

**PHYLOGENETIC EVIDENCE FOR AN ASSOCIATION BETWEEN TUNNELING
BEHAVIOR AND THE EVOLUTION OF HORNS IN DUNG BEETLES
(COLEOPTERA: SCARABAEIDAE: SCARABAEINAE)**

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Abstract

Dung beetles employ numerous behavioral strategies to sequester dung away from other insects, and these have been broadly grouped into two categories: species that dig tunnels beneath the dung (tunnelers) and species that roll dung on the surface of the soil (rollers). Many species also are armed with rigid exoskeletal outgrowths called horns. Horns function as weapons, and horn sizes can be extreme. One widespread pattern within dung beetles is that tunneling species often have horns, whereas rolling species almost always do not, suggesting that residing (and fighting) inside tunnels at the dung deposition site may be an important ecological prerequisite for the evolution of horns in dung beetles. Here, we test explicitly for an historical association between tunneling behavior and the evolution of horns using a recent phylogeny for the scarabaeine dung beetles. We show that all eight of the independent gains of horns included in our analyses occurred on branches of the phylogeny reconstructed as tunneling, and that one of the three evolutionary losses of horns occurred on a branch that had lost tunneling behavior. We interpret this as evidence for a biologically meaningful association between tunneling behavior and the evolution of enlarged or exaggerated weapons such as horns, supporting the ideas of Eberhard and others that beetle horns may be most “beneficial” when used within the confines of restricted spaces such as burrows or tunnels.

Males in many animal species produce elaborate morphological weapons that aid in competition with rival males over access to females (Darwin 1871; Geist 1978; Eberhard 1979; Lincoln 1994; Sneddon *et al.* 1997). Male investment into the production of these structures is predicted to be favored whenever individuals with long or large weapons derive a performance advantage over individuals with smaller weapons, and when the net reproductive benefits of having such structures outweigh the allocation and survivorship costs of their production (Parker 1979, 1983; West-Eberhard 1983; Andersson 1994; Andersson and Iwasa 1996). This means that for many animals, weapon production is only cost-effective when male contests occur over physically restricted or economically defendable resources or substrates. For example, male lucanid beetles use enlarged mandibles in fights over localized plant wounds or sap flows on the sides of tree trunks (Mathieu 1969; Otte and Stayman 1979; Fearn 1996; Suzuki 1996), male fiddler crabs use their enlarged claws in fights over burrows in the sand (Crane 1975; Christy 1983; Oliveira and Custodio 1998), and males of many

ungulates use their antlers/horns in fights over groups/harems of females (Geist 1966, 1978; Clutton-Brock *et al.* 1980; Lincoln 1994).

For many dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae), this restricted substrate is likely to be a tunnel in the soil with a sequestered dung resource. Male dung beetles often possess horns (d'Orbigny 1913; Paulian 1935; Arrow 1951; Howden and Gill 1993; Kohlmann and Solis 2001)¹. Dung beetle horns can reach extreme sizes, and horn development is expensive: growing a horn extends larval development time, increasing the risk of mortality due to nematodes and pathogens in the soil and dung (Hunt and Simmons 1997), and horn growth can stunt the relative growth of other morphological structures including eyes, wings, antennae, genitalia, and testes (Emlen 2001; Knell *et al.* 2004; Moczek and Nijhout 2004; Emlen *et al.* 2005; Tomkins *et al.* 2005). However, costs of horn growth appear to be offset in many species because horns aid males in contests and, as a result, males with the longest horns win disproportionate access to females (Rasmussen 1994; Emlen 1997; Moczek and Emlen 2000; Hunt and Simmons 2001; Pomfret and Knell 2005).

Contests involving horns have now been studied in at least ten species of dung beetle (seven species of *Onthophagus* Latreille [Fabre 1899; Cook 1990; Emlen 1997; Kotiaho 2000; Moczek and Emlen 2000; Hunt and Simmons 2002]; *Euoniticellus intermedius* Reiche [Lailvaux *et al.* 2005; Pomfret and Knell 2005], *Coprophanæus ensifer* Germar [Otronen 1988], and *Phanaeus difformis* Leconte [Rasmussen 1994]), and in all of these, both contests and matings occur inside underground burrows where females reside and provision eggs on gathered dung (*e.g.*, Fabre 1899; Halffter and Matthews 1966). Direct observations of these fights suggest that horns are used to assist in blocking tunnel entrances or in prying opponents away from tunnel walls and pushing them out of tunnels (*e.g.*, Rasmussen 1994; Emlen 1997; Moczek and Emlen 2000). This is similar to the use of horns by males of several species of rhinoceros beetles (Scarabaeidae: Dynastinae) and 'dor' beetles (Scarabaeoidea: Geotrupidae) that also battle over tunnels or burrows (*e.g.*, Daguerre 1931; Palmer 1978; Eberhard 1979, 1982, 1987).

