

Diet alters male horn allometry in the beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae)

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SUMMARY

Darwin considered the horns of male beetles to be among the most striking examples of sexual selection. As with antlers in deer or elk, beetle horns scale positively with male body size, with the result that large males have disproportionately longer horns than small males. It is generally assumed that such scaling relationships ('static allometries') are insensitive to short-term changes in the environment, and for this reason they are regularly used as diagnostic attributes of populations or species. Here I report breeding experiments on horned beetles that demonstrate that the scaling relationship between male horn length and body size changes when larval nutrition changes. Males reared on a low-quality diet had longer horn lengths at any given body size than sibling males reared on a high-quality diet. Such 'allometry plasticity' may explain seasonal changes observed in this same scaling relationship in a natural population. These experiments demonstrate that scaling relationships of sexually selected traits can respond facultatively to variation in the environment, thereby revealing a new mechanism by which males regulate the production of exaggerated secondary sexual traits.

1. INTRODUCTION

Sexual selection is credited with the evolution of nature's most outrageous traits, including the elongated tails of male peacocks (Petrie & Williams 1993) and birds of paradise (Pruett-Jones & Pruett-Jones 1990), the branched antlers of male elk (Simpson 1953), and the formidable horns of more than a thousand species of beetle (Huxley 1932; Arrow 1951; Eberhard 1979). Sexually selected traits generally exhibit extraordinary intrapopulation phenotypic variation, and discerning the contributions of genetic and environmental factors to this variation remains crucial for understanding how these traits evolve. For many sexually selected traits, variation in trait expression is partially caused by differences in the nutritional status, body size or overall condition of the male bearers ('conditional expression'; e.g. Andersson 1989; Göransson *et al.* 1990; Hill 1990; Ligon *et al.* 1990; Møller 1991). This has important consequences for sexual selection, because it can cause the magnitude of a trait to become positively correlated with a male's physical condition, rendering these traits useful metrics for discriminatory mate choice or rival assessment (reviewed by Andersson 1994).

What is frequently overlooked, however, is that conditionally expressed traits are often sensitive to many different environmental factors (e.g. temperature, moisture, diet). Trait variance caused by some of these factors may alter the relationship between trait size and male condition, and hence the reliability of

that trait as an indicator of male quality (e.g. by reducing the correlation between these variables). It is therefore useful to know precisely how external conditions affect male expression of secondary sexual traits. Unfortunately, the genetic and developmental mechanisms regulating the expression of these traits remain poorly understood for all but a few species (but see Suttie & Kay 1983; Kodric-Brown 1989; Hill 1990; Ligon *et al.* 1990; Møller 1991 for exceptions).

Previously I showed that the horns of one beetle species (*Onthophagus acuminatus* Har. [Coleoptera: Scarabaeidae]) are conditionally expressed (Emlen 1994a); the length of a male's horns depends on his adult body size, which is in turn determined primarily by the environmental (i.e. nutritional) conditions experienced during larval development. Males experiencing favourable conditions have both longer horns and larger adult body sizes than males who experience poorer conditions, resulting in a positive scaling relationship between horn length and male body size (figure 1).

Here I demonstrate an entirely different mechanism by which males vary expression of horns, adding a new level of complexity to studies concerned with ornaments or weapons as reliable indicators of male quality. I show that variation in diet not only influences the absolute length of a male's horns (traditional 'conditional expression'; figure 2a), but also the length of the horns *in relation to body size* (figure 2b). The scaling relationship between male horn length and body size (i.e. the 'static' allometry *sensu* Cock 1966; Gould 1966) shifted in response to experimental manipulation of larval diet, such that males fed a low-quality diet had longer horns at any given body size than sibling males

