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Seasonal activity and sexual selection in an urban dung beetle

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Onthophagus orpheus Panzer (Coleoptera: Scarabaeidae) is the most abundant dung beetle in urban forests in central Massachusetts, but little is known about its behavioral ecology. We measured individuals throughout the breeding season to characterize male horn allometry and track seasonal variation in population abundance, adult sex ratio (ASR), and male morph ratio. Large major males have a forked thoracic horn that they use in male–male fights over ownership of breeding tunnels; small minor males have rudimentary horns; and females are hornless. Unlike many onthophagine dung beetles that exhibit sigmoidal horn allometries with distinct horned and hornless male morphs, *O. orpheus* exhibits a segmented horn allometry in which many males have intermediate-sized horns. Abundance peaked in July, and average densities were comparable to those observed for other horned *Onthophagus* species that experience intense male–male competition. The season-wide ASR was significantly female-biased, and males exhibited size-dependent seasonal activity. These ecological conditions are likely to promote a highly competitive, defense-based mating system that favors the development of sexually selected horns. Because of its prevalence in urban forests across the eastern United States and the expected increases in resource availability (i.e., dog dung) in urban environments, we highlight *O. orpheus* as an emerging model species for investigating the effects of urbanization on mating dynamics.

Keywords: allometry, male dimorphism, male–male competition, Onthophagus orpheus, sex ratio

Introduction

Sexual selection has driven the evolution of a diverse array of exaggerated traits, including horns in male beetles that can be longer than the rest of their body (Emlen 2008, McCullough et al. 2015). These traits evolve in complex, dynamic environments where ecological conditions can vary over space and time (Miller and Svensson 2014). However, our understanding of how demographic parameters fluctuate across a breeding season remains limited. This information is important not only for understanding the evolution of mating systems but also because it may inform conservation efforts or management of invasive species. For example, human activities can significantly alter animal population abundance (Tucker et al. 2021), and density-dependent sexual selection can influence the risk of extinction or dispersal rates (Kokko and Rankin 2006, Knell 2009a). Our ability to preserve threatened species or minimize the costs of introduced species, therefore, depends on our understanding of how ecological variability impacts the strength, form, and direction of sexual selection.

Sex ratio is a key ecological factor in determining a species' mating system by influencing the intensity and direction of sexual selection (Emlen and Oring 1977, Kvarnemo and Ahnesjö 1996). Of the various ways to measure sex ratio, the operational sex ratio (OSR) is arguably the most relevant for understanding mating dynamics and the strength of sexual selection because it directly measures the proportion of males to females that are ready to mate in a population at a given time (Jennions and Fromhage 2017). Male–male competition is predicted to be the most intense in populations with a male-biased OSR, in which there is a limited number of sexually receptive females. Empirical studies have confirmed that a male-biased OSR is associated with the presence of sexually selected weaponry (Pomfret and Knell 2008, Painting et al. 2014, Barretto et al. 2022) and higher male aggression (Weir et al. 2011; but note that aggression then decreases when the OSR becomes extremely male-biased). Although the OSR is a useful and widely used term in sexual selection studies, it is often difficult to estimate in practice because many animals do not produce obvious visual, olfactory, or auditory cues that indicate whether or not they are sexually active (Székely et al. 2014, Kappeler et al. 2023). By contrast, the adult sex ratio (ASR) denotes the proportion of males to females among adult individuals, which is much easier to assess, and therefore may provide a more useful measure for understanding sexual interactions and breeding system variation (Székely et al. 2014, Kappeler et al. 2023, Zhang et al. 2024).

Population density, independent of sex ratio, is another important ecological factor impacting the strength of sexual

selection because it affects how often individuals encounter potential mates and rivals (Kokko and Rankin 2006, Knell 2009a). Male aggression is predicted to be highest at intermediate population densities. When density is low, selection should favor males that invest in traits that improve their ability to locate mates, and when density is high, male–male competition should shift from aggressive contests to scrambles if males are no longer able to economically defend potential mates (Knell 2009a). The strength of sexual selection may therefore fluctuate across the breeding season, even if the sex ratio remains constant (Miller and Svensson 2014).

