

Douglas J. Emlen

Alternative reproductive tactics and male-dimorphism in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae)

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Abstract Adult dung beetles (*Onthophagus acuminatus*) exhibit continuous variation in body size resulting from differential nutritional conditions experienced during larval development. Males of this species have a pair of horns that protrude from the base of the head, and the lengths of these horns are bimodally distributed in natural populations. Males growing larger than a threshold body size develop long horns, and males that do not achieve this size grow only rudimentary horns or no horns at all. Previous studies of other horned beetle species have shown that horned and hornless males often have different types of reproductive behavior. Here I describe the mating behaviors of the two male morphs of *O. acuminatus* during encounters with females. Females excavate tunnels beneath dung, where they feed, mate and provision eggs. Large, horned males were found to guard entrances to tunnels containing females. These males fought with all other males that attempted to enter these tunnels. In contrast, small, hornless males encountered females by sneaking into tunnels guarded by other males. In many instances, this was accomplished by digging new tunnels that intercepted the guarded tunnels below ground. Side-tunneling behavior allowed sneaking males to enter tunnels beneath the guarding male, and mate with females undetected. Both overall body size and relative horn length significantly affected the outcome of fights over tunnel ownership. These results suggest that alternative reproductive tactics may favor divergence in male horn morphology, with long horns favored in males large enough to guard tunnels, and hornlessness favored in smaller males that adopt the “sneaking” behavioral alternative.

Key words Alternative reproductive behavior · Male dimorphism · Male competition · Horned beetles · *Onthophagus*

Introduction

Males in many animal species show variation in morphology which is associated with differences in behavior (e.g., Austad 1984; Dominey 1984; Travis 1994). For example, large and small males frequently utilize strikingly different behaviors to encounter and mate with females (Dominey 1980; Rubenstein 1980, 1987; Howard 1984; Gross 1985; Kodric-Brown 1986; Arak 1988; Reynolds et al. 1993). Occasionally, variation in male morphology is dimorphic, and two or more distinct male forms co-occur in populations with intermediate forms scarce or lacking (Shuster 1987; Ryan and Causey 1989; Zimmerer and Kallman 1989; Danforth 1991). Species exhibiting dimorphic variation can be especially revealing to the investigator because they generally implicate morphological specializations for alternative behavioral or ecological situations (e.g., fighting and dispersing in thrips, Crespi 1988; and beetles, Eberhard 1982; Siva-Jothy 1987; soft and hard seed diets in finches, Smith 1993; and high and low levels of predation in barnacles, Lively 1986a,b; rotifers, Gilbert and Stemberger 1984; and *Daphnia*, Grant and Bayly 1981; Black and Dodson 1990; Spitze 1992).

A classic example of morphological dimorphism involves the horns of some male beetles (Bates 1863; Darwin 1871; Wallace 1878; Fabre 1899; Inukai 1924; Huxley 1931; Beebe 1944; Arrow 1951; Clark 1977; Eberhard 1982; Cook 1987; Siva-Jothy 1987). Not only are horned beetles sexually dimorphic (females in most species do not have horns), but many species exhibit dimorphic variation within males (Goldsmith 1987; Cook 1987, 1990; Eberhard and Gutierrez 1991; Emlen 1994a; Rasmussen 1994; Kawano 1995). In these species large males possess fully developed horns, while small males have only rudimentary horns, or no horns.