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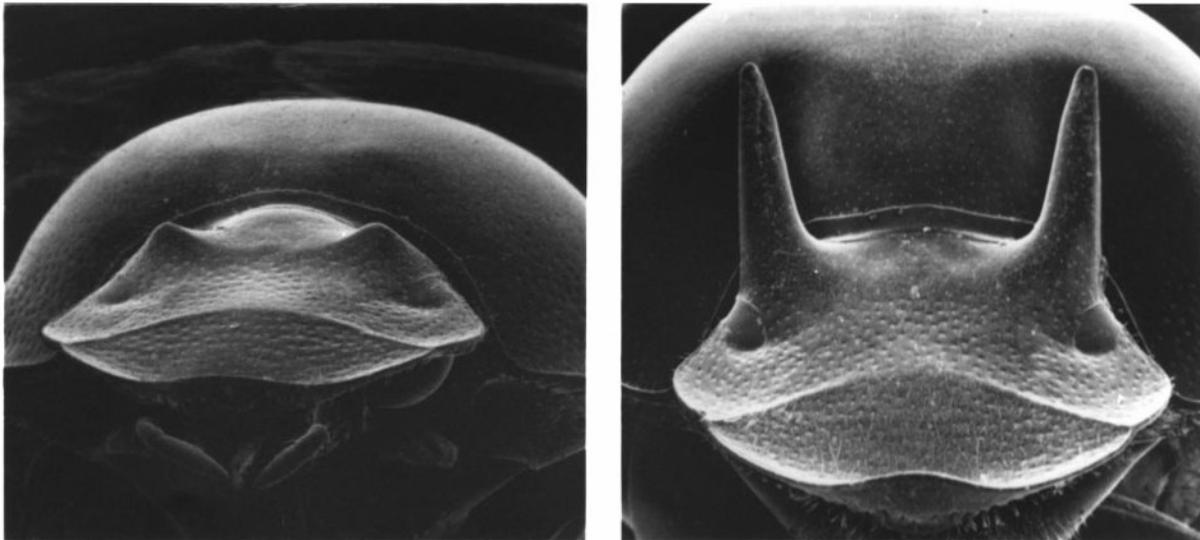
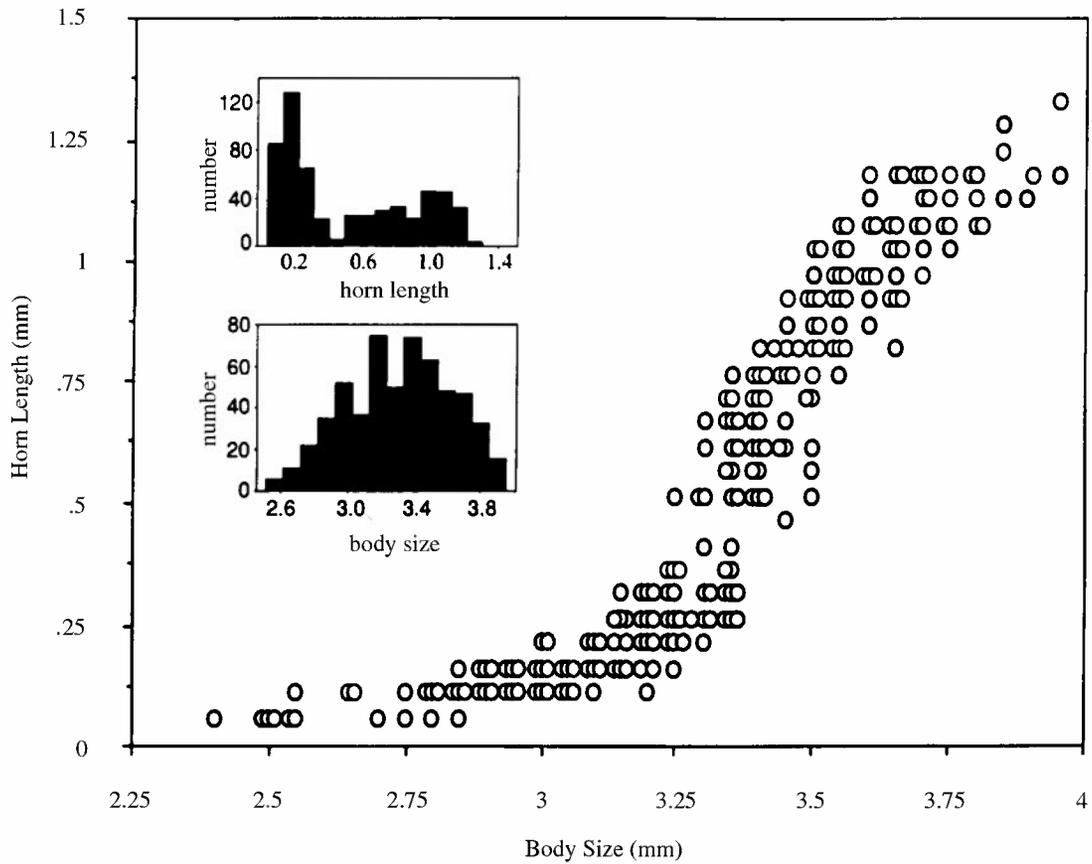


Figure 1. Scaling relationship between horn length and body size (prothorax width) for 600 male *Onthophagus acuminatus* (Coleoptera: Scarabaeidae) sampled from Barro Colorado Island, Panama. The sigmoidal relationship causes male horn lengths to be bimodally distributed (top insert) and separates males into hornless and horned adult shapes. (Photographs: Jorge Ceballos).

reared on a higher-quality diet. I draw on results from a companion study to suggest a possible selective context for this unprecedented developmental mechanism.