The recurrent association between male horns and fights over burrows led to the suggestion that tunneling behavior may have been an important ecological prerequisite for the evolution of horns in dung beetles (Eberhard 1979; Emlen 2000; Emlen *et al.* 2005). This hypothesis proposes that the evolution of tunneling behavior adjacent to or underneath the dung resource may have resulted in situations (*i.e.*, contests inside restricted burrows) that consistently favored male investment into large body weapons; males with horns or other projections could block tunnel entrances or expel intruders more effectively than those lacking these ornaments, and in so doing could guard access to resident females. In contrast, beetles that fight in the open (*e.g.*, above ground) may not have experienced net selection for large horns because the benefits of horns in these contests would be smaller and, therefore, less likely to outweigh horn costs. Specifically, this hypothesis predicts that gains of horns will be more likely to occur in lineages of beetles that fight over restricted substrates such as tunnels than in lineages that

¹ Females of a surprising number of dung beetle species also produce horns, and in a few species (*e.g.*, *Onthophagus sagittarius* Fabricius, *Heteronitis castelnaui* Harold, *Liatongus monstrosus* Bates) females produce larger horns than males. Females in at least one of these species (*O. sagittarius*) use their horns in fights with rival females inside burrows, but the majority of species with female horns have yet to be studied behaviorally, and so we restrict our current analyses to discussions of the evolution of male horns.

fight in the open. Concomitantly, it also predicts that lineages of tunnelers that ancestrally had horns will lose their horns if they shift from fighting inside tunnels to fighting in the open.

Dung beetles are ideal for testing these hypotheses. Historically, dung beetles are thought to have experienced intense competition for their food resources (Halffter and Edmonds 1982; Doube 1990; Cambefort and Hanski 1991), and today the majority of extant species utilize one of two behavioral strategies to escape this competition: they either dig a tunnel into the soil beneath or adjacent to the dung and stash dung in the burrow to sequester it away from other insects ('tunnelers'), or they carve and mold dung into a ball and roll it away from the dung source ('rollers'; Halffter and Matthews 1966; Halffter and Edmonds 1982; Doube 1990; Cambefort 1991; Cambefort and Hanski 1991). These two behavioral strategies were long thought to represent a single and relatively ancient evolutionary split, with currently defined tribes of Scarabaeinae belonging to either tunnelers (six 'dichotomiine' tribes) or rollers (six 'canthonine' tribes, with one reversal from rolling to tunneling in the Eurysternini) (Halffter and Matthews 1966; Halffter and Edmonds 1982; Cambefort and Hanski 1991).

However, a recent phylogenetic analysis of the scarabaeine dung beetles based on 200 morphological characters of 46 species representing 45 genera and 11 tribes of dung beetles (Philips *et al.* 2004) revealed a much richer history of evolution. Their result suggests that the ancestors of the dung beetles were tunnelers, and that the behavioral transition from tunneling to ball forming and rolling occurred independently as many as seven times. Here, we use this same phylogeny to test for an historical relationship between tunneling behavior and the evolution of horns.

Methods

Both behavioral strategy (tunneling or rolling) and horns (presence or absence) (Table 1) were mapped onto the phylogeny as discrete characters with two states using MacClade 4.0 (Maddison and Maddison 1999). Horns were defined broadly to include any projections (pronounced ridges or carinae or obvious protruberances as well as more typical "horns") on the head or pronotum of males. Based on the taxa at the base of the tree (as reconstructed by Philips *et al.* 2004), this method implies that the ancestor of the dung beetles was a tunneler and that there were seven subsequent transitions from tunneling to ball-rolling behavior (as reconstructed in Philips *et al.* 2004). This method also suggests that the ancestor of dung beetles was hornless (but see Emlen *et al.* 2006).