D.J. Emlen¹Department of Ecology and Evolutionary Biology,
Princeton University, Princeton, NJ 08544-1003, USA*Present address:*¹Division of Biological Sciences, The University of Montana,
Missoula, MT 59812-1002, USA

Fax: +406 243-4184; e-mail: demlen@selway.umt.edu

Beetle horns have been shown to function in intra-sexual combat over access to females (Palmer 1978; Eberhard 1979, 1987; Brown and Bartalon 1986; Goldsmith 1987; Siva-Jothy 1987; Conner 1988), and the existence of a "hornless" class of smaller males suggests that these individuals may employ an alternative, less aggressive behavioral tactic. In the species examined thus far, hornless males do employ reproductive behaviors that differ from that of horned males. Hornless males dispense with courtship and transfer spermatozoa more rapidly (Cook 1990), search for females in sub-optimal locations ("satellite" tactics; Eberhard 1982; Goldsmith 1987; Siva-Jothy 1987), and sneak around fighting males (Rasmussen 1994). However, why these behaviors are associated with hornlessness remains unclear, and the behavioral repertoires of the vast majority of horned beetle species have yet to be explored.

Onthophagus acuminatus Har. (Coleoptera: Scarabaeidae) is a horned beetle common in lowland tropical forests of Central America, where it feeds on dung from howler monkeys. Large males of this species possess a pair of frontal horns, while horns are greatly reduced in small males (Emlen 1994a, 1997). Variation in adult body size in *O. acuminatus* was found to be predominantly determined by environmental factors related to larval nutrition (Emlen 1994a, 1996). Male horns are facultatively expressed, and depend on the body size attained by an individual: larvae growing larger than a genetically-determined threshold size metamorphose into adults with long horns, and larvae not reaching this size metamorphose into adults lacking or with very short horns (Emlen 1994a, 1996).

The facultative adoption of either a horned or a hornless morphology by males strongly suggests that these males may be morphologically specialized for alternative behaviors or ecological situations. Here I determine whether horned and hornless male *O. acuminatus* differ in reproductive behavior. I present results from a series of experiments comparing the tactics employed by these two classes of males to encounter and mate with females. In addition, as a first step towards identifying the functional significance (if any) of horned and hornless male morphologies, I measure whether these males differ in their ability to perform one of these behaviors. Taken together, these results identify an "alternative" male mating behavior that may be functionally associated with a hornless beetle morphology, and suggest that alternative male reproductive tactics may contribute to the maintenance of dimorphic variation in male horns.

Methods

Observing underground behavior

Females of *O. acuminatus* excavate vertical tunnels directly beneath dung that are used for feeding, mating, and provisioning eggs (Emlen 1994b). In order to clearly observe beetles in tunnels I

constructed glass observation chambers. These chambers were similar to "ant farms" (see Klemperer 1981; Hunter et al. 1991; Emlen 1993 for examples) in that they consisted of two parallel panes of glass separated by 5 mm and filled with soil. Wide boxes made from clear plexiglass fit over the tops of these farms, allowing beetles to walk freely on the "soil" surface. Pieces of howler monkey dung were placed over the soil, and beetles of known sizes and sexes introduced. In all cases, beetles tunneled readily into the soil between the panes of glass, and all behavior occurring both above and below the surface could be viewed clearly. Because tunneling behavior naturally occurs in darkness, all observations were conducted using red-filtered light (beetles cannot detect red light; Crowson 1981).

Behavioral observations included ad libitum, focal-animal, and scan samples (Altmann 1974) until beetles either became dormant or tried to leave the arena (often 2–4 days later). At this time tunnels were traced onto clear acetate overlays. All beetles were wild-collected from the Barro Colorado Island Nature Monument, Panama (where this study was conducted), and no individuals were used more than once. Beetle behavior was observed under approximately natural conditions, as well as in four sets of experimental situations.

General observations

To approximate natural conditions, I constructed boxes consisting of several adjacent glass chambers (methods described in Emlen 1993). These boxes were buried in the forest so that the tops of the chambers were flush with the forest floor. When filled with soil, boxes provided a smooth, dirt surface which could later be disassembled into separate glass-walled "slices". Boxes were buried beneath trees where the howler monkeys slept. In the mornings, when dung fell to the forest floor, pieces were re-located on to the surfaces of the boxes. Beetles were allowed to colonize dung and tunnel undisturbed. Boxes were then returned to the laboratory, and all below ground behaviors were observed under red light. Twenty-two of these boxes were monitored to characterize the natural repertoire of tunneling, feeding and mating behavior. From these observations, two male reproductive tactics were identified, labeled "guarding" and "sneaking" (Fig. 1).