The horned beetle *O. acuminatus* is a common diurnal inhabitant of the forest understorey of the Barro Colorado Island Nature Monument, Panama, where it feeds primarily on dung from howler monkeys (*Alouatta palliata*) (Howden & Young 1981; Gill 1991; Emlen 1994a). Beetles fly to monkey dung after it falls to the forest floor, and females dig vertical tunnels in which

they sequester dung for larval provisioning (Emlen 1994a, b). Adult males possess a pair of cylindrical horns that extend vertically from the base of the head. Natural variation in the lengths of these horns is bimodally distributed, and the scaling relationship between horn length and body size has a 'broken', or sigmoid, shape characteristic of many species with morphological dimorphism (e.g. Wilson 1971; Wheeler & Nijhout 1981; Eberhard & Gutiérrez 1991). Males larger than a 'threshold' body size (in this case,

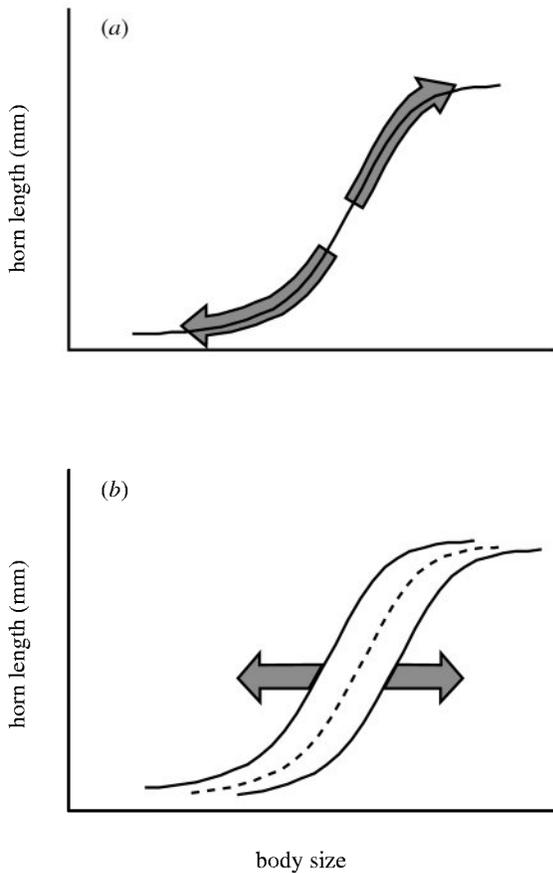


Figure 2. Illustration of the two types of conditional expression of beetle horns. (a) Traditional conditional expression: male horn length depends on the body size attained during development. Environmental conditions affect male horn expression through their effects on body size, not through changes in the scaling relationship. (b) Allometry plasticity: the scaling relationship between horn length and body size is sensitive to changes in the environment, so that males produce relatively longer horns under some conditions than they do under others.

3.35 mm prothorax width) have prominent horns; males smaller than this size have only minute horns, or no horns at all.

Male *O. acuminatus* utilize two very different behavioural tactics to encounter and mate with females: they either guard entrances to tunnels containing females, or they sneak into guarded tunnels and mate with females on the sly (Emlen 1994*b*, 1997). Males larger than most of their competitors guard tunnels; males smaller than most competitors sneak. On Barro Colorado Island (BCI), the body size where males stop guarding and begin sneaking roughly corresponds with the body size separating horned from hornless adult morphologies so that, on average, horned males guard tunnels, and hornless males sneak.

