 (mean \pm SD) for plants but only 0.45 ± 0.11 for animals. Second, the predicted advance (in days) in phenology given a realistic future climate-warming scenario was much greater for plants than for animals (Fig. 3c and 3d, data from table 6 in Sparks and Carey, 1995). Climate warming is predicted to advance plant phenology by an average of 19.5 ± 0.9 days in response, but that for animals by only 6.6 ± 1.3 days ($P \ll 0.001$).

These data are derived from a limited set of species at a single site but nonetheless support Bradshaw's (1972) general expectation that plants are more tightly coupled to environmental variation than are animals. The observed pattern might alternatively result from

TABLE 2. Results of ANCOVA on the relationship between upper distributional limits, maximum mid-intertidal temperature, and functional group (algae, sessile invertebrate, or mobile invertebrate).*

| Factor | DF | F | P |
|---------------------------------------|------|------|-------------|
| Functional group | 2 | 9.64 | <0.001 |
| Mid-intertidal temperature | 1 | 41.8 | $\ll 0.001$ |
| Functional group \times temperature | 2 | 5.11 | 0.015 |
| Species [functional group] | 5 | 22.9 | $\ll 0.001$ |
| Error | 29** | | |

* For this analysis, species (see Fig. 2) were nested within functional group. The significant functional group \times temperature interaction indicates that the upper limits of species in different functional groups differed in their sensitivity to thermal stress. In exploratory analyses (ANCOVA) between functional group pairs, mobile invertebrates responded differently to the stress gradient than both algae and sessile invertebrates (temperature by functional group interactions: $F_{1,18} = 4.69$, $p = 0.047$, and $F_{1,18} = 12.6$, $p = 0.003$, for mobile animals vs. algae and mobile vs. sessile animals, respectively). The responses of algae and sessile invertebrates were not different (temperature by functional group interaction: $F_{1,22} = 0.33$, $p = 0.576$).

** Not all species were present at each of the six sampling sites.

differential climatic change in the wintering grounds of migratory animals or from the error associated with defining the return of migrating species (Sparks and Carey, 1995). However, phenologies of non-migratory animals also showed poor fits with climate data as well as showed limited predicted response to climate change.

These phenological patterns raise interesting suggestions regarding potential changes in the distribution and abundance of plant and animal populations in response to climate change. For example, climate warming might have a bigger impact on the intertidal zonation of sessile than of mobile species. Whether climate warming is having a bigger impact on plants than on animals in terrestrial systems remains to be determined; however, distributions of plants and animals

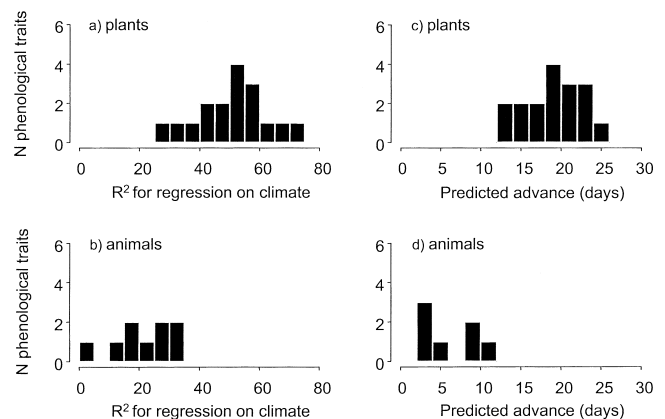


FIG. 3. Relative phenological sensitivity of (a) plants and (b) animals to climate change over two centuries. Plotted in are histograms of R^2 values (%) for regressions of time of onset of phenological variables on climate variables for plants (a) and animals (b). Predicted advance (in days) of phenological variables in response to a simulated climate warming for (c) plants and (d) animals. Data were collected (see Sparks and Carey, 1995) at the Marsham family estates (England).

shifted dramatically and individualistically following de-glaciation in the late Quaternary (Graham and Grimm, 1990).