Dung beetles (Coleoptera: Scarabaeidae) in the genus *Onthophagus* are a valuable system for studying sexual selection because of their complex mating behaviors and diversity in horn expression. Females dig tunnels beneath fresh dung pads where they mate and build brood balls in which to lay their eggs (Halffter and Edmonds 1982). Males compete with other males over ownership of these breeding tunnels, and one-on-one fighting inside tunnels has favored the evolution of horns (Emlen and Philips 2006). Comparative phylogenetic studies indicate that horns have been gained independently numerous times in the genus *Onthophagus*, and extant species vary tremendously in the location, shape, size, and allometry of their horns (Emlen, Hunt, et al. 2005, Emlen, Marangelo, et al. 2005, Emlen et al. 2007).

Allometry describes how horn size scales with body size and can provide insights into the patterns of selection within and among species (Sherratt et al. 2022). Among the 2000 described *Onthophagus* species are examples with linear, segmented, and sigmoidal horn allometries, as well as species with reversed polarity where females and small males produce horns, but large males are hornless (Emlen, Hunt, et al. 2005, Toh et al. 2022). Research on the mating behaviors of *Onthophagus* dung beetles has focused predominantly on species with sigmoidal allometries, such as *O. acuminatus* Harold (Emlen 1997a) and *O. taurus* Schreber (Hunt and Simmons 1998, Moczek and Emlen 2000, Zhang et al. 2024), so little is known about whether variation in horn allometries corresponds with variation in mating behaviors.

When horns scale sigmoidally with body size, it results in a bimodal distribution of horn sizes with 2 distinct morphs: minor males with no or only rudimentary horns, and major males with fully developed horns (Emlen 1997b, Moczek and Emlen 2000, Buzatto et al. 2024). The discrete male morphologies correspond with alternative reproductive tactics that favor opposite horn phenotypes, with long horns being advantageous for major males that aggressively fight for ownership of breeding tunnels, and hornlessness being advantageous for minor males that rely on sneaking behaviors to mate inside the tunnels of larger males (Moczek and Emlen 2000). At the inflection of the sigmoidal curve, horn size changes dramatically over a narrow range of body size, so very few males have intermediate-sized horns (Buzatto et al. 2024). This pattern may reflect selection against males with intermediate-sized horns because they are likely to perform poorly at both the fighting and sneaking tactics (Moczek and Emlen 2000). By contrast, when horns exhibit a segmented allometry, male dimorphism is less obvious because many males have intermediate-sized horns (Knell 2009b). Because behavioral studies of onthophagine dung beetles have focused on species with sigmoidal horn allometries, we still know relatively little about alternative reproductive behaviors in species with other types of horn allometries.

Onthophagus orpheus Panzer is a metallic green, purple, or bronze beetle that is native to the eastern United States and exhibits both sexual dimorphism and male horn dimorphism (Price and Ratcliffe 2023). Large males develop an enlarged, flattened, and bifurcated pronotal horn that projects forward over the head; small males develop only rudimentary horns; and females are hornless (Fig. 1). Previous research found that *O. orpheus* is the second-most abundant dung beetle in old-growth forests in New Jersey (Price 2004), and this study finds that *O. orpheus* is the most abundant dung beetle in urban forests in central Massachusetts. Despite its prevalence across the eastern United States (GBIF.org 2025), little is known about the behavioral ecology of this species.

The goal of this study was to describe the ecology and population structure of *O. orpheus* across its breeding season. We investigate male dimorphism by exploring horn allometry and report patterns in seasonal abundance, sex ratio, and male morph ratio. This information expands our understanding of the evolutionary ecology of onthophagine dung beetles and provides a foundation for developing *O. orpheus* as a model dung beetle species for studying the impact of urbanization on sexual selection and behavior.