However, monthly samples revealed significant fluctuations in the composition of the BCI population: beetles were significantly larger during the wet–dry and dry–wet season transition periods than they were during either the wet or the dry seasons (Emlen 1994*b*). In theory, these changes in the average body sizes of rival males should shift the body size at which

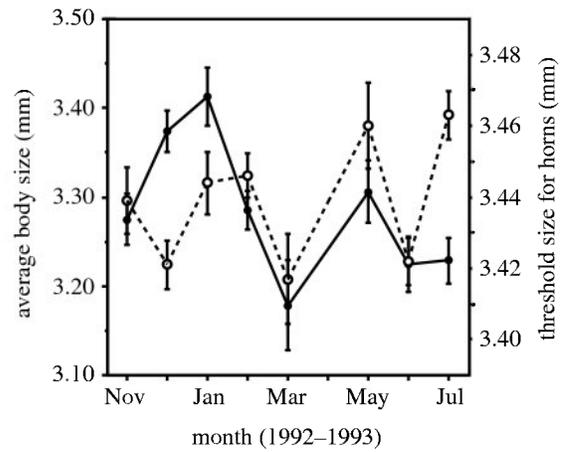


Figure 3. Monthly samples of male *O. acuminatus* collected from Barro Colorado Island, Panama, showing seasonal fluctuations in the average body size of beetles in the population (closed circles), and in the threshold body size separating horned from hornless males (open circles). Bars indicate standard errors. The body size distribution of this population shifted significantly during the course of the year (one-factor ANOVA: $F_{7,909} = 6.119$, $p = 0.0001$), as did the position of the scaling relationship between male horn length and body size (measured as changes in the relative lengths of male horns; one-factor ANOVA: $F_{7,909} = 3.579$, $p = 0.0008$; see text for methods). Shifts in the position of the horn allometry are shown here as changes in the threshold body size at which males began producing horns (the point of inflection of a sigmoid curve fit to each of the monthly samples; see Emlen 1994*b*, 1996 for methods). Seasonal fluctuations in the threshold size for horns roughly tracked similar fluctuations in the body size distribution of the population, although the correlation was not significant ($r = 0.156$, $n = 8$).

males stop guarding and begin sneaking. Unless the scaling relationship between male horn length and body size also shifts, this would result in a poor match between male morphology and male behaviour, with intermediate-sized males often having a horn morphology inappropriate for the behavioural tactic they employ. Remarkably, the scaling relationship did shift significantly during this same year (Emlen 1994*b*). Furthermore, the direction of these shifts strongly suggested that the position of the allometry was in some way tracking the seasonal fluctuations in the body size distribution of the population (figure 3); when the average body size was large, the sigmoidal allometry shifted to the right (males began horn production at a larger ‘threshold’ body size): when the average body size was small, the allometry shifted to the left (males began horn production at a smaller body size).

Two observations indicated that these seasonal shifts in the scaling relationship between horn length and body size might be a plastic response to variation in the environment. First, in an experiment selecting for variation in the allometry, four selected and two control lines all showed large, correlated fluctuations across generations (Emlen 1996). This suggested that the scaling relationships of these genetic lines were all shifting in response to some environmental parameter not controlled for in the laboratory. Second, the seasonal shifts observed in the natural population occurred too rapidly for an evolutionary change to be

likely (on the order of a single beetle generation). I tested directly for phenotypic plasticity in the expression of male horn allometry by bringing beetles into the laboratory and subjecting larvae to controlled variation in two nutritional factors. I chose to vary diet quality and diet amount because each of these factors strongly affects growth in this species (Emlen 1994*a, b*), because each varies under natural conditions, and because each could have varied during the artificial selection experiment described above (see methods of Emlen 1996).

2. MATERIALS AND METHODS

(a) *Experimental methods*

Beetles were reared in the laboratory (Emlen 1994*a, b*) by placing pairs of adults in deep containers filled with potting soil and supplied with dung. Females dug tunnels in the containers, pulled small pieces of dung below ground and packed these into a series of dense 'brood balls' (Halffter & Edmonds 1982). Each brood ball contained a single egg, and constituted the total food supply for the developing larva. Brood balls were extracted from containers by sifting the soil, and each was buried individually in a soil-filled cup for the duration of development (mean development time \pm s.d. = 29.6 ± 2.37 d, $n = 191$). Body sizes (prothorax widths) and horn lengths of all males were measured on emergence with a stereomicroscope ocular micrometer (correlation coefficients for blind repeated measurements of 27 males: prothorax width, $r = 0.995$; horn length, $r = 0.997$), and the horn length–body size scaling relationships were compared across experimental treatments. Females do not produce horns, and were not included in these analyses.

