

Likelihood models for discriminating alternative phenotypes in morphologically dimorphic species

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ABSTRACT

Question: How can we numerically discriminate with explicit confidence the alternative phenotypes in dimorphic species with bimodal threshold traits?

Mathematical method: A bimodal distribution of a dimorphic trait is parameterized by mixture distribution models for normal and gamma distributions. Likelihood ratios of the alternative phenotypes for a given trait size are computed from the mixture models. The likelihood models are tested in several horn-dimorphic beetles and compared with existing piece-wise linear regression methods.

Key assumptions: The bimodal distribution represents a mixture of two discrete distributions. The alternative phenotypes have normal or gamma distributions.

Conclusions: Likelihood methods effectively model the way in which alternative phenotypes are expressed in taxa with bimodal trait size frequency distributions. New likelihood models estimate the probability that a given trait size represents a given phenotype in normal to skewed bimodal frequency distributions. These prove theoretically and empirically superior to linear regression methods. Likelihood methods model the behaviour of threshold mechanisms in natural populations and will enhance exploration of the evolutionary significance of intraspecific conditional phenotypes.

Keywords: alternative tactics, horn dimorphism, intrasexual polyphenism, likelihood models, threshold traits.

INTRODUCTION

The aim of this paper is to introduce new numerical methods that discriminate the alternative phenotypes in dimorphic species with explicit confidence. Our models estimate likelihood ratios of the alternative phenotypes across bimodal frequency distributions and are relevant to diverse taxa that express discontinuous morphologies.

The likelihood method should prove broadly useful for exploring the evolutionary significance of conditional strategies and threshold traits, including, for example, how and why alternative intrasexual phenotypes arise and evolve in relation to ecological factors,

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such as the social environment in which they are framed (Gross, 1996; Emlen and Nijhout, 2000). Moreover, intrasexual conditional polyphenisms are thought to constitute an important source of morphological and behavioural specializations and of phylogenetic diversification (West-Eberhard, 1989, 1992, 2003).

The present models will apply to intrasexual dimorphisms that are common among insects and other invertebrates (Emlen and Nijhout, 2000) and which are well documented in vertebrate species, such as bill-dimorphic African finches (Smith, 1987). Male horns in certain beetle taxa exhibit polymorphism and have yielded unique perspectives concerning the evolutionary behaviour of threshold traits (e.g. Emlen, 1996; Moczek and Emlen, 1999; Emlen and Nijhout, 2000). Here we employ the likelihood models to examine a selected suite of male horn-dimorphic beetle species to illustrate the utility of this new approach.

Varied studies of laboratory, exotic and natural populations of horn-dimorphic beetles show that parameters of horn allometry evolve rapidly in response to diverse ecological factors (Kawano, 1995; Emlen, 1996; Moczek, 1998; Moczek and Nijhout, 2003; Rowland, 2003). Changes in both the position and shape of the horn allometry occur in advance of primary sexual characters and, presumably, reproductive isolation. The latter changes may represent some of the earliest features of morphological divergence in these and other groups (Moczek, 2003; Rowland, 2003; but see Kawano, 1995). Interspecific competition and character displacement appear to have generated marked divergence of threshold parameters in the horn scaling alternatives of several sympatric species-pairs of the elaborately horned dynastine scarab genera *Chalcosoma*, *Xylotrupes* and others (Kawano, 1995, 2003; Rowland, 2003). In *Onthophagus* dung beetles, both intra- and interspecific competition appear to have generated significant threshold divergence between allopatric populations within a matter of decades (Moczek *et al.*, 2002; Moczek 2003; Moczek and Nijhout, 2003).

Intrasexual horn dimorphism occurs in beetles as a consequence of the male's capacity to develop along alternative ontogenetic pathways. Horn expression is determined by a condition-dependent threshold mechanism that is sensitive to larval size (Eberhard, 1982; Moczek, 1998; Emlen and Nijhout, 1999; Moczek and Emlen, 1999) and is associated in *Onthophagus* dung beetles with the timing and titre of juvenile hormone (Emlen and Nijhout, 1999). Individuals below a critical threshold body size produce horns that are proportionally smaller than those of males of larger body sizes. In sigmoidal allometries, the scaling relationship of horn size increases rapidly over a narrow body size range. This produces two phenotypic modes in the horn size frequency distribution that are separated by a nadir, or intermode, wherein relatively fewer individuals of intermediate horn sizes are expressed (Figs. 1–6). In theory, this threshold mechanism maximizes genotypic fitness by allowing individuals to select the phenotypic alternative that provides the maximum fitness for a given body size or status (Emlen, 1996; Gross, 1996).

Male horn-dimorphism in beetles appears to operate in concert with diverse suites of correlated tactics, such as alternative reproductive behaviours (Eberhard, 1982; Siva-Jothy, 1987; Cook, 1990; Rasmussen, 1994; Emlen, 1997; Simmons *et al.*, 1999; Hunt and Simmons, 2000; Moczek and Emlen, 2000). To identify such correlated suites of alternative tactics and to associate their differential expression to ecological and other variables, it is important to determine, where possible, which individual males belong to which alternative horn phenotype. However, such determination has been problematic in species with sigmoidal allometries because the prevailing numerical methods produce only single, absolute cutscores that are insensitive to continuous variation of horn size across the allometric and frequency distributions.

