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Gallery and acoustic traits related to female body size mediate male mate choice in a bark beetle

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Male preference for mating with large females and its benefits on fitness have been shown in several animal taxa. However, the mechanisms underlying this preference are less well known. *Dendroctonus valens*, a primarily monogamous bark beetle whose females initiate tunnels beneath the bark of host trees, provides a useful system for testing how male mate choice is based on size. Field observations and laboratory experiments demonstrated that *D. valens* males preferentially entered tunnels containing large females, and that large females were more fecund than small females. Behavioural assays showed that males could discern tunnel size, and preferred larger artificially constructed tunnels in a two-choice assay. Males were also able to walk more quickly through larger diameter tunnels. Volatiles and chirping sounds associated with females were also analysed. Female body size was positively associated with the intensity of the female's chirp, but not with the quantity of pheromones released. Playback of this chirp showed males preferred female-produced sound to a silent control, and that males could discriminate between soft and loud sounds. Male *D. valens* appear to have evolved strategies of mate selection by relying on dual cues, tunnel size and acoustic signals, to obtain a large partner to increase fitness.

Sexual selection by females has been examined extensively to understand its role in fitness, but mechanisms and fitness values of mate selection by males have been less well studied (Andersson, 1994; Thornhill & Alcock, 1983). The distinct reproductive roles and energetic commitments to gametes of the two sexes have largely been characterized in terms of competitive males and choosy females (Andersson, 1994; Edward & Chapman, 2011; Miller & Svensson, 2014). Hence, the operation of sexual selection on females due to male mate choice has received comparatively little attention (Clutton-Brock, 2007). However, male sperm production and mating rates are also constrained by limits, which may favour discrimination by males to obtain high-quality females, even in situations in which this would be less expected such as polygyny or absence of male parental care (Bonduriansky, 2001; Edward & Chapman, 2011). Recent studies show that both intrasexual competition between females and male choice of mating partners are common (Andersson, 1994; Clutton-Brock, 2007; Dural, Cetinkaya, & Gulbetekin, 2015; Schnell, Smith, Hanlon, & Harcourt, 2015; Wittman & Fedorka, 2015). Males may be more selective if they receive direct benefits associated with a choice, such as more offspring from mating with more fecund females (Ceballos & Kiørboe, 2010; Monaghan, Metcalfe, & Houston, 1996), and when males provide valuable nutrients to females or when male parental investment increases (Clutton-Brock & Vincent, 1991; Gwynne, 1993; Simmons, 1992).

Body size plays an important role in the sexual selection of many species, as reproductive success within many arthropods is often positively correlated with body size (Andersson, 1994; Honek, 1993; Nali, Zamudio, Haddad, & Prado, 2014; O'Dea, Jennions, & Head, 2014; Thornhill & Alcock, 1983). One assumption that guides interpretation is that larger individuals are expected to be preferred (Byrne & Rice, 2006; Schäfer, Misof, & Uhl, 2008). Large female body size generally indicates high fecundity and large females are attractive to higher-quality males (Gotthard, 2008; Tammaru, Esperk, & Castellanos, 2002). Likewise, larger males may benefit from male–male contests, in which they have a higher chance of acceptance by choosy females and often have greater quantity or quality of sperm or associated nuptial gifts (Iyengar & Eisner, 2004; Sutherland, Hogg, & Waas, 2007).

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In addition to visual cues, sound often contributes to mate selection, helping some insects, birds and mammals locate high-quality partners (Mhatre, Montealegre, Balakrishnan, & Robert, 2012; Wilkins, Seddon, & Safran, 2013; Wyman, Mooring, McCowan, Penedo, & Hart, 2008). Moreover, size and sound intensity are often correlated, such as in various crickets (Gray, 1997), toads (Cynx & Gell, 2004), birds (Ritschard, Riebel, & Brumm, 2010), bats (Schuchmann & Siemers, 2010) and bison (Wyman et al., 2008). For example, male field crickets produce three types of acoustic signals: aggressive chirps, calling song and courtship song (Alexander, 1961). Females will locate a male by his calling song and use his courtship song to evaluate him before mating. Females prefer large males whose chirps indicate their large size by their amplitude and the number of pulses per chirp (Alexander, 1961; Gray, 1997; Huber & Thorson, 1985).