To vary diet quality I gave breeding pairs either howler monkey dung alone ('high' quality), or a 50:50 mixture of howler monkey dung and cow manure ('low' quality). Although *O. acuminatus* on BCI primarily feed on dung from howler monkeys, this species has been collected in cow manure at the perimeter of the protected forest (on the mainland surrounding Barro Colorado Island), as well as in other parts of its range (personal observation). Cow manure was considered low quality food because a prior study revealed that beetles fed 100% cow manure had poor survivorship and emerged at very small body sizes (Emlen 1994*b*). For the present study, dilution of howler monkey dung by 50% with cow manure was sufficient to reduce the body sizes of beetles with only a minimal reduction in survivorship. Twenty-six beetle pairs were randomly given dung from one of the two treatments and allowed to breed for three days. During this time, beetles pulled dung into tunnels beneath the soil surface to form the brood balls. After three days the soil was sifted, and all brood balls were removed. The same beetle pairs were then given a new supply of dung from the alternative treatment, and bred for an additional three days. All brood balls from both treatments were buried individually in soil-filled cups for the duration of larval development ($n = 328$ brood balls).

To vary food amount, I manipulated the sizes of larval brood balls (methods described more fully in Emlen 1994*a*). Thirty beetle pairs were bred as above, except that beetles were given only howler monkey dung. Eight brood balls were collected from each breeding pair and divided among two experimental treatments: I added dung to four of the brood balls from each pair (mean volume \pm s.d. for 'large' brood balls = 2.41 ± 0.74 cm³), and removed dung from the remaining four brood balls of each pair (mean volume \pm s.d. for 'small' brood balls = 0.37 ± 0.07 cm³). Once size-adjusted,

all brood balls were stored individually in soil-filled cups as above ($n = 240$ brood balls).

(b) *Analyses*

To test for treatment effects on the scaling relationship between horn length and body size, I needed to incorporate measures of both horn length and body size into a single value effectively describing male shape. In particular, I needed to compare the relative horn lengths of individual males after accounting for their respective body sizes. To do this, I used data from wild-caught males to describe the average relationship between male horn length and body size. The equation giving the best fit to this relationship:

$$\text{horn length} = 0.743 + \left\{ \frac{2.24}{1 + \left(\frac{2.24}{0.04} - 1 \right) \exp(-0.892 [\text{body size} - 2.35]^{2.02})} \right\} \quad (1)$$

(see Emlen 1996 for derivation of this equation) was used to calculate 'average' horn lengths for males of all possible body sizes. Individual males could then be characterized as having unusually long or short horns for their respective body sizes by comparing their actual horn length to the horn length expected for an 'average' male of the same body size (i.e. by calculating residual horn lengths from equation (1)).

Residual horn lengths were calculated for all emerging males as actual horn length minus the horn length predicted for a male of the same body size from equation (1). As shifts in the position of the allometry are manifest as changes in the relative lengths of male horns (Emlen 1996), residual horn length provided an appropriate metric for comparing males in the different treatment populations. Residual horn lengths of males from each of the treatment populations were compared using analyses of variance (ANOVA); the sample variance of males reared on high-quality food was compared to that of males reared on low-quality food, and the sample variance of males reared on large amounts of food was compared to that of males reared on small amounts. To account for the possible non-independence of sibling males, I used a nested (hierarchical) ANOVA design (Zar 1984), with diet treatment nested within family.

3. RESULTS

Diet quality significantly affected the horn length–body size allometry, whereas diet amount did not (figure 4). Males reared on large amounts of food were larger than males reared on smaller food amounts (nested ANOVA on progeny body size, food amount nested within family: $F_{23,38} = 10.583$, $p = 0.0001$), but the relationships between horn length and body size did not differ (nested ANOVA on progeny residual horn length, food amount nested within family: $F_{23,38} = 0.811$, $p = 0.6974$). However, experimental manipulation of diet quality affected both adult body size and horn length–body size allometry. Males reared on high-quality food were larger (nested ANOVA on progeny body size, diet quality nested within family: $F_{17,61} = 3.756$, $p = 0.0001$), but also had disproportionately shorter horn lengths (nested ANOVA on progeny residual horn length, diet quality nested within family: $F_{17,61} = 3.082$, $p = 0.0006$) than did males reared on low-quality food. Consequently, males expressed different scaling relationships between horn length and body size, depending on the nutritive quality (but not amount) of dung experienced as larvae.