Methods

We collected adult *O. orpheus* using live pitfall traps at 2 urban forests in Worcester, Massachusetts: Hadwen Arboretum (42.258°N, −71.832°W) and Cascades Park (42.287°N, −71.864°W). Pitfall traps consisted of a 1 liter Nalgene bottle that was buried to the rim in soil, covered with 19 mm plastic mesh, and secured with landscape staples. Traps were baited with a 90-ml aliquot of either cow dung or dog dung that was

Fig. 1. *Onthophagus orpheus* A) major male with arrow pointing to large bifurcated thoracic horn, B) minor male with arrow pointing to rudimentary thoracic horn, and C) hornless female with arrow pointing to clypeal ridge that spans the entire width of the head (ridge lacking in males). (Photo credit: Steve King).

placed directly on the plastic mesh and secured with a landscape staple. A small amount of dung was also placed inside the trap to provide food for the captured beetles. Traps were deployed twice per month over a 24-h period from April to November 2024. Eight traps were deployed at each site (4 with dog dung, 4 with cow dung), spaced at least 10 m apart.

To minimize variation in dung quality, which could affect bait attractiveness, we collected all cow dung for the study in May 2023. Fresh cow dung was collected in pastures from ivermectin-free cattle, homogenized, and frozen in clean plastic containers until used. Dog dung was collected throughout the season from two domestic dogs fed a dry kibble diet and monthly antihelminthic tablet (Simparica Trio). Fresh dog dung was collected in waste bags and frozen until used.

After collection, beetles were brought to the laboratory for species identification and morphological measurements. *O. orpheus* individuals were sexed based on the presence (males) or absence (females) of a thoracic horn, and the presence (females) or absence (males) of a clypeal ridge that spans the entire width of the head (Fig. 1). Voucher specimens were deposited in the entomology collection of the Harvard Museum of Comparative Zoology.

Males were anaesthetized on ice, weighed to the nearest 0.01 mg on a digital balance (Mettler Toledo XSR105DU), and photographed in the dorsal position with a Leica M125c dissecting microscope and Leica K5C camera attached to a computer running Leica Application Suite X Imaging Software version 3.7.6.25997. Horn size and body size were measured to the nearest 0.01 mm using the "draw scalebar" annotation tool in Leica Application Suite X. Each trait was measured independently 3 times, and the averages were used in the analyses. Prothorax width was used as a proxy for body size, and horn length was used as a measure of horn size (Fig. 2). Horn length was measured as the straight-line distance from the horn tip to the horn base, where the outer margins of the horn meet the pronotum (see Fig. 2). We also measured horn width, or the distance between the outer horn tines, as an alternative measure of horn size. We were unable to measure horn width in one male because of a broken horn tine, so we only report results using horn length. Our results are qualitatively the same using either measure of horn size. All analyses were conducted on log-transformed measurements in R version 2024.09.0+375 (R Core Team 2024).

Visual inspection of the log–log scatterplots suggested that the relationship between horn size and body size was nonlinear, so we followed the recommendations of Knell (2009b) to explore this nonlinear allometry. To evaluate male dimorphism, we fit a segmented regression between horn size and body size using the R package *segmented* (Muggeo 2008, McCullough and Simmons 2016). Males with a log prothorax width greater than or equal to the break-point were classified as majors, and the remaining males were classified as minors. We then calculated allometric slopes and intercepts for each male morph using ordinary least squares regression in the R package *smatr* (Warton et al. 2012).

We performed chi-square tests to assess seasonal variation in sex ratio and male morph ratio, and a one-way analysis of variance to evaluate seasonal variation in male size. Seasonal analyses were based on composite monthly data from May to September. We only collected one individual in October, so this month was excluded from the analyses.