Experiments 1 and 2: reproductive behavior of horned and hornless males

To compare the reproductive behavior of horned and hornless males, I observed their methods of mate-acquisition both without, and with competition from a rival male. In the first experiment, one male and one female were placed in each of 12 observation chambers. Seven of these males were hornless, five were horned, and females were selected at random. Beetles were observed for a minimum of three half-hour intervals (maximum of six intervals), during which time all behaviors were recorded.

In the second experiment, two males (one horned and one hornless) were placed together in each observation chamber with a single female, and behaviors of all individuals were monitored as above. This second experiment tested for behavioral differences arising as a result of direct competition for access to females. Because dung always had large numbers of *O. acuminatus* (Emlen 1994b), and because horned and hornless males occurred in approximately equal frequencies on Barro Colorado Island (Emlen 1994a,b, 1997), this experiment accurately reflected natural conditions experienced by males.

Experiments 3 and 4: tunnel-guarding performance and male morphology

To examine whether males in this species differ in their ability to perform the "guarding" tactic, I measured whether natural variation in two aspects of male morphology (body size and horn length)

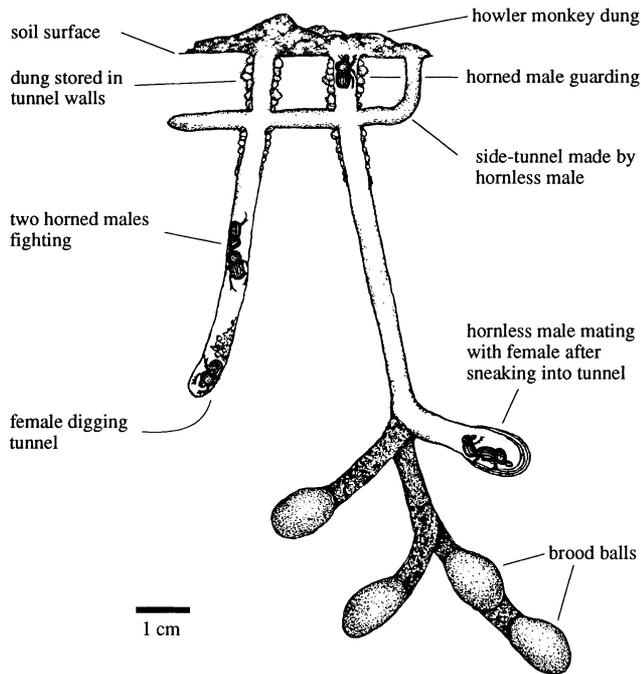


Fig. 1 Biology of *Onthophagus acuminatus* illustrating the two reproductive tactics used by males. Horned males fight to guard possession of tunnels containing females (“guarding”), and males able to successfully guard tunnels mate repeatedly with occupant females. Hornless males sneak into tunnels by digging horizontal side-tunnels that intercept primary tunnels underground (“sneaking”). In this way hornless males sometimes enter main tunnels beneath the guarding male and mate with the female undetected

affected male guarding ability. To identify an appropriate measure for body size, I used a principal components analysis including five measured traits (elytra width, elytra length, prothorax width, head width, body weight) and 368 male beetles. All of these measures were found to be strongly positively correlated (Emlen 1994b), and the first principal component (considered by some authors to be a measure of overall body size; Bookstein 1989; Klingenberg 1996) explained 90% of the overall variance. The width of the prothorax was the trait most strongly correlated with the first principal component ($r = 0.981$; Emlen 1994b), and was used subsequently as a linear approximation of overall body size. Horn length was measured as the linear distance between the base and the tip of the horn. Both prothorax width and horn length could be measured to the nearest 0.05 mm.

