

NOTES AND COMMENTS

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IS A JACK-OF-ALL-TEMPERATURES A MASTER OF NONE?

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The relative evolutionary advantage of generalized versus specialized phenotypes is a central issue in organismal biology. Most theoretical models in this area make the appealing, but largely intuitive, assumption that a "jack-of-all-trades is a master-of-none." In other words, the ability to perform a broad variety of tasks can be achieved only at the sacrifice of maximal performance. Often considered as a corollary of the Principle of Allocation (Levins, 1968), this assumption of trade-offs has been widely applied (MacArthur, 1972; Huey and Slatkin, 1976; Pianka, 1978) but rarely tested (Strickler, 1979; Mitter and Futuyma, 1983; Webb, 1983) by evolutionary ecologists and morphologists.

In ectotherms, body temperature influences the performance of many important physiological systems such as locomotion, digestion, and growth (Brett, 1971; Fry, 1971; Dawson, 1975; Huey and Stevenson, 1979; Huey, 1982). The ecological, physiological, and behavioral consequences of this thermal sensitivity are important (Park, 1954; Christian and Tracy, 1981; Hertz et al., 1982; Huey, 1982).

The Principle of Allocation can be readily applied to thermal physiology: an individual that performs well (relative to other individuals) in its optimal temperature zone should perform relatively poorly at non-optimal temperatures (Huey and Slatkin, 1976 Fig. 1a). Ectotherms that perform well over a narrow versus a broad range of temperatures can be classified as thermal specialists and generalists, respectively (Fig. 1a). The assumption here of trade-offs is appealing because thermodynamic constraints on enzyme structure probably hinder the evolution of molecules that function well over a broad range of temperatures (Somero, 1978; Heinrich, 1981; but see below).

An alternative pattern of thermal sensitivity can be imagined: an individual that performs relatively well at its optimal temperature might in fact perform relatively well at all other temperatures (Fig. 1b; see Mitter and Futuyma, 1983). The occurrence of such a pattern would clearly contradict the Principle and suggest that a "jack-of-all-temperatures is a master of all."

Knowing which of the patterns in Figure 1 best describes phenotypes is of considerable interest. The extreme scenarios can be distinguished by measur-

ing the performance of individuals at a variety of temperatures and then determining whether the rank order for performances of different individuals either changes (as in Fig. 1a) or remains constant (Fig. 1b) at different body temperatures.

Here we present a test of the Principle of Allocation as it applies to thermal biology by deter-

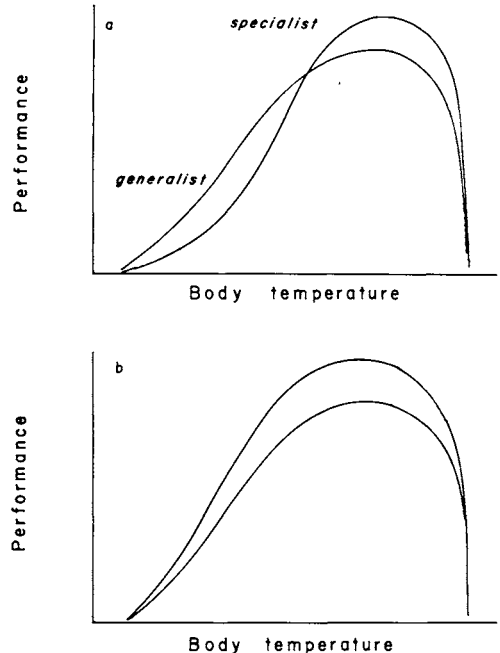


FIG. 1. Hypothetical performance curves of ectotherms as function of body temperature. (a) Example predicted from the Principle of Allocation, involving a tradeoff between maximum performance and breadth of performance. The categories "specialist" and "generalist" are not discrete but are endpoints on a continuum. (b) Example contradicting the Principle, in which traits that promote performance at one temperature promote performance at all temperatures.

