

Status-dependent selection in the dimorphic beetle *Onthophagus taurus*

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The occurrence of alternative reproductive phenotypes is widespread in most animal taxa. The majority of known examples best fit the notion of alternative tactics within a conditional strategy where the fitness pay-offs depend on an individual's competitive ability or status. Individuals are proposed as 'choosing' the tactic that maximizes their fitness, given their status relative to others in the population. Theoretically, status-dependent selection should determine when an animal should switch between alternative tactics. While a number of studies have demonstrated unequal fitness pay-offs associated with alternative tactics, none, to our knowledge, have examined the fitness functions necessary for predicting when individuals should switch between tactics. Here, we use a dimorphic male beetle in order to provide the first empirically derived fitness function across alternative reproductive phenotypes. Our data provide empirical support for a game-theoretic conditional strategy that has evolved under status-dependent selection.

Keywords: alternative reproductive phenotypes; conditional strategy; status-dependent selection; *Onthophagus taurus*

1. INTRODUCTION

Variation in male phenotype and reproductive behaviour is found in many species where males compete for access to mates. Game theory offers three means by which phenotypic diversity within a sex may arise: alternative strategies, a mixed strategy or a conditional strategy (Gross 1996). Each of these strategies has a clear set of conditions that are necessary if they are to be maintained in the population. These conditions enable alternative reproductive phenotypes to be studied in relation to their costs and benefits to evolutionary fitness (Gross 1996).

Individuals adopting alternative strategies are required to be genetically polymorphic, with at least one of the alternatives being negatively frequency-dependent, thereby yielding an evolutionarily stable strategy frequency of alternative phenotypes at which the average fitnesses of the alternatives are equal (Maynard Smith 1982; Gross 1996). Individuals adopting a mixed strategy are required to be genetically monomorphic, but display a probabilistic mix of the alternative reproductive tactics. Again, alternative tactics should yield average equal fitnesses that are provided by frequency-dependent selection on the frequency with which each is played (Maynard Smith 1982; Gross 1996). A number of studies have provided partial support for the maintenance of alternative phenotypes through alternative strategies, such as genetic determination of phenotypes (Shuster & Wade 1991; Ryan *et al.* 1992; Lank *et al.* 1995), equal fitness pay-offs (Gross 1985; Shuster & Wade 1991; Ryan *et al.* 1992) and the operation of frequency-dependent selection (Gross 1991; Sinervo & Lively 1996). However, further tests are needed for each of these systems in order to satisfy all the requirements necessary for alternative strategies to operate (Gross 1996). Likewise, while a mixed reproductive strategy is theoretically conceivable,

there is currently no empirical support for such a strategy operating within a sex (Gross 1996).

The majority of known alternative reproductive phenotypes are most readily interpreted as alternative tactics within a conditional strategy (Gross 1996). Individuals must be genetically monomorphic in order for alternative tactics to constitute a conditional strategy, and are required to make a decision regarding the tactic they employ based on their relative status in the population. The average fitnesses of the tactics should be unequal, but the chosen tactic should result in higher fitness for the individual relative to the alternative (Gross 1996). Gross (1996) proposed that, within a conditional strategy, the ability of individuals in choosing the appropriate tactic occurs through status-dependent selection. When the relative fitnesses of the alternative tactics depend on the competitive state of an individual and this state also determines the fitness that can be attained from a given phenotype, individuals will differ in their 'status'. Theoretically, the rate of increase in fitness with status (the fitness function) should differ between alternative tactics. The point at which the fitness functions of the alternative tactics intersect will be the evolutionarily stable switch point at which both tactics yield equal fitness. Thus, the tactic that yields the highest fitness for the individual will change with status so that individuals of high status will obtain greater fitness by adopting one tactic, while individuals of low status obtain greater fitness by adopting the alternative tactic. An individual is able to express the phenotype that maximizes their fitness by incorporating information about their status relative to a switch point (Gross 1996).

While a large number of studies have demonstrated unequal fitness pay-offs associated with alternative tactics (Brockman *et al.* 1994; Moran *et al.* 1996; Elisabeth & Taborsky 1997; Foote *et al.* 1997; Tsunenori 1998; Coltman *et al.* 1999; Fuller 1999), to our knowledge, no study to date has fulfilled the complete set of criteria required for demonstrating a conditional strategy convincingly (Gross

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1996). Furthermore, many systems have demonstrated that individuals increase their fitness through status-dependent selection. Thus, studies demonstrating the operation of status-dependent selection are urgently required for many systems claiming a conditional strategy.