Finally, we investigated male fighting behavior by staging fights between 2 major males over ownership of an artificial
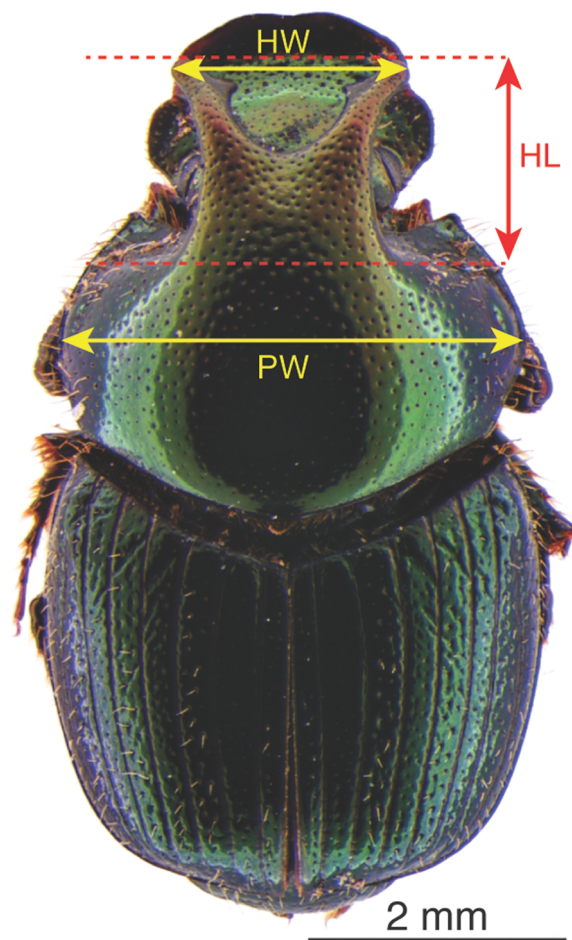
Fig. 2. Dorsal view of a major male with annotations indicating horn and body size measurements. The dotted lines denote the tip and base of the horn, which were drawn on each image to measure horn length. HL, horn length; HW, horn width; PW, prothorax width (body size).

breeding tunnel (McCullough and Simmons 2016). Tunnels were made using clear vinyl tubing (6 mm internal diameter) that was sealed at the bottom with nylon mesh. The tunnel was plugged with another piece of tubing filled with fresh dog dung to mimic the brood balls built by females and lure males to the bottom of the tunnel. Tunneling behavior naturally occurs underground, so fights were recorded with a video camera (Sony Handycam HDR-CX405) in a dark room under dim, red-filtered light.

Results

O. orpheus emergence began in May, peaked in July, and ended in October (Fig. 3). We expect that *O. orpheus* typically engages in a single breeding season and overwinters as pupae. However, several females survived in the laboratory for nine months (August 2024 to May 2025), which suggests that the species can also overwinter as adults and potentially engage in 2 breeding seasons.

We collected a total of 452 individuals (174 males, 278 females). This species was the most abundant dung beetle species at our 2 study sites, accounting for 68.8% of all individuals collected. The sex ratio was significantly female-biased in June, July, and August (binomial tests: $P < 0.05$), but unbiased in May

and September (binomial tests: $P > 0.05$) when beetles were less abundant. Overall, there was no significant seasonal variation in sex ratio (Fig. 3; $\chi^2 = 1.99$, df = 4, $P = 0.74$). The season-wide ASR, calculated as the number of males divided by the total number of males and females collected, was 0.38.
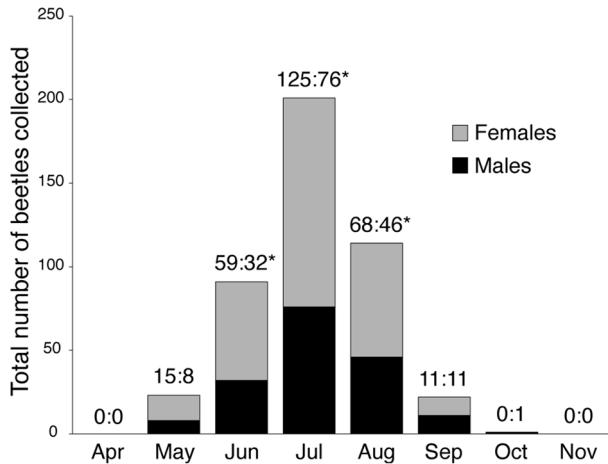
Fig. 3. Stacked bar plot showing seasonal activity and variation in sex ratio. Bar heights and reported ratios (female:male) represent the total number of beetles collected each month, with females represented in gray and males represented in black. Asterisks denote sex ratios that are significantly female-biased (binomial test: $P < 0.05$).

