

Environmental control of horn length dimorphism in the beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae)

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SUMMARY

Impressive examples of male ornamentation occur in horned beetles. Many beetle species are characterized by substantial amounts of phenotypic variation in horn length, and in some species this variation is bimodally distributed so that males may be separated into two groups on the basis of horn length. Two discrete male morphs are present in natural populations of *Onthophagus acuminatus* (Coleoptera: Scarabaeidae), a dung beetle common to lowland tropical forests of Panama. Large males possess a pair of frontal horns, which in small males are greatly reduced in length or are lacking. This paper presents results from experiments designed to assess the relative importance of genetic and environmental factors as determinants of male horn morphology. Experimental manipulation of food quantity, a factor known to influence body size, showed that male horn length variation in *O. acuminatus* was influenced primarily by environmental factors. Horn lengths of male progeny were a function of individual differences in body size (the manipulated variable) and not of the horn lengths of their fathers, in both experimental and control populations. These results support recent theories on sexual selection which predict that male ornaments will evolve to be reliable indicators of male quality. The utility of incorporating studies of developmental mechanism into analyses of morphological evolution is discussed.

1. INTRODUCTION

A large number of evolutionarily interesting morphological characters show discontinuous variation, with strikingly different forms maintained simultaneously in single populations (e.g. sexual dimorphisms (Charnov & Bull 1977), insect wing dimorphisms (reviewed in Harrison 1980; Roff 1986) and social insect castes (Wheeler 1991)). Species with morphological dimorphisms offer the opportunity for direct study of the selective and developmental processes responsible for divergence within a lineage, and these have already received both experimental and theoretical attention (see, for example, Grant & Bayly 1981; Denno *et al.* 1986; Lively 1986*a, b*; Crespi 1988; Shuster 1989; Hazel *et al.* 1990).

From these and other studies it is clear that two very different types of dimorphisms exist: (i) those where morphs are allelically determined ('genetic' polymorphisms: e.g. isopods (Shuster 1989; Shuster & Wade 1991), barnacles (Lively 1986*a*) fish (Gross 1985; Zimmerer & Kallman 1989; Ryan *et al.* 1992) and birds (Smith 1993); and (ii) those where morphs are environmentally determined (e.g. insects (Smith 1978; Hazel & West 1979; Sims 1983; Denno *et al.* 1986; Crespi 1988; Greene 1989), amphibians (Collins & Cheek 1983) and daphnia (Grant & Bayly 1981)).

Recent theoretical work suggests that both allelically and environmentally determined dimorphisms result

from genetically based 'switches' which regulate the expression of alternative sets of genes during development (West-Eberhard 1992). Determination of which morph a developing individual becomes (i.e. which sets of genes are expressed) can be influenced by environmental or genetic factors, or some combination of the two (West-Eberhard 1992). In systems with environmental determination, this switch is influenced predominantly by external cues correlated with a particular selective situation. In systems with allelic determination, the switch is influenced by internal genetic cues. Despite the possible similarity of their mechanisms, allelically and environmentally determined dimorphisms are very different evolutionarily (Dominey 1984; Shuster 1989), and correct interpretation of the adaptive significance of a particular dimorphism will often require an understanding of which of the two underlying processes is involved.

A classical morphological dimorphism occurs in the horns of some male beetles (Darwin 1871; Wallace 1878; Beebe 1944; Arrow 1951; Eberhard & Gutierrez 1991). Large males possess head or thoracic horns, which are greatly reduced in length or lacking in smaller males. In all species studied so far, males use horns as weapons in intraspecific combat (see, for example, Palmer 1978; Eberhard 1982, 1987; Brown & Bartalon 1986; Conner 1989). With such clear sexually selected advantages to both large horns and large size, the continued persistence of small, hornless

males poses an interesting evolutionary problem. Previous research has recognized that the genetic nature of variation underlying horn length is critical to the adaptive explanation for the maintenance of this dimorphism. Gadgil (1972) explicitly assumed that horned and hornless males were allelically determined alternatives maintained by frequency-dependent selection. Later, Eberhard (1982, 1987) and then Cook (1987, 1990) argued that horn dimorphism was environmentally determined, based on the observation that horn lengths were closely correlated with body size, a variable known to be affected by nutrition and other external factors.