In earlier studies, visual estimation of the nadir value in the bimodal trait size frequency

distribution provided a means of discriminating between the alternative male phenotypes in horned beetles and other taxa (e.g. Huxley, 1927; Siva-Jothy, 1987). More recently, piece-wise linear regression (Eberhard and Gutierrez, 1991; Kotiaho and Tomkins, 2001) and logistic regression models (Emlen, 1996; Moczek, 2002; Rowland, 2003) that parameterize horn size scaling relationships have been employed to estimate the location in the allometry of the developmental switchpoint between phenotypes. A recent report by Kotiaho and Tomkins (2001) reviewed these methods and derived an optimized model for estimating switchpoints. However, all of the above methods rely on the identification of a single, absolute cutscore for discriminating alternative phenotypes. Moreover, the above methods are liable to fall short because they do not adequately model the way in which threshold traits with sigmoidal allometries are expressed.

In male horn-dimorphic beetles with sigmoidal allometries, the alternative phenotypes are at least partially uncoupled developmentally and are thought to be produced by alternative subsets of genes. Individuals inherit both subsets, but express one or the other depending on conditions encountered as larvae develop (Emlen and Nijhout, 2000). The sigmoidal allometry produces two phenotypic modes in the horn size frequency distribution separated by an intermode within which there are relatively fewer individuals of intermediate horn sizes. Thus, the bimodal horn size frequency distribution represents the sum of the two separate frequency distributions and the relative proportion of the two alternative phenotypes is fractional for each point where their frequency distributions overlap (Fig. 1). These distributions overlap in part due to genetic and environmental variation in the switchpoints of different individuals; that is, there is no single switchpoint. We suggest that existing models which rely on a single absolute cutscore fail to represent the behaviour of threshold mechanisms expressed in natural populations. In the region where two morph frequency distributions overlap, male morphology is best represented by a probability distribution that reflects the relative proportions of the two alternative phenotypes for a given horn size. In taxa with sigmoid scaling relationships, classification of individual males to either phenotypic alternative decreases in certainty as horn size approaches the inflection region of the allometry and nadir region of the frequency distribution.

The single absolute cutscore employed by the above methods misclassifies each phenotype according to the distribution parameters of the alternative phenotypes in the region of overlap. There is always one side of the single cutscore in which the individuals immediately adjacent to the cutscore carry at least a 50% chance of misclassification. To eliminate these large errors, we developed a method that estimates the likelihood ratios of the two phenotypes across the bimodal horn size frequency distribution.

Here we demonstrate our new numerical models in male horn-dimorphic beetles. The likelihood models discriminate minor and major males on the basis of horn size with explicit confidence. These models are generalizable and can be applied to a multitude of taxa with sigmoid threshold trait allometries. The principle of these models in the example of male horn-dimorphic beetles is that horn size frequency distribution can be modelled as mixtures of two distributions that correspond to the alternative minor and major male horn phenotypes. The probabilities that a given horn size represents a minor or major male phenotype are complementary functions described by the likelihood ratio at any given horn size under the distribution curve (Fig. 1). The proportions of minor and major males of horned beetles and the shape of the horn size frequency distribution can vary in natural populations according to circadian (Siva-Jothy, 1987), seasonal (Eberhard, 1982; Emlen, 1996) and other factors. Therefore, the likelihood cutscores will also vary according to such factors.

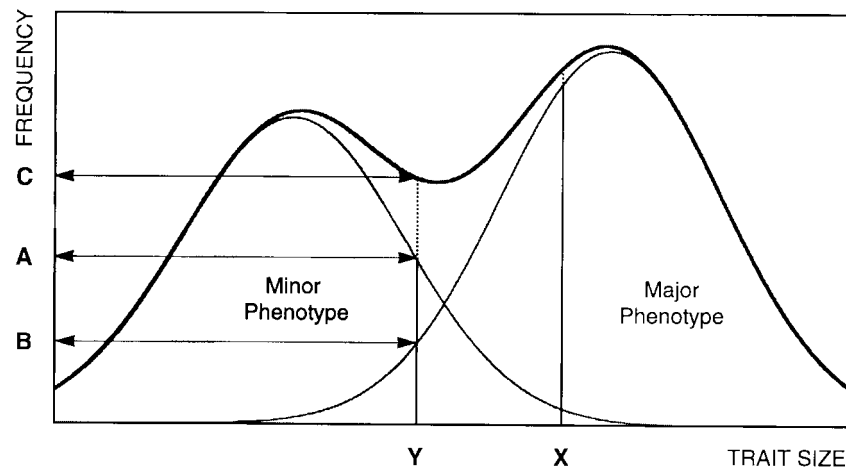


Fig. 1. Bimodal frequency distribution (heavy curve) of threshold trait sizes is the sum of the distributions of the alternative 'minor' and 'major' phenotypes (thin curves). At trait size 'Y', sample frequency 'C' represents the sum of the number of minor males with that trait size (frequency 'A') plus the number of major males with that trait size (frequency 'B'). The likelihood ratio of minor males to major males at trait size 'Y' is 2:1. The likelihood ratio of minor males to major males at trait size 'X' is 5:95 (1:19) (see text, models <c> and <d>).

