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INDIVIDUAL-LEVEL SELECTION AS A CAUSE OF COPE'S RULE OF PHYLETIC SIZE INCREASE

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Abstract.—Cope's rule, the tendency for species within a lineage to evolve towards larger body size, has been widely reported in the fossil record, but the mechanisms leading to such phyletic size increase remain unclear. Here we show that selection acting on individual organisms generally favors larger body size. We performed an analysis of the strength of directional selection on size compared with other quantitative traits by evaluating 854 selection estimates from 42 studies of contemporaneous natural populations. For size, more than 79% of selection estimates exceed zero, whereas for other morphological traits positive and negative values are similar in frequency. The selective advantage of increased size occurs for traits implicated in both natural selection (e.g., differences in survival) and sexual selection (e.g., differences in mating success). The predominance of positive directional selection on size within populations could translate into a macroevolutionary trend toward increased size and thereby explain Cope's rule.

Key words.—Body size evolution, directional selection, macroevolution, microevolution, natural selection, selection gradient, sexual selection.

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An organism's size impacts nearly every aspect of its biology, from its physiology to its ecology and evolution (reviewed in Peters 1983; LaBarbera 1986; Bonner 1988). Because of the biological significance of body size, many studies have explored selection and microevolution on size in contemporaneous populations in nature (reviewed in Blanckenhorn 2000). These studies illustrate a diversity of types of selection and microevolution in size, including directional selection favoring increased size (Bumpus 1899) or decreased size (Reznick et al. 1990), temporal fluctuations in the direction of selection (Gibbs and Grant 1987), and stabilizing selection towards intermediate size (Karn and Penrose 1951). However, general patterns or tendencies in the direction of selection on size in natural populations have not been explored.

Understanding if and how selection generally acts on individual body size is important for explaining macroevolutionary trends. Among the most pervasive patterns in the history of life is a tendency for species within a lineage to evolve toward larger body size, a pattern known as Cope's rule (Cope 1896; Benton 2002). Cope's rule has been documented in diverse plant and invertebrate and vertebrate animal taxa (Newell 1949; Hallam 1975; Chaloner and Sheerin 1979; Bonner 1988; McFadden 1992; Alroy 1998; McShea 1998; Benton 2002; for exceptions to Cope's rule, see Lomolino 1985; Arnold et al. 1995; Jablonski 1997; Dommergues et al. 2002; Knouft and Page 2003). Although Cope's rule is often ascribed to the putative selective advantages accruing to larger individuals (Brown and Maurer 1986; Bonner 1988; Hallam 1990), its causes remain unclear and subject to contention (Stanley 1973; Gould 1997; Benton 2002). Thus, whether bigger individuals are generally fitter and whether any such individual-level selective advantage of larger size can potentially explain the trends toward increased body size observed in many fossil lineages remains unclear.

Here we use a recently compiled database of phenotypic selection studies (Kingsolver et al. 2001) to compare the strength of directional selection on size and on other morphological traits within natural populations. We asked two questions. First, are there any general tendencies related to selection on size within natural populations? Second, could individual-level selection provide a mechanism for Cope's rule?

MATERIALS AND METHODS

A recent study (Kingsolver et al. 2001) synthesized published estimates of phenotypic selection in the field (database available at http://www.bio.unc.edu/faculty/kingsolver/lab/). Criteria for inclusion were (1) natural variation in quantitative traits within each study population, (2) measurements of fitness in natural field conditions, and (3) estimation of selection in terms of standardized selection differentials or gradients. Linear selection gradients (β) are particularly useful measures of the strength of directional selection (Lande and Arnold 1983). Selection gradients are directly related to the evolutionary response to selection in models for the evolution of quantitative traits (Lande 1979; Lande and Arnold 1983; Arnold and Wade 1984). The linear selection gradient β relates variation in the trait (in units of standard deviation of the trait) to variation in relative fitness w; thus β provides a standardized metric of directional selection that facilitates comparisons among different traits and study systems. In addition, β indicates selection directly on the trait of interest, controlling statistically for indirect selection due to correlated traits (Lande and Arnold 1983); this is important here because size is often correlated with many other phenotypic traits (Gould 1977).

