

The discrimination of alternative male morphologies

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Male dimorphisms represent alternative selective regimes within a sex. As such, they can be used as a powerful tool in testing evolutionary theory. However, to realize this potential, we need to be able to accurately discriminate individuals into two separate morphs. In this article we discuss the existing methods and propose a new one. We test our method with data from three dimorphic species and compare these results to results with existing methods. We conclude that existing methods often misclassify a large proportion of individuals, but applying our method notably reduces these errors. *Key words*: male dimorphism, morph discrimination, sexual selection, alternative reproductive strategies. [*Behav Ecol* 12:553–557 (2001)]

Alternative reproductive behaviors are frequently associated with two or more distinct morphologies that occur within a sex (Alcock, 1996b; Emlen, 1997; Gross, 1985, 1991). In a few species, the morphologies associated with the different behavioral tactics are extreme, such as the order of magnitude difference in body mass of par and anadromous salmon (Gage et al., 1995; Gross, 1985). However, in most species dimorphic variability is limited to specific traits that vary discontinuously with body size. Discriminating between one morph and another in these species can be difficult, and this stimulated early researchers to formulate explicit methods of detecting dimorphisms. The first of these was the inspection of the modality of the character distribution; bimodality in character length (e.g., forceps lengths in the earwig *Forficula auricularia*) associated with unimodality in a linear measure of body size was considered indicative of a dimorphism (Bateson and Brindley, 1892; Huxley, 1932).

Because male dimorphisms represent alternative selective regimes within a sex, they can be used as powerful tests of evolutionary theory (Gage et al., 1995; Gross, 1996; Simmons et al., 1999; Tomkins and Simmons, 1996). However, in modern evolutionary biology, visual examination of the modality of character distributions are frequently inadequate and imprecise. This is because in many cases the character distributions are not strictly discontinuous, but instead all character sizes are expressed by at least some individuals (Figures 1–3; see also Eberhard and Gutiérrez, 1991; Emlen, 1996; Simmons et al., 1999; Tomkins, 1999; Tomkins and Simmons, 1996). Thus, to test evolutionary theories with dimorphic species, we need accurate statistical methods to detect dimorphisms and discriminate between alternative phenotypes.

Eberhard and Gutiérrez (1991) pioneered a method of statistically detecting and testing for dimorphisms. Before this method only a handful of studies had attempted any statistical determination between alternative morphologies (Cook, 1987; Eberhard, 1987; Goldsmith, 1985; Ollason, 1972). Eberhard and Gutiérrez's (1991) model (which will be referred to as model 1) is as follows:

$$Y = \alpha + \beta_1 X + \beta_2 (X - X_D) D + \beta_3 D + \epsilon, \quad (1)$$

in which Y and X are a linear measure of character size and a linear measure of body size, respectively; X_D is the proposed switch point (the body size at which one phenotype gives way to another); $D = 0$ if $X < X_D$, $D = 1$ if $X \geq X_D$; α is constant; β is the regression coefficient, and ϵ is the error (Eberhard and Gutiérrez, 1991).

This model provides a statistical test for the existence of dimorphic variation in a character associated with body size. First, model 1 tests whether there is a body size switch point, X_D , at which the distribution of the character size Y becomes discontinuous. This switch point can be found by first iterating the X_D that gives the best fit (highest R^2) for model 1 and then testing if this X_D fitted in model 1 gives a regression coefficient, β_3 , that is significantly different from zero (Eberhard and Gutiérrez, 1991).

Second, model 1 tests if there is a body size switch point, X_D , at which the linear slope between body size, X , and character length, Y , changes. If the β_3 of the previous test was significant, then the change in the slope at the body size X_D may be examined by testing the regression coefficient β_2 against zero. A significant deviation from zero indicates that, in addition to the discontinuity of the character length, there is also a change in the slope. If the β_3 of the previous test was not significant, then the term $\beta_3 D$ in model 1 may be left out, and the change in the slope at the body size X_D may be examined with the reduced model by testing the regression coefficient β_2 against zero. The above methods enable the statistical determination of whether a dimorphism exists, and they also establish the exact body size at which individuals are most likely to switch from one morph to the other.