To my knowledge, the study reported here is the first to test specifically for the genetic basis of a beetle horn dimorphism. I use a combination of father–son regressions and nutrition manipulation experiments to examine the relative contributions of genetic and environmental factors to male horn length variation. These experiments directly measure the extent to which expression of a major secondary sexual character, beetle horns, reflects the nutritional history of individual males. The results have important implications for recent theory on the mechanisms of sexual selection and the role of ornaments as reliable indicators of male quality or competitive ability.

2. MATERIALS AND METHODS

(a) *Biology and terminology*

Onthophagus acuminatus Har., is a small, black dung beetle common to lowland tropical forests of Panama. Males of *O. acuminatus* are dimorphic in horn length (figure 1; I use 'dimorphic' to describe bimodally distributed variation which is almost, if not entirely, discrete). Large males possess a pair of frontal horns (≥ 0.4 mm) which vary in length as a function of body size (measured as prothorax width; $y = 1.13x - 3.13$, $r^2 = 0.75$, $n = 258$). Horn lengths of small males (< 0.4 mm) are described by a different allometric relation ($y = 0.35x - 0.90$, $r^2 = 0.69$, $n = 303$; comparison of slopes, Student's t test, $t = 20.379$, d.f. = 557, $p \ll 0.001$), and from personal observations these males appear functionally hornless.

Beetles dig tunnels in the soil beneath fresh dung of howler monkeys (*Alouatta palliata*). Dung is pulled into these tunnels and packed into dense, ovoid masses, and a single egg is laid in each mass. Each 'brood ball' ('brood mass' of Halfiter & Edmonds (1982)) constitutes the total food available to a single larva, and natural brood ball size variation significantly affects the size of emerging adults (D. J. Emlen, unpublished data).

(b) *Experimental methods*

All experiments were conducted at the Barro Colorado Island field station of the Smithsonian Tropical Research Institute, Panama. Female *O. acuminatus* store sperm (D. J. Emlen, unpublished observation). To ensure that females were unmated, a generation of beetles was reared in the laboratory before all described experiments. Females were isolated from males on emergence, and fed howler monkey dung until sexually mature.

To measure the heritability of male horn lengths, each of 40 females was paired randomly with a single wild-caught

male and allowed to breed. Pairs were put in 25 cm \times 10 cm cylindrical buckets three quarters full of moist potting soil and provided with unlimited fresh howler monkey dung. After 3 days the soil was sifted and all brood balls were removed. Brood balls were placed individually in plastic soil-filled cups and allowed to develop. Body sizes (prothorax width) and horn lengths of all male progeny were measured to the nearest 0.05 mm by using a Wild® stereo-microscope ocular micrometer (correlation coefficients for blind, repeated measurements of 27 males: horn length, $r = 0.997$; body size, $r = 0.995$). Laboratory conditions closely mimicked the natural larval environment of *O. acuminatus*: larvae were reared from naturally produced brood balls which were isolated from other individuals and buried in soil. Consequently, laboratory estimates of heritability should be similar to heritabilities occurring in the field.

To test for an effect of the nutritional environment on progeny horn morphology, 30 beetle pairs were reared under conditions identical to those above except that the sizes of brood balls were experimentally manipulated. Each of 13 horned and 17 hornless wild-caught males was used as a sire (\bar{X} horn length \pm s.d. for horned males = 0.89 ± 0.21 mm; \bar{X} horn length \pm s.d. for hornless males = 0.17 ± 0.08 mm), and each of 30 lab-reared (unmated) females was paired randomly with one of these males and allowed to breed.