Do plants and animals differ in macro-evolutionary responses to the environment (Niklas, 1997)? If plants and animals are indeed sensitive to different kinds of stresses or at least have different sensitivities, then the timing of their mass extinctions might differ.

The timing of mass extinctions has been studied intensively. Five mass extinctions have generally been recognized for marine invertebrates (Jablonski, 1991), and two mass extinctions (plus some minor ones) are recognized for terrestrial vertebrates (Benton, 1989). However, only three mass extinctions (late Ordovician, Permian-Triassic, Cretaceous-Tertiary) are currently receiving strong support (R. Bambach and A. Knoll, reported in Kerr, 2001). What about plants? Niklas (1997) states that nine "episodes of intense species extinction" characterize the history of vascular land plants and that none of these extinctions coincides with any of the major extinctions (post-Silurian) of marine invertebrates or of terrestrial vertebrates (see fig. 8.14 in Niklas, 1997). However, recent data suggests that plants actually experienced only two major extinctions (Permian-Triassic, Cretaceous-Tertiary; A. H. Knoll, personal communication), which are in fact synchronous with the mass extinctions of marine and terrestrial animals. Given that several mass extinctions have recently "gone extinct" (*e.g.*, Kerr, 2001), it now seems premature to evaluate whether extinction patterns of plants and animals actually show differential sensitivity to environmental changes.

CONCLUDING REMARKS

We have examined some physiological, ecological, and evolutionary consequences of one fundamental difference between animals and plants, namely, the fact that animals (but not plants) can use their behavior and mobility to evade environmental stresses and to maximize time in suitable environments. Our review is based largely on a classic synthesis by A. D. Bradshaw (1972), in which he drew attention to the evolutionary consequences of various key biological differences (not just behavioral ones) between plants and animals.

The generalizations given here are largely well known, but nevertheless are worth repeating. Most importantly, behavior and mobility can be an effective defense against diverse biotic and environmental stresses. Consequently, any organism—be it a plant or a sessile invertebrate—that has limited capacities in this regard may need to amplify evolutionarily its use of other mechanisms (*e.g.*, greater tolerance, plasticity, or repair capacity) to deal with stresses (Bradshaw, 1972). However, comparing quantitative responses of plants and animals has proven remarkably difficult.

We would be remiss not to reiterate that plants and animals differ, of course, in many ways other than in behavioral and locomotor capacities (Bradshaw, 1972). For example, they differ in dispersal distance (Brad-

shaw, 1972), breeding system (Lande and Schemske, 1985), modular construction (Harper, 1977, 1986), and ploidy (Ramsey and Schemske, 1998), to say nothing of their vast physiological differences. All of these differences should have major ecological and evolutionary consequences (Bradshaw, 1972; Harper, 1977, 1986), will undoubtedly interact with differences in behavior and locomotion, and should be well worthy of detailed investigation. Someone interested in embarking on such an investigation would be well advised to start with a careful reading of Bradshaw (1972).

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REFERENCES

- Baldwin, J. and P. W. Hochachka. 1970. Functional significance of isoenzymes in thermal acclimation: Acetylcholinesterase from trout brain. *Biochem. J.* 116:883–887.
- Bartholomew, G. A. 1964. The roles of physiology and behaviour in the maintenance of homeostasis in the desert environment. *Symp. Soc. Exp. Biol.* 18:7–29.
- Bazzaz, F. A. 1991. Habitat selection in plants. *Am. Nat.* 137:S116–S130.
- Benton, M. J. 1989. Mass extinctions among tetrapods and the quality of the fossil record. *Proc. R. Soc. London, ser. B* 191:109–135.
- Boston, R. S., P. V. Viitanen, and E. Vierling. 1996. Molecular chaperones and protein folding in plants. *Plant Mol. Biol.* 32:191–222.
- Bowers, J. E. 1982. Catastrophic freezes in the Sonoran Desert. *Desert Plants* 2:232–236.
- Bradshaw, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. *Adv. Genetics* 13:115–155.
- Bradshaw, A. D. 1972. Some of the evolutionary consequences of being a plant. *Evol. Biol.* 5:25–47.
- Buckley, B. A., M.-E. Owen, and G. E. Hofmann. 2001. Adjusting the thermostat: The threshold induction temperature for the heat-shock response in intertidal mussels (genus *Mytilus*) changes as a function of thermal history. *J. Exp. Biol.* 204:3571–3579.
- Bunning, E. 1967. *The physiological clock*. Springer-Verlag, New York, New York.
- Chai, P. and R. B. Srygley. 1990. Predation and the flight, mor-