Male dung beetles (*Onthophagus taurus*) are dimorphic in their body plan, with large 'major' males developing head horns and small 'minor' males remaining hornless (Hunt & Simmons 1997). The alternative phenotypes are associated with alternative mate-securing tactics, with major males fighting for access to females and minor males sneaking copulations (Moczek & Emlen 2000). Competitive ability is dependent on both body size and horn length within horned males (Moczek & Emlen 2000). Alternative phenotypes are also associated with alternative parental tactics, with major males assisting females in the provisioning of their offspring (Hunt & Simmons 2000). The behavioural switch between paternal non-provisioning and provisioning occurs at the pronotum width where males begin to develop horns, and it seems likely that the switch between alternative mate-securing tactics similarly coincides with the development of horns. The development of horns is determined by a hormonal switch, which governs the developmental trajectory of larvae (Emlen & Nijhout 1999). The hormonal switch is triggered by the amount of dung provided in the brood mass; larvae developing in small brood masses do not have the resources for growing large (Hunt & Simmons 1997; Moczek & Emlen 1999) and receive a pulse of ecdysteroid that inhibits the development of horns (Emlen & Nijhout 1999). Experiments manipulating brood mass size have shown that the switch between alternative phenotypes is facultative and that individuals are genetically monomorphic for the expression of alternative phenotypes (Hunt & Simmons 1997; Moczek & Emlen 1999).

In this study we provide, to the authors' knowledge, the first empirically derived fitness functions across alternative phenotypes in the dung beetle *O. taurus*. We show that the fitness function across the alternatives is nonlinear and that the average fitnesses of the two tactics are unequal. Our results support the hypothesis that alternative reproductive tactics in *O. taurus* are maintained through status-dependent selection within a conditional strategy. Thus, by gauging their nutritional environment larvae appear to choose the developmental trajectory that will theoretically yield them the greatest fitness returns for their future adult status.

2. METHODS

(a) *Experimental animals*

Approximately 500 females were collected from cattle pastures using baited pit traps in Margaret River, Western Australia. The females were maintained in the laboratory for 2 weeks with constant access to fresh cow dung in order to ensure that all individuals were reproductively mature and in optimal condition. The females were then established in individual breeding chambers (PVC piping of 25 cm in length and 6 cm in diameter) that were three-quarters filled with moist sand and 0.25 l of cow dung, and maintained for 1 week. The chambers were then sieved and brood masses were removed. The brood

masses were buried in moist sand and maintained at 25 °C until emergence. Emerging beetles were collected and the females maintained for 2 weeks in single-sex populations with constant access to fresh dung. Prior to use in experiments, the pronotum widths of all females were measured using digital callipers.

Approximately 4000 males were collected from the same cattle pasture in Margaret River when virgin females had begun to emerge. The males were maintained in populations for 2 weeks with constant access to fresh dung. Prior to use in experiments, the pronotum widths and horn lengths of the males were measured using digital callipers and an eyepiece graticule in a binocular microscope, respectively.

(b) *Statistical determination of male morphology*

We used the method of Eberhard & Gutiérrez (1991) for determining the position of the morphological switch point between major and minor males in the field sample of males used for our experiments. First, the relationship between their pronotum widths and horn lengths was examined in order to assess nonlinearity across males. Nonlinearity is expected if there is a critical body size at which beetles switch to producing a major phenotype. In order to assess linearity we fitted the partial regression equation

$$\ln^* = \alpha_0 + \alpha_1 x^* + \alpha_2 x^{*2} + \varepsilon, \quad (2.1)$$

where \ln^* is the natural log of horn length, x^* is the natural log of pronotum width, the α_i s are the regression coefficients and ε is the random component with an assumed normal distribution, a mean of zero and a homogeneous variance (Eberhard & Gutiérrez 1991). An α_2 that differs significantly from zero confirms nonlinearity and the possible existence of a switch point. The relationship between pronotum width and horn length differed significantly from linearity in our sample of male *O. taurus* ($\alpha_2 = 12.211.00$, $t = 12.18$, $n = 1500$ and $p = 0.0001$).