To test for correlated evolution between these two characters, we used the concentrated changes test (Maddison 1990) as implemented in MacClade 4.0. Specifically, we tested whether evolutionary gains of male horns were concentrated on branches of the tree that were also scored as tunneling. Because this analysis requires a fully resolved tree topology, we performed concentrated changes tests separately on each of two equally parsimonious trees included in the consensus tree of Philips *et al.* (2004). The third equally parsimonious tree was not included because it was not thought to be a likely hypothesis of evolution in the scarabaeine dung beetles (see Philips *et al.* 2004 for more details).

Results and Discussion

Beetle lineages that battle conspecifics inside the confines of tunnels evolved horns eight separate times, whereas those that fought above ground did not gain

Table 1. Species included in the phylogeny with behavior and morphology indicated.

Taxon	Behavior	Morphology	Taxon	Behavior	Morphology
<i>Amphistomus</i> sp. (van Lansberge)	roller		<i>Eurysternus velutinus</i> (Bates)	tunneler	
<i>Anachalcus comexus</i> (Klug)	roller		<i>Garreta nitens</i> (Olivier)	roller	
<i>Anomipsoides cavifrons</i> (Burmeister) ¹	tunneler	horns	<i>Glyphoderus sterculinus</i> (Westwood) ¹	tunneler	horns
<i>Anomipsus panamensis</i> (Paulian) or near	tunneler		<i>Helicopris hamadryas</i> (Fabricius)	tunneler	horns
<i>Archnodes</i> sp.	roller		<i>Heteronitis castelnau</i> (Harold)	tunneler	horns
<i>Ateuchus lecontei</i> (Harold)	tunneler		<i>Kheper subaeneus</i> (Janssens)	roller	
<i>Bdelyropsis bowditchi</i> (Paulian)	roller		<i>Lepanus ustulatus</i> (van Lansberge)	roller	
<i>Bubas bubalus</i> (Olivier)	tunneler	horns	<i>Liatoragus militaris</i> (Castelnau)	tunneler	horns
<i>Canthidium perceptibile</i> (Howden & Young)	tunneler		<i>Metacatharsius opacus</i> (Waterhouse)	tunneler	horns
<i>Canthon imitator</i> (Robinson)	roller		<i>Neosisyphus regardi</i> (Klug)	roller	
<i>Cephalodesmus laticollis</i> (Pascoe) ¹	re-locator		<i>Oniticellus pictus</i> (Hausmann)	dweller	
<i>Circellium bacchus</i> (Fabricius)	roller		<i>Onitis fulgidus</i> (Klug)	tunneler	horns
<i>Copris</i> sp.	tunneler	horns	<i>Oxysternon festivum</i> (L.)	tunneler	
<i>Coptodactyla lesnei</i> (Paulian)	tunneler	horns	<i>Pedaria</i> sp.	tunneler	
<i>Coptorhina klugi</i> (Hope)	tunneler	horns	<i>Phanaeus difformis</i> (LeConte)	tunneler	horns
<i>Cyptochirus ambiguus</i> (Kirby)	tunneler	horns	<i>Scaptocnemis segregis</i> (Peringuey)	tunneler	
<i>Demarziella imitatrix</i> (Balthasar)	tunneler	horns	<i>Scarabaeus flavicornis</i> (Boheman)	roller	
<i>Diastellopalpus thomsoni</i> (Bates) or near	tunneler	horns	<i>Scatinus quadridentatus</i> (Balthasar)	tunneler	
<i>Dichotomius satanus</i> (Harold)	tunneler	horns	<i>Sisyphus</i> sp.	roller	
<i>Digitonthophagus gazella</i> (Fabricius)	tunneler	horns	<i>Sulcophanaeus velutinus</i> (Murry)	tunneler	horns
<i>Drepanocerus</i> sp.	tunneler	horns	<i>Synapsis molus</i> (Fischer) ¹	re-locator	
<i>Epirinus silvestris</i> (Cambefort)	roller		<i>Tiniocellus spinipes</i> (Roth)	tunneler	
<i>Euoniticellus intermedius</i> (Reiche)	tunneler	horns	<i>Tragiscus dimidiatus</i> (Klug)	dweller	
<i>Eurysternus confusus</i> (Jessop)	tunneler		<i>Xinidium dentilabrum</i> (Harold)	tunneler	horns