- phology, and temperature of Neotropical rainforest butterflies. *Am. Nat.* 135:748–765.
- Coleman, J. S., S. A. Heckathorn, and R. L. Hallberg. 1995. Heat-shock proteins and thermotolerance: Linking molecular and ecological perspectives. *TREE* 10:305–306.
- Darwin, C. and F. Darwin. 1880. *The power of movement in plants*. John Murray, London.
- Dicke, M. 1999. Evolution of induced indirect defense of plants. In R. Tollrian and C. D. Harvell (eds.), *The ecology and evolution of inducible defenses*, pp. 62–88. Princeton University Press, Princeton, New Jersey.
- Dudley, S. A. and J. Schmitt. 1995. Genetic differentiation in morphological responses to simulated foliage shade between populations of *Impatiens capensis* from open and woodland sites. *Funct. Ecol.* 9:655–666.
- Ehleringer, J. and I. Forseth. 1980. Solar tracking by plants. *Science* 210:1094–1098.
- Feder, M. E. 1999. Organismal, ecological, and evolutionary aspects of heat-shock proteins and the stress response: Established conclusions and unresolved issues. *Amer. Zool.* 39:857–864.
- Feder, M. E., N. Blair, and H. Figueras. 1996. Oviposition site selection: Unresponsiveness of *Drosophila* to cues of potential thermal stress. *Anim. Behav.* 53:585–588.
- Feder, M. E. and G. Hofmann. 1999. Heat-shock proteins, molecular chaperones, and the stress response: Evolutionary and ecological physiology. *Annu. Rev. Physiol.* 61:243–282.
- Fisher, R. A. 1958. *The genetical theory of natural selection*. Dover, New York, New York.
- Frost, S. D. W. 1999. The immune system as an inducible defense. In R. Tollrian and C. D. Harvell (eds.), *The ecology and evolution of inducible defenses*, pp. 104–126. Princeton University Press, Princeton, New Jersey.
- Graham, R. W. and E. C. Grimm. 1990. Effects of global climate change on the patterns of terrestrial biological communities. *TREE* 5:289–292.
- Harley, C. 2001. Environmental modification of biological interactions: A comparison across scales. Ph.D. Diss., University of Washington, Seattle, Washington.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, London.
- Harper, J. L. 1986. Modules, branches and the capture of resources. In J. B. C. Jackson, L. W. Buss, and R. E. Cook (eds.), *Population biology of clonal organisms*. Yale University Press, New Haven, Connecticut.
- Hart, J. W. 1990. *Plant tropisms and other growth movements*. Unwin Hyman, London.
- Harvell, C. D. 1990. The ecology and evolution of inducible defenses. *Q. Rev. Biol.* 65:323–340.
- Hausladen, A. and R. G. Alscher. 1994. Cold-hardiness specific glutathione-reductase in isozymes in red spruce thermal-dependence of kinetic parameters and possible regulatory mechanisms. *Plant Physiology* 105:215–223.
- Heath, J. E. 1965. Temperature regulation and diurnal activity in horned lizards. *Univ. Calif. Publ. Zool.* 64:97–136.
- Heatwole, H. 1976. *Reptile ecology*. University of Queensland Press, St. Lucia, Queensland, Australia.
- Helfman, G. S. 1986. Behavioral responses of prey fishes during predator-prey interactions. In M. E. Feder and G. V. Lauder (eds.), *Predator-prey relationships: Perspectives and approaches from the study of lower vertebrates*, pp. 135–156. University of Chicago Press, Chicago, Illinois.
- Helmuth, B. S. T. 1998. Intertidal mussel microclimates: Predicting the body temperature of a sessile invertebrate. *Ecol. Monogr.* 58:51–74.
- Hochachka, P. W. and G. N. Somero. 1984. *Biochemical adaptation*. Princeton University Press, New Jersey.
- Hoffmann, A. A. and P. A. Parsons. 1991. *Evolutionary genetics and environmental stress*. Oxford University Press, Oxford.
- Huey, R. B. 1991. Physiological consequences of habitat selection. *Am. Nat.* 137:S91–S115.
- Huey, R. B., D. Berrigan, G. W. Gilchrist, and J. C. Herron. 1999. Testing the adaptive significance of acclimation: A strong inference approach. *Amer. Zool.* 29:323–336.
