

TESTING SYMMORPHOSIS: DOES STRUCTURE MATCH FUNCTIONAL REQUIREMENTS?

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"Symmorphosis" proposes that biological design will be optimized, such that each structural element in a functional chain matches the maximal requirements of the overall functional system. Taylor and Weibel (1981 p. 3) defined this principle "as a state of structural design commensurate to functional needs resulting from regulated morphogenesis, whereby the formation . . . of structural elements is regulated to satisfy but not exceed the requirements of the functional system." They considered symmorphosis to be "a rather general principle of regulated economical construction which should apply to all levels of biological organization" and suggested that it may serve as a unifying principle for anatomy, as homeostasis has done for physiology (Taylor and Weibel, 1981 p. 3). Calder (1984) argued further that symmorphosis may provide a theoretical basis for scaling relationships (but see Heusner [1983]). Although Weibel and Taylor's (1981) initial empirical test (see below) was contradictory, symmorphosis has attracted considerable attention and is becoming established in the secondary literature (Calder, 1984; Schmidt-Nielsen, 1984; Weibel, 1984b).

Symmorphosis was motivated by Taylor and Weibel's (1981 p. 3) "firm belief that animals are built reasonably" and their conviction that "structural design is optimized," because "maintaining biological structures with their often high turnover rates is costly." The principle is thus philosophically related to optimality arguments and may have widespread appeal (e.g., Rosen, 1968; Maynard Smith, 1978; Alexander, 1982). However, the validity of optimality criteria in evolutionary biology has been challenged (e.g., Gould and Lewontin, 1979; Lewontin, 1979; Bernstein, 1984), and one may wonder whether "symmorphosis" is a likely evolutionary outcome. Certainly, structures and functional capacities are matched to some extent (Olson and Miller, 1958; Alexander, 1975; Frazzetta, 1975), but how close is this matching, and is structural design optimized?

For an initial empirical test of symmorphosis, Weibel and Taylor focused on the mammalian respiratory system. They predicted that "the structural design of the respiratory system should . . . be matched to the functional requirements," with "the structural design (being) a rate-limiting factor for O₂ flow at each level," and "no excess capacity at any organizational level" (Weibel and Taylor, 1981 pp. 3, 152). In other words, no *single* component should constitute a rate-limiting step.

Weibel and Taylor (1981) measured maximal functional capacity of the respiratory system as $\dot{V}O_{2\max}$,

the maximal rate of O₂ consumption attained during exercise of progressively increasing intensity. $\dot{V}O_{2\max}$ sets an upper limit to the intensity of work (e.g., running speed) that can be sustained aerobically for prolonged periods, and hence should be of considerable selective importance (Bennett et al., 1984; Garland, 1987). Weibel and Taylor measured several structural indices, emphasizing a morphometric estimate of pulmonary diffusing capacity (DLO₂), but also quantifying the distribution of mitochondria and capillaries in various muscles.

Weibel and Taylor proposed two comparative tests of symmorphosis. First, for animals differing in size, the scaling of respiratory structures should parallel the scaling of maximal oxygen consumption. Second, for animals of similar size, differences in structural capacities should match differences in $\dot{V}O_{2\max}$. Weibel and Taylor (1981) formally tested only the first approach and found that structure and function did not scale congruently. Weibel and Taylor (1981 pp. 62, 154) mentioned comparisons of similar-sized pairs of species (e.g., horses versus cows; see also Weibel, 1984a, 1984b), but did not explicitly test the second approach; we do so herein.

Our new test of the principle uses Weibel and Taylor's (1981) original data plus some published subsequently (Weibel et al., 1983) and focuses on interspecific variation about allometric equations. We find few positive correlations between structural indices (e.g., DLO₂) and maximal functional requirements ($\dot{V}O_{2\max}$). Thus, our analysis also contradicts symmorphosis. We therefore reconsider the utility of symmorphosis as an evolutionary principle and conclude that such "optimal design" may be an unlikely evolutionary outcome.