¹ These species are known to horizontally re-locate dung (e.g., drag or push dung pellets; Ocampo and Phillips 2005; Ocampo 2005). However, they behave like tunnelers in other respects (e.g., they dig tunnels before they provision them with dung). Because fights in these species are still likely to occur inside tunnels, we did not distinguish them from true tunnelers in the present analyses.

horns even a single time. All eight gains of horns occurred on branches of the tree that were also scored as tunneling (Fig. 1), and this pattern was significant for both of the fully resolved trees of Philips *et al.* (2004) (8/8 gains of horns, trees 1 and 2: $P = 0.05$). The converse pattern was also significant: none of the eight gains of horns occurred on branches of the tree scored as ball rolling (0/8 gains of horns, trees 1 and 2: $P = 0.05$). Despite the fact that 27% of the included taxa were rollers and 45% of the taxa had horns, not one lineage of rollers included an evolutionary gain of horns.

We interpret this as evidence that the confinement of contests to restricted spaces such as tunnels may have been an important prerequisite for the evolution of horns in the Scarabaeinae. It may be that only in these confined spaces are horns sufficiently effective at aiding males in contests and that the benefits of horns outweigh the substantial costs of their production.

Two of the taxa included in this study (*Oniticellus pictus* Hausmann, *Tragiscus dimidiatus* Klug) form nests directly within dung ('dwellers') (Davis 1989, 1997; Philips *et al.* 2004). Although both of these species are derived from a lineage of tunnelers, neither presently excavates burrows into the soil. Dwelling behavior, like ball rolling, brings fights out of tunnels and into more malleable/open substrates (tunnels inside dung are not as confining or resistant to pushing/prying behavior as burrows excavated into the soil; D. J. Emlen, pers. obs.). For this reason, rolling and dwelling behaviors may be ecologically similar with respect to sexual selection on horns: both may be less likely to favor the evolution of large weapons than tunneling. Interestingly, one of these dwelling species (*O. pictus*) is a hornless species within a horned clade (Fig. 1). Thus, it has *secondarily lost horns*—consistent with an evolutionary association between tunneling behavior and horns.

Other ecological factors, such as low population densities (and hence fewer conflicts over burrows), may also result in weaker selection for large weapons in dung beetles. We mention this possibility because both of the other two losses of horns (Fig. 1) occurred in species that are likely to have especially low population densities. *Synapsis tmolus* Fischer is found in the semi-arid steppes of central Asia, and *Scaptocnemis segregis* Peringuey is a species confined to high elevation forests in East Africa. These are two habitats with typically low numbers of scarabaeine individuals, and we suggest that selection for large weapons could have been relaxed in these lineages.

What about other beetles with horns? In fact, a great many of the dynastid and geotrupid beetles with horns use them in contests over some form of burrow (Lameere 1904; Eberhard 1979), either in the soil (*e.g.*, *Aegopsis nigricollis* Sternberg [Eberhard 1987]; *Typhoeus typhoeus* Linnaeus [Palmer 1978]; *Diloboderus abderus* Sturm [Daguerre 1931; Rowland, J. M., pers. comm.]) or in hollowed-out stems of palms or sugar cane (*Podischnus agenor* Olivier [Eberhard 1982]; *Scapanes australis* Boisduval [Prior *et al.* 2000; Rowland *et al.* 2005]). Thus, it is possible that defense of burrows may be a widespread phenomenon selecting for male investment in elaborate or exaggerated weapons in beetles. However, tunnels clearly are not the only situation that can favor male investment in horns. Many extant species of rhinoceros and stag beetle fight over branches or emergent plant shoots (*e.g.*, *Golofa porteri* Hope) (Eberhard 1978; Howden and Campbell 1974) or for plant wounds and sap flows on tree trunks (*e.g.*, *Lucanus spp.* [Otte and Stayman 1979; Fearn 1996; Suzuki 1996], *Allomyrina dichotoma* [L.] [Iguchi 2001; Hongo 2003])—all substrates with a relatively confined zone of contact that, like tunnels, is likely to be economically defensible (*e.g.*, Thornhill and