Every 3 days, soil in each of the cups was sifted, and all brood balls removed. The soil was then re-moistened as needed, the cups re-filled, and beetles given a new supply of dung. This procedure was repeated until all pairs had produced eight brood balls. These were assigned randomly to one of two treatments.

Four of the brood balls from each pair were enlarged, by adding howler monkey dung, so that they were greater than two standard deviations above the natural mean brood ball size (large treatment: $\bar{X} \pm$ s.d. = 2.41 ± 0.74 cm³). Dung was removed from the remaining four brood balls of each pair until sizes were all more than two standard deviations below the natural mean (small treatment: $\bar{X} \pm$ s.d. = 0.37 ± 0.07 cm³). Brood balls were then placed individually in soil-filled cups (as above) and allowed to develop. To control for any possible position effects, cups from the two treatments were intermixed uniformly in the laboratory. Progeny body sizes and horn lengths were measured as above.

(c) *Analyses*

Parent–offspring regressions were used to predict male progeny horn lengths from father horn lengths. Because siblings are more closely related to each other than to other male progeny, they were not considered statistically independent for these analyses. Consequently, only a single value was used for each family in calculation of the regressions: results for all male siblings were pooled, and the mean progeny horn length for each family used. Significant regressions would suggest a heritable component to horn length variation, its magnitude being estimated by twice the slope (Falconer 1989).

A paired t -test (two-tailed) was used to test for an effect of brood ball size manipulation on progeny horn lengths. For each family, the mean progeny horn length for males reared in small brood balls was compared with the mean horn length for males reared in large brood balls. Significant within-family differences in horn length between progeny reared in large and small brood balls would indicate an environmental effect on horn length determination. Heritabilities were also calculated by parent–offspring regression for each of the two experimentally manipulated populations.

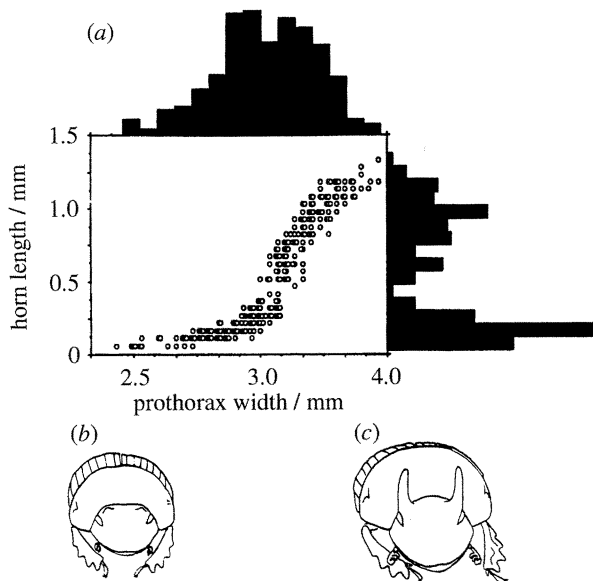


Figure 1. (a) Relation between horn length and body size for 561 male *Onthophagus acuminatus* (Coleoptera: Scarabaeidae) from Barro Colorado Island, Panama. The sigmoidal relation can be approximated by two separate linear allometries corresponding to (b) hornless and (c) horned male morphologies. The separate allometries and bimodal horn length frequency distribution (right) result in the co-occurrence of two discrete male shapes within populations.