In our analysis we considered estimates of directional selection gradients (β) for morphological traits or for combinations of morphological traits (e.g., resulting from principal components analyses). Each author independently classified the estimates into two categories, based on the trait names in the database: Overall Size traits, for traits that represent

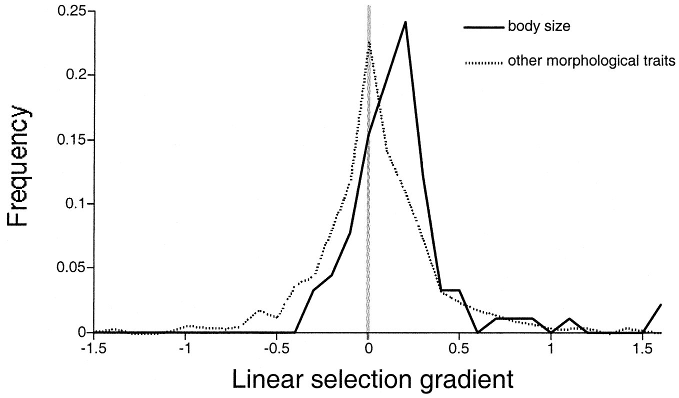

FIG. 1. Frequency distributions of linear selection gradients (β) for size and for other morphological traits. Values were binned at intervals of 0.05. Values of β for size are significantly greater than those for other morphological traits (Wilcoxon rank sum test: $Z = 4.4001$, $P < 0.0001$).

indicators of overall size (e.g., body length, plant height, body mass, total biomass); and Other Morphological traits. In our analyses traits that indicate size of body components (e.g., wing length, flower height, leg length, etc) were classified as Other Morphological traits; thus our analyses are likely to be conservative. In each analysis we use nonparametric statistics (one-tailed Wilcoxon rank-sum test) to compare β estimates for Overall Size compared with Other Morphological traits.

For studies that estimated selection on both size and other morphological traits within the same study, we use the median value of β over all traits and time periods within each study, separately for size traits and for all other morphological traits. In one case, data from two different publications by the same principal authors represented selection estimates for the same study populations, the same time periods, and the same traits; these data were combined and considered as a single study in our analysis. We compared paired values of the median β for size trait and for other morphological traits for each study using a one-tailed Wilcoxon signed-rank test.

RESULTS

The database used in the present analyses contained 854 estimates of β involving morphological traits, representing 39 species from 42 studies (Kingsolver et al. 2001). The traits were classified as representing either aspects of overall size ($n = 91$ estimates, for 23 species in 24 studies) or other morphological traits ($n = 763$ estimates, from 35 species in 38 studies).

Frequency distributions of β for size and for other morphological traits reveal a striking pattern (Fig. 1). The distribution of β for other morphological traits is symmetric about zero, with 50% of the values greater than zero, and a median value of 0.02. This is not surprising, because one would not expect a consistent bias in the direction of selection for arbitrary quantitative traits (Kingsolver et al. 2001). By contrast, the distribution of β for overall size is strongly shifted to positive values: 79% of the values are greater than zero, and the median β is 0.15. Values of β for size are significantly greater than those for other morphological traits (Wilcoxon rank sum test: $Z = 4.4001$, $P < 0.0001$). If we restrict our analysis to studies that estimated selection on both size and other morphological traits within the same study (20 studies), a similar pattern emerges. For example, the median β for size is 0.15, and 80% of the β values are greater than zero ($n = 83$ estimates); whereas the median β for other morphological traits is 0.04, and 57% of the β values are greater than zero ($n = 363$ estimates). For this subset of studies, values of β for size are again significantly greater than those for other morphological traits (Wilcoxon rank sum test: $Z = 3.0759$, $P < 0.0001$). If we pair median β values for size and for other morphological traits for each study that measured selection on both, we again find that median β values for size are greater than median β values for other traits (Wilcoxon signed-rank test: $V = 151$, $n = 20$ studies, $P = 0.048$).