MATERIALS AND METHODS

Weibel and Taylor (1981) published data on both $\dot{V}O_{2\max}$ and pulmonary diffusing capacity (DLO₂) for 12 species of viverrids and bovids, and subsequently, Weibel et al. (1983) published similar data for four canids. We analyzed species means to promote statistical independence among values (Clutton-Brock and Harvey, 1984; Felsenstein, 1985). To test correspondence of structure and function, we first removed the confounding effects of body size by log₁₀ transforming all characters and computing residual deviations from least-squares linear regressions (allometric equations) of each character on body mass (Clutton-Brock and Harvey, 1984; Garland, 1984). We then asked whether species with a high $\dot{V}O_{2\max}$ for their size also have a relatively high DLO₂? If symmorphosis is correct, the residuals should be positively correlated.

A digression concerning our use of least-squares regressions is necessary (see Rayner [1985] for a recent

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review). One assumption of least-squares regression analysis is that the independent variable is measured without error (i.e., the ratio of the error variance in the dependent variable to the error variance in the independent variable equals infinity). Obviously, this cannot be true in any study employing body mass as the independent variable. Error in independent variables leads to underestimation of true slopes. Thus, some might have preferred us to use a different regression model (review in Rayner [1985]), such as the reduced major axis (RMA). RMA slopes can be calculated as the ratio of standard deviations or, equivalently, the regression slope divided by the correlation coefficient, and, hence, these are always greater than regression slopes (unless r is unity).

Unfortunately, as noted by Kuhry and Marcus (1977 p. 204), RMA also makes an assumption about error variances, namely that the ratio of error variances is proportional to the ratio of total variances. For $\log_{10}(\dot{V}O_2\text{max})$ and $\log_{10}(\text{body mass})$ ($N = 16$; see Results), the ratio of total variances is $0.437/0.631 = 0.693$. Thus, for the assumption inherent in RMA analysis to hold, the error variance in body mass would have to be greater than that in $\dot{V}O_2\text{max}$. This seems highly unlikely, because body mass can usually be measured quite precisely, as compared with errors inherent in measurements of $\dot{V}O_2\text{max}$, DLO_2 or the other morphometric variables analyzed herein (see Weibel and Taylor, 1981). Using regression also seems appropriate because we wished to remove correlations with body mass, and the regression line is the only line that minimizes vertical deviations of the independent variable about the line. Moreover, regression slopes are employed in analysis of covariance. In summary, we favor regression analysis for the present applications (see also Garland [1984, 1985]). Nevertheless, we repeated all computations of allometric equations, residuals, and subsequent correlation analyses using RMA equations. In no case did the results change qualitatively. We present both regression and RMA slopes for allometric equations but present only the residual analyses based on least-squares regression equations.

RESULTS

Using the enlarged data set of 16 species, we first repeated Weibel and Taylor's (1981) scaling test. For these species (body mass $[M] = 0.5\text{--}232$ kg), $\dot{V}O_2\text{max}$ scales as $2.28M^{0.787}$ ($r^2 = 89.6\%$, $P < 0.0001$; Fig. 1A), but pulmonary diffusing capacity scales as $0.0471M^{1.025}$ ($r^2 = 98.7\%$, $P < 0.0001$; Fig. 1B). These slopes are statistically indistinguishable from those presented originally for 12 species (Weibel and Taylor, 1981). As Weibel and Taylor noted, the slope for DLO_2 is significantly greater than that for $\dot{V}O_2\text{max}$, which contradicts predictions of symmorphosis. (RMA slopes are 0.832 for $\dot{V}O_2\text{max}$ and 1.032 for DLO_2 . Clarke's [1980] test comparing these yields $t = 2.52$, $d.f. = 13.01$, $0.05 > P > 0.02$.)

Next we examined the full data set for interfamilial patterns. Significant differences in $\dot{V}O_2\text{max}$ among families, with corresponding differences in DLO_2 , would be consistent with symmorphosis. Such is not the case. Rather, canids have a significantly higher $\dot{V}O_2\text{max}$ than either bovids or viverrids (Fig. 1A), but their DLO_2 is not correspondingly higher (Fig. 1B). The $\dot{V}O_2\text{max}$ of

viverrids is also marginally higher ($P = 0.06$) than that of bovids, but their DLO_2 is not.