- Huey, R. B., C. R. Peterson, S. J. Arnold, and W. P. Porter. 1989. Hot rocks and not-so-hot rocks: Retreat-site selection by garter snakes and its thermal consequences. *Ecology* 70:931–944.
- Jablonski, D. 1991. Extinctions: A paleontological perspective. *Science* 253:754–757.
- Jones, J. S., J. A. Coyne, and L. Partridge. 1987. Estimation of the thermal niche of *Drosophila melanogaster* using a temperature-sensitive mutant. *Am. Nat.* 130:83–90.
- Kagawa, T., T. Sakai, N. Suetsuga, K. Oikawa, S. Ishiguro, T. Kato, S. Tabata et al. 2001. *Arabidopsis* NPL1: A phototropin homolog controlling the chloroplast high-light avoidance response. *Science* 291:2138–2141.
- Kalish, S., F. M. Hanzawa, S. J. Tonsor, D. A. Thiede, and S. Voigt. 1999. Ant-mediated seed dispersal alters spatial pattern of seed relatedness in an outcrossing population of *Trillium grandiflorum*. *Ecology* 80:2620–2634.
- Kerr, R. A. 2001. Paleontology: Paring down the big five mass extinctions. *Science* 294:2072b–2073b.
- Kessler, A. and I. T. Baldwin. 2001. Defensive function of herbivore-induced plant volatile emissions in nature. *Science* 291:2141–2144.
- Kingsolver, J. G., H. E. Hoekstra, J. M. Joekstra, D. Berrigan, S. N. Vignieri, C. E. Hill, A. Hoang et al. 2001. The strength of phenotypic selection in natural populations. *Am. Nat.* 157:245–261.
- Kingsolver, J. G. and R. B. Huey. 1998. Evolutionary analyses of morphological and physiological plasticity in thermally variable environments. *Amer. Zool.* 38:545–560.
- Körner, C. 1999. *Alpine plant life*. Springer-Verlag, Heidelberg.
- Lande, R. and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210–1226.
- Lande, R. and D. W. Schemske. 1985. The evolution of self-fertilization and inbreeding depression in plants. I. Genetic models. *Evolution* 39:24–40.
- Larcher, W., U. Heber, and K. A. Santarius. 1973. Limiting temperatures for life functions. In H. Precht, J. C. Christophersen, H. Hensel, and W. Larcher (eds.), *Temperature and life*, pp. 193–231. Springer-Verlag, New York, New York.
- Lee, R. E., G. J. Warren, and L. V. Gusta. 1995. *Biological ice nucleation and its applications*. APS Press, St. Paul, Minnesota.
- Leigh, E. G., Jr., R. T. Paine, J. F. Quinn, and T. H. Suchanek. 1987. Wave energy and intertidal productivity. *Proc. Natl. Acad. Sci. U.S.A.* 84:1314–1318.
- Leopold, A. C., M. J. Jaffe, C. J. Brokaw, and G. Goebe. 2000. Many modes of movement. *Science* 288:2131–2132.
- Leroi, A. M., A. F. Bennett, and R. E. Lenski. 1994. Temperature acclimation and competitive fitness: An experimental test of the Beneficial Acclimation Assumption. *Proc. Natl. Acad. Sci. U.S.A.* 91:1917–1921.
- Levin, D. A. 1978. Some genetic consequences of being a plant. In P. F. Brussard (ed.), *Ecological energetics: The interface*, pp. 189–212. Springer-Verlag, New York, New York.
- Levins, R. 1968. *Evolution in changing environments*. Princeton University Press, Princeton, New Jersey.
- Levins, R. 1969. Thermal acclimation and heat resistance in *Drosophila* species. *Am. Nat.* 103.
- Levitt, J. 1972. *Responses of plants to environmental stresses*. Academic Press, New York.
- Levitt, J. 1980. *Responses of plants to environmental stresses*. Academic Press, New York.
- Lewis, J. R. 1964. *The ecology of rocky shores*. English Universities Press Ltd., London.
- Lewis, J. R. 1986. Latitudinal trends in reproduction, recruitment and population characteristics of some rocky littoral molluscs and cirripedes. *Hydrobiology* 142:1–13.
- Lin, J. J. and G. N. Somero. 1995. Temperature-dependent changes in expression of thermostable and thermolabile isozymes of cytosolic malate dehydrogenase in the eurythermal goby fish *Gillichthys mirabilis*. *Physiol. Zool.* 68:114–128.
- Lutova, M. I. 1995. Thermostability and kinetic properties of enzymes during temperature adaptation in plants. *Russ. J. Plant Physiol.* 42:821–832.
- Never, L., K. D. Scharf, D. Gagliardi, P. Vergne, E. Czarnedcka