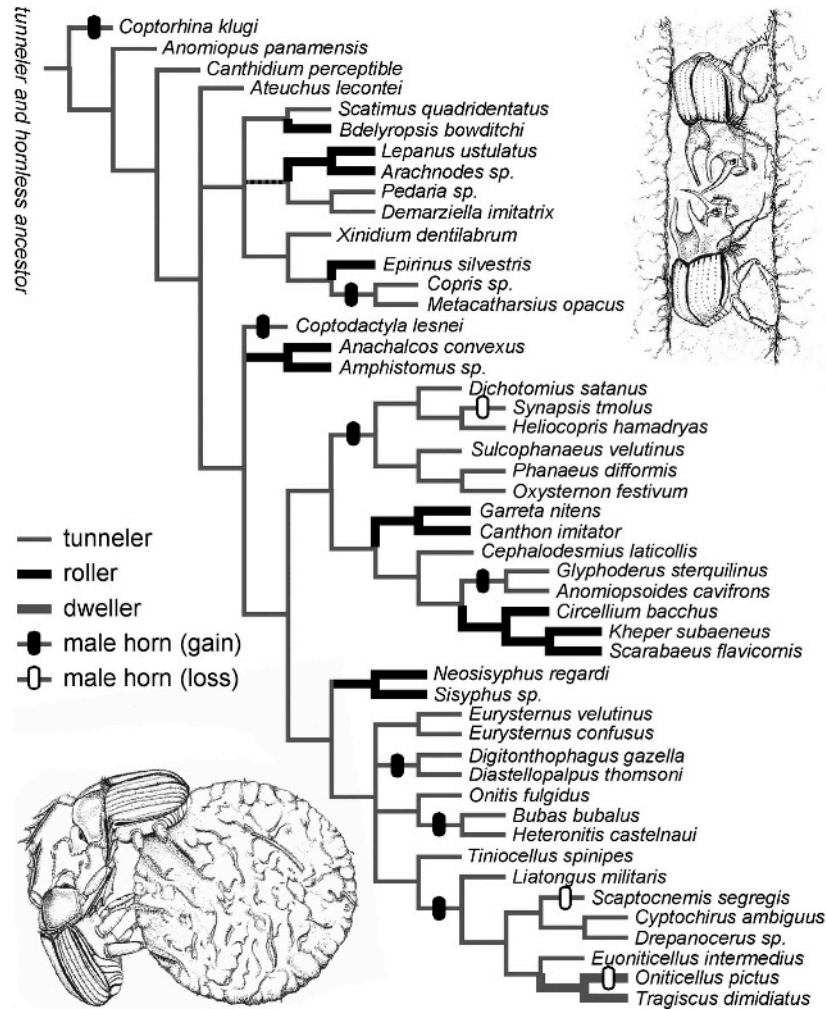


Fig. 1. Phylogenetic hypothesis for the relationships among 46 species of dung beetles illustrating evolutionary transitions from tunneling (thin gray branches) to non-tunneling ("roller") behavior and gains of male horns (closed, vertical bubble) or losses of male horns (open, vertical bubble). Non-tunnelers either roll balls (thick black branches) or form nests directly within dung (thick gray branches), both of which resulted in male contests occurring above ground. Gains of horns were significantly concentrated on branches of the tree that were also scored as tunneling (8/8 gains of horns), and one of the three losses of horns occurred on a branch scored as non-tunneling. Phylogeny from Philips *et al.* 2004.

Alcock 1983). Tree branches and sap flows have the added feature that they are elevated, which may have led to selection for additional functions of horns, such as lifting and dropping opponents from the contest (Beebe 1944; Eberhard 1978, 1979; Suzuki 1996). Which came first? And did these changes in the ecological

context of contests influence the evolution of horns? Additional behavioral and comparative studies will be needed to more fully test these ideas.