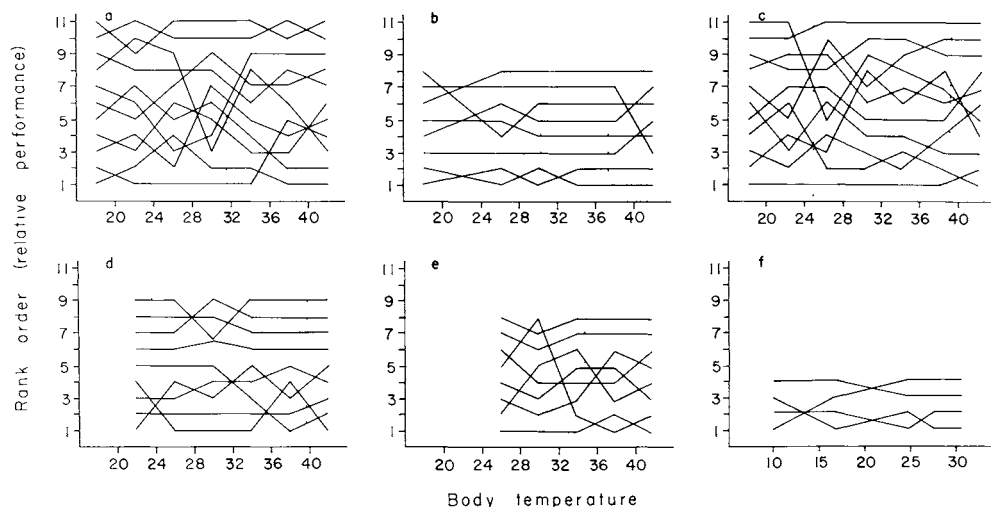


Fig. 2. Rank order is positively correlated across temperature intervals for relative running performance of individual agamid lizards (a–e, all $P < .001$) and for multiplication rates of clones of *Amoeba* (f, $P < .05$). (a) represents *Stellio stellio* from 170 m (Kendall coefficient of concordance = .761), (b) *S. stellio* from 530 m ($W = .852$), (c) *Stellio stellio* from 920 m ($W = .791$), (d) = *S. stellio* from 1,500 m ($W = .846$), and (e) *Agama savignyi* from 330 m ($W = .689$). Vertical dotted lines delimit the maximum and minimum activity temperatures of lizards in nature (from Hertz and Nevo, 1981): Kendall coefficients for the activity temperature ranges are .927, .989, .833, .871, and .929, respectively. *Agama savignyi* generally do not run at low body temperature (see Hertz et al., 1982).

mining which of the two patterns in Figure 1 best describes patterns in the thermal sensitivity of locomotor performance of lizards (*Stellio stellio*, *Agama savignyi*; Hertz et al., 1983) and of the multiplication rates of protozoans (*Amoeba*; Sopina, 1976). The relative performance of an individual at ecologically important tasks such as locomotion (Webb, 1976; Christian and Tracy, 1981) should correlate with fitness (see Arnold, 1983).

We first examine data on the thermal sensitivity of sprint speed in some agamid lizards from Israel. In a previous analysis, we examined the correspondence between geographic variation in the thermal environment and in the thermal sensitivity of locomotion in five populations of *Stellio* and *Agama* (Hertz et al., 1983). Using data from that analysis, we have now determined absolute speeds of each lizard at the following temperature levels: 18, 22, 26, 30, 34, 38, and 42 C. Because body size influences absolute speed in *Stellio* (Huey and Hertz, 1982), we then calculated the relative speed of each individual at each temperature by analyzing the residuals in regressions involving log speed versus log body mass (see Harvey et al., 1980).

Data on the thermal sensitivity of locomotor performance of agamid lizards are inconsistent with predictions based on the Principle of Allocation (Fig. 1a) but strongly support the alternative hypothesis that a jack-of-all-temperatures is a master

of all (Fig. 1b). Overall, the rank orders of relative running performance are highly correlated across temperature (Kendall coefficients of concordance, all $P < .001$) for all four populations of *S. stellio* and for *A. savignyi* (Fig. 2a–e). Thus lizards that run quickly at one temperature tend to run quickly at all temperatures, as in Figure 1b. This pattern is even stronger if the analysis is restricted to ecologically relevant temperatures (Feder, 1978; Huey, 1982)—that is, to the range of actual activity temperatures of lizards in nature (vertical dotted lines in Fig. 2). Using a similar analysis, but for different purposes and without correcting for body size, Bennett (1980) found a parallel trend for running performance of several species of lizards from other families.