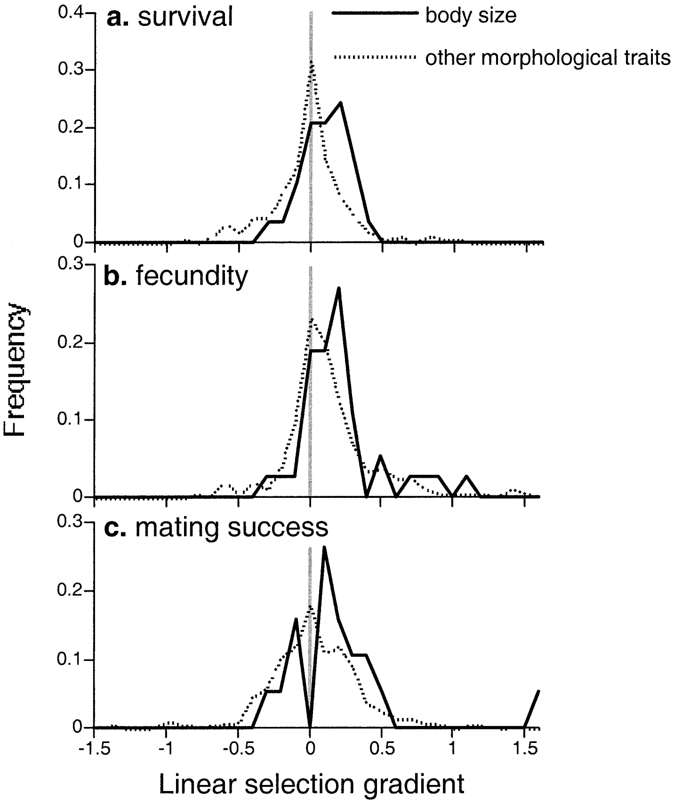

FIG. 2. Frequency distributions of linear selection gradients (β) for size and for other morphological traits for traits related to (a) survival, (b) fecundity, (c) mating success. In each case, values of β for size are significantly greater (Wilcoxon rank sum tests) than those for other morphological traits (survival: $Z = 3.16$, $P = 0.0008$; fecundity: $Z = 1.8868$, $P = 0.0296$; mating success: $Z = 1.9897$, $P = 0.0466$). Values were binned at intervals of 0.05. The bimodality in graph (c) is likely an artifact of binning.

This qualitative pattern of selection on size and other traits also holds for different taxonomic groups (e.g., invertebrates, plants, and vertebrates), and for different components of fitness (e.g., survival, fecundity, or mating success; Fig. 2). Thus, values of β for size are significantly greater than those for other morphological traits for selection due to differences in survival (Wilcoxon rank sum test: $Z = 3.16$, $P = 0.0008$), differences in fecundity ($Z = 1.8868$, $P = 0.0296$), and differences in mating success ($Z = 1.9897$, $P = 0.0466$). For example, the median β for viability selection (selection due to differences in survival) on size is 0.08, with 76% of the values greater than zero ($n = 29$ estimates); whereas for viability selection other morphological traits the median β is −0.01, with 47% of the values greater than zero ($n = 193$). Similarly, the median β for sexual selection (selection due to differences in mating success) on size is 0.13, with 74% of the values greater than zero ($n = 19$ estimates); whereas for sexual selection other morphological traits the median β is 0.02, with 53% of the values greater than zero ($n = 366$).

Discussion

Unlike the pattern of selection on other quantitative traits (Hoekstra et al. 2001; Kingsolver et al. 2001), there is a strong bias towards positive directional selection for overall size. We found that bigger size is associated with higher fitness in most natural populations that have been studied (Fig. 1) and that both natural and sexual selection generally favor increasing size (Fig. 2). Moreover, the above patterns hold within as well as across studies: when we restricted our analysis to studies that estimated selection on both size and other morphological traits in the same organism, we found that the strength of selection on size was greater than that for other morphological traits (see Results). Thus, our results are not likely to be an artifact of the particular species studied or of the particular methods employed to quantify selection in our dataset.