Male dimorphisms (in insects particularly) tend to be conditionally expressed (Eberhard, 1982), or what Gross (1996) has described as "status dependent." The condition for the expression of alternative behaviors and morphologies is generally body size, which is linked to the status of the individual. For example, in the dung beetle *Onthophagus acuminatus* the unconscious strategy of beetles can be summarized as two tactics: if small, sneak copulations and do not grow horns, but if large, grow horns and guard females (Emlen, 1997). Thus, body size is usually the variable underlying the expression of many dimorphic traits. Model 1 therefore provides the important information about where the body size switch point lies, at which one morph changes to another. The accuracy of this methodology is, however, dependent on a tight relationship between body size and the dimorphic trait (Eberhard and Gutiérrez, 1991; Tomkins, 1999; Tomkins and Simmons,

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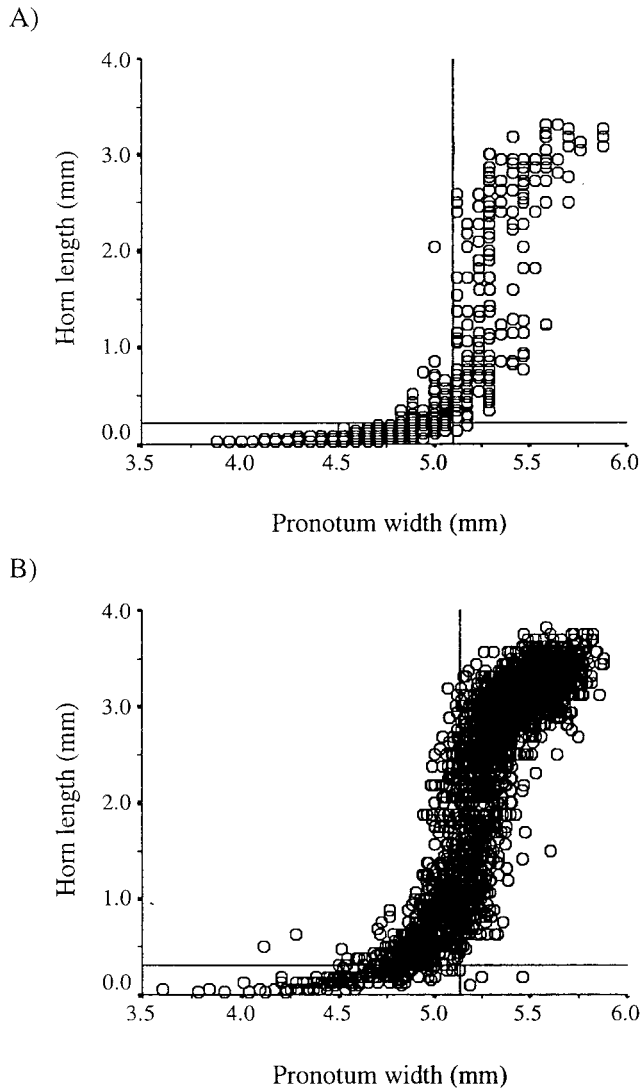


Figure 1
The relationship between pronotum width and horn length from (A) field and (B) laboratory populations of *O. taurus*. (A) The vertical line illustrates the switch point (5.100) derived from the Eberhard and Gutiérrez (1991) original model (model 1), and the horizontal line illustrates the switch point (0.22) derived from our modification of the model (model 2). (B) The vertical line illustrates the switch point (5.135) derived from model 1, and the horizontal line illustrates the switch point (0.31) derived from model 2.

1996). When there is variance in the switch points of individuals within a population, either environmental or genetic in origin (Tomkins, 1999), a large overlap in body size will exist, and many individuals will be misclassified by model 1 (Eberhard and Gutiérrez, 1991; Tomkins, 1999; Tomkins and Simmons, 1996).

For example, in Figure 1, the vertical lines in the graphs indicate the best switch point based on model 1. To the left of the line, individuals are classified as minor morphs, and to the right of the line as major morphs. It is evident that some of the individuals even with the longest horns are erroneously classified as minors (top left of the lines). In addition, some individuals with very small horns are classified as majors (bottom right of the lines). Similar misclassification of minors as majors is evident in Figures 2 and 3. Unfortunately, the overlaps between morphs are very common (Alcock, 1996a; Eber-