The segmented regression identified a break-point at a log prothorax width of 0.545 (standard error = 0.004). Using this body size threshold, 74 males were classified as majors and 99 were classified as minors (Fig. 4). Horns exhibited significant positive allometry for both male morphs, but the slope was significantly steeper for minors ($\beta = 7.95$; 95% CI = [6.68 to 9.21]) compared to majors ($\beta = 2.41$; 95% CI = [1.75 to 3.07]).

There were significantly more minor males than major males in June (binomial test: $P < 0.001$), which resulted in a significant difference in male morph ratio across the breeding season (Fig. 5; $\chi^2 = 16.62$, df = 4, $P = 0.002$). There was also seasonal variation in male size, with average male body size being smallest in June and largest in August (Fig. 6; $F = 4.43$, $P = 0.002$).

Males engaged in aggressive, head-to-head fights over access to the artificial breeding tunnel. Males either wedged their head (clypeus) underneath the opponent's horn and rapidly jerked their head upward to pry the opponent off the tunnel wall (Supplementary Video 1), or interlocked their horn tines and engaged in a head-to-head pushing match to shove the opponent down or out of the tunnel (Supplementary Video 2). Fights typically lasted 1 to 2 min and ended with 1 male being evicted from the tunnel.

Discussion

This study reports the seasonal activity, population structure, and male dimorphism of *O. orpheus*—the most abundant dung beetle in urban forests in central Massachusetts. Beetle
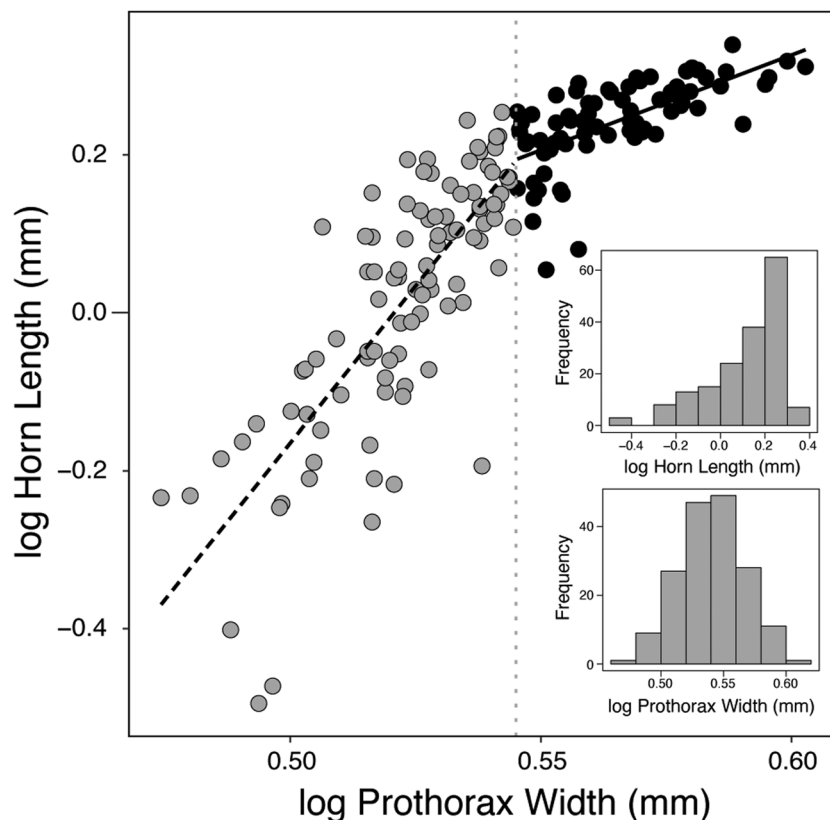