Likelihood cutscores are applicable between samples and can be used prospectively where samples are expected to have similar distribution characteristics, such as under experimental control.

METHODS

Four species of male horn-dimorphic beetles were selected for this study that represent differing shapes of the frequency distributions and differing scaling relationships of horn size to body size. Details concerning the samples of *Xylotrupes gideon* and *X. ulysses australicus* are given in Rowland (2003). The *Phanaeus vindex* sample was trapped by Dr. Truman Fincher in Arlington, Georgia on 24 October 1998. The *Onthophagus taurus* data represent 217 bivariate data from Stern and Emlen (1999, figure 5). *Xylotrupes gideon*, *P. vindex* and *O. taurus* are strongly horn-dimorphic species that vary considerably in shapes of the frequency distribution. In *X. gideon* (Fig. 2), the shape of the distribution appears symmetric around the mean in both the minor and major males. In *P. vindex* (Fig. 3), the distribution is skewed moderately right in the major males. In *O. taurus*, the shape of the distributions is skewed strongly left in the minor males and strongly right in the major males (Figs. 4, 5). *Xylotrupes ulysses australicus* (Fig. 6) is a weakly dimorphic species with extensive overlap of the minor and major male frequency distributions, impeding estimation of their shapes (Rowland, 2003). This choice of species and samples represents two contrasting frequency distribution shapes found broadly in horned beetles, normal and strongly skewed, as well as intermediates between these extremes.

To fit these varying shapes, we propose model <c> to simulate normal distributions and model <d>, which employs the gamma function, to simulate skewed distributions. Both

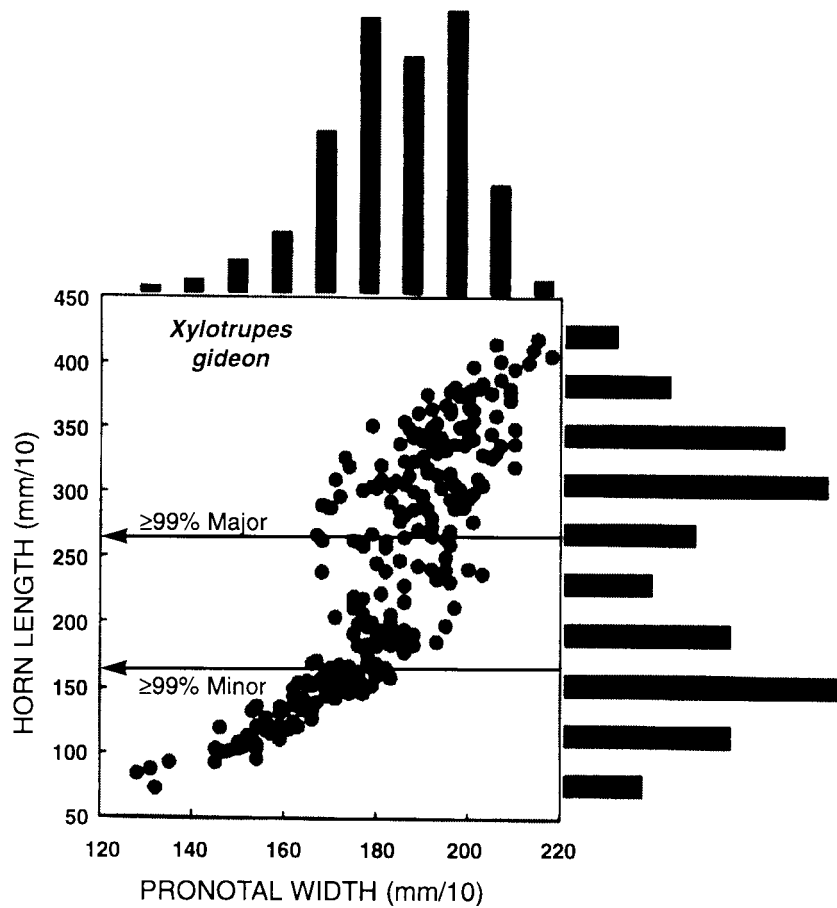


Fig. 2. Allometric relationship and frequency distributions of horn size and body size in *Xylotrupes gideon* from Lampung Province, Sumatra, Indonesia ($n = 177$). Horizontal lines represent 99% likelihood cutscores for minor and major males derived by model <c> (see text). At least 99% of individuals above the upper cutscore represent the major phenotype and at least 99% of individuals below the lower cutscore represent the minor phenotype.

models were tested in all four species and their performances are compared by chi-square and likelihood goodness-of-fit methods and other criteria.