3. RESULTS

Heritable variation in horn length was not detected in either the control population, by simple regression of mean progeny horn length on paternal horn length ($b \pm \text{s.e.} = 0.003 \pm 0.10$, $r^2 = 0.000$, $p = 0.9773$, $n = 38$; figure 2), or the experimental treatment populations (large brood ball treatment, $b \pm \text{s.e.} = 0.091 \pm 0.129$, $r^2 = 0.023$, $p = 0.4921$, $n = 22$; small brood ball treatment, $b \pm \text{s.e.} = -0.011 \pm 0.027$, $r^2 = 0.008$, $p = 0.6853$, $n = 22$; figure 3). Heritability of body size, estimated by simple regression of mean progeny size on mid-parent size, was also not sig-

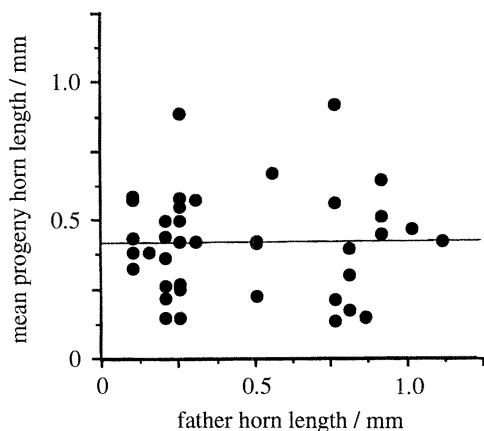


Figure 2. Relation between father horn length and progeny horn length for beetles reared in unmanipulated brood balls. The regression of father horn length on mean progeny horn length was not significant (simple regression, $b \pm \text{s.e.} = 0.003 \pm 0.10$, $r^2 = 0.000$, $p = 0.9773$, $n = 38$), showing no detectable effect of father horn length on progeny horn length.

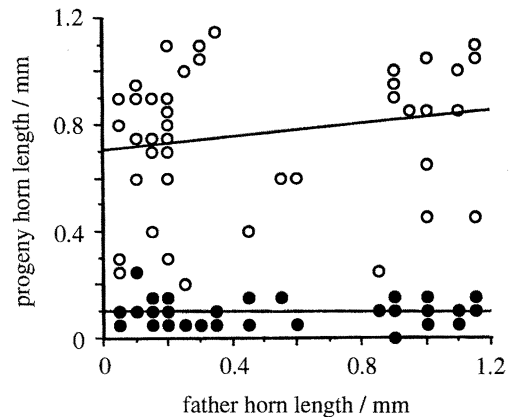


Figure 3. Effect of experimental manipulation of larval food quantity (brood ball size) on progeny horn length. Horn lengths of male progeny reared in large brood balls (open circles) were significantly larger than those of males reared in small brood balls (filled circles). A paired t -test was used to compare the family mean horn lengths of male progeny reared in large and small brood balls for the 22 families which produced sons in both of the experimental treatments (of the initial 30 pairs, six produced males in only one of the treatments and two produced only daughters). Because treatment variances were not equal, family means were calculated from \log_{10} -transformed horn lengths: $t_{22} = 16.055$, two-tailed $p = 0.0001$). Neither of the parent-offspring regressions for large and small brood ball treatments were significant (simple regression on family means: large brood balls, $b \pm \text{s.e.} = 0.091 \pm 0.129$, $r^2 = 0.023$, $p = 0.4921$, $n = 22$; small brood balls, $b \pm \text{s.e.} = -0.011 \pm 0.027$, $r^2 = 0.008$, $p = 0.6853$, $n = 22$), indicating no effects of father horn length on progeny horn length.