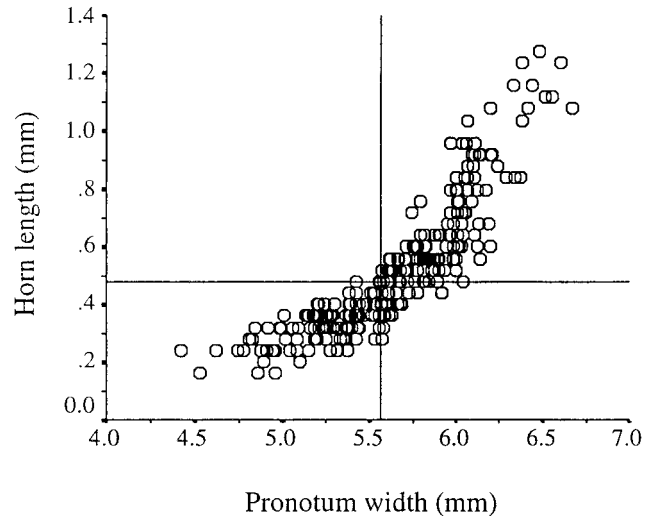


Figure 2
The relationship between pronotum width and horn length in *O. binodis*. The vertical line illustrates the switch point (5.565) derived from the Eberhard and Gutiérrez (1991) original model, and the horizontal line illustrates the switch point (0.48) derived from our modification of model 1 (model 2).

hard and Gutiérrez, 1991; Emlen, 1996; Hunt and Simmons, 1998a; Moczek and Emlen, 1999; Simmons et al., 1999; Tomkins and Simmons, 1999) and are the reason that further statistical discrimination is needed.

Thus, for establishing the body size switch point for a dimorphic trait, which is essential for understanding the ontogeny and evolution of dimorphisms, model 1 is the appropriate model. However, model 1 is not as effective in identifying individuals as either belonging to one morph or another. We suggest a modified methodology that specifically aims for the discrimination of morphs based on the dimorphic character itself, rather than on body size. By modifying model 1 to substitute Y with X and X with Y , we find the switch point in the dimorphic character size that defines the dimorphism, rather than the switch point in body size that defines the dimorphism. In this model (which will be referred to as model 2),

$$X = \alpha + \beta_1 Y + \beta_2 (Y - Y_D) D + \beta_3 D + \epsilon. \quad (2)$$

The terms are as defined in the original model 1 with the exception that the suggested switch point is Y_D and $D = 0$ if $Y < Y_D$, and $D = 1$ if $Y \geq Y_D$. Repeating the calculations discussed with model 1 allows one to statistically test the existence of dimorphism and to find the best switch point that determines the dimorphism similarly as with the model 1. The only difference between the results is that now the switch point is found directly for the dimorphic character itself rather than for a correlate of it—namely, body size.

It may seem inappropriate to use linear regression models and regress X on Y (i.e., independent body size on dependent character size). However, because in the majority of morphometric studies, Y is not strictly dependent on X , and X is not measured without error (the two basic assumptions of linear regression models; Sokal and Rohlf, 1981; Zar, 1996), there is statistical justification for regressing X on Y as well as Y on X .

We illustrate the utility of our modification of the model 1 in the discrimination between morphs by comparing the two models with data from three species: two species of dung beetles with a horn dimorphism (*Onthophagus taurus* [two samples] and *Onthophagus binodis*) and a species of earwig with a forceps dimorphism (*Forficula auricularia*). The first sample of *O. taurus* (Figure 1A) consists of individuals from a field

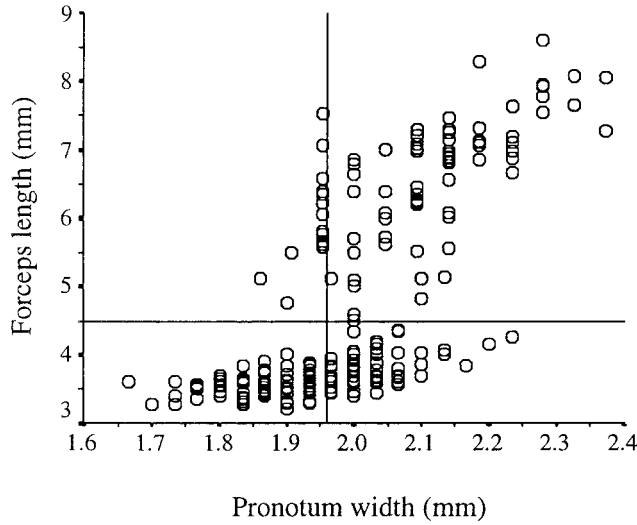


Figure 3
The relationship between pronotum width and forceps length in *O. auricularia*. The vertical line illustrates the switch point (1.960) derived from the Eberhard and Gutiérrez (1991) original model, and the horizontal line illustrates the switch point (4.50) derived from our modification of model 1 (model 2).