Model <c>, the mixture normal distribution: $f(x) = (1 - p)f_1(x) + pf_2(x)$, where

$$f_1(x) = \frac{1}{\sigma_1 \sqrt{2\pi}} e^{-\frac{1}{2} \left(\frac{x - \mu_1}{\sigma_1} \right)^2}, \text{ for minor males,}$$

$$f_2(x) = \frac{1}{\sigma_2 \sqrt{2\pi}} e^{-\frac{1}{2} \left(\frac{x - \mu_2}{\sigma_2} \right)^2}, \text{ for major males; and}$$

where x = horn length; p = fraction of major males; μ_1 , μ_2 = means and σ_1 , σ_2 = standard deviations of minor male and major male normal distributions of horn length, respectively.

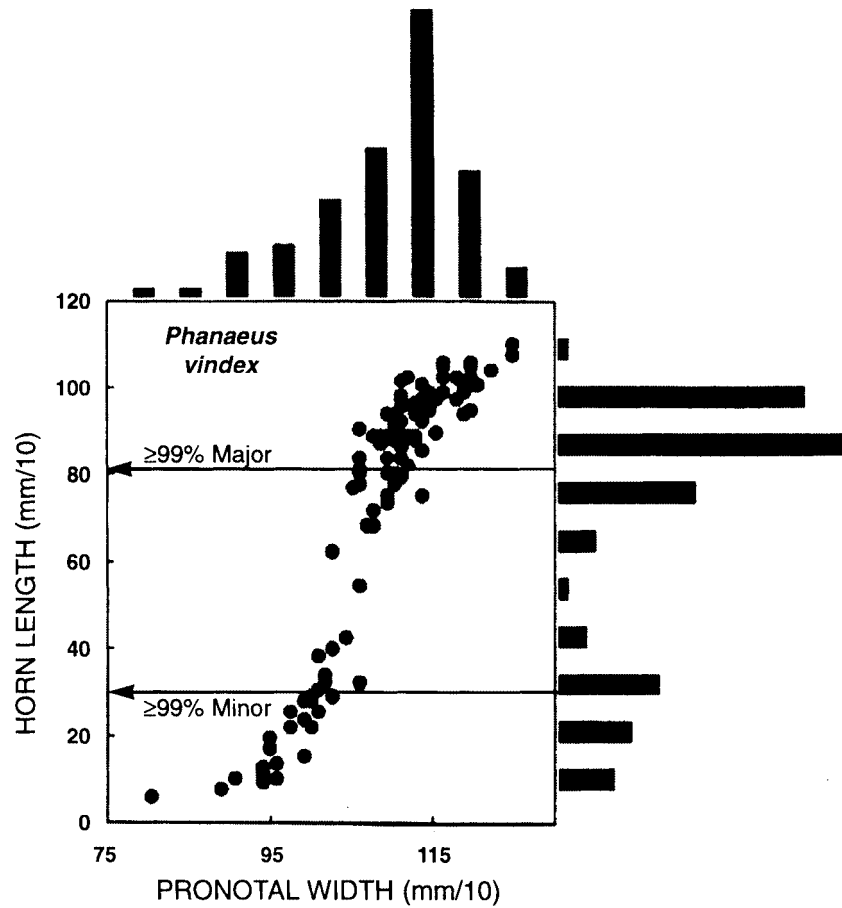


Fig. 3. Allometric relationship and frequency distributions of horn size and body size in *Phanaeus vindex* from Arlington, Georgia, USA ($n = 108$). Horizontal lines represent 99% likelihood cutscores for minor and major males derived by model <d> (see text). At least 99% of individuals above the upper cutscore represent the major phenotype and at least 99% of individuals below the lower cutscore represent the minor phenotype.

Model <d>, the mixture gamma distribution: $f(x) = (1 - p)f_1(x) + pf_2(x)$, where

$$f_1(x) = \frac{1}{\Gamma(\lambda_1)} \left(\frac{x - LB}{\theta_1} \right)^{\lambda_1 - 1} \frac{1}{\theta_1} e^{-\left(\frac{x - LB}{\theta_1} \right)}, \text{ for minor males,}$$

$$f_2(x) = \frac{1}{\Gamma(\lambda_2)} \left(\frac{UB - x}{\theta_2} \right)^{\lambda_2 - 1} \frac{1}{\theta_2} e^{-\left(\frac{UB - x}{\theta_2} \right)}, \text{ for major males; and}$$

where LB = lower bound of minor male horn lengths; UB = upper bound of major male horn lengths; θ_i , λ_i = scale and shape parameters for i th gamma distribution, $i = 1, 2$. Although the theoretical distributions of minor and major male horn lengths extend beyond LB and UB, the interval $LB \leq x \leq UB$ is restricted within rational limits. The means