Although the pattern we observed is not an artifact of the particular species or study method used, several potential biases occur in these data. First, the studies used in our analysis were weighted heavily toward birds, plants, and insects; taxa such as mammals were poorly represented. Such taxonomic biases may be important if different taxa tend to experience different forms of selection on body size. For example, certain mammalian lineages appear to evolve toward *smaller* body size on islands (Lomolino 1985; Brown 1995). Second, most studies used in our analysis estimated selection for only a single component of fitness. More integrated measures of fitness, in which multiple components are evaluated, could reveal counter selection against body size (see below). Finally, several sources of bias may affect estimates of selection gradients. For example, study systems and traits are not chosen at random, and publication bias may exclude studies with small sample sizes or nonsignificant results; these effects will tend to inflate our estimates of the strength of selection compared with ''randomly'' chosen traits or study systems. Conversely, measurement error will reduce the estimated magnitude of the selection gradients (Kingsolver et al. 2001). Despite these potential biases in the dataset, it is not clear how any of the above factors could have generated the observed different patterns of selection on size compared with other morphological traits (Fig. 1, 2).

Our results clearly indicate consistent directional selection favoring larger size in many study systems. Generally, opposing selective forces are thought eventually to counterbalance selection for larger size. Although cases of directional selection favoring decreased size (Reznick et al. 1990) and temporal fluctuations in the direction of selection on size have been observed (Gibbs and Grant 1987), selection for decreased size was uncommon at best in our analysis, and the pattern of selection that we observed is not consistent with alternating selection (Fig. 1). Similarly, individual cases of stabilizing selection on body size have been observed (Karn and Penrose 1951). Demonstrating such stabilizing selection toward intermediate size requires information about both directional and quadratic components of selection on body size (Lande 1983). Only a few studies in our database estimated both directional (β) and quadratic (γ) selection gradients for overall size (a total of 30 joint estimates of β and γ). The majority (80%) of these γ estimates are negative, but in combination with the β estimates these are not consistent with stabilizing selection towards the population mean phenotype in most cases. Thus, individual level selection on size does not appear to be the primary mechanism preventing organisms from evolving toward larger size.

Another factor that may constrain evolution of larger size is opposing selection on traits that are genetically correlated with body size. Development time is a key trait that is often positively correlated with body size but which may be under opposing selection. Unfortunately, only a handful of studies have simultaneously measured selection on both size and development time in the same study system (Kingsolver et al. 2001). Nevertheless, we examined whether selection for decreased development time opposes selection for increased size by using the available estimates of selection on life-history and phenological traits (Kingsolver et al. 2001). We divided these estimates into two categories: Development Time, for traits associated with age or time to adulthood, maturity, or reproduction; and Other Life History (LH) traits, for the remaining life-history and phenological traits. There are many fewer values than for size and other morphological traits, with 32 estimates of β (from seven studies) for Development Time and 96 estimates of β (from 12 studies) for Other LH traits. Moreover, the majority of available estimates for Development Time (69%) and Other LH traits (59%) are for plants. However these limited data reveal a clear pattern: estimates for Other LH traits are symmetric about zero, with a median of 0.01 and 46% of the estimates less than zero, whereas estimates for Development Time are shifted towards negative values, with a median of −0.145 and 84% of the estimates less than zero. Thus, these limited data suggest that consistent selection for increased size may sometimes be opposed by consistent selection for decreased development time, resulting in no evolutionary change in size. How frequently, or in what taxa or ecological conditions, selection for decreased developmental time opposes selection for larger size remains unclear.

Given the predominance of positive directional selection on size within populations (Fig. 1, 2), why is larger size selectively advantageous? Larger size may be advantageous in prey capture or predator escape (Benton 2002), resource competition (Bonner 1988) and utilization (Brown and Maurer 1986), resistance to extreme environmental conditions (Peters 1983), fecundity (Andersson 1994), and competition for mates (Andersson 1994). In combination with genetic variation in size (Mousseau et al. 2000), positive directional selection for overall size would tend to generate microevolutionary increases in mean size within populations and species. Indeed, a selection gradient of 0.15 (the median value for β in our analysis) for a trait with a moderate heritability of 33.3% would generate an evolutionary increase in the mean size within a population by 0.05 standard deviations in a single generation (=0.05 haldanes; Gingerich 1993). An evolutionary rate of 0.05 haldanes falls well within the range of estimated rates of microevolution of quantitative traits, including body size, in a variety of systems (Hendry and Kinnison 1999).