Next, we examined the data for the presence of a switch point, i.e. a pronotum width at which beetles switched their developmental pathways in order to grow horns. We fitted the partial regression equation

$$y = \beta_0 + \beta_1 x + \beta_2 (x - x^0)D + \beta_3 D + \varepsilon, \quad (2.2)$$

where y is horn length, x is pronotum width, x^0 is the proposed switch point, with $D = 0$ when $x < x^0$ and $D = 1$ otherwise, the β_i s are the regression coefficients and ε is the random component (Eberhard & Gutiérrez 1991). In order to determine which switch point gave the best fit, 20 different hypothetical switch points (ranging from 4.7 to 5.3 mm) were substituted into equation (2.2) and an adjusted R^2 calculated for each. This produced a range of R^2 values (0.685–0.707) from which the pronotum width corresponding to the maximum R^2 value was taken as the most likely switch point. This occurred over a range of pronotum widths (4.90–4.94 mm inclusive), the mean of which was 4.92 ± 0.007 mm (figure 1).

β_3 was significantly greater than zero in equation (2.2) when using this switch point ($\beta_3 = -0.07 \pm 0.03$, $t = 2.30$, $n = 1500$ and $p = 0.02$), thereby confirming the presence of a switch point at which horn size was discontinuous (Eberhard & Gutiérrez 1991). Finally, we tested the change in the linear slope of horn length and pronotum width at the switch point by fitting a modified version of equation (2.2) in which $\beta_3 D$ is removed and the significance of β_2 assessed (Eberhard & Gutiérrez 1991). There was a significant change in the linear slope at the switch point ($\beta_2 = 3.79 \pm 0.07$, $t = 56.70$, $n = 1500$ and $p = 0.0001$). Thus,

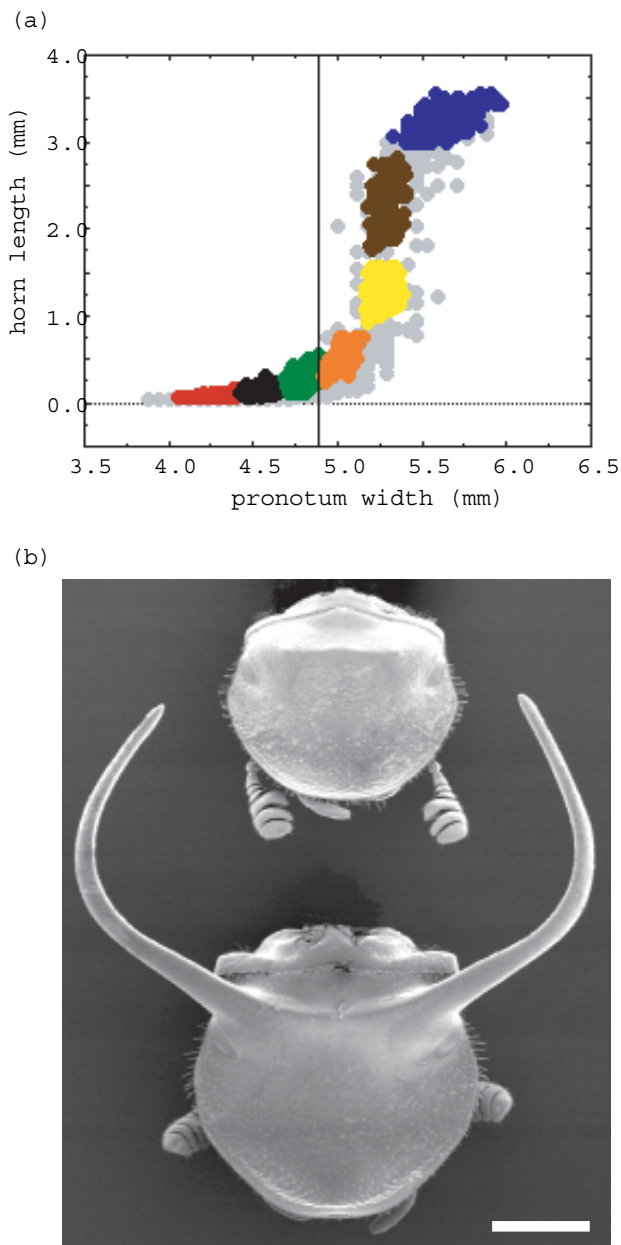


Figure 1. (a) The scaling relationship between pronotum width and horn length found in the natural population from which beetles were drawn (grey symbols). Individuals selected for experimental populations are depicted in the seven phenotypic classes (which are distinguished by colour). The position of the morphological switch point between alternative phenotypes is shown by the vertical line (see §2b for calculation). (b) Scanning electron micrographs of the heads of a minor male (top) showing the rudimentary 'nodes' from which the horns arise in major males (bottom). The scale bar represents 1 mm.

males with a pronotum width ≥ 4.92 mm were classified as major males and males with a pronotum width < 4.92 mm were classified as minor males (figure 1).