In the third experiment, I measured the consequences of variation in body size on the ability of males to guard tunnels by staging contests between individuals with different body sizes ($n = 10$ contests). However, body size and horn length are positively correlated in natural populations (Emlen 1994a, 1997). To control for possible confounding effects of horn length, I compared guarding abilities only between pairs of males with the same horn length but different body sizes (i.e., by pairing those males with the largest and smallest body sizes for a given horn length).

The general observations indicated that fights only occur inside tunnels, and that intruding males needed to maneuver past the resident beetle before they could push the resident beetle out of the tunnel from below (62 observed fights). Therefore, all staged contests were performed in natural tunnels made by females, and to provide a conservative estimate of the effects of male morphology, the predicted loser was always placed in the tunnel first. In each contest, the male with the smaller size was placed in the tunnel first, and the second contestant added immediately (< 1 min) after. All males were wild-caught, and no male was ever used in more than one contest. Winners were defined as the male remaining in the

tunnel with the female when the other male exited the arena. Fight outcomes were compared for larger and smaller males using a chi-square test.

In a fourth experiment, I measured the effects of natural variation in horn length on male guarding performance. To control for possible confounding effects of variation in body size, I chose 26 pairs of males differing in horn length but not in body size, and compared the number of fights won by the longer- and shorter-horned contestants. As in experiment 3, the predicted loser (i.e. the male with the shorter horn length) was placed into tunnels first, and the second male added less than one minute later. Staged contests encompassed an extensive range of horn length differences: the difference in horn length between competitors ranged from 0.05 mm (less than 5%) to 0.45 mm (over 50%). I therefore measured the effect of horns on male guarding performance by regressing the proportion of fights won by the longer-horned male against the difference in horn length between contestants (proportions were arc-sine transformed prior to analysis; Zar 1984). A significant regression would indicate that the effect of horns on male guarding performance increases with increasing difference in horn length between opponents. Differences in horn length were measured in both absolute units and as proportions of total length. The two methods yielded similar results, so only the absolute measures are presented.

Results

Males of *O. acuminatus* employed two very different tactics to encounter and mate with females (Fig. 1): they either attempted to monopolize access to a female by guarding the entrance to her tunnel (guarding), or they attempted to bypass guarding males (sneaking). Guarding behavior entailed remaining inside a tunnel with a female, and fighting intruding males over possession of the tunnel. Guarding males blocked tunnel entrances and periodically “patrolled” the length of the tunnel. Rival males could gain possession of a tunnel only by forcibly evicting the resident male, and both fights and turnovers were frequent. Fights over tunnel occupancy entailed repeated butting, wrestling and pushing of opponents, and fights continued until one of the contestants left the tunnel.

Sneaking involved bypassing the guarding male. The primary method of sneaking into tunnels was to dig side-tunnels that intercepted guarded tunnels below ground (Fig. 1). New tunnels were dug immediately adjacent (< 2 cm) to a guarded tunnel. These tunnels then turned horizontally 1–2 cm below ground, and often intercepted primary tunnels beneath the guarding male (16/24 side-tunnels). In this fashion, sneaking males sometimes bypassed the guarding male and mated with females undetected (observed in four instances). Side tunnels were not artifacts from observing beetles in two-dimensional observation chambers: side-tunnels were always present in tunnel castes formed by injecting silicone latex into natural tunnels in the forest floor (Emlen 1994b). In addition, latex castes revealed that individual side-tunnels often intercepted several different primary tunnels, suggesting that sneaking males may visit multiple guarded burrows (Emlen 1994b).

A second method of sneaking into tunnels involved entering guarded tunnels directly. Occasionally, if the

guarding male was away from the tunnel (e.g., in the dung) or off to the side of the tunnel, a hornless male managed to enter tunnels unchallenged (8/27 hornless male entrance attempts). Once inside, these males generally went directly to the female and mated (observed for 5 of the 8 entrances).