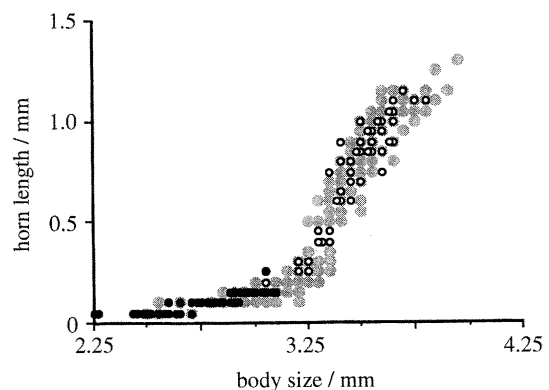


Figure 4. Relation between body size and horn length for beetles reared from artificially enlarged and reduced brood balls. Manipulation of larval food quantity (brood ball size) had a significant effect on progeny body size ($\bar{X} \pm \text{s.d.}$ for progeny reared in large brood balls = 3.42 ± 0.15 mm, $n = 103$; $\bar{X} \pm \text{s.d.}$ for progeny reared in small brood balls = 2.73 ± 0.215 mm, $n = 86$; paired t -test for family means, $t_{29} = 27.138$, two-tailed $p = 0.0001$). Despite the large nutritional effect on body size variation, all progeny showed horn lengths within the narrow range of variation present in the natural population (grey circles). The close matching of progeny horn lengths to artificially enlarged (open circles) and reduced (filled circles) body sizes suggests that developing individuals contain within them a relation dictating horn length for a range of body sizes.

nificantly different from 0 ($b \pm \text{s.e.} = -0.106 \pm 0.113$, $r^2 = 0.022$, $p = 0.353$, $n = 40$).

In contrast, brood ball size manipulation sig-

nificantly affected progeny horn lengths (figure 3). Horn lengths for males reared in large brood balls were over seven times larger than those of full siblings reared in small brood balls ($\bar{X} \pm \text{s.d.}$ for large brood balls = 0.765 ± 0.26 mm, $n = 48$; $\bar{X} \pm \text{s.d.}$ for small brood balls = 0.1 ± 0.045 mm, $n = 43$; paired t -test on family means, $t_{22} = 16.055$, two-tailed $p = 0.0001$). Furthermore, every father which sired male progeny in both of the experimental treatments produced horned sons from the large brood ball treatment and hornless sons from the small brood ball treatment. Changing larval food conditions predictably altered progeny morphology, and clearly demonstrated an effect of rearing environment upon horn length variation. All progeny horn lengths fell within the horn length/body size distribution present in the natural population (figure 4). The close matching of progeny horn lengths to artificially enlarged and artificially reduced body sizes suggests that each family contained the potential to produce 'appropriate' horn lengths for a range of body sizes.

4. DISCUSSION

(a) *Horn length determination in O. acuminatus*

Horn lengths in male progeny were not predicted by father horn length variation: heritabilities estimated by father-son regression were not significantly different from 0. Progeny horn lengths were affected significantly by the experimental manipulation of larval food abundance, an environmental factor influencing body size. The negligible effects of father horn length and large effects of larval nutrition suggest that variation in male horn length is largely caused by environmental factors. Consequently, male dimorphism in *O. acuminatus* appears consistent with environmentally influenced 'developmental switch' mechanisms for dimorphism described by Stearns (1982) and West-Eberhard (1992).

Results from a complementary behavioural study provide a selective context for this dimorphism. Horned males fight for possession of subterranean tunnels beneath dung and the females within them. Hornless males are unable to defend tunnels successfully, and sneak into tunnels of horned males either by sliding past the guarding male undetected or by burrowing into the tunnel beneath the soil surface (D. J. Emlen, unpublished observations). Success in using horns is a function of male size (D. J. Emlen, unpublished results), and body size in *O. acuminatus* is influenced primarily by environmental factors. Under these conditions, where body size is uncorrelated with genotype, developmental mechanisms which conditionally express horns in relation to size should be selectively favoured over mechanisms with genetic determination of horn length.

(b) *Sexual selection and the heritability of male ornaments*

The low heritabilities for beetle horn length found in this study add beetle horns to the list of male traits

already shown to have large environmental components of expression (see, for example, Møller 1991; Johnson *et al.* 1993; Nicoletto 1993). Several recent models predict that sexual selection should favour the evolution of male ornaments with little or no heritable variation, because these traits will be more reliable indicators of male quality than genetically determined, condition-insensitive traits (Hamilton & Zuk 1982; Dominey 1983; Nur & Hasson 1984; Kodric-Brown & Brown 1984; Andersson 1986). However, for each of the above models, the evolution of conditional expression in a male trait involves female preference for that trait. Extensive observations of the natural behaviour of *O. acuminatus* provide no evidence for any form of female discrimination based on male horns (D. J. Emlen, unpublished results).