- Verner, and W. B. Gurley. 1996. The Hsf world: Classification and properties of plant heat stress transcription factors. *Cell Stress* Chap. 1:215–223.
- Newell, R. C. 1979. *Biology of intertidal animals*. Marine Ecological Surveys Ltd., Faversham, Kent, U.K.
- Niklas, K. J. 1992. *Plant biomechanics—an engineering approach to plant form and function*. University of Chicago Press, Chicago.
- Niklas, K. J. 1997. *The evolutionary biology of plants*. University of Chicago Press, Chicago.
- Patterson, B. D. and D. Graham. 1987. Temperature and metabolism. In D. D. Davies (ed.), *The biochemistry of plants*, pp. 153–199. Academic Press, Inc., San Diego.
- Pitekla, L. F. and J. W. Ashmun. 1985. Physiology and integration of ramets in clonal plants. In R. E. Cook (ed.), *Population biology and evolution of clonal organisms*, pp. 399–435. Yale University Press, New Haven, Connecticut.
- Porter, W. P. and C. R. Tracy. 1983. Biophysical analyses of energetics, time-space utilization, and distributional limits. In R. B. Huey, E. R. Pianka, and T. W. Schoener (eds.), *Lizard ecology: Studies of a model organism*, pp. 55–83. Harvard University Press, Cambridge.
- Ramsey, J. and D. W. Schemske. 1998. Pathways, mechanisms and rates of polyploid formation in flowering plants. *Annu. Rev. Ecol. Syst.* 29:477–501.
- Ray, T. S. 1992. Foraging behaviour in tropical herbaceous climbers (Araceae). *J. Ecol.* 80:189–203.
- Relyea, R. A. 2001. Morphological and behavioral plasticity of larval anurans in response to different predators. *Ecology* 82:541–554.
- Roberts, D. A., G. E. Hofmann, and G. N. Somero. 1997. Heat-shock protein expression in *Mytilus californianus*: Acclimatization (seasonal and tidal-height comparisons) and acclimation effects. *Biol. Bull.* 192:309–320.
- Roth, G. 1986. Neural mechanisms of prey recognition: An example in amphibians. In M. E. Feder and G. V. Lauder (eds.), *Predator-prey relationships: Perspectives and approaches from the study of lower vertebrates*, pp. 42–68. University of Chicago Press, Chicago, Illinois.
- Sabehat, A., D. Weiss, and S. Lurie. 1998. Heat-shock proteins and cross-tolerance in plants. *Physiol. Plant.* 103:437–441.
- Salzman, A. G. 1985. Habitat selection in a clonal plant. *Science* 228:603–606.
- Schlichting, C. D. and M. Pigliucci. 1998. *Phenotypic evolution: A reaction norm perspective*. Sinauer Associates, Inc., Sunderland.
- Somero, G. N. 1995. Proteins and temperature. *Annu. Rev. Physiol.* 57:43–68.