Sneaking behavior was characterized by brief (< 10 min) tenure of males inside tunnels. Even when sneaking males succeeded in entering a tunnel undetected, they exited tunnels immediately after mating. Most of the time, however, sneaking males were caught by the guarding male and evicted before encountering the female (19/27 entrance attempts at the top of the burrow; 30/43 total observed entries, also including use of side-tunnels). Sneaking males then returned to their original side-tunnels, or made new side-tunnels, and remained inactive until several hours later when they tried to enter the primary tunnel again.

Experiments 1 and 2: reproductive behavior of horned and hornless males

When males were placed alone with females (experiment 1), both horned and hornless males remained inside tunnels with females and mated repeatedly (Fig. 2a). There were no fights in this experiment because there were no rival males. However, remaining inside tunnels was still considered “guarding” because sneaking males exit tunnels immediately after mating, even when they do not encounter a guarding male.

When males competed for access to females (experiment 2), only the horned males successfully defended the tunnels. In all nine trials where both a horned and a hornless male competed for a single female, the horned male guarded the tunnel entrance and evicted the smaller, hornless male in the process (2×2 contingency

table with Yates’ correction for continuity: $\chi^2 = 14.22$, $P = 0.000$; Fig. 2b).

Results from experiment 2 were consistent with the general observations described above. Horned males always guarded tunnels. When horned males were evicted from a tunnel, they abandoned the vicinity of that tunnel, and generally attempted to gain possession of another tunnel (30/31 evictions). In contrast, when hornless males were evicted from a tunnel, they generally remained nearby before attempting to sneak back into guarded tunnels (27/34 evictions). This tendency to leave a tunnel after a fight was one of the most characteristic differences in behavior between horned and hornless males (2×2 contingency table with Yates’ correction for continuity: $\chi^2 = 35.339$, $P = 0.001$).

With one exception, all males using side-tunneling behavior were hornless (23/24 total observations [including general observations and experiments], binomial probability: $P < 0.001$), and all nine hornless males from experiment 2 (males competing for access to females) used this tactic.

Matings generally occurred inside tunnels (55/56 observed matings). Females never rejected a mating attempt from any male, suggesting that active, precopulatory mate choice may not be important in this species. Courtship consisted of the male “drumming” his forelegs over the back and sides of the female, and copulation durations were brief ($\bar{x} \pm SD = 123 \pm 35$ s, $n = 21$). There was no difference in copulation duration between horned and hornless males (Mann-Whitney test, $U_{14,7} = 44$, $P = 0.71$), suggesting that females do not discriminate among horned and hornless males by preferentially terminating copulations. Female mating behavior, and this conspicuous absence of direct female choice, will be discussed more fully in a later paper.

In experiment 2, which had equal frequencies of horned and hornless males (one of each per observation chamber), 75% of the observed matings were by the horned male (9/12). However, this need not reflect the relative reproductive success of horned and hornless males under natural conditions, because morph frequencies may vary, and because sneaking males may sometimes intercept several different primary tunnels (which was not possible in this experiment).

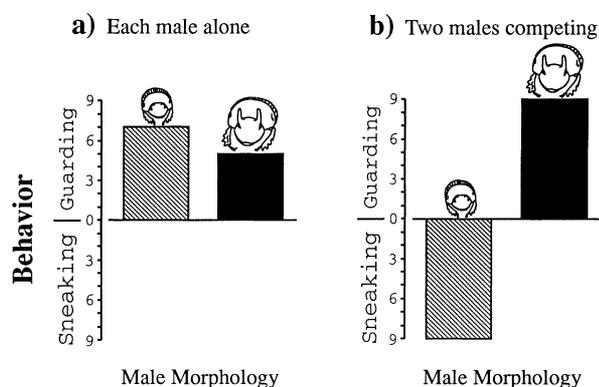


Fig. 2 Reproductive behaviors used by horned and hornless males to gain access to females. **a** When males were alone with females, all males remained inside primary tunnels with females (“guarding”). **b** However, when males competed for access to a female, only the horned males were able to successfully guard tunnels. In these situations the hornless males sneaked into guarded tunnels by digging new tunnels that intercepted the guarded tunnels below ground