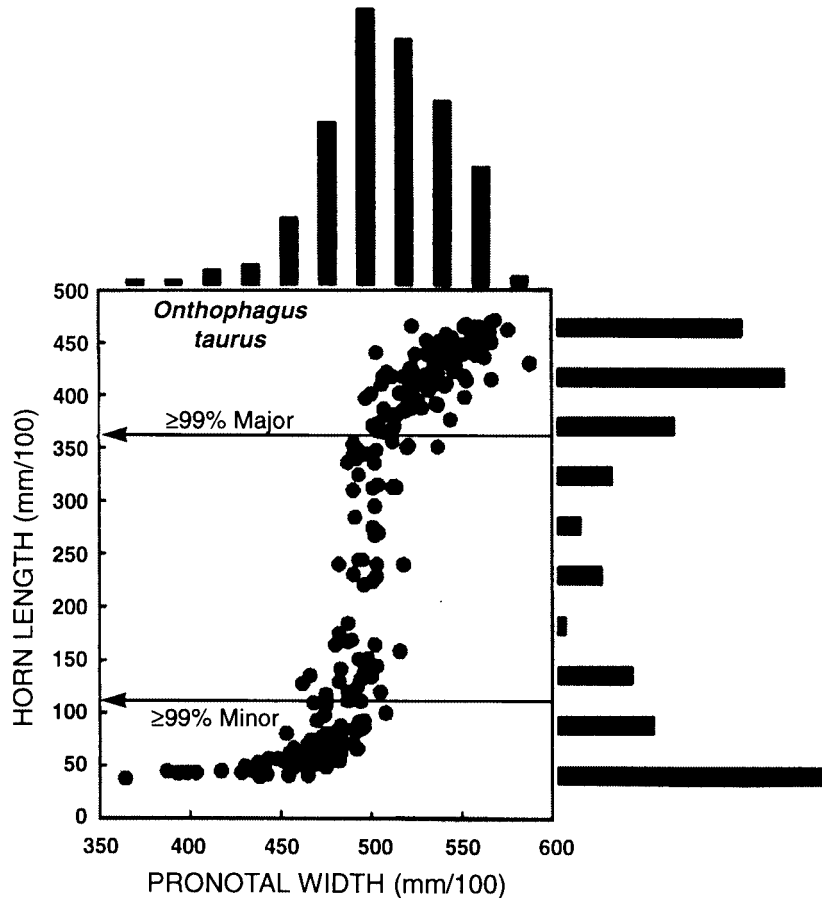


Fig. 4. Allometric relationship and frequency distributions of horn size and body size in *Onthophagus taurus*; data represent bivariate data from data in Stern and Emlen (1999, figure 5) ($n = 217$). Horizontal lines represent 99% likelihood cutscores for minor and major males derived by model <d> (see text). At least 99% of individuals above the upper cutscore represent the major phenotype and at least 99% of individuals below the lower cutscore represent the minor phenotype.

of the minor and major male horn sizes in terms of these parameters are $LB + \theta_1 \lambda_1$ and $UB - \theta_2 \lambda_2$ respectively; the standard deviations are $\theta_1 \sqrt{\lambda_1}$ and $\theta_2 \sqrt{\lambda_2}$.

Functions <c> and <d> describe the shape of the bimodal distribution. The number of minor (L_1) and major (L_2) males at a given horn size (x) is proportional to the following expressions of likelihood, and the fraction of males that are major males at a given horn length is $L_2/(L_1 + L_2)$.

$$L_1(\text{minor}) = (1 - p)f_1(x)$$

$$L_2(\text{major}) = pf_2(x)$$

The cutscores for major males in either model <c> or <d> are obtained as the x values such that $L_2/(L_1 + L_2) = 0.95, 0.99$ or 0.999 . In terms of likelihood ratios, $L_2/L_1 = 19, 99$ or 999 for major male cutscores, and $L_2/L_1 = 1/19, 1/99$ or $1/999$ for minor male cutscores.