(c) *Experimental populations*

Beetles arrive at fresh dung *en masse*, with as many as 25 individuals per minute after deposition arriving at experimental dung pads in the field (Hunt *et al.* 1999). The arriving sex ratio

is typically constant at 1:1. However, minor males arrive in excess of major males and also remain in the dung longer than major males (Hunt *et al.* 1999). Thus, minor males make up *ca.* 60% of the breeding male population (Hunt *et al.* 1999; Simmons *et al.* 1999). Females excavate breeding tunnels immediately on arrival at the dung pad.

In order to ensure that fertilization success was examined across the full range of male phenotypes, we selected males across seven classes based on pronotum width (class 1 = 4.05–4.40 mm, class 2 = 4.41–4.67 mm, class 3 = 4.70–4.90 mm, class 4 = 4.91–5.15 mm, class 5 = 5.16–5.36 mm, class 6 = 5.16–5.36 mm and class 7 = 5.40 mm) and horn length (class 1 = 0.06–0.16 mm, class 2 = 0.06–0.31 mm, class 3 = 0.13–0.56 mm, class 4 = 0.25–0.75 mm, class 5 = 0.94–1.75 mm, class 6 = 1.76–2.81 mm and class 7 = 3.0–3.56 mm) (figure 1). Based on the fit of the data to the models of Eberhard & Gutiérrez (1991) described above, males in classes 1–3 represent the minor phenotype and those in classes 4–7 represent the major phenotype. Populations that consisted of 10 males selected from across the phenotypic size range (two males from classes 1–3 and one male from classes 4–7) and 10 randomly selected laboratory-reared virgin females were established. The frequency of minor to major males and males to females in our populations thereby simulated the natural frequencies found in field populations (Hunt *et al.* 1999; Simmons *et al.* 1999).

We measured the reproductive success of focal males within populations using the sterile male technique (Boorman & Parker 1976). Preliminary experiments involving a range of doses from 5 to 20 krad of gamma irradiation from a ^{60}Co source showed that 11 krad was the optimal dose for these experiments; $99.11 \pm 0.89\%$ of eggs fertilized by sperm from irradiated males failed to hatch, but the dose had no impact on male viability for the first 5 days following irradiation (irradiated proportion surviving, 0.95 ± 0.04 and normal proportion surviving, 1.0 ± 0.0) ($t = 1.45$, d.f. = 18 and $p = 0.16$). Neither irradiation nor the time since irradiation influenced the time taken for males to initiate courtship (main effect irradiation, $F_{1,39} = 2.50$ and $p = 0.12$, time since irradiation, $F_{2,39} = 0.08$ and $p = 0.92$ and interaction $F_{2,39} = 1.15$ and $p = 0.33$) or their ability to obtain matings (28.57% of normal males ($n = 21$) mated during 60 min of observation as compared with 33.3% of irradiated males ($n = 24$)) ($\chi^2_1 = 0.12$ and $p = 0.74$).

An individual from one phenotypic class was selected for each population and irradiated; background males were normal and focal males were irradiated. A total of 10 replicate populations were established for each of the seven male phenotypes. A further 10 replicate populations per male phenotype were established, in which the focal male remained fertile but the remaining nine background males were irradiated. Natural levels of fertility and sterility were assessed for the irradiated and fertile populations for 10 populations, half of which were where all males were fertile and half of which were where all males were irradiated.

The populations were housed in individual plastic buckets (26 cm in height and 27 cm in diameter) that were three-quarters filled with moist sand and 1 litre of cow dung. Virgin females were introduced and allowed to establish breeding tunnels before males were added. The populations were maintained for 5 days before being sieved and their brood masses collected. The females in each population were re-established for a further week and then sieved and their brood masses collected again. The brood masses were maintained for 4 days at 25 °C before scoring each as fertile or sterile.

Table 1. The mean \pm s.e. untransformed proportion of offspring sired by focal males separated by the morph and irradiation status of the background and focal males.