Experiments 3 and 4: guarding performance and male morphology

Body size significantly affected male performance at guarding tunnels (experiment 3; Fig. 3). These contests controlled for possible confounding effects of male horn length by using pairs of males that differed in body size but not horn length. In males with the same horn lengths, body size significantly affected the outcome of fights, with the larger male winning 9 out of 10 staged contests (chi-square test: $\chi^2 = 6.40$, $P = 0.011$).

Natural variation in male horn length also affected guarding ability. Specifically, long horns improved male

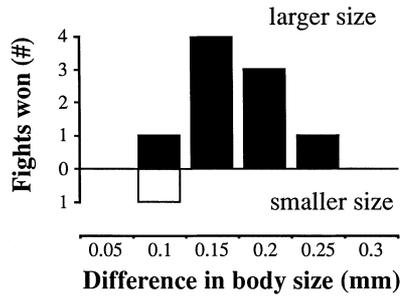


Fig. 3 Effect of male body size on guarding performance. Results are from 10 staged contests between males with the same horn length but different body sizes

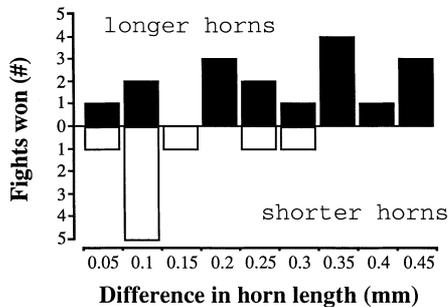


Fig. 4 Effect of male horn length on guarding performance. Results are from 26 staged contests between same-sized males with different horn lengths

guarding performance when the confounding effects of body size were removed, and when the difference in horn lengths between contestants was large (experiment 4; Fig. 4). The probability of a male winning a fight was significantly and positively affected by the difference in horn length between contestants (simple regression, $r = 0.696$, $F = 6.573$, $P = 0.037$). Males with relatively long horns were more likely to win contests over tunnel ownership than males with relatively short horns.

Discussion

Males in natural populations of the beetle *O. acuminatus* occur in two forms. Populations on Barro Colorado Island, Panama, contain approximately equal numbers of males with a pair of fully developed horns, and males with only rudimentary horns or no horns at all (Emlen 1994a, 1997). Here I show that horned and hornless males employ two very different behavioral tactics to encounter and mate with females. Large, horned males guard entrances to tunnels containing females (Fig. 1). Guarding a tunnel enabled a male to mate repeatedly with the female as she provisioned burrows with dung and oviposited. Guarding frequently involved fighting intruding males over tunnel occupancy, and was similar to behavior described for other horned dung beetles living in burrows (*Onthophagus binodis*: Cook 1990;

Onthophagus taurus: Fabre 1899; Moczek 1996; D.J. Emlen, unpublished work; *Phanaeus difformis*: Rasmussen 1994; *Typhoeus typhoeus*: Palmer 1978).

Smaller, hornless males also remained inside tunnels with females when given the opportunity (i.e., when there was no competition from rival males; Fig. 2a). However, whenever males competed for access to females (the typical situation in natural populations; Emlen 1994b), hornless males always adopted a non-aggressive alternative tactic that was never employed by the larger, horned males (Fig. 2b). Hornless males sneaked into guarded tunnels either by digging side-tunnels that intercepted guarded tunnels below ground (Fig. 1), or by sliding past guarding males at the tunnel entrance. Sliding past guarding males was similar to sneaking behavior described for hornless males in other horned beetle species (e.g., Rasmussen 1994; Moczek 1996; A.P. Moczek and D.J. Emlen, unpublished work), but this is the first characterization of a sneaking tactic involving hornless males digging their own tunnels, and intercepting guarded burrows beneath the soil surface. It was impossible to estimate the profitability of sneaking into tunnels, as compared with guarding, using the present methods. Below-ground behaviors could only be observed inside glass-walled observation chambers. These chambers restricted the directions of side-tunnels, and may have influenced the likelihood of a sneaking male intercepting a guarded tunnel. However, castes from natural tunnels indicated that side-tunneling males can intercept multiple guarded tunnels with a single side-tunnel, suggesting that sneaking males may repeatedly visit numerous tunnels. More direct measures are needed (e.g., using genetic markers) to adequately assess the relative fertilization success of guarding and sneaking males.