Fig. 4. Allometric relationship between body size and horn length. The vertical dotted line represents the break-point in body size that separates major and minor males (log Prothorax width = 0.545). Gray points represent minor males ($n = 99$), and black points represent major males ($n = 74$). The allometric slope was significantly steeper in minor males ($\beta = 7.95$; 95% CI = [6.68 to 9.21]) than in major males ($\beta = 2.41$; 95% CI = [1.75 to 3.07]). Inserts show frequency distributions of horn lengths (top) and body sizes (bottom).
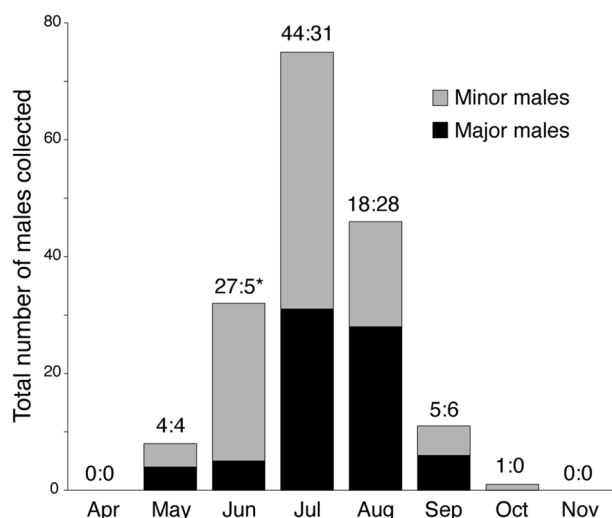
Fig. 5. Stacked bar plot showing seasonal variation in morph ratio. Bar heights and reported ratios (minor:major) represent the total number of males collected each month, with minor males represented in gray and major males represented in black. Asterisk denotes a significant difference in the number of minor and major males (binomial test: $P < 0.001$).
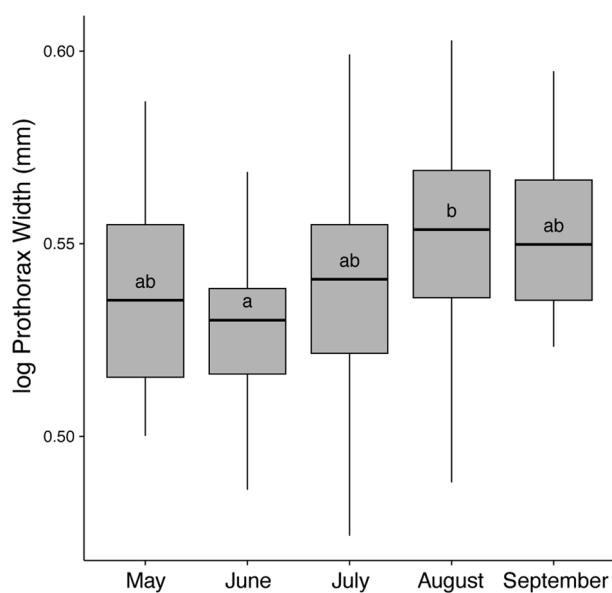
Fig. 6. Boxplot showing seasonal variation in male body size. Different letters denote means that are significantly different from each other (Tukey's test: $P < 0.05$). Male body size was smallest in June and largest in August ($F = 4.43$, $P = 0.002$).

abundance peaked in July, and the sex ratio was significantly female-biased through most of the breeding season. Males are morphologically dimorphic, with clear major and minor morphs based on nonlinear horn allometry. We discuss how these factors have influenced the mating system and behavioral ecology of this understudied species.