(Sample sizes are in parentheses.)

irradiation sequence	focal male morph	
	major	minor
normal-irradiated	0.081 \pm 0.007 (40)	0.037 \pm 0.003 (30)
irradiated-normal	0.138 \pm 0.007 (40)	0.012 \pm 0.003 (30)

3. RESULTS

On average, only $2.40 \pm 0.2\%$ of the brood masses recovered from populations where all the males were irradiated contained viable eggs (z). In contrast, $93.6 \pm 1.1\%$ of the brood masses recovered from populations where all the males were fertile contained viable eggs (p). The proportion of eggs fertilized by irradiated sperm in the experimental populations was calculated as $P_R = 1 - [(x-z)/(p-z)]$, where x was the observed proportion of brood masses with viable eggs (Cook *et al.* 1997). When the focal male was irradiated this gave his fertilization success relative to the population. When he was fertile, $1 - P_R$ gave his fertilization success. Values less than or greater than unity can be generated when $z > x$, so we corrected the data according to Cook *et al.* (1997). The proportions were arcsine transformed for statistical analysis.

The data were first examined in order to determine whether, on average, alternative male phenotypes experienced different reproductive pay-offs. We examined the variation in the proportion of offspring sired by males using a two-factor ANOVA with male morph (major or minor) as a main effect. Irradiation generally influences fertilization capacity thereby necessitating the replication of experiments using reciprocal crosses (Boorman & Parker 1976). Thus, we entered irradiation sequence (normal-irradiated or irradiated-normal) as the second main effect in the model. There was a significant effect of male morph ($F_{1,136} = 252.68$ and $p = 0.0001$) but not irradiation sequence ($F_{1,136} = 0.003$ and $p = 0.96$) on fertilization success. Nevertheless, there was a significant interaction ($F_{1,136} = 65.88$ and $p = 0.0001$) (see table 1). Irradiation appeared to decrease the fertilization capacity of major males, but increase the fertilization capacity of minor males. The alternative phenotypes experienced unequal fitness pay-offs; on average, major males sired more offspring than did minor males and this effect was the same, irrespective of the irradiation sequence used (table 1).

Analysis of covariance revealed a significant interaction between male morph and pronotum width on the proportion of offspring sired ($F_{1,135} = 15.73$ and $p < 0.001$), indicating that the slope of the function of fitness on body size differed between alternative male phenotypes. Again, irradiation order (normal-irradiated or irradiated-normal) was included as a main effect in this analysis. We therefore examined fitness functions within morphs using

partial regression analysis with male pronotum width and horn length as independent variables and the proportion of offspring sired as the dependent variable. Irradiation order was entered as a dummy variable in order to control for its effect. Note that pronotum width and horn length are strongly correlated both phenotypically (figure 1) and genetically (J. S. Kotiaho, J. Hunt, J. L. Tomkins and L. W. Simmons, unpublished data) so that they can be considered as a single trait (Roff 1997). Nevertheless, it is useful to examine the partial effects of these traits in determining fitness as this can identify the precise target on which selection acts. Fertilization success was not related to pronotum width or horn length amongst minor males (to the left of the switch point in figure 1) after controlling for the effect of irradiation ($t_{59} = 5.72$ and $p = 0.0001$) (partial effect of pronotum, $t_{59} = 0.06$ and $p = 0.95$ and partial effect of horn length, $t_{59} = 0.32$ and $p = 0.75$) (figure 2a). In contrast, fertilization success increased with horn length amongst major males ($t_{79} = 2.80$ and $p = 0.007$), whereas pronotum width did not have an independent partial effect on fertilization success ($t_{79} = 0.13$ and $p = 0.89$). The irradiation effect was again significant ($t_{79} = 7.78$ and $p = 0.0001$) (figure 2a). Clearly the function of body size on fitness differed between morphs.

The extended regression models of Eberhard & Gutiérrez (1991) described in §2(b) essentially look for nonlinearity between two variables before statistically evaluating the point at which the elevation and slope of the relations between the two variables change. We thus used this approach for statistically determining the point at which increases in male size began to increase male fitness. The relationship between pronotum width and fertilization success shown in figure 2a differed significantly from linearity ($\alpha_2 = 8.11 \pm 3.61$, $t = 2.25$, $n = 132$ and $p = 0.03$), and the switch point explaining the greatest variance ($R^2 = 0.72$) occurred over a range of pronotum widths (4.91–4.96 mm, inclusive) with a mean pronotum width of 4.94 ± 0.008 mm. The relation between pronotum width and fertilization success is characterized by a change in the linear slope at the switch point ($\beta_2 = 0.21 \pm 0.06$, $t = 3.74$, $n = 140$ and $p = 0.0003$) and a discontinuity of fertilization success ($\beta_3 = 0.11 \pm 0.03$, $t = 4.22$, $n = 140$ and $p = 0.0001$) (figure 2a). Importantly, this switch point in the fitness function did not differ significantly from the morphological switch point for the development of horns ($t_9 = 1.64$ and $p = 0.13$) (see figure 1).