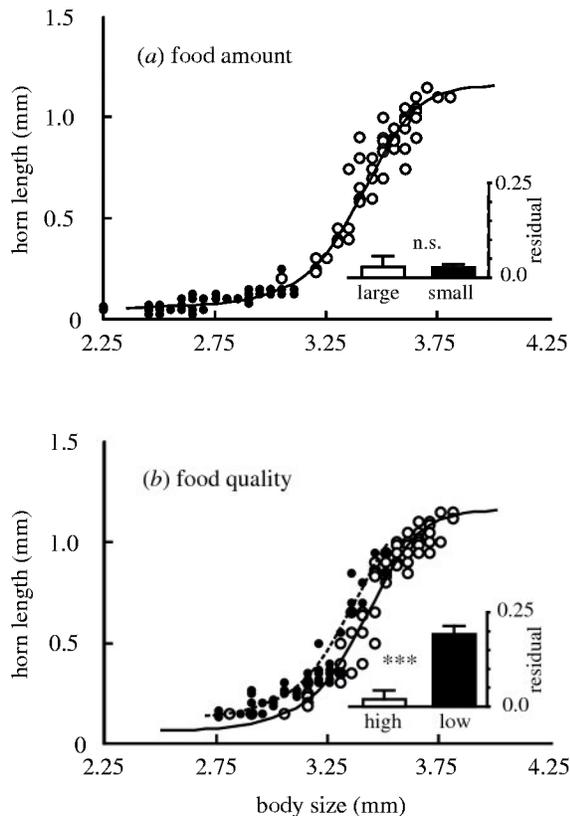


Figure 4. Effects of induced variation in larval food amount and food quality on the scaling relationship between horn length and body size. Residual horn lengths were calculated for all emerging males as actual horn length minus the horn length predicted for a male of the same size using the equation shown by the solid curved line in each figure. Residual horn lengths were pooled for all males within each treatment population (bar graph inserts), and compared across treatments using analyses of variance (see text). (a) Relative horn lengths of males fed small (closed circles) and large (open circles) food amounts did not differ (nested ANOVA, food amount nested within family: $F_{23,38} = 0.811$, $p = 0.6974$). (b) In contrast, males fed low-quality food (closed circles) had longer horn lengths for their body sizes than males fed high-quality food (open circles) (nested ANOVA, food quality nested within family: $F_{17,61} = 3.082$, $p = 0.0006$), resulting in a lateral displacement of the position of the allometry of these males (approximated by the dashed line). Consequently, the scaling relationship between horn length and body size is altered depending on the nutritive quality (but not amount) of dung experienced as larvae.

Although male residual horn length has been shown to exhibit heritable variation under artificial selection (Emlen 1996), such variation was not detected under the present experimental conditions. Family effects were not significant in any of the comparisons (diet amount experiment: progeny body size, $F_{29,38} = 0.265$, $p = 0.9995$, progeny residual horn length, $F_{29,38} = 1.679$, $p = 0.1030$; diet quality experiment: progeny body size, $F_{25,17} = 0.932$, $p = 0.5739$, progeny residual horn length, $F_{25,17} = 0.892$, $p = 0.6120$).

4. DISCUSSION

This study demonstrates an environmentally induced lability of a bivariate scaling relationship. The allometric relationship between male horn length and

body size shifted, so that over a similar range of body sizes, male beetles fed high-quality food had relatively shorter horn lengths than sibling males reared on poorer quality food.

(a) Relevance to sexual selection theory

A current focus in the study of sexual selection concerns how costly or exaggerated male traits are inherited and, in particular, whether these traits are conditionally expressed (Zeh & Zeh 1988; Kodric-Brown 1989; Hill 1990; Andersson 1994). One important class of models for trait evolution by sexual selection, the 'indicator' models (also called 'honest advertisement' and 'handicap' models; reviewed by Andersson 1994), predicts that secondary sexual traits can spread and persist within a population if variation in the expression of the trait honestly reveals, or indicates, underlying differences in the viability, physical condition and/or genetic quality of males (reviewed by Andersson 1994). These models have received recent support because it is now apparent that many secondary sexual traits are conditionally expressed, at least to some degree (M. Andersson 1986; S. Andersson 1989; Kodric-Brown 1989; Göransson *et al.* 1990; Hill 1990; Ligon *et al.* 1990; Møller 1991). Here I show that the process of conditional expression can be much more complicated than is generally considered.

Male horns in *O. acuminatus* exhibit traditional conditional expression: a male's horn length depends on how large it grows to be, which is directly influenced by the nutritional conditions that it encounters during development (figure 2a). This results in a tight (though nonlinear) correlation between male horn length and body size in natural populations (figure 1), and implies that variation in male horn length should indicate true differences in male fighting ability.

However, male horns in this species are conditionally expressed in an additional way (figure 2b). I show here that the scaling relationship between horn length and body size is itself sensitive to changes in the environment. Males consistently altered their pattern of allocation to horns in response to changes in one nutrition factor (diet quality), but not to changes in another (diet amount).