Sex ratio and population density can have significant effects on a species' mating system by influencing the level of competition for mates and encounter rates with potential mates and rivals (Emlen and Oring 1977, Kvarnemo and Ahnesjö 1996, Kokko and Rankin 2006, Knell 2009a). Male–male competition is predicted to be the most intense in populations with a male-biased sex ratio, which should favor higher male aggression and

the evolution of exaggerated weaponry (Pomfret and Knell 2008, Weir et al. 2011, Painting et al. 2014). We were, therefore, surprised that the sex ratio in our study was female-biased, rather than male-biased, because *O. orpheus* has a mating system that is characterized by the development of exaggerated horns and male–male competition for breeding tunnels. Across the entire season, less than 40% of all *O. orpheus* individuals collected were males. These results contrast with findings from a comparative study of a community of South African dung beetles that found that horned species tended to have a male-biased or unbiased OSR, whereas every hornless species had a female-biased OSR (Pomfret and Knell 2008).

All field-collected beetles were assumed to be sexually receptive, so in this study, the ASR was considered equivalent to the OSR. Most females produced viable brood balls when returned to the laboratory (EL McCullough, personal observation), which confirms they were sexually mature and mated. However, we cannot rule out the possibility that females (or males) have a refractory period after mating. We therefore acknowledge that the ASR may differ from the OSR in *O. orpheus*, but we doubt the discrepancy will be substantial enough to alter our overall conclusion about the species' mating dynamics. Because females are significantly more abundant than males, males are unlikely to be mate limited.

Although the sex ratio did not vary significantly across the breeding season, there was significant seasonal variation in abundance. Male–male competition is predicted to increase with population density due to higher encounter rates with potential mates and conspecific competitors (Kokko and Rankin 2006, Knell 2009a). We therefore predict the strength of sexual selection in *O. orpheus* will track seasonal changes in population density, becoming most intense during the middle of the breeding season (Miller and Svensson 2014). Future studies should examine whether levels of male aggressiveness or rates of female remating vary across the breeding season due to concomitant changes in population abundance.

When *O. orpheus* abundance peaked in July, we collected on average 6.3 beetles per pitfall trap. Bait size (50 g) mimicked the size of a typical dung pad from dogs at our study sites, so the densities observed in our traps (126 individuals/kg dung) should provide a biologically meaningful estimate of beetle densities in naturally occurring dung pads. Our density estimate for *O. orpheus* is similar to the densities observed for the horned dung beetle *O. taurus* in the eastern United States (Moczek 2003). *O. taurus* is native to the Mediterranean but has been introduced to the United States and Australia (Silva et al. 2016). Drastically different population densities between the exotic ranges have driven rapid changes in the body size threshold that separate horned and hornless male morphs (Moczek 2003). Low-density populations in the United States have a larger body size threshold and therefore are comprised of a higher proportion of horned major males, whereas high-density populations in Australia have a smaller body size threshold and therefore are comprised of a higher proportion of hornless minor males. These patterns suggest that male dung beetles benefit from producing horns in low-density populations where they can monopolize access to females (Moczek 2003, see also Pomfret and Knell 2008). Consistent with our observations in *O. orpheus*, the low-density populations of *O. taurus* in the eastern United States also had a female-biased ASR (Moczek 2003). Collectively, these results suggest the ecological conditions experienced by our population of *O. orpheus* will promote a highly

competitive, defense-based mating system that favors the development of sexually selected horns.