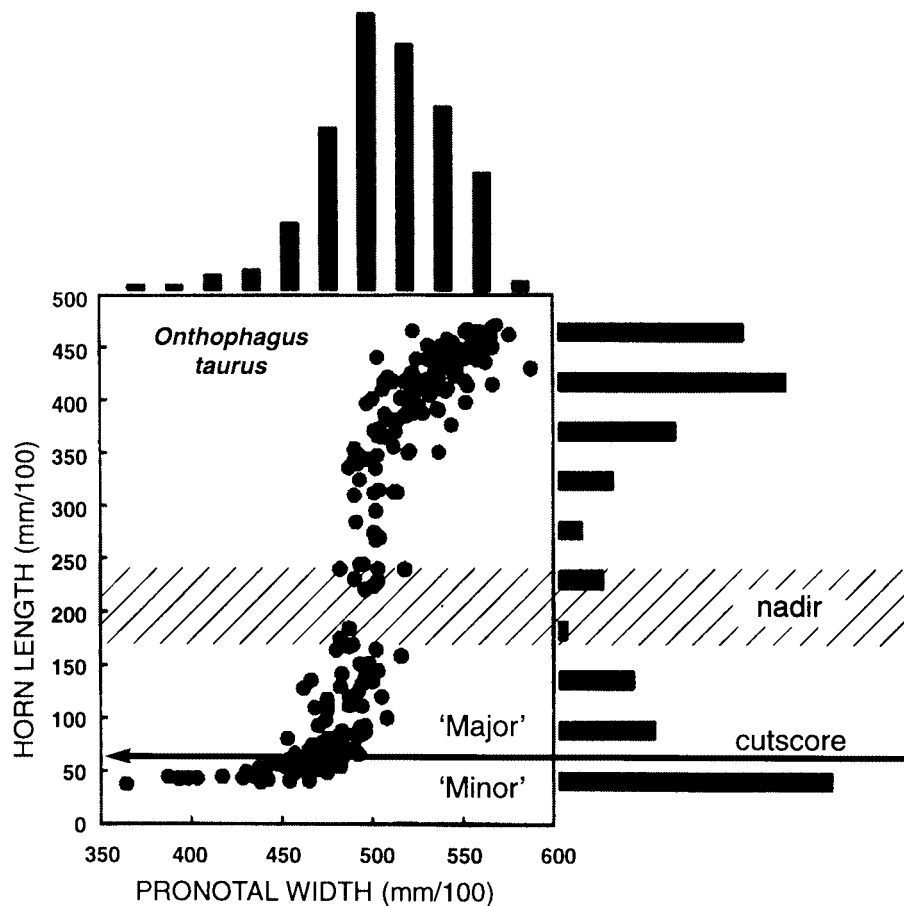


Fig. 5. Allometric relationship and frequency distributions of horn size and body size in *Onthophagus taurus* from data in Stern and Emlen (1999, figure 5) ($n = 217$). This figure shows the single horn size cutscore (solid line) used to discriminate minor and major males of *O. taurus* by Hunt and Simmons (2000) and Kotiaho and Tomkins (2001). This cutscore does not correspond to the nadir region of the frequency distribution (sloping lines). The nadir region closely, but imprecisely, corresponds to the developmental switchpoint between minor and major males. The single cutscore misclassifies few major males as minor males, but misclassifies a great many minor males as major males.

RESULTS

Chi-square and likelihood goodness-of-fit tests preferred model <c> for *X. gideon*, in which the morph frequency distributions appear normal (Fig. 2), and model <d> for *O. taurus*, in which the distributions are strongly skewed (Fig. 4). In the samples with intermediate frequency distributions, chi-square and likelihood goodness-of-fit preferred different models and thus the models were chosen on the basis of additional rationale specific to each case. In *X. ulysses australicus*, model <d> did not detect the nadir region of the distribution and did not produce cutscores. In *P. vindex*, both models produced cutscores, but we favoured model <d> because it proved more conservative. While chi-square and likelihood goodness-of-fit will probably suffice to select the appropriate