Finally, we considered interspecific variation about allometric equations. (The residuals generated showed neither significant departures from normality [Kolmogorov-Smirnov tests] nor heteroscedasticity.) Figure 1C plots residual $\dot{V}O_2\text{max}$ versus residual DLO_2 . Given symmorphosis, a significant positive correlation is expected; such is not the case. Because phylogeny may confound such comparisons (review in Huey [1987]), we repeated these residual analyses for the nine Bovidae ($r = -0.054$) and four Canidae ($r = 0.981$) separately. The latter correlation is statistically significant, but should be viewed with caution because only four species are involved and because a Spearman rank-order correlation ($r_s = 0.400$) is insignificant.

Weibel and Taylor (1981 pp. 138–139) also provided data on volume densities of mitochondria and number of capillaries per mm^2 cross-sectional area of muscle for four muscles in 12 species. The former should index tissue capacities for aerobic production of ATP; the latter is an index of capacities for oxygen transport within muscle tissue. These data serve as another test of symmorphosis, which predicts that each of these characters should be positively related to DLO_2 to $\dot{V}O_2\text{max}$, and to each other.

Contrary to predictions of symmorphosis, a correlation matrix of residuals from allometric equations shows that $\dot{V}O_2\text{max}$ (column 1 in Table 1) is not positively correlated with variation in any structural character. Treating each correlation among structural indices as independent (a liberal test), only 14 of 45 possible correlations are significantly positive. Capillarity is positively correlated among muscles and with DLO_2 . Mitochondrial densities, however, are generally uncorrelated among tissues or with DLO_2 . Mitochondrial densities and capillarity are positively correlated within three of four tissues. However, these characters are not positively correlated between muscles; the previously reported positive correlation (Weibel and Taylor, 1981; Hoppeler et al., 1984) apparently reflects negative scaling of both characters with body mass. Similar results were obtained using only the nine bovids.

Finally, we conducted a principle-component analysis of the correlation matrix of residuals in Table 1. Symmorphosis predicts that all characters should load heavily and with the same sign on at least one factor. Such is not the case. Only DLO_2 and the four capillarities load heavily (component correlations = 0.824 to 0.922) on the first factor, which accounts for 41.5% of the total variance. $\dot{V}O_2\text{max}$ (0.739) and three muscle mitochondrial volume densities (component correlations = 0.570 to 0.704) load heavily on the second factor (25.7% of variance), but longissimus dorsi mitochondria (component correlation = -0.705) load negatively.

DISCUSSION

Both Weibel and Taylor's (1981) original analysis of scaling patterns and our analysis of residuals from allometric equations contradict predictions of symmorphosis: structure and function do not seem closely matched in interspecific comparisons of mammals. Moreover, other studies find evidence for single rate-limiting steps in some species, whereas symmorphosis