4. DISCUSSION

Game theoretic models for the evolution of conditional strategies predict that individuals within a population are able to assess information about their relative ability for obtaining fitness through alternative phenotypes and express the phenotype that yields the maximum fitness for their status (Gross 1996). Thus, conditional strategies arise due to status-dependent selection where the relative fitnesses of the alternative phenotypes are dependent on the competitive state of the individuals expressing them (Gross 1996). Theory predicts that, on average, alternative tactics will yield unequal fitnesses and be characterized by discrete fitness functions (X and Y in figure 2b). The point at which these fitness functions intersect will

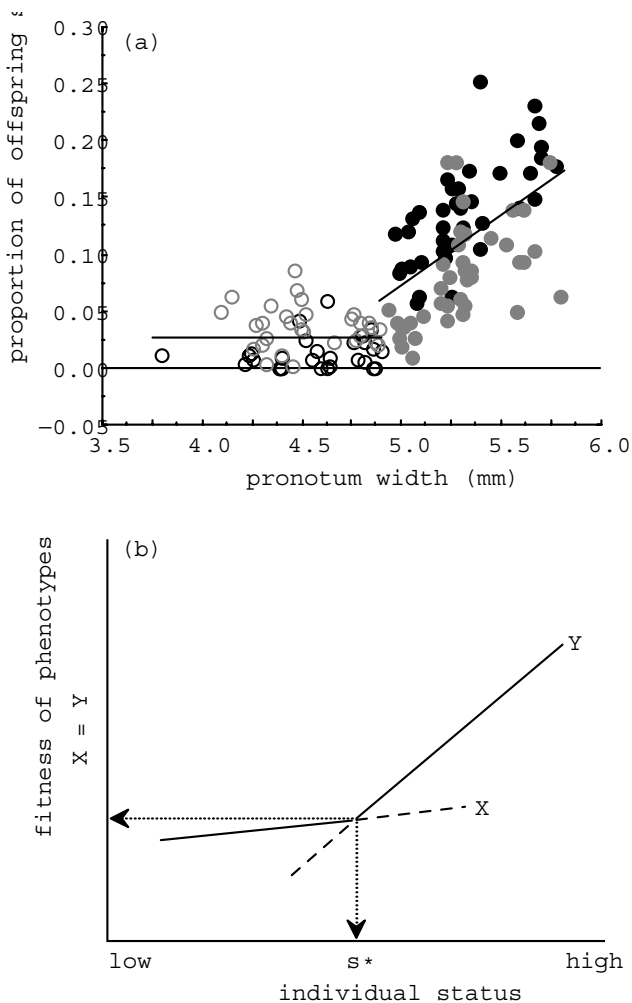


Figure 2. (a) The fitness functions for focal major (fertile, solid black symbols; sterile, solid grey symbols) and minor males (fertile, open black symbols; sterile, open grey symbols). The data are the untransformed proportions of offspring emerging from a population that were sired by focal males of different pronotum widths. The solid lines are the least squares regression slopes for the data on either side of the change in the relation between fitness and pronotum width (see the text for more details). (b) Gross' (1991) model of status-dependent selection. The alternative reproductive tactics X and Y have status-dependent fitness functions, where the fitness of a given tactic depends on the status of the individual adopting the tactic. The fitness functions are different between the alternative tactics, but at the point of intersection both tactics have equal fitnesses (s^*). Individuals of status $< s^*$ that adopted phenotype Y would have a lower fitness than those adopting the alternative phenotype X , even though, on average, phenotype X has the lower pay-off (see the text for more details).

represent the evolutionarily stable switch point at which both tactics yield equal fitness (s^*) (figure 2b). High-status individuals receive greater fitness returns above this switch point by adopting tactic X rather than tactic Y , and individuals receive greater fitness returns below this switch point by adopting tactic Y rather than tactic X (figure 2b). Thus, it is theoretically possible for an individual to express the phenotype and reproductive tactic that will maximize their fitness by incorporating information about their status relative to other individuals in the population (Gross 1996).