Behavioral observations confirmed that *O. orpheus* males engage in head-to-head fights over access to breeding tunnels. Similar to the fighting behavior described in *Onthophagus* species with exaggerated head horns (e.g., *O. acuminatus* and *O. taurus*), *O. orpheus* males used their head (clypeus) to butt opponents and jerk them out of the tunnel (Emlen 1997a, Moczek and Emlen 2000). We also noticed that *O. orpheus* males sometimes interdigitated their bifurcated thoracic horns, which may improve their grip on opponents when pushing them down or out of the tunnel. We collected one male with a broken thoracic horn and another male with a chipped clypeus, which suggests that both the horn and clypeus are sexually selected weapons that are susceptible to damage (Lane and McCullough 2025). We note that fights were staged only between major males, so future work is needed to compare the fighting behavior of males across the full range of body sizes. Future studies should also investigate reproductive behaviors in observation chambers, rather than artificial tunnels, to determine whether males dig side tunnels or adopt other alternative reproductive tactics to gain access to females (Emlen 1997a).

Dung beetles in the genus *Onthophagus* are famous for their diversity in the patterns of horn expression and allometric relationships describing how horn size scales with body size (Emlen, Hunt, et al. 2005, Emlen et al. 2007). We found that *O. orpheus* horns exhibit a segmented (or breakpoint) allometry, and that the allometric slope was significantly shallower in major males compared with minor males. This pattern of a decrease in allometric slope with increasing body size is common among male-dimorphic insects that undergo complete metamorphosis (Kochensparger et al. 2024), and is consistent with the hypothesis that large males face a resource ceiling during development that limits the continued exaggeration of weapon size (Nijhout and Wheeler 1996). Although *O. orpheus* males can be separated into major and minor morphs based on different horn allometries, whether the 2 morphological morphs correspond to distinct behaviors warrants further investigation.

We found that *O. orpheus* minor males were relatively more abundant than major males in June, and average male body size was smallest in June and largest in August. This size-dependent seasonal activity is consistent with observations in other horned beetles in which minor males are more active earlier in the season than major males (Eberhard 1982, Akamine 2019). These patterns may be the result of intense male–male competition that has favored minor males that employ alternative reproductive behaviors, such as earlier emergence, to avoid direct combat with major males (Eberhard 1982, Siva-Jothy 1987). Future work is needed to determine if the 2 morphological morphs in *O. orpheus* correspond to other alternative behaviors, such as a switch in parental provisioning strategies (Hunt and Simmons 1998, 2000).

Overall, we find that the ecological conditions in *O. orpheus* are conducive to a mating system characterized by intense male–male competition that has driven the evolution of exaggerated horns. We report significant seasonal variation in beetle abundance and the ratio of major and minor males, which can cause the strength of sexual selection to fluctuate across the breeding season (Miller and Svensson 2014). We also expect *O. orpheus* will be a valuable system for investigating the effects of urbanization on mating dynamics because this species is prevalent in urban forests across the eastern United States (GBIF.org 2025), and the availability of food resources (i.e., dog dung) is expected to increase with urbanization (Carpaneto et al. 2005, Cronin et al. 2022). Future studies should explore how population density, male investment in horns, and rates of female remating in *O. orpheus* are influenced by urbanization and differences in resource availability (Cronin et al. 2022). Urban environments offer fertile ground for studying ecological and evolutionary responses to rapidly changing conditions. This study highlights *O. orpheus* as an emerging model species for studying sexual selection and behavior in urban environments.

Author contributions

Erin L. McCullough (Conceptualization [lead], Formal analysis [lead], Investigation [equal], Visualization [lead], Writing—original draft [lead], Writing—review & editing [supporting]), Beatrice Altopp (Investigation [equal], Writing—review & editing [supporting]), Madelyn S. McInnis (Investigation [equal], Writing—review & editing [supporting]), and Luna J. Pagan (Investigation [equal], Writing—review & editing [supporting])

Supplementary material

Supplementary material is available at *Annals of the Entomological Society of America* online.

Conflicts of interest

Data Availability

All data and code for the analyses reported in this article are available on Dryad: https://doi.org/10.5061/dryad.xgxd254sn.

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