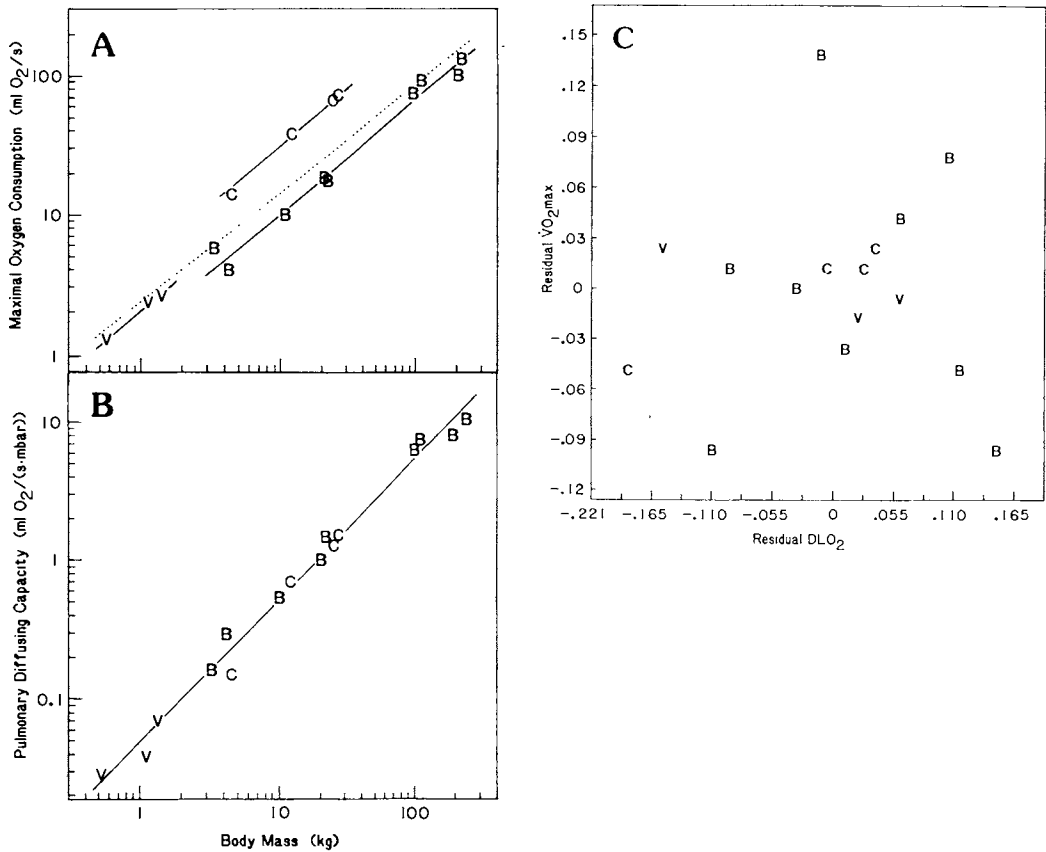


FIG. 1. A) Log-log plot of maximal oxygen consumption versus body mass for 16 species of mammals. Solid lines show results of analysis of covariance on \log_{10} -transformed data (pooled within-groups slope \pm 95% confidence interval = 0.833 ± 0.069); families do not differ significantly in slope ($P > 0.05$), but canids have a significantly higher $\dot{V}O_{2max}$ than bovids ($P < 0.0001$) or viverrids, which are marginally higher than bovids ($P = 0.0629$). Dotted line is least-squares regression for all points (slope = 0.787 ± 0.154). B) Pulmonary diffusing capacity does not differ significantly (slope or intercept) among families (ANCOVA, $P > 0.49$), and scales as $M^{1.025 \pm 0.068}$. C) Residual variation in $\dot{V}O_{2max}$ (from ANCOVA regression lines in A) versus residual variation in DLO_2 ; the correlation, predicted to be positive given symmorphosis, is insignificant ($r = 0.061$, $P = 0.821$).

predicts that no single step will be rate-limiting. For example, $\dot{V}O_{2max}$ in goats appears to be limited by muscle oxidative capacities, whereas ventilation, pulmonary gas exchange, cardiac output, and tissue capillary gas exchange appear to be in excess (Jones et al., 1985; Lindstedt and Jones, 1987). In contrast, pulmonary factors may be limiting in some species (Dempsey et al., 1985). Finally, comparisons of trained versus untrained animals often reveal compensatory changes only in selected traits (Blomqvist and Saltin, 1983; Saltin and Gollnick, 1983; Hoppeler et al., 1984; Sillau, 1985), suggesting that traits that did not change were "excessive" prior to training. In lizards, a high $\dot{V}O_{2max}$ is sometimes, but not always, paralleled by expected structural differences (e.g., relative heart or muscle mass; Bennett et al., 1984; Garland, 1984, 1987 and references therein).

At least two general explanations may account for the lack of correspondence between theory and data (see also Lindstedt and Jones [1987]). First, symmorphosis may be a valid principle, but the available data

are unsuitable for testing it. This seems unlikely, because Weibel and Taylor's choice of structural and functional indices appears sound, as discussed in their original publication. Moreover, Blomqvist and Saltin (1983) argue that pulmonary diffusing capacity is in fact a likely limiting factor for $\dot{V}O_{2max}$. Finally, all measurements were carried out by a single group of scientists, using the same species and mostly the same individuals. Comparative data of this quality are rare.