Our experiments with *O. taurus* provide two lines of evidence that support Gross's (1996) model for the evolution of a conditional strategy under status-dependent selection. First, we found that, on average, alternative tactics yielded unequal fitness; major males obtained 11% of fertilizations compared with only 2.5% for minor males. This undoubtedly reflects differential mating access since, with equal access to fertilization, success does not vary between morphs (Tomkins & Simmons 2000). Second, where the fitness functions of two alternative tactics are themselves linear, status-dependent selection should generate a fitness function across the full range of male phenotypes that is nonlinear and that will have a change in slope where alternative fitness functions intercept (figure 2b). The fitness function for *O. taurus* shown in figure 2a is consistent with this expectation. Moreover, we should expect males to switch tactics at a body size (or status) where fitness gains can be increased by adopting the competitive tactic. Our data show that the morphological switch point from hornless to horned males is convergent with the point where fitness begins to increase with body size. We already know that male morphology is facultative rather than genetic (Hunt & Simmons 1997; Emlen & Nijhout 1999; Moczek & Emlen 1999), so the evidence for *O. taurus* is entirely consistent with game theoretic models for the evolution of a conditional strategy. The final piece of evidence required under status-dependent selection models, that the fitness of alternatives is equal at the switch point, will require careful selection of focal animals of the same switch point body size that differ in their expression of horns.

Competitive ability amongst major male *O. taurus* that adopt the fighting tactic is a function of body size and the length of their head horns (Moczek & Emlen 2000). Thus, selection is predicted to favour increased horn length amongst major males. It has been suggested that selection may favour decreasing horn length in minor males that adopt the alternative tactic of sneaking copulations because being hornless may enable minor males to move through tunnels more rapidly (Moczek & Emlen 2000). Indeed, Moczek & Emlen (2000) found that smaller horned males were, on average, able to travel 1.1s faster within a tunnel of standardized length. Thus, Moczek & Emlen (2000) suggested that disruptive selection may be important in the evolution of horn dimorphism between alternative reproductive tactics. Our data show that horn length is an important trait generating increased fitness for major males; the partial effect of horn length on fitness was significant while the partial effect of body size was not. Thus, there does appear to be directional selection for increased horn length amongst major males. If the increased agility of relatively small horned males reported by Moczek & Emlen (2000) were a significant selective agent, there should be a negative relationship between horn length and fitness amongst minor males. However, our data show that, amongst minor males, horn length has no significant influence on reproductive success, thereby providing no evidence for the notion of directional selection for decreased horn length in minor males and disruptive selection favouring alternate horn morphologies between the morphs of *O. taurus*.

The notion of disruptive selection favouring alternative morphologies that suit alternative mating tactics currently has little empirical support. Gross's (1985) original study of coho salmon suggested that disruptive selection may be important since smaller sneaks were able to gain closer proximity to females than large sneaks, while the reverse was true for fighting anadromous males. However, Foote *et al.*'s (1997) study showed that proximity to females has no impact on fertilization success and, thus, fitness gain. Moreover, there is a positive rather than negative relationship between parr fertilization success and parr body size in Atlantic salmon (Thomaz *et al.* 1997), indicating that selection is directional for increased male size under both tactics. Our results for *O. taurus* and those for salmon show how an understanding of fitness functions rather than behaviour is essential in interpreting the patterns of selection acting on alternative mating tactics.