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References Cited

- Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton, NJ.
- Andersson, M., and Y. Iwasa. 1996. Sexual selection. *Trends in Ecology and Evolution* 11:53–58.
- Arrow, G. J. 1951. *Horned Beetles*. The Hague.
- Beebe, W. 1944. The function of secondary sexual characters in two species of Dynastinae (Coleoptera). *Zoologica* 29:53–58.
- Cambefort, Y. 1991. Biogeography and evolution [pp. 51–68]. In: *Dung Beetle Ecology*. I. Hanski and Y. Cambefort (eds.). Princeton University Press, Princeton, NJ.
- Cambefort, Y., and I. Hanski. 1991. Dung beetle population biology [pp. 36–50]. In: *Dung Beetle Ecology*. I. Hanski and Y. Cambefort (eds.). Princeton University Press, Princeton, NJ.
- Christy, J. H. 1983. Female choice and the breeding behavior of the fiddler crab *Uca beebei*. *Journal of Crustacean Biology* 7:624–635.
- Clutton-Brock, T. H., S. D. Albon, and P. Harvey. 1980. Antlers, body size and breeding group size in the Cervidae. *Nature* 285:565–567.
- Cook, D. 1990. Differences in courtship, mating and postcopulatory behavior between male morphs in the dung beetle *Onthophagus binodis* Thunberg (Coleoptera: Scarabaeidae). *Animal Behaviour* 40:428–436.
- Crane, J. 1975. *Fiddler Crabs of the World*. Princeton University Press, Princeton, NJ.
- d'Orbigny, H. 1913. Synopsis des Onthophagides d'Afrique. *Annales de la Société Entomologique de France* 132:1–795.
- Daguerre, J. B. 1931. Costumbres nupicales del *Diloboderus abderus* Sturm. *Revista de la Sociedad Entomologia Argentina* 3:253–256.
- Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. Random House, Modern Library, New York, NY.
- Davis, A. L. V. 1989. Nesting of Afrotropical *Oniticellus* (Coleoptera, Scarabaeidae) and its evolutionary trend from soil to dung. *Ecological Entomology* 14:11–21.
- Davis, A. L. V. 1997. Climatic and biogeographical associations of southern African dung beetles. *African Journal of Ecology* 35:10–38.
- Doube, B. M. 1990. A functional classification for analysis of the structure of dung beetle assemblages. *Ecological Entomology* 15:371–383.
- Eberhard, W. G. 1978. Fighting behavior of male *Golofa porteri* beetles (Scarabaeidae: Dynastinae). *Psyche* 83:292–298.
- Eberhard, W. G. 1979. The function of horns in *Podischmus agenor* (Dynastinae) and other beetles [pp. 231–259]. In: *Sexual Selection and Reproductive Competition in Insects*. M. S. Blum and N. A. Blum (eds.). Academic Press, New York, NY.
- Eberhard, W. G. 1982. Beetle horn dimorphism making the best of a bad lot. *American Naturalist* 119:420–426.