The possibility that trait allometries may be sensitive to specific changes in the environment has not previously been considered, and presents new possibilities for studies of sexual selection. For example, by identifying those conditions that influence the production of a trait, and those that do not, scientists can begin to relate aspects of the ecology of a species with patterns of selection on the exaggerated morphology of males. Here I use results from a companion field study to begin to provide such a context for plasticity of horn allometry in *O. acuminatus*.

(b) Sexual selection in *Onthophagus acuminatus* populations

Why might horn allometry respond to food quality but not to food amount? To address this we must

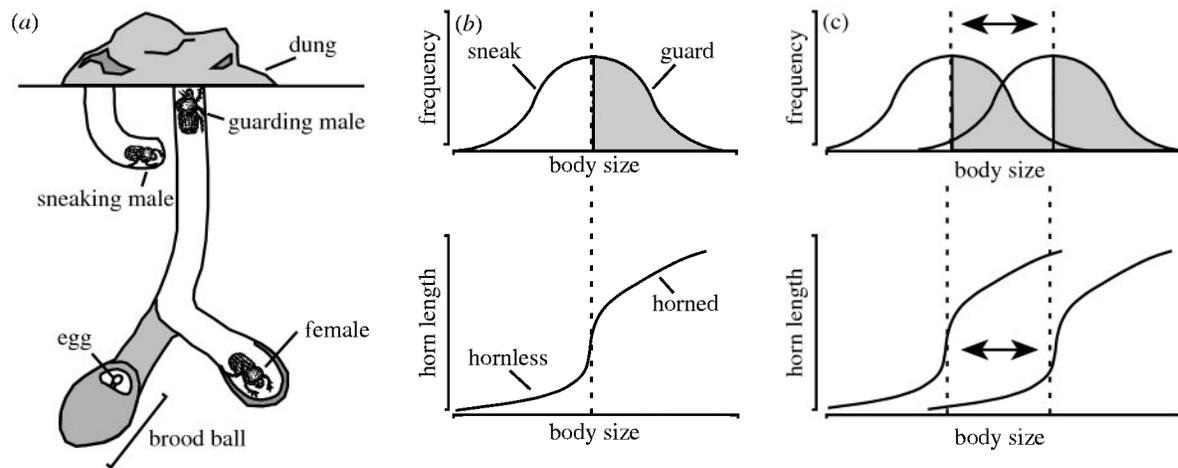


Figure 5. Model for sexual selection on male horns and horn allometry in *O. acuminatus*. (a) Illustration of the two reproductive behavioural tactics employed by males. Females dig tunnels beneath pieces of howler monkey dung, and pull dung to the ends of the tunnels to provision larvae. Males encounter females either by 'guarding' the entrances to these tunnels, or by 'sneaking' into tunnels through side-tunnels that intercept guarded tunnels below ground. Guarding and sneaking behaviours select differently for male horns. Horns help guarding males by blocking the entrance from intruders, whereas horns hinder sneaking males by bumping against tunnel walls as they move underground (Emlen 1994*b*, 1997). Disruptive selection should favour a correlation between male behaviour and male horn morphology, with all guarding males horned, and all sneaking males hornless. (b) Male behaviour depends on relative body size. Larger males guard (shaded area under top curve) and smaller males sneak (open area). Horn morphology and behaviour correlate perfectly whenever the horn length–body size allometry (bottom) is positioned along the body size axis such that the body size separating horned from hornless morphologies (i.e. the inflection of the sigmoid curve) coincides with the body size where males switch from guarding to sneaking behaviours (dashed line). (c) Environmental factors that change the body size distribution of the population (e.g. seasonal changes in the quality of howler monkey dung) should shift the 'optimal' relationship between horn length and body size.

understand (i) how food quality and amount vary under natural conditions, and (ii) whether this variation is likely to affect how selection acts on horns.

The amount of dung available to a larva depends primarily on the amount of dung the parent female has access to during provisioning. On BCI, competition for howler monkey dung is erratic, and can be extreme. Whether females have access to dung for 15 min or 10 h depends on how many other dung beetles arrive to compete for it, and this, it turns out, is extraordinarily variable (Emlen 1994*b*; D. J. Emlen, unpublished data). For example, when the morning rains occur before the dung drops to the forest floor, or when the dung falls through heavy foliage so that lots of fragments remain stuck to branches, many thousands of beetles arrive (presumably because the odour persists at the site; personal observation). When the rains occur just after the dung falls, or when the monkeys are low down in the trees, so that dung falls directly to the forest floor (without fragmenting on branches), very few beetles find the site. Hence dung availability to a provisioning parent female can vary tremendously from day to day, as well as from site to site. Consequently, while the amount of dung provided to a developing male larva may influence how large he grows to be, it is not likely to reveal much about how large other males growing in other parts of the population will be.