On the other hand, the adequacy of $\dot{V}O_{2max}$ alone as a functional index has been questioned (Cooper et al., 1984; Bennett and Lindstedt's comments in discussion following Lindstedt and Jones [1987]). In addition, not all factors important in gas exchange have been measured simultaneously in previous studies. Such variables as pulmonary transit time (Lindstedt, 1984; Dempsey et al., 1985), blood flow, perfusion distribution, O₂-diffusion facilitation, aspects of ventilation, or the pressure gradient for O₂ transfer for alveolar air to capillary blood (Weibel and Taylor, 1981; Weibel, 1984a, 1984b; Taylor and Weibel, pers. comm.) may

TABLE 1. Correlation matrix among residuals from allometric equations for 12 species of mammals. Characters are maximal oxygen consumption ($\dot{V}O_{2\max}$), pulmonary diffusing capacity (DLO_2), mitochondrial volume densities (-Mito), and capillaries per mm^2 cross-sectional area of muscle fibers (-Cap) in diaphragm (D), semi-tendinosus (S), longissimus dorsi (LD), and vastus medialis (VM). See Weibel and Taylor (1981) for original units. Correlations significantly positive ($P < 0.05$) by a one-tailed t-test are in boldface.

	$\dot{V}O_{2\max}$	DLO_2	D-Mito	D-Cap	S-Mito	S-Cap	LD-Mito	LD-Cap	VM-Mito	VM-Cap
$\dot{V}O_{2\max}$	—									
DLO_2	-0.301	—								
D-Mito	0.365	0.103	—							
D-Cap	-0.248	0.648	0.619	—						
S-Mito	0.263	0.385	0.509	0.296	—					
S-Cap	-0.175	0.865	0.032	0.536	0.515	—				
LD-Mito	-0.449	0.189	-0.079	0.115	-0.398	0.056	—			
LD-Cap	-0.691	0.693	0.040	0.612	0.053	0.581	0.533	—		
VM-Mito	0.419	0.144	0.111	0.239	0.236	0.288	-0.420	-0.176	—	
VM-Cap	-0.254	0.814	0.152	0.751	0.022	0.715	0.320	0.562	0.194	—

exhibit size related and/or interspecific differences, resulting in tighter matching than is now apparent. Another possibility is that total mitochondrial volumes or capillary numbers (per muscle [cf. Weibel and Taylor, 1981 pp. 125-127, 141-144, 146] or per whole animal [Lindstedt and Jones, 1987; but see Weibel and Taylor (1981 p. 156)]) may correlate with $\dot{V}O_{2\max}$ and/or DLO_2 among species, although per gram or per cross-sectional area values do not. Unfortunately, data on muscle masses were not available in the original report (Weibel and Taylor, 1981). Assessment of the foregoing possibilities must await further studies.

Second, symmorphosis itself may be invalid, because some or all of its premises are unrealistic. Premise I: Because the maintenance of structures in excess of functional needs is wasteful, natural selection should optimize design, such that structures and maximal functional demands will be closely matched at all levels. Unfortunately, as noted by Weibel (1984b), the energetic cost of building and maintaining excessive structure is not well known. Whether the "waste" of maintaining (say) 10% more mitochondria than could be used at $\dot{V}O_{2\max}$ has a significant negative impact on lifetime reproductive output (and hence is selected against) is unclear and debatable (cf. Diamond, 1986). Moreover, whether maximum efficiency or optimality, rather than adequacy or sufficiency, is a primary criterion of natural selection, is also unclear and debatable (Darwin, 1859 p. 201; Lewontin, 1979; Gans, 1983; Bartholomew, 1986). In any case, genetic or developmental constraints (either or both often termed "historical" or "phylogenetic" constraints) may prevent natural selection from achieving optimal evolutionary solutions (Gould and Lewontin, 1979; Lande, 1979; Lauder, 1981; Mayr, 1983; Burger, 1986). Premise II: All components within a system (e.g., the respiratory system) are designed primarily for the overall functioning of that system alone (e.g., oxygen transport), such that the capacities of a given component do not represent adaptive compromises to conflicting functional demands. Given the interdependence of most morphological, physiological, and biochemical systems, including the respiratory system (Weibel and Taylor, 1981; Weibel, 1984b; Lindstedt and Jones,

1987,) this will often be false (Gans, 1983; Alexander, 1975; Frazzetta, 1975).