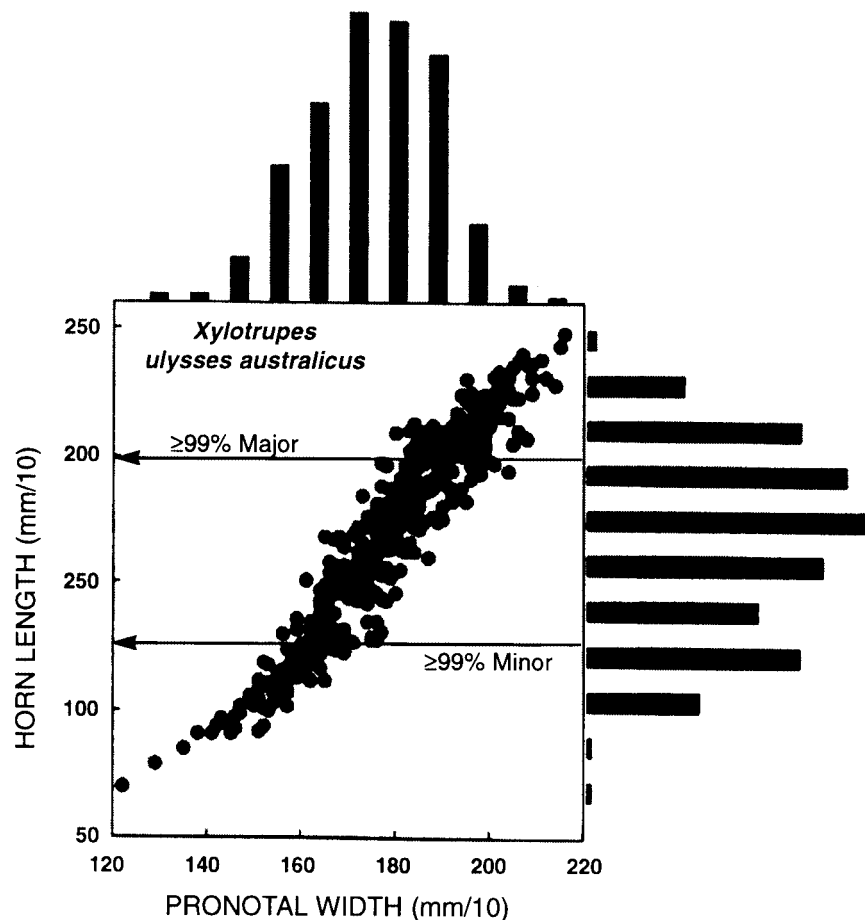


Fig. 6. Allometric relationship and frequency distributions of horn size and body size in *Xylotrupes ulysses australicus* from Bundaberg, Queensland, Australia ($n = 426$). Horizontal lines represent 99% likelihood cutscores for minor and major males derived by model <c> (see text). At least 99% of individuals above the upper cutscore represent the major phenotype and at least 99% of individuals below the lower cutscore represent the minor phenotype.

model for many taxa, we found it necessary to apply additional rationale to select the best model for two of the present samples. Thus we do not here suggest absolute rules.

Using 99% likelihood cutscores, model <c> estimates that at least 99% of *X. gideon* males with horn lengths smaller than 16.8 mm represent the minor phenotype and at least 99% of the males with horns larger than 25.9 mm represent the major phenotype (Fig. 2; Table 1). Model <c> estimates that at least 99% of *X. ulysses australicus* males with horn lengths smaller than 12.4 mm represent the minor phenotype and males with horns larger than 19.9 mm represent the major phenotype (Fig. 6; Table 1). Model <d> estimates that with lower and upper bounds of 0.50 mm and 11.1 mm, at least 99% of *P. vindex* males with horn lengths smaller than 3.2 mm represent the minor phenotype and males with horns larger than 8.1 mm represent the major phenotype (Fig. 3; Table 1). Model <d> estimates that with lower and upper bounds of 0.37 mm and 4.72 mm, at least 99% of *O. taurus* males

Table 1. Distribution parameters and likelihood cutscores for alternative male phenotypes in selected taxa of horned beetles

Parameter	<i>Xylotrupes gideon</i> (<i>n</i> = 177, <i>p</i> = 0.56)	<i>X. ulysses australicus</i> (<i>n</i> = 420, <i>p</i> = 0.61)	<i>Phanaeus vindex</i> (<i>n</i> = 108, <i>p</i> = 0.73)	<i>Onthophagus taurus</i> (<i>n</i> = 217, <i>p</i> = 0.55)
Minor males				
Normal μ/σ , or Gamma θ/λ	15.5/3.15	13.1/2.36	1.14/1.79	0.501/1.14
LB			LB = 0.50	LB = 0.37
Major males				
Normal μ/σ , or Gamma θ/λ	31.3/4.80	19.5/2.20	0.66/3.01	0.495/1.57
UB			UB = 11.1	UB = 4.72
0.95 Likelihood cutscores	minor < 18.9 major > 24.9	minor < 13.7 major > 18.4	minor < 4.0 major > 7.2	minor < 1.52 major > 3.13
0.99 Likelihood cutscores	minor < 16.8 major > 25.9	minor < 12.4 major > 19.9	minor < 3.2 major > 8.1	minor < 1.07 major > 3.59
0.999 Likelihood cutscores	minor < 13.3 major > 27.6	minor < 10.7 major > 22.0	minor < 1.9 major > 10.2	minor – major > 4.31

Note: The numerical model <c> estimates the μ and σ parameters in *Xylotrupes* and *Phanaeus* and numerical model <d> estimates the θ and λ parameters in *Onthophagus* for minor and major male horn length distributions. The probabilities that a given horn length represents a minor or major male are complementary functions that are described by the likelihood ratio at any given horn length under the distribution curve (see text). The horn length cutscores for three likelihood ratios (95%, 99%, 99.9%) of the alternative phenotypes are presented for four species with differing allometric shapes. *p* = proportion of major males in each sample; units are millimetres; LB = lower bound; UB = upper bound.

with horn lengths smaller than 1.07 mm represent the minor phenotype and males with horns larger than 3.59 mm represent the major phenotype (Fig. 4; Table 1). The horn length cutscores for 95%, 99% and 99.9% likelihood ratios of the alternative phenotypes of each species are reported in Table 1.

DISCUSSION

Here we introduce numerical models for probabilistic discrimination of the alternative phenotypes in taxa that express discontinuous morphologies and then demonstrate their use in a suite of male horn-dimorphic beetles. The likelihood models estimate the probability that an individual with a given trait size represents a given phenotype across normal to skewed bimodal trait size distributions. These provide a significant refinement compared with single cutscore methods, which are liable to large errors in discriminating alternative phenotypes (Figs. 4, 5). The likelihood models are intended to help discriminate and correlate alternative suites of morphological, behavioural, physiological and life-history tactics. Specific applications in male horn-dimorphic beetles, for example, include comparative studies of sexual characters and behaviours (e.g. Simmons *et al.*, 1999; Hunt and Simmons, 2000,

2002; Tomkins and Simmons, 2002; Hongo, 2003) and fitness functions such as fluctuating asymmetry (e.g. Hunt and Simmons, 1997, 1998). This method will also aid such studies in, for example, forceps-dimorphic male dermapterans where classification of alternative male phenotypes was confounded by broad overlaps in threshold trait sizes (e.g. Tomkins and Simmons, 1996; Tomkins, 1999). In the above examples, all the individuals in the samples were classified as either one phenotype or another by means of a single, absolute cutscore (Fig. 5). The present likelihood models are more sensitive because they classify individuals according to each phenotype with a defined level of probability (Figs. 1–6).