In contrast, the quality of dung on BCI varies much more consistently and gradually, and does appear to affect the entire population simultaneously. Dung quality varies seasonally because the howler monkeys alter their foraging behaviour: monkey diets shift from

mixtures of fruits and leaves to primarily leaves, depending on the fruit and leaf-flush phenologies of the available food plants (Milton 1982, 1991). Howler monkey digestive efficiencies differ for fruit and leaf diets (Milton *et al.* 1980), and monkey dung from these diets has different energy contents (Nagy & Milton 1979). By affecting all growing beetles similarly, seasonal changes in dung quality probably contribute to the large, seasonal fluctuations in the body size distribution observed in the natural beetle population (figure 3; Emlen 1994*b*). If so, then the quality of dung available to a growing male, in addition to influencing that male's own body size, might also contain information about the likely sizes of other males growing simultaneously. Consequently, dung quality (but not amount) may at least partially predict changes in the size distribution of the beetle population.

But why are the sizes of other males in the population so important? Sexual selection on male horns results from male reproductive behaviours (Emlen 1994*b*, 1997). Males employ two distinct tactics to encounter females (guarding and sneaking), for which different horn lengths are appropriate (figure 5*a*). Horns aid males in tunnel defence (guarding), but appear to hinder sneaking (Emlen 1994*b*, 1997). Disruptive selection generated by this mating system should favour males able to facultatively express horns only when they are likely to guard tunnels.

On BCI, whether a male guards or sneaks appears to depend on his relative body size: males larger than most of their competitors guard, and males smaller than most of their competitors sneak. In this situation, male mating tactic and male horn morphology will

best coincide whenever males begin horn production at the same body size that they switch between guarding and sneaking tactics (figure 5*b*).

However, the size distribution of the natural population fluctuates significantly during the course of the year (figure 3; Emlen 1994*b*). Such changes in the average sizes of males in the population might be expected to favour corresponding shifts in the scaling relationship between horn length and body size (figure 5*c*), so that intermediate-sized males continue to produce horn morphologies appropriate for the behavioural tactic they employ. If fluctuations in the body size distribution of the wild population are even partially caused by seasonal changes in dung quality, then the plasticity of allometry revealed in this study would produce exactly this response: when dung quality is high and most individuals grow large, males would begin horn production at a larger critical body size than when dung quality was low and most individuals were small. In this situation males able to modify their horn production in response to variation in dung quality might produce more appropriate horn lengths, on average, than males responding to less predictive environmental variables, or males not responding at all.

In fact, the scaling relationship of the BCI population did shift significantly during this same year, and in roughly the same directions as the changes in the body size distribution of the population: during the seasons when the average body sizes were the largest (the dry–wet and wet–dry season transition periods), the allometry had shifted to the right, whereas when the average body sizes were smallest (the dry season and late wet season), the allometry had shifted to the left (figure 3; Emlen 1994*b*). Further studies are needed to directly link natural changes in howler monkey dung with these shifts in horn allometry. However, this pattern suggests that the plastic mechanism identified in this laboratory study may be responsible for the seasonal shifts in horn allometry observed in the natural population. Consequently, I suggest that diet-induced shifts in the male horn length–body size allometry of *O. acuminatus* may be adaptive responses to predictable seasonal fluctuations in the horn selection environment.

(c) Are scaling relationships in other taxa similarly flexible?

Plasticity in the expression of scaling relationships might be expected for other sexually selected male traits, such as antlers in deer and tail length in birds, because selection for these allometries also depends on a male's relative body size or condition. I suggest that such plasticity may have been overlooked. Bi- or multivariate scaling relationships are frequently estimated from museum specimens or other samples collected over a wide geographic range and over long time periods. This would tend to obscure any environmental effects on patterns of trait expression by averaging over many different sets of conditions. Studies that avoid these problems, for example by sampling over a brief period and from a single

population, also tend to be conducted in the laboratory under uniform environmental conditions. Hence it is possible that plasticity of trait allometries is a general phenomenon, but that the nature of sampling has rendered its detection unlikely.

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