In arguing for condition-dependent male ornaments, Nur & Hasson (1984) and Kodric-Brown & Brown (1984) include traits such as antlers in deer by suggesting that antlers may improve both male competitive ability and male attractiveness to females. This is reasonable because traits such as antlers or horns, by advertising competitive ability, may indicate overall genetic quality. However, recent studies have not supported a role for female preference based on antler size (Clutton-Brock *et al.* 1989; Balmford *et al.* 1992), suggesting that intrasexual selection alone could favour condition-dependent trait expression. Furthermore, because males in poor condition are not likely to win contests even if they bear horns, males should benefit directly by investing in costly weaponry only when they are in good condition. This has also been suggested by the results of studies of fluctuating asymmetry in beetle horns and bird spurs (Møller 1992).

(c) *Implications for horn evolution*

Male horn lengths in *O. acuminatus* showed no detectable heritable variation, and therefore appear to be incapable of direct evolutionary response to selection on horn length. However, this does not mean that horns in *O. acuminatus* have no genetic basis. Heritable variation may exist in the relation between horn length and body size. To the degree that individuals differ genetically in the shape of the growth curve relating horn length to body size, natural selection should favour those genotypes with the most appropriate developmental trajectories, the 'character' subject to selection in this case would not be horn length per se, but horn length in relation to body size.

This distinction illustrates the fundamental difference between allelically and environmentally determined mechanisms for phenotypic dimorphism. At one extreme (allelic determination), morphs may be considered to be genetically separate entities competing with each other for persistence within a lineage. At the opposite extreme (environmental determination), morphs are manifestations of the same genotype under different external circumstances. Phenotypic dimorphisms produced by these two mechanisms require different selective conditions for stable maintenance, and may evolve differently in response to the same

selective situations. For example, the assumption that morphs, to be maintained, must on average receive equal payoffs (see, for example, Gadgil 1972) is only justified when the morphs are allelically determined (Dominey 1984; Shuster 1989). In contrast, an unpredictable selection environment is critical for the maintenance of environmentally cued mechanisms of dimorphism (see, for example, Levins 1968; Stearns 1982; Lively 1986*b*), but not necessary (and possibly detrimental) for the maintenance of allelically determined mechanisms.

Consequently, identification of the selection pressures maintaining dimorphic variation may require an understanding of the developmental processes underlying the particular dimorphism. As a first step towards understanding the evolution of dimorphic horn length variation in *Onthophagus acuminatus*, these experiments demonstrate that horned and hornless male morphs are facultative developmental alternatives correlated with individual differences in body size.