Published data on the thermal sensitivity of multiplication rates of several species of amoebae (Sopina, 1976) were also inconsistent with the Principle of Allocation, suggesting that our results may have some generality. Rank order of multiplication rates for a clone (from Fig. 2 of Sopina, 1976) at different temperatures remains correlated across temperature intervals (Fig. 2f, $P < .05$), as in Figure 1b. (Body sizes were unspecified in Sopina [1976], so these patterns are not corrected for potential size effects.)

These analyses fail to demonstrate a tradeoff between maximal performance and thermal general-

ization. In fact, the results are the opposite of those expected: a "jack-of-all-temperatures" seems to be a "master of all." We suggest several alternative interpretations for the apparent positive relationship between maximum performance and breadth of performance:

(1) The Principle of Allocation could be an important evolutionary constraint on thermal physiology, but its influence could be difficult to detect in phenotypic comparisons of individual organisms. Some individuals might simply run faster than others because of differences in health, condition, or motivation; and such developmental influences could mask an inverse (but relatively weak) relationship between maximum performance and breadth of performance. (Nevertheless, the effects of the Principle might be detectable with inter-specific comparisons, where developmental influences might be less influential [S. C. Stearns, pers. comm.].) This general rationale might conceivably account for the data on lizard locomotion (Bennett, 1980; herein), but it is unlikely to explain the data on multiplication rates of amoebae (Sopina, 1976). Clones, not single individuals, were used to generate multiplication rates of amoebae.

(2) The Principle of Allocation could be an important evolutionary constraint on thermal physiology, but it involves trade-offs between different dimensions rather than within a single dimension. For example, traits that promote speed in the optimal temperature zone could actually promote speed at other temperatures (Fig. 1b), but at the sacrifice of the performance of other physiological dimensions (such as endurance). This line of reasoning is conceptually similar to the concept of antagonistic pleiotropy, which describes the effects of genes having positive effects on some traits but negative effects on other traits (Rose, 1982). We cannot evaluate our data with respect to this explanation, and we note that this hypothesis may in general be difficult to test—if only because the variety of physiological dimensions that could be involved is large.

(3) The Principle of Allocation could be an unimportant or nonexistent constraint on evolution, at least with respect to the animals and physiological traits considered here. Enzymes with histidine residues are in fact relatively insensitive to temperature (Reeves, 1977), suggesting that the evolution of thermally generalized enzymes is sometimes possible (Hochachka and Somero, 1973); but whether such enzymes are inefficient is unclear. Moreover, organismal traits that promote maximal performance at one temperature might in fact have positive effects on performance at other temperatures. For example, morphological traits (such as limb proportions, distribution of muscle fiber types) that enhance speed at one temperature could simultaneously enhance speed at other temperatures. Thus even if the Principle operates at the biochemical level of physiology, its effect on phenotypic performance might be masked by compensatory adaptations at higher levels of physiological organization (Mitter and Futuyma, 1983).

Our data constitute a phenotypic but not a genetic test of the Principle of Allocation as applied to thermal biology. A genetic test (S. J. Arnold, pers. comm.) would involve determining the genetic covariance between maximum performance and breadth (see Falconer, 1982). The general approach we have developed here might be useful in such an analysis, and perhaps this challenge to the universality of the Principle of Allocation might prompt such needed studies.

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ALLOZYMES AND SONG DIALECTS: A REASSESSMENT

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The hypothesis that song dialects act as barriers to gene flow, promoting genetic differentiation among bird populations with different dialects, has received intensive study (Marler and Tamura, 1962; Nottebohm, 1969; Nottebohm and Selander, 1972; Baker, 1974, 1975, 1982a, 1982b; Baptista, 1975; Baker and Mewaldt, 1978, 1981; Payne, 1981; Petrinovich et al., 1981). Several hypotheses have been advanced to explain the origin of song dialects (review in Payne, 1981). For example, Baker (1975) and Baptista (1975) suggested that young white-

crowned sparrows (*Zonotrichia leucophrys*) colonize vacant habitats before completion of song learning, and that these colonists acquire a different song, or dialect. Positive assortative mating would then insure the genetic integrity of the dialect group, and possibly maintain local adaptation when and if dialect groups come into contact (Nottebohm, 1970). Jenkins (1982a) proposed that male saddlebacks (*Philesturnus carunculatus*) dispersed to demes with different song dialects, thereby effecting outbreeding through negative assortative mating (see