Table 1
Statistical tests for dimorphism in *O. taurus* from a field and laboratory population: multiple regressions

Source	β	SE of β	t	Significance
<i>Model 1, field population</i>				
Best switch point ($X_D = 5.100$); dependent variable: horn length (mm); $R^2 = .768$				
Constant	-1.617	0.533	-3.031	.003
Pronotum width	0.378	0.112	3.368	.001
$(X - X_D)D$	3.377	0.223	15.118	.000
D	0.505	0.076	6.647	.000
<i>Model 1, laboratory population</i>				
Best switch point ($X_D = 5.135$), dependent variable: horn length (mm); $R^2 = .790$				
Constant	-7.098	0.381	-18.643	.000
Pronotum width	1.604	0.078	20.693	.000
$(X - X_D)D$	1.086	0.097	11.214	.000
D	0.949	0.031	30.932	.000
<i>Model 2, field population</i>				
Best switch point ($Y_D = 0.201$), dependent variable: pronotum width (mm); $R^2 = .830$				
Constant	4.308	0.023	188.650	.000
Horn length	3.426	0.190	17.990	.000
$(Y - Y_D)D$	-3.258	0.191	-17.084	.000
D	0.052	0.026	2.022	.044
<i>Model 2, laboratory population</i>				
Best switch point ($Y_D = 0.31$), dependent variable: pronotum width (mm); $R^2 = .783$				
Constant	4.142	0.027	150.726	.000
Horn length	2.754	0.156	17.631	.000
$(Y - Y_D)D$	-2.558	0.156	-16.376	.000
D	-0.091	0.026	-3.518	.000

The $(X - X_D)D$ tests the change in the slope, and D tests the discontinuity at the switch point X_D . $(Y - Y_D)D$ tests the change in the slope, and D tests the discontinuity at the switch point Y_D .

population in Margaret River in southwestern Western Australia. These data were first presented in Simmons et al. (1999). The second sample of *O. taurus* (Figure 1B) consists of second generation, laboratory-reared individuals also originating from Margaret River. The sample of *O. binodis* consists of first-generation laboratory-reared individuals originating from Walpole in southwestern Western Australia. The *F. auricularia* were collected from West Wideopen Island in the Farnes group on the northeastern coast of England, and the data were presented first in Tomkins and Simmons (1996).

The best fitting switch point for field-collected *O. taurus*, using model 1, occurred at the pronotum width of 5.100 mm, and the dimorphism at this point was best characterized as being discontinuous (β_3 significantly different from zero) and having a change in the slope (β_2 significantly different from zero; Tables 1 and 2). Using model 2, the best fitting switch point occurred at the horn length of 0.201 mm, and the dimorphism at this point was best characterized as being discontinuous (β_3 significantly different from zero) and having a change in the slope (β_2 significantly different from zero) (Tables 1 and 2). Using model 1, the best fitting switch point for the laboratory-reared *O. taurus* occurred at the pronotum width of 5.135 mm, and the dimorphism at this point was best characterized as being discontinuous (β_3 significantly different from zero) and having a change in the slope (β_2 significantly different from zero; Tables 1 and 2). Using model 2, the best fitting switch point occurred at the horn length of 0.310 mm, and the dimorphism at this point was best characterized as being discontinuous (β_3 significantly different from zero) and having a change in the slope (β_2 significantly different from zero; Tables 1 and 2).

Table 2
Statistical tests for dimorphism in *O. taurus* from field and laboratory populations: ANOVAs

ANOVA	df	SS	MS	F	Significance
<i>Model 1, field population</i>					
Best switch point ($X_D = 5.100$); dependent variable: horn length (mm); predictors: constant, pronotum width, $(X - X_D)D$, D					
Regression	3	363.962	121.321	516.075	.000
Residual	469	110.254	0.235		
Total	472	474.216			
<i>Model 1, laboratory population</i>					
Best switch point ($X_D = 5.135$); dependent variable: horn length (mm); predictors: constant, pronotum width, $(X - X_D)D$, D					
Regression	3	3433.18	1144.39	4637.29	.000
Residual	3707	914.82	0.247		
Total	3710	4348.00			
<i>Model 2, field population</i>					
Best switch point ($Y_D = 0.201$); dependent variable: pronotum width (mm); predictors: constant, horn length, $(Y - Y_D)D$, D					
Regression	3	54.833	18.278	762.981	.000
Residual	469	11.235	0.024		
Total	472	66.068			
<i>Model 2, laboratory population</i>					
Best switch point ($Y_D = 0.31$); dependent variable: pronotum width (mm); predictors: constant, horn length, $(Y - Y_D)D$, D					
Regression	3	220.942	73.647	4459.916	.000
Residual	3707	61.214	1.651E-02		
Total	3710	282.157			