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REFERENCES

- Andersson, M. 1986 Evolution of condition-dependent sex ornaments and mating preferences: sexual selection based on viability differences. *Evolution* **40**, 804–816.
- Arrow, G. H. 1951 *Horned beetles*. The Hague: Junk.
- Balmford, A., Albon, S. & Blakeman, S. 1992 Correlates of male mating success and female choice in a lek-breeding antelope. *Behav. Ecol.* **3**, 112–123.
- Beebe, W. 1944 The function of secondary sexual characters in two species of *Dynastinae* (Coleoptera). *Zoologica* **29**, 53–58.
- Brown, L. & Bartalon, J. 1986 Behavioral correlates of male morphology in a horned beetle. *Am. Nat.* **127**, 565–570.
- Charnov, E. L. & Bull, J. J. 1977 When is sex environmentally determined? *Nature, Lond.* **266**, 828–830.
- Clutton-Brock, T. H., Hiraiwa-Hasegawa, M. & Robertson, A. 1989 Mate choice on fallow deer leks. *Nature, Lond.* **340**, 463–465.
- Collins, J. P. & Cheek, J. E. 1983 Effect of food and density on development of typical and cannibalistic salamander larvae in *Ambystoma tigrinum nebulosum*. *Am. Zool.* **23**, 77–84.
- Conner, J. 1989 Density-dependent sexual selection in the fungus beetle, *Bolitotherus cornutus*. *Evolution* **43**, 1378–1386.
- Cook, D. F. 1987 Sexual selection in dung beetles. I. A multivariate study of morphological variation in two species of *Onthophagus*. *Aust. J. Zool.* **36**, 123–132.
- Cook, D. F. 1990 Differences in courtship, mating and postcopulatory behaviour between male morphs of the dung beetle *Onthophagus binodis* Thunberg (Coleoptera: Scarabaeidae). *Anim. Behav.* **40**, 428–436.
- Crespi, B. J. 1988 Adaptation, compromise, and constraint: the development, morphometrics, and behavioral basis of a fighter-flier polymorphism in male *Hoplothrips karnyi* (Insecta: Thysanoptera). *Behav. Ecol. Sociobiol.* **23**, 93–104.
- Darwin, C. 1871 *The descent of man, and selection in relation to sex*. London: J. Murray.
- Denno, R. F., Douglass, L. W. & Jacobs, D. 1986 Effects of crowding and host plant nutrition on a wing-dimorphic planthopper. *Ecology* **67**, 116–123.
- Dominey, W. J. 1983 Sexual selection, additive genetic variance and the “phenotypic handicap”. *J. theor. Biol.* **101**, 495–502.
- Dominey, W. J. 1984 Alternative mating tactics and evolutionarily stable strategies. *Am. Zool.* **24**, 385–396.
- Eberhard, W. G. 1982 Beetle horn dimorphism: making the best of a bad lot. *Am. Nat.* **119**, 420–426.
- Eberhard, W. G. 1987 Use of horns in fights by the dimorphic males of *Ageopsis nigricollis* (Coleoptera, Scarabaeidae, Dynastinae). *J. Kansas ent. Soc.* **60**, 504–509.
- Eberhard, W. G. & Gutierrez, E. 1991 Male dimorphism in beetles and earwigs and the question of developmental constraints. *Evolution* **45**, 18–28.
- Falconer, D. S. 1989 *Introduction to quantitative genetics*. New York: John Wiley and Sons.
- Gadgil, M. 1972 Male dimorphism as a consequence of sexual selection. *Am. Nat.* **106**, 574–580.
- Grant, J. W. G. & Bayly, I. A. E. 1981 Predator induction of crests in morphs of the *Daphnia carinata* King complex. *Limnol. Oceanogr.* **26**, 201–218.
- Greene, E. 1989 A diet-induced developmental polymorphism in a caterpillar. *Science, Wash.* **243**, 643–646.
- Gross, M. R. 1985 Disruptive selection for alternative life histories in salmon. *Nature, Lond.* **313**, 47–48.
- Halfiter, G. & Edmonds, W. D. 1982 *The nesting behavior of dung beetles (Scarabaeinae): an ecological and evolutive approach*. Instituto De Ecologia, Mexico D.F.
- Hamilton, W. D. & Zuk, M. 1982 Heritable true fitness and bright birds: a role for parasites? *Science, Wash.* **218**, 384–387.
- Harrison, R. G. 1980 Dispersal polymorphisms in insects. *A. Rev. Ecol. Syst.* **11**, 95–118.
- Hazel, W. N. & West, D. A. 1979 Environmental control of pupal colour in swallowtail butterflies (Lepidoptera: Papilioninae): *Battus philenor* (L.) and *Papilio polyxenes* Fabr. *Ecol. Ent.* **4**, 393–400.
- Hazel, W. N., Smock, R. & Johnson, M. D. 1990 A polygenic model for the evolution and maintenance of conditional strategies. *Proc. R. Soc. Lond. B*, **242**, 181–187.
- Johnson, K. J., Thornhill, R., Ligon, J. D. & Zuk, M. 1993 The direction of mothers’ and daughters’ preferences and the heritability of male ornaments in red jungle fowl (*Gallus gallus*). *Behav. Ecol.* **4**, 254–259.
- Kodric-Brown, A. & Brown, J. H. 1984 Truth in advertising: the kinds of traits favoured by sexual selection. *Am. Nat.* **124**, 309–323.
- Levins, R. 1968 *Evolution in changing environments*. Princeton University Press.
- Lively, C. M. 1986*a* Predator-induced shell dimorphism in the acorn barnacle *Chthamalus anisopoma*. *Evolution* **40**, 232–242.
- Lively, C. M. 1986*b* Canalization versus developmental conversion in a spatially variable environment. *Am. Nat.* **128**, 561–572.
- Møller, A. P. 1991 Sexual selection in the monogamous barn swallow (*Hirundo rustica*). I. Determinants of tail ornament size. *Evolution* **45**, 1823–1836.
- Møller, A. P. 1992 Patterns of fluctuating asymmetry in weapons: evidence for reliable signalling of quality in beetle horns and bird spurs. *Proc. R. Soc. Lond. B* **248**, 199–206.