- Eberhard, W. G. 1987.** Use of horns in fights by the dimorphic males of *Ageopsis nigricollis* (Coleoptera, Scarabaeidae, Dynastinae). *Journal of the Kansas Entomological Society* 60:504–509.
- Emlen, D. J. 1997.** Alternative reproductive tactics and male-dimorphism in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Behavioral Ecology and Sociobiology* 41:335–341.
- Emlen, D. J. 2000.** Integrating development with evolution: A case study with beetle horns. *Bioscience* 50:403–418.
- Emlen, D. J. 2001.** Costs and the diversification of exaggerated animal structures. *Science* 291:1534–1536.
- Emlen, D. J., J. Marangelo, B. Ball, and C. W. Cunningham. 2005.** Diversity in the weapons of sexual selection: Horn evolution in the beetle genus *Onthophagus* (Coleoptera: Scarabaeidae). *Evolution* 59:1060–1084.
- Emlen, D. J., Q. Szafran, L. S. Corley, and I. Dworkin. 2006.** Insulin signaling and limb-patterning: Candidate pathways for the origin and evolutionary diversification of beetle 'horns'. *Heredity* 97:179–191.
- Fabre, J. H. 1899.** *Souvenirs Entomologiques VI*. Librairie Delgrave, Paris.
- Fearn, S. 1996.** Observations on the life history and habits of the stag beetle *Lamprima aurata* (Latrielle) (Coleoptera: Lucanidae) in Tasmania. *Australian Entomologist* 24:133–139.
- Geist, V. 1966.** The evolution of horn-like organs. *Behaviour* 27:175–214.
- Geist, V. 1978.** On weapons, combat and ecology [pp. 1–30]. In: *Aggression, Dominance and Individual Spacing*. L. Kramer, P. Pliner, and T. Alloway (eds.). Plenum Press, New York, NY.
- Halfiter, G., and W. D. Edmonds. 1982.** *The Nesting Behavior of Dung Beetles (Scarabaeidae): An Ecological and Evolutionary Approach*. Instituto de Ecologia, Mexico, D.F.
- Halfiter, G., and E. G. Matthews. 1966.** The natural history of the dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). *Folia Entologica Mexicana* 12–14:1–313.
- Hongo, Y. 2003.** Appraising behaviour during male-male interaction in the Japanese horned beetle *Trypoxylus dichotomus septentrionalis* (Kono). *Behaviour* 140:501–517.
- Howden, H. F., and B. D. Gill. 1993.** Mesoamerican *Onthophagus* Latreille in the *Dicranus* and *Mirabilis* groups (Coleoptera: Scarabaeidae). *Canadian Entomologist* 125:1091–1114.
- Howden, H. F., and J. M. Campbell. 1974.** Observations on some Scarabaeoidea in the Colombia Sierra Nevada De Santa Marta. *Coleopterists Bulletin* 28:109–114.
- Hunt, J., and L. W. Simmons. 1997.** Patterns of fluctuating asymmetry in beetle horns: an experimental examination of the honest signalling hypothesis. *Behavioral Ecology and Sociobiology* 41:109–114.
- Hunt, J., and L. Simmons. 2001.** Status-dependent selection in the dimorphic beetle *Onthophagus taurus*. *Proceedings of the Royal Society Series B* 268:2409–2414.
- Hunt, J., and L. W. Simmons. 2002.** Behavioural dynamics of biparental care in the dung beetle *Onthophagus taurus*. *Animal Behaviour* 64:65–75.
- Iguchi, Y. 2001.** Differences in the frequency of fights between minor and major males in the horned beetle *Trypoxylus dichotomus septentrionalis* (Coleoptera: Scarabaeidae). *Entomological Review of Japan* 56:11–14.
- Knell, R. J., J. C. Pomfret, and J. L. Tomkins. 2004.** The limits of elaboration: curved allometries reveal the constraints on mandible size in stag beetles. *Proceedings of the Royal Society of London, Series B* 271:523–528.
- Kohlmann, B., and A. Solis. 2001.** El genero *Onthophagus* (Coleoptera: Scarabaeidae) en Costa Rica. *Giornale Italiano di Entomologia* 49:1–261.
- Kotiaho, J. S. 2000.** Testing the assumptions of conditional handicap theory: Costs and condition dependence of a sexually selected trait. *Behavioral Ecology and Sociobiology* 48:188–194.
- Lailvaux, S. P., J. Hathway, J. Pomfret, and R. J. Knell. 2005.** Horn size predicts physical performance in the beetle *Euoniticellus intermedius* (Coleoptera: Scarabaeidae). *Functional Ecology* 19:632–639.