The $(X - X_D)D$ tests the change in the slope, and D tests the discontinuity at the switch point X_D . $(Y - Y_D)D$ tests the change in the slope, and D tests the discontinuity at the switch point Y_D .

Table 3
Statistical tests for dimorphism in *O. binodis*: multiple regressions

Source	β	SE of β	t	Significance
Model 1: best switch point ($X_D = 5.565$); dependent variable: horn length (mm); $R^2 = .849$				
Constant	-0.697	0.183	-3.804	.000
Pronotum width	0.196	0.035	5.597	.000
$(X - X_D)D$	0.535	0.045	11.907	.000
D	2.340E-03	0.018	0.128	.899
Model 2: best switch point ($Y_D = 0.48$); dependent variable: pronotum width (mm); $R^2 = .845$				
Constant	4.320	.071	60.976	.000
Horn length	2.917	.206	14.137	.000
$(Y - Y_D)D$	-1.906	.218	-8.758	.000
D	1.827E-02	.038	.483	.630

The $(X - X_D)D$ tests the change in the slope, and D tests the discontinuity at the switch point X_D . $(Y - Y_D)D$ tests the change in the slope, and D tests the discontinuity at the switch point Y_D .

The best fitting switch point for *O. binodis* using model 1 occurred at the pronotum width of 5.565 mm, and the dimorphism at this point was best characterized as being continuous (β_3 not significantly different from zero) but having a change in the slope (β_2 significantly different from zero) (Tables 3 and 4). Using model 2, the best fitting switch point occurred at the horn length of 0.48 mm, and the dimorphism at this point was best characterized as being continuous (β_3 not significantly different from zero) but having a change in the slope (β_2 significantly different from zero; Tables 3 and 4).

The best fitting switch point for *F. auricularia*, based on model 1, occurred at the pronotum width of 1.959 mm, and the dimorphism at this point was best characterized as being discontinuous (β_3 significantly different from zero) and having a change in the slope (β_2 significantly different from zero; Tables 5 and 6). Using model 2, the best fitting switch point occurred at the forceps length of 4.50 mm, and the dimorphism at this point was best characterized as being discontinuous (β_3 significantly different from zero) and having a change in the slope (β_2 significantly different from zero; Tables 5 and 6).

Table 5
Statistical tests for dimorphism in *F. auricularia*: multiple regressions

Source	β	SE of β	t	Significance
Model 1: best switch point ($X_D = 1.959$); dependent variable: forceps length (mm); $R^2 = .563$				
Constant	-8.605	2.875	-2.993	.003
Pronotum width	6.688	1.532	4.365	.000
$(X - X_D)D$	5.212	1.777	2.933	.004
D	-0.688	.215	-3.194	.002
Model 2: best switch point ($Y_D = 4.50$); dependent variable: pronotum width (mm); $R^2 = .609$				
Constant	.984	.110	8.960	.000
Forceps length	.259	.030	8.680	.000
$(Y - Y_D)D$	-.173	.032	-5.479	.000
D	-.229	.034	-6.693	.000

The $(X - X_D)D$ tests the change in the slope, and D tests the discontinuity at the switch point X_D . $(Y - Y_D)D$ tests the change in the slope, and D tests the discontinuity at the switch point Y_D .

Table 4
Statistical tests for dimorphism in *O. binodis*: ANOVAs

ANOVA	df	SS	MS	F	Significance
Model 1: best switch point ($X_D = 5.565$); predictors: constant, pronotum width, $(X - X_D)D$, D ; dependent variable: horn length (mm)					
Regression	3	11.923	3.974	516.285	.000
Residual	273	2.102	7.698E-03		
Total	276	14.024			
Model 2: best switch point ($Y_D = 0.48$); predictors: constant, horn length, $(Y - Y_D)D$, D ; dependent variable: pronotum width (mm)					
Regression	3	38.616	12.872	500.718	.000
Residual	273	7.018	2.571E-02		
Total	276	45.634			

The $(X - X_D)D$ tests the change in the slope, and D tests the discontinuity at the switch point X_D . $(Y - Y_D)D$ tests the change in the slope, and D tests the discontinuity at the switch point Y_D .