- Nicoletto, P. F. 1993 Female sexual response to condition-dependent ornaments in the guppy, *Poecilia reticulata*. *Anim. Behav.* **46**, 441–450.
- Nur, N. & Hasson, O. 1984 Phenotypic plasticity and the handicap principle. *J. theor. Biol.* **110**, 275–297.
- Palmer, T. J. 1978 A horned beetle which fights. *Nature, Lond.* **274**, 583–584.
- Roff, D. A. 1986 The evolution of wing dimorphism in insects. *Evolution* **40**, 1009–1020.
- Ryan, M. J., Pease, C. M. & Morris, M. R. 1992 A genetic polymorphism in the swordtail *Xiphophorus nigrensis*: testing the prediction of equal fitnesses. *Am. Nat.* **139**, 21–31.
- Shuster, S. M. 1989 Male alternative reproductive strategies in a marine isopod crustacean (*Paracerceis sculpta*): the use of genetic markers to measure differences in fertilization success among α -, β -, and γ - males. *Evolution* **43**, 1683–1698.
- Shuster, S. M. & Wade, J. L. 1991 Equal mating success among male reproductive strategies in a marine isopod. *Nature, Lond.* **350**, 608–610.
- Sims, S. R. 1983 The genetic and environmental basis of pupal colour dimorphism in *Papilio zelicaon*. *Heredity* **50**, 159–168.
- Smith, A. G. 1978 Environmental factors influencing pupal colour in Lepidoptera. I. Experiments with *Papilio polytes*, *Papilio demoleus*, and *Papilio polyxenes*. *Proc. R. Soc. Lond. B* **200**, 295–329.
- Smith, T. B. 1993 Disruptive selection and the genetic basis of bill size polymorphism in the African finch *Pyrenestes*. *Nature, Lond.* **363**, 616–620.
- Stearns, S. C. 1982 The role of development in the evolution of life histories. In *Evolution and development* (ed. J. T. Bonner), pp. 237–258. Berlin: Springer-Verlag.
- Wallace, A. R. 1878 *Tropical nature and other essays*. London: Macmillan.
- West-Eberhard, M. J. 1992 Behavior and evolution. In *Molds, molecules and metazoa: growing points in evolutionary biology* (ed. P. R. Grant & H. S. Horn), pp. 57–75. Princeton University Press.
- Wheeler, D. E. 1991 Developmental basis of worker caste polymorphism in ants. *Am. Nat.* **138**, 1218–1238.
- Zimmerer, E. J. & Kallman, K. D. 1989 Genetic basis for alternative reproductive tactics in the pygmy swordtail, *Xiphophorus nigrensis*. *Evolution* **43**, 1298–1307.

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