The likelihood methods may significantly alter interpretation of reproductive tactics in the onthophagine dung beetle *Onthophagus taurus*, an important model species for exploring the evolutionary behaviour of threshold traits. Hunt and Simmons (2000) pointed out that in previous studies, only males from the opposite extremes of the allometric distributions were used in experiments to discriminate and correlate alternative behavioural and morphological tactics. Their study was the first to examine comparative behaviours of several graduated size classes of males across the entire range of body and horn sizes. Employing this design with *O. taurus*, they found that while horn size varied continuously, male reproductive behaviour varied in a discontinuous, 'all-or-none' fashion. Males below 5 mm pronotal width (an indicator of body size) did not provision brood masses, whereas males above that size engaged in a fixed amount of provisioning. These results provided the first such empirical evidence that alternative male horn phenotypes are produced by discrete ontogenetic programs and that intermediate horn sizes do not necessarily reflect intermediate underlying programs.

While Hunt and Simmons (2000) found that the onset of horn development coincides precisely with the onset of brood provisioning, it appears they incorrectly concluded that this point corresponds to the switchpoint between minor and major male phenotypic alternatives. Indeed, there is a profound increase in the slope of the horn allometry at approximately 5 mm pronotal size (Hunt and Simmons, 2000, figure 1) (*c.* 4.7 mm in the data herein; Figs. 4, 5), which concurs with the switchpoint identified in *O. taurus* by Kotiaho and Tomkins (2001). However, extension of this point in the allometric distribution to the horn size frequency distribution shows it to be located far outside the nadir region of the bimodal horn size distribution (Fig. 5). In fact, the point these methods identify occurs near the peak of the minor male horn size frequency distribution.

The point of onset of rapid horn growth and brood provisioning behaviour identified by Hunt and Simmons (2000) and Kotiaho and Tomkins (2001) do not correspond with the minor to major male developmental switchpoint in *O. taurus* as estimated by the logistic regression parameterization methods (see data in Emlen, 1996; Moczek, 2003), the likelihood ratio methods herein (Fig. 4) or as visually estimated by the location of the nadir of the bimodal frequency distribution (Fig. 5). The methods of Hunt and Simmons (2000) and Kotiaho and Tomkins (2001), rather than identifying the developmental switchpoint between minor and major male phenotypes, instead identify the first point in the bivariate distribution where the allometric trajectory changes abruptly. In *O. taurus*, that point occurs within the minor male phenotype distribution (Figs. 4, 5).

Our interpretation of the results of Hunt and Simmons (2000) and Kotiaho and Tomkins (2001) suggests that onset of rapid horn development and male brood provisioning in *O. taurus*, rather than representing major male tactics, may represent subordinate threshold phenomena within the minor male developmental program. In fact, our likelihood ratio model estimates that the onset of these tactics corresponds to a point in the horn size

frequency distribution in which the likelihood ratio of minor to major males is greater than 99:1 (Figs. 4, 5).

In summary, study of the evolutionary significance of threshold traits has been limited by the methods available for assigning individuals to the respective tactics. In particular, previous methods provide a single absolute value to discriminate between tactics. This single cutscore is insufficient for two reasons. First, it assumes that all individuals above the cutscore possess one discrete attribute and all individuals below it possess another – an assumption that is clearly inaccurate given that the distributions of the alternative phenotypes overlap in most dimorphic systems. Second, the numerical estimate for this cut-off often does not agree with observations of behaviour.

Here we provide a new method for assigning individuals to alternate tactics – a likelihood method that explicitly accounts for overlap of the tactic frequency distributions. It also assigns probabilities in accordance with the extent of distribution overlap. We introduce two models – one for normal and one for skewed tactic frequency distributions – and demonstrate their efficacy using allometry data for four male horn-dimorphic beetle species.

We suggest that likelihood methods such as these will complement existing methods, and enhance future explorations of the evolutionary significance of intraspecific conditional phenotypes. We are presently developing the mixture distribution concept as an element in an expanded model that couples trait size with body size through the bivariate scaling function. Hopefully, a coherent numerical system can be developed that will effectively model demographic and evolutionary change in the expression of alternative phenotypes and non-linear scaling relationships. Such a system will be useful, for instance, in investigating the biological significance of the skewed distributions of the threshold trait alternatives addressed in this study.

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