In Figures 1–3, we have plotted the horn lengths of *O. taurus* and *O. binodis* and the forceps length of *F. auricularia* on their respective pronotum widths. As pointed out earlier, it is immediately clear from the figures that the switch points calculated by using model 1 misclassify a substantial proportion of the males. However, by using our model 2, misclassification is notably reduced.

As morphological dimorphisms are frequently associated with alternative reproductive behaviors (Alcock et al., 1977; Cook, 1990; Emlen, 1997; Goldsmith, 1987; Hunt and Simmons, 1998b, 2000; Hunt et al., 1999), only a combination of behavioral and morphological studies can ultimately confirm the correct position of a switch point. In dung beetles, the dimorphism in horn lengths has been shown to be associated with different behaviors. In *O. acuminatus*, major morphs with large horns defend the tunnels in which a female constructs a brood mass, while minor morphs try to sneak copulations (Emlen, 1997). In *O. taurus* and *O. binodis*, major and minor morphs use different tactics in helping the female in brood mass construction; major males help females, whereas minor males do not help (Cook, 1990; Hunt and Simmons, 1998b). However, only one study has examined whether the change in male morphology from one morph to another coincides with the change from one behavior to another. Hunt

Table 6
Statistical tests for dimorphism in *F. auricularia*: ANOVAs

ANOVA	df	SS	MS	F	Significance
Model 1: best switch point ($X_D = 1.959$); predictors: constant, pronotum width, $(X - X_D)D$, D ; dependent variable: forceps length (mm)					
Regression	3	292.687	97.562	99.524	.000
Residual	226	221.546	.980		
Total	229	514.233			
Model 2: best switch point ($Y_D = 4.50$); predictors: constant, forceps length, $(Y - Y_D)D$, D ; dependent variable: pronotum width (mm)					
Regression	3	2.475	.825	117.436	.000
Residual	226	1.588	7.026E-03		
Total	229	4.063			

The $(X - X_D)D$ tests the change in the slope, and D tests the discontinuity at the switch point X_D . $(Y - Y_D)D$ tests the change in the slope, and D tests the discontinuity at the switch point Y_D .

and Simmons (2000) showed that in *O. taurus* the start of horn development coincided with a behavioral change from a nonhelping minor to a helping major morph; furthermore, the change in helping was not continuous but showed an abrupt discontinuity. This abrupt change in behavior accompanied with much less abrupt change in horn lengths (Figure 1) suggests that the biologically correct switch point from minor to major morph in *O. taurus* occurs immediately at the start of horn development and not across a body size threshold per se.

From Hunt and Simmons's study (2000), it is obvious that model 1 sometimes misclassifies many males of *O. taurus* (Figure 1). However, our model 2 performs better and provides us with a horn length switch point that coincides well with the behavioral switch described by Hunt and Simmons (2000).

Other methods of describing dimorphisms in *Onthophagus* have been used. For example, Emlen (1996) modified logistic regressions and nonlinear regressions to determine a switch point for both the pronotum width and the horn length (inflection point and curve height, respectively, in Emlen, 1996). However, in these models the switch point is located at the inflection point of the sigmoidal distribution of horn lengths plotted on pronotum width (Emlen, 1996). Although this model is useful for calculating relative horn size, it may be unsuitable for finding the correct switch point. It is likely that the positions of behavioral and morphological switch points in *O. taurus* are also applicable to other *Onthophagus* species with approximately similar sigmoidal relationships between horn length and pronotum width. Hence, the determination of switch points based on inflection of the sigmoid (Emlen, 1996) is likely to overestimate the position of the real switch point and misclassify a proportion of small majors as minors.

Eberhard and Gutiérrez's (1991) model (model 1) is based on the notion of conditional expression determined by body size. This model is not redundant because it determines the lateral position of the point across which most individuals are likely to change phenotypes, providing a vital component of understanding the evolution and ontogeny of dimorphisms. Our modification (model 2) is not based on body size but rather directly on the dimorphic character of interest and thus is not affected by overlaps in body size between morphs. In all of the four data sets that we analyzed, our modification (model 2) performed better in classifying the morphs than the original model. Our modification provides additional information about the dimorphism and has its primary advantage in discriminating accurately between the alternative phenotypes.

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