The predominance of positive directional selection on size of individuals within populations, if unopposed, could also translate into a macroevolutionary trend toward increased size of an entire lineage. The evolutionary rate of 0.05 haldanes calculated above, if extrapolated over evolutionary time, could account for a substantial increase in the size of a lineage. Directional selection of this magnitude, if applied continuously, would increase the mean size of individuals in a population by five standard deviations in only 100 generations—an evolutionary shift far beyond the original range of phenotypic variation in size in the original population. Such rapid evolution, if extrapolated over long periods of time, could easily explain observed patterns of phyletic size increase in fossil lineages. In fossil horses, for example, mean body size (as estimated by the size of the first molar tooth) increased by about 10% per million years or per 500,000 generations (McFadden 1992). Because coefficients of variation (standard deviation/mean) for these characters are on the order of 5–10% (McFadden 1992), this represents an evolutionary change of only 1–2 standard deviations per 500,000 generations. Over this same time period, direction selection of the magnitude measured in our analysis would transform a lineage's size by 25,000 standard deviations (rates of evolution calculated from fossil data are generally much lower than those calculated from contemporary populations owing to time-averaging; Gingerich 1983). Thus, positive directional selection on body size seen in contemporaneous populations is more than potent enough to explain phyletic size increase observed in the fossil record (for similar examples illustrating how quantitative genetic estimates in extant taxa correspond to the tempo and mode of evolution observed in the fossil record, see Lande 1976, 1979).

Our results therefore potentially explain Cope's rule, the tendency for species within a lineage to evolve toward larger body size. Cope's rule has been ascribed to many causes, including individual selective advantages of being large (Brown and Maurer 1986; Bonner 1988; Hallam 1990), clade selection (Stanley 1973), and statistical artifact (Gould 1997). Our data suggest that bigger individuals are fitter and demonstrate how a microevolutionary process (individual-level selection for larger body size) can potentially explain a macroevolutionary pattern (a tendency for lineages to evolve toward larger body size).

Given our evidence that selection generally favors larger size, why are many extant taxa not at their maximum size (e.g., see Bonner 1988)? Extinction may ultimately prevent organisms from evolving toward larger size (Bonner 1988; Brown 1995). Indeed, mass extinctions often appear to be size selective, such that larger individuals are more vulnerable (Bakker 1977; Martin 1984; LaBarbera 1986; Arnold et al. 1995). For example, although dinosaurs and rudist bivalves went extinct during the end-Cretaceous mass extinction, and large mammals (mammoths, mastodons, giant slots) disappeared during the end-Pleistocene mass extinction, smaller phylogenic relatives living in the same environments with the above taxa survived these events (but see Jablonski and Raup 1995; Jablonski 1996). Presumably, the larger an organism, the greater its resource requirements become, and limiting resources may contribute to extinction (Bonner 1988). Thus, mass extinction may help explain why organisms remain relatively small in the face of individual-level selection for larger body size.

Finally, an additional reason why many extant taxa may not be at their maximum size is because, as mentioned above, selection for decreased development time may often oppose selection for increased size, resulting in an absence of evolutionary change in size. Indeed, different taxa might vary in the relative strength of selection on size versus selection on development time, and such variation may explain why Cope's rule has been documented in some taxa but not in others. In particular, in taxa such as mammals in which Cope's rule apparently holds (Alroy 1998), selection for increased size may predominate over selection for decreased development time, whereas in taxa such as Cretaceous molluscs in which Cope's rule apparently does not hold (Jablonski 1997), selection for decreased development time may offset selection for increased size. Future studies are needed to determine whether the relative strength of selection on size versus selection on development time varies across taxa, and whether any such variation can explain why Cope's rule appears to hold in some systems but not in others.

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