Females appeared to mate with hornless males just as readily as with horned males. No female ever rejected matings with any male, and copulation durations were not different for horned and hornless males. These results are consistent with a mating system characterized by intense inter-male competition over access to females, and where smaller, competitively inferior males adopt a non-aggressive behavioral alternative to encounter females.

Do guarding and sneaking tactics favor horned and hornless male morphologies, respectively? As a first step towards addressing this question, this study measured the effect of natural variation in male horn morphology on male performance at guarding tunnels. In staged contests that controlled for confounding effects of variation in body size, males with relatively longer horns won significantly more fights over tunnel ownership than same-sized males with relatively shorter horns. This suggests that for males large enough to guard tunnels, long horns will be beneficial.

But why should smaller, sneaking males be hornless? One possibility is that males without horns sneak more effectively than males with horns. Horns scrape against tunnel walls as beetles run below ground (Emlen 1994b;

Moczek 1996). Sneaking males depend on rapidly entering and exiting tunnels for their reproductive success, and horns may hinder their sneaking performance. Although this remains to be tested for *O. acuminatus*, experiments conducted on the related species *Onthophagus taurus* demonstrated that for same-sized males, males with short horns moved significantly faster inside tunnels than males with longer horns (Moczek 1996; A.P. Moczek and D.J. Emlen, unpublished work).

A second possibility is that horns are costly to produce. Relatively small males were not successful at guarding tunnels, and presumably derive little benefit from possessing horns. If horns are expensive to produce, then this might favor males able to facultatively omit horn growth whenever developmental conditions preclude the attainment of large body sizes. At least two costs of beetle horns have already been established. First, production of horns significantly extends the development time of *O. taurus* males, and results in increased larval mortality from soil-dwelling nematodes (Hunt and Simmons in press). Second, allocation of developmental resources to horns in both *O. acuminatus* and *O. taurus* results in reduced allocation to other morphological traits, specifically eyes: males with relatively longer horns developed with significantly smaller eyes than males with relatively shorter horns (D.J. Emlen and H.F. Nijhout, unpublished work). Such costs to horn production suggest that sneaking males might benefit by not developing horns.

One prerequisite for the maintenance of dimorphism is that organisms experience a fitness tradeoff across environments (Levins 1968; West-Eberhard 1979, 1992; Stearns 1982; Lively 1986b). If animals encounter several discrete environment types, or ecological or behavioral situations, and these different environments favor different morphologies, then distinct morphological alternatives can evolve within a single population – each specialized for one of the different environments. Such fitness tradeoffs have been demonstrated for several dimorphic species. For example, soft and hard seed diets have favored two divergent bill morphologies within populations of African finches (Smith 1993), and high and low levels of predation have favored alternative shell morphologies in barnacles (Lively 1986a), and spined and spineless morphologies in rotifers (Gilbert and Stemberger 1984) and *Daphnia* (Grant and Bayly 1981; Black and Dodson 1990; Spitz 1992). It is possible that the alternative reproductive tactics characterized in this study produce a similar situation in *O. acuminatus*. If guarding and sneaking behaviors favor horned and hornless male morphologies, respectively, then the reproductive behavior of males may have contributed to the evolution of male horn length dimorphism in this species.

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