- Lameere, A. 1904. L'Evolution des ornements sexuels. Academie Royale de Belgique, Bulletin 1904:1327–1364.
- Lincoln, G. A. 1994. Teeth, horns and antlers: the weapons of sex [pp. 131–158]. In: *The Differences Between the Sexes*. R. V. Short and E. Balaban (eds.). Cambridge University Press, Cambridge, MA.
- Maddison, W. P. 1990. A method for testing the correlated evolution of two binary characters: Are gains or losses concentrated on certain branches of a phylogenetic tree? *Evolution* 44:539–557.
- Maddison, W. P., and D. R. Maddison. 1999. MacClade: analysis of phylogeny and character evolution. Sinauer Associates, Sunderland, MA.
- Mathieu, J. M. 1969. Mating behavior of five species of Lucanidae (Coleoptera: Insecta). *Canadian Entomologist* 101:1054–1062.
- Moczek, A. P., and D. J. Emlen. 2000. Male horn dimorphism in the scarab beetle, *Onthophagus taurus*: Do alternative reproductive tactics favour alternative phenotypes? *Animal Behaviour* 59:459–466.
- Moczek, A. P., and H. F. Nijhout. 2004. Tradeoffs during the development of primary and secondary sexual traits in a horn dimorphic beetle. *American Naturalist* 163:184–191.
- Ocampo, F. C. 2005. Revision of the southern South American endemic genus *Anomiopsoides* Blackwelder 1944 (Coleoptera: Scarabaeidae: Scarabaeinae: Eucraniini) with description of its food relocation behavior. *Journal of Natural History* 39:2537–2557.
- Ocampo, F. C., and T. K. Philips. 2005. Food relocation behavior of the Argentinian dung beetle genus *Eucranium* Brullé and comparison with the southwest African *Scarabaeus* (*Pachysoma*) MacLeay (Coleoptera: Scarabaeidae: Scarabaeinae). *Revista de la Sociedad Entomológica Argentina* 64:53–59.
- Oliveira, R. F., and M. R. Custodio. 1998. Claw size, waving display and female choice in the European fiddler crab, *Uca tangeri*. *Ethology, Ecology and Evolution* 10:241–251.
- Otronen, M. 1988. Intra- and intersexual interactions at breeding burrows in the horned beetle *Coprophanaeus ensifer*. *Animal Behaviour* 36:741–748.
- Otte, D., and K. Stayman. 1979. Beetle horns: Some patterns in functional morphology [pp. 259–292]. In: *Sexual Selection and Reproductive Competition in Insects*. M. S. Blum and N. A. Blum (eds.). Academic Press, New York, NY.
- Palmer, T. J. 1978. A horned beetle which fights. *Nature* 274:583–584.
- Parker, G. A. 1979. Sexual selection and sexual conflict [pp. 123–166]. In: *Sexual Selection and Reproductive Competition in Insects*. M. S. Blum and N. A. Blum (eds.). Academic Press, New York, NY.
- Parker, G. A. 1983. Arms races in evolution: an ESS to the opponent-independent costs game. *Journal of Theoretical Biology* 101:619–648.
- Paulian, R. 1935. Le polymorphisme des males de Coléoptères [pp. 1–33]. In: *Exposés de Biométrie et Statistique Biologique IV. Actualités Scientifiques et Industrielles*. G. Tessier (ed.). Hermann, Paris.
- Philips, T. K., E. Pretorius, and C. H. Scholtz. 2004. A phylogenetic analysis of dung beetles (Scarabaeinae: Scarabaeidae): unrolling an evolutionary history. *Invertebrate Systematics* 18:53–88.
- Philips, T. K., D. W. Edmonds, and C. H. Scholtz. 2004. Phylogenetic analysis of the New World Phanaeini (Scarabaeidae: Scarabaeinae): Hypotheses on origins and relationships. *Insect Systematics and Evolution* 35:43–63.
- Pomfret, J., and R. J. Knell. 2005. Sexual selection and horn allometry in the dung beetle *Euoniticellus intermedius*. *Animal Behaviour* 71:567–576.
- Prior, R., J.-P. Morin, D. Rochat, L. Beaudoin-Ollivier, T. Stathers, T. Kakul, S. Embupa, and R. Nanguai. 2000. New aspects of the biology of the Melanesian rhinoceros beetle *Scapanes australis* (Col., Dynastidae) and evidence for field attraction to males. *Journal of Applied Entomology* 124:41–50.
- Rasmussen, J. L. 1994. The influence of horn and body size on the reproductive behavior of the horned rainbow scarab beetle *Phanaeus difformis* (Coleoptera: Scarabaeidae). *Journal of Insect Behavior* 7:67–82.

- Rowland, J. M., C. R. Qualls, and L. Beaudoin-Ollivier. 2005.** Discrimination of alternative male phenotypes in *Scapanes australis* (Boisduval) (Coleoptera: Scarabaeidae). *Australian Journal of Entomology* 44:22–28.
- Sneddon, L. U., F. A. Huntingford, and A. C. Taylor. 1997.** Weapon size versus body size as a predictor of winning fights between shore crabs, *Carcinus maenas*. *Behavioral Ecology and Sociobiology* 41:237–242.
- Suzuki, T. 1996.** Some ecological notes of *Cyclommatus metallifer* in Sulawesi, Indonesia: Adult feeding habits and possibility of guarding behavior in stag beetles. *Gekkan-Mushi* 305:16–19.
- Thornhill, R., and J. Alcock. 1983.** *The Evolution of Insect Mating Systems*. Harvard University Press, Cambridge, MA.
- Tomkins, J. L., J. S. Kotiaho, and N. R. LeBas. 2005.** Phenotypic plasticity in the developmental integration of morphological tradeoffs and secondary sexual trait compensation. *Proceedings of the Royal Society of London, Series B* 272:543–551.
- West-Eberhard, M.-J. 1983.** Sexual selection, social competition and speciation. *Quarterly Review of Biology* 58:155–183.