- Somero, G. N., E. Dahlhoff, and J. J. Lin. 1996. Stenotherms and eurytherms: Mechanisms establishing thermal optima and tolerance ranges. In I. A. Johnston and A. F. Bennett (eds.), *Animals and temperature: Phenotypic and evolutionary adaptation*, pp. 53–78. Cambridge University Press, Cambridge.
- Sparks, T. H. and P. D. Carey. 1995. The responses of species to climate over two centuries: An analysis of the Marsham phenological record, 1736–1947. *J. Ecol.* 83:321–329.
- Stanton, M. L. and C. Galen. 1989. Consequences of flower heliotropism for reproduction in an alpine buttercup. *Oecologia* 78:477–485.
- Stevenson, R. D. 1985. The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. *Am. Nat.* 126:362–386.
- Stillman, J. H. and G. N. Somero. 1996. Adaptation to temperature stress and aerial exposure in congeneric species of intertidal porcelain crabs (genus *Petrolisthes*): Correlation of physiology, biochemistry and morphology with vertical distribution. *J. Exp. Biol.* 199.
- Sultan, S. E. 1987. Evolutionary implications of phenotypic plasticity in plants. *Evol. Biol.* 21:127–178.
- Sultan, S. E. 2001. Phenotypic plasticity for fitness components in *Polygonum* species of contrasting ecological breadth. *Ecology* 82:328–343.
- Sultan, S. E. and F. A. Bazzaz. 1993. Phenotypic plasticity in *Polygonum persicaria*. I. Diversity and uniformity in genotypic norms of reaction to light. *Evolution* 47:1009–1031.
- Teeri, J. A. 1980. Adaptation of kinetic properties of enzymes to temperature variability. In N. C. Turner and P. J. Kramer (eds.), *Adaptation of plants to water and high temperature stress*, pp. 251–260. John Wiley & Sons, New York.
- Tollrian, R. and C. D. Harvell. 1999. *The ecology and evolution of inducible defenses*. Princeton University Press, New Jersey.
- Tomanek, L. and G. N. Somero. 1999. Evolutionary and acclimation-induced variation in the heat-shock responses of congeneric marine snails (genus *Tegula*) from different thermal habitats: Implications for limits of thermotolerance and biogeography. *J. Exp. Biol.* 202:2925–2936.
- Tsuchiya, M. 1983. Mass mortality in a population of the mussel *Mytilus edulis* L. caused by high temperature on rocky shores. *J. Exp. Mar. Biol. Ecol.* 66:101–111.
- Went, F. W. 1957. *The experimental control of plant growth*. Ronald Press, New York.
- Wetley, D. S. 1984. Sun and shade mediate competition in the barnacles *Chthamalus* and *Semibalanus*: A field experiment. *Biol. Bull.* 167:176–185.
- Withers, P. C. 1992. *Comparative animal physiology*. Saunders College Publishing, New York.