Although symmorphosis has heuristic value as a working hypothesis (Lindstedt and Jones, 1987), it should not presently be considered an established principle; available data appear largely contradictory. Moreover, for the reasons given above, "symmorphosis" may be an unlikely evolutionary outcome. Some components within a system may exhibit "excessive construction" (Gans, 1979), whereas others constitute "limiting factors." Furthermore, given the vicissitudes of evolutionary change, factors that are limiting (or in excess) may well differ among species (or populations). This possibility has been recognized previously (e.g., Saltin and Rowell, 1980; Garland, 1984) and may account for some of the conflicting results obtained by those studying limitations to $\dot{V}O_{2\max}$ in different species (cf. Weibel and Taylor, 1981; Blomqvist and Saltin, 1983; Saltin and Gollnick, 1983; Hillman and Withers, 1985; Jones et al., 1985).

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SELECTION FOR SEXUAL ISOLATION BETWEEN GEOGRAPHIC FORMS OF
DROSOPHILA MOJAVENSIS. II. EFFECTS OF SELECTION OF MATING
PREFERENCE AND PROPENSITY

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The situation in which behavioral differences prevent interspecific mating has been called sexual isolation (Dobzhansky, 1970). Although examples of this phenomenon abound, many questions concerning sexual isolation remain unanswered. These relate to the manner of its evolutionary development (Barton and Charlesworth, 1984; Carson and Templeton, 1984; Dobzhansky, 1940; Kaneshiro, 1976; Lambert and Paterson, 1984; Muller, 1942; Paterson, 1982; Sved, 1981; Thornhill and Alcock, 1983; West-Eberhard, 1983), and to the types of behavioral interactions by which it is effected (Crossley, 1974; Gilbert and Starmer, 1985; Manning, 1965; Merrell, 1950, 1960; Spencer et al., 1986; Spiess, 1970, 1982; Spieth and Ringo, 1983; Wood and Ringo, 1980). This report describes the first step in an exploration of the relative roles of preference and propensity in an artificially increased sexual isolation and, thus, primarily addresses the latter issue.

Drosophila mojavensis comprises three geographic forms occurring in the United States, the Baja California peninsula, and mainland Mexico. The forms differ from each other in morphology, genetics, ecology, and extent of sexual isolation from the sibling species, *D. arizonensis* (Heed, 1982; Koepfer, 1987; Wasserman and Koepfer, 1980; Zouros, 1973). There is also a small amount of naturally occurring sexual isolation between the peninsular and mainland forms of *D. mojavensis*.

In a previous study (Koepfer, 1987), *D. mojavensis* from Baja California and from Sonora on the mainland were selected for increased sexual isolation from each other, while controls were maintained with maximum outbreeding. Response to selection was rapid and asymmetrical in that postselection isolation was very high between peninsular males and mainland females but nonexistent in the reciprocal pairing. Results of that work indicated that selection had affected both peninsular males and mainland females, but the testing regimen was not adequate for sharply defining the behavioral components that had been altered. In addition, isolation had increased somewhat between pen-

insular and mainland control lines, indicating either that the control-line regimen itself or the initial method of establishing control and selected lines had influenced isolation. The heightened control-line isolation also made it difficult to delineate the specific effects of selection on behavior.

Selected and control lines have been maintained in mass culture since cessation of that experiment. They were retested after three and one-half years in such culture, and isolation between control lines has returned to the level exhibited at the start of the experiment. This indicates that there was an effect due to the control-line regimen but that this effect was transitory. Isolation between selected peninsular males and Sonoran females is still high; the selectively induced behavioral change has been stable in the absence of continued selection pressure.

The study described here begins a "behavioral dissection" of the post-selection isolation between peninsular males and mainland females. The aim is to elucidate the effects of the selective regimen on mating preference and propensity, or sex drive, and to evaluate the relative importance of these behavioral components for mate choice in the selected and control lines. Mainland *D. mojavensis* is referred to as S; *D. mojavensis* from Baja California is called B; selected flies are referred to as B_s and S_s; control-line flies are B_c and S_c. Mating propensity is defined as the probability that an individual will mate homogamically within a given time interval. Homogamic indicates B × B or S × S, i.e., a member of the same geographic form, whether control or selected. Preference refers to a bias toward mating with a particular type. Definitions of propensity and preference are modified from DeBenedictis (1977).

MATERIALS AND METHODS

Flies were reared and tested on banana medium supplemented with *Opuntia* cactus, at 23°C, under a 12:12 light:dark cycle. For testing, both no-choice and male-choice methods were utilized (Spieth and Ringo, 1983). In each case, males were tested singly, thereby