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REFERENCES

- Boorman, E. & Parker, G. A. 1976 Sperm (ejaculate) competition in *Drosophila melanogaster*, and the reproductive value of females to males in relation to female age and mating status. *Ecol. Entomol.* **1**, 145–155.
- Brockman, H. J., Colson, T. & Potts, W. 1994 Sperm competition in horseshoe crabs (*Limulus polyphemus*). *Behav. Ecol. Sociobiol.* **35**, 153–160.
- Coltman, D. W., Bancroft, D. R., Robertson, A., Clutton-Brock, T. H. & Pemberton, J. M. 1999 Male reproductive success in a promiscuous mammal: behavioural estimates compared with genetic paternity. *Mol. Ecol.* **8**, 1199–1209.
- Cook, P. A., Harvey, I. F. & Parker, G. A. 1997 Predicting variation in sperm precedence. *Phil. Trans. R. Soc. Lond. B* **352**, 771–780. (DOI 10.1098/rstb.1997.0061.)
- Eberhard, W. G. & Gutiérrez, E. E. 1991 Male dimorphisms in beetles and earwigs and the question of developmental constraints. *Evolution* **45**, 18–28.
- Elisabeth, M. & Taborsky, M. 1997 Alternative male mating tactics in a cichlid, *Pelvicachromis pulcher*: a comparison of reproductive effort and success. *Behav. Ecol. Sociobiol.* **41**, 311–319.
- Emlen, D. J. & Nijhout, H. F. 1999 Hormonal control of male horn length dimorphism in the dung beetle *Onthophagus taurus* (Coleoptera: Scarabaeidae). *J. Insect. Physiol.* **45**, 45–53.
- Foote, C. J., Brown, G. S. & Wood, C. C. 1997 Spawning success of males using alternative mating tactics in sockeye salmon, *Oncorhynchus nerka*. *Can. J. Fish. Aquat. Sci.* **54**, 1785–1795.
- Fuller, R. C. 1999 Costs of group spawning to guarding males in the rainbow darter, *Etheostoma caeruleum*. *Copeia* **1999**, 1084–1088.
- Gross, M. R. 1985 Disruptive selection for alternative life histories in salmon. *Nature* **313**, 47–48.
- Gross, M. R. 1991 Evolution of alternative reproductive strategies: frequency-dependent sexual selection in the male bluegill sunfish. *Phil. Trans. R. Soc. Lond. B* **332**, 59–66.
- Gross, M. R. 1996 Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol. Evol.* **11**, 92–98.
- Hunt, J. & Simmons, L. W. 1997 Patterns of fluctuating asymmetry in beetle horns: an experimental examination of the honest signalling hypothesis. *Behav. Ecol. Sociobiol.* **41**, 109–114.
- Hunt, J. & Simmons, L. W. 2000 Maternal and paternal effects on offspring phenotype in the dung beetle *Onthophagus taurus*. *Evolution* **54**, 936–941.
- Hunt, J., Kotiaho, J. S. & Tomkins, J. L. 1999 Dung pad residence time covaries with male morphology in the dung beetle *Onthophagus taurus*. *Ecol. Entomol.* **24**, 174–180.
- Lank, D. B., Smith, C. M., Hanotte, O., Burke, T. & Cooke, F. 1995 Genetic polymorphism for alternative mating behaviour in lekking male ruff, *Philomachus pugnax*. *Nature* **378**, 50–62.
- Maynard Smith, J. 1982 *Evolution and the theory of games*. Cambridge University Press.
- Moczek, A. P. & Emlen, D. J. 1999 Proximate determination of male horn dimorphism in the beetle *Onthophagus taurus* (Coleoptera: Scarabaeidae). *J. Evol. Biol.* **12**, 27–37.
- Moczek, A. P. & Emlen, D. J. 2000 Male horn dimorphisms in the scarab beetle, *Onthophagus taurus*: do alternative reproductive tactics favour alternative phenotypes. *Anim. Behav.* **59**, 459–466.
- Moran, P., Pendas, A. M., Beall, E. & Garcia-Vazquez, E. 1996 Genetic assessment of the reproductive success of Atlantic salmon precocious parr by means of VNTR loci. *Heredity* **77**, 655–660.
- Roff, D. A. 1997 *Evolutionary quantitative genetics*. London: Chapman & Hall.
- Ryan, M. J., Pease, C. M. & Morris, M. R. 1992 A genetic polymorphism in the swordtail *Xiphiphorus nigrensis*: testing the prediction of equal fitnesses. *Am. Nat.* **139**, 21–31.
- Shuster, S. M. & Wade, M. J. 1991 Equal mating success among male reproductive strategies in a marine isopod. *Nature* **350**, 608–610.
- Simmons, L. W., Tomkins, J. L. & Hunt, J. 1999 Sperm competition games played by dimorphic male beetles. *Proc. R. Soc. Lond. B* **266**, 145–150. (DOI 10.1098/rspb.1999.0614.)
- Sinervo, B. & Lively, C. M. 1996 The rock–paper–scissors game and the evolution of alternative male strategies. *Nature* **380**, 240–243.
- Thomaz, D., Beall, E. & Burke, T. 1997 Alternative reproductive tactics in Atlantic salmon: factors affecting mature parr success. *Proc. R. Soc. Lond. B* **264**, 219–226. (DOI 10.1098/rspb.1997.0031.)
- Tomkins, J. L. & Simmons, L. W. 2000 Sperm competition games played by dimorphic male beetles: fertilization gains with equal mating access. *Proc. R. Soc. Lond. B* **267**, 1547–1553. (DOI 10.1098/rspb.2000.1177.)
- Tsunenori, K. 1998 Reproductive success and two modes of mating in the sand-bubbler crab *Scopimera globosa*. *J. Exp. Mar. Biol. Ecol.* **22**, 197–207.