Bark beetles (Coleoptera: Curculionidae: Scolytinae) exhibit a high diversity of mating systems (Kirkendall, 1983). Most species in the genus *Dendroctonus* are thought to be monogamous: each female initiates a single gallery under bark, where she is subsequently joined by a male which mates with her (Kirkendall, 1983; Liu, Zhang, & Sun, 2006; Wood, 1982). Acoustic communication in *Dendroctonus* is used in competition for mates by both sexes, acquisition of nutrients and habitat, and release of long-range pheromone (McGhehey, 1968; Rudinsky & Michael, 1974; Ryker, 1988; Ryker & Rudinsky, 1976). Both male and female red turpentine beetles, *Dendroctonus valens*, produce sounds by stridulation, with both sexes producing agreement sounds when in contact with each other, and additionally males produce an aggressive/rivalry sound (Lindeman & Yack, 2015; Liu, Xin, Xu, Raffa, & Sun, 2016; Ryker, 1988; Ryker & Rudinsky, 1976; Wang, Zhao, Luo, Zhang, & Kong, 2012).

Dendroctonus valens, a native of North America, is one of the most destructive invasive bark beetles in China, where it has killed over 7 million *Pinus tabuliformis* (Qiu, 2013; Yan, Sun, Owen, & Zhang, 2005). Adults infest healthy trees and freshly cut stumps (Liu et al., 2006, 2008; Owen, Smith, & Seybold, 2010). This insect is apparently monogamous, and exhibits some parental care (Kirkendall, 1983; Liu et al., 2006; Reid & Roitberg, 1994; Wood, 1982). As in other *Dendroctonus* species (Latty & Reid, 2010), the female constructs a gallery before being joined by a male (Liu et al., 2006). The male usually remains in the gallery after mating and blocks the entrance, resulting in monogamy being their typical mating habit. Moreover, we have observed that males of any size join females and are never expelled, indicating that *D. valens* females are not choosy ($N = 45$ males; personal observation). This differs from many other *Dendroctonus* species, in which females sometimes force the male out of their burrows (Ryker, 1984; Rudinsky & Ryker, 1976). Both sexes of *D. valens* produce sounds, with males producing agreement chirps when they are attracted to females and aggressive/rivalry chirps during fighting over territories, while females produce agreement chirps when a male is digging and chirping in her gallery entrance or she is stimulated by pheromones (Liu et al., 2016; Ryker, 1988; Ryker & Rudinsky, 1976). In addition to sound, pheromones also contribute to mate location, especially over long distances, and function in host location, aggregation and resource partitioning (Chen, Salcedo, & Sun, 2012; Liu, Wang, Xu, & Sun, 2011; Liu et al., 2016; Liu, Xu, Miao, & Sun, 2013; Wood, 1982; Xu, Liu, & Sun, 2014).

We evaluated the extent and underlying mechanisms of preference by male *D. valens* for large females. First, we conducted field observations and a laboratory experiment to determine preference. Second, we tested whether there are benefits to mating with large females. Third, we explored visual, olfactory and acoustic cues that may potentially influence mate selection by males.

METHODS

Field Trapping and Insect Rearing

Field trapping was conducted in the same way as in our previous studies (Liu et al., 2013; Sun, Miao, Zhang, Zhang, & Gillette, 2004) in a natural stand of *P. tabuliformis* at Beishe Mountain, located at the base of the Luliang Mountains (37°48′N, 111°57′E, mean elevation 1400 m), west of Gujiao City, Shanxi Province, China, from early May to early June in 2010 and 2011. Traps were checked every other day; *D. valens* were collected alive, and the sexes were separated by listening for the sex-specific stridulation produced by males (Liu et al., 2013; McGhehey, 1968). Insects were stored in plastic boxes with holes for ventilation and provided with fresh phloem for food. The boxes were kept in an environmental chamber at 25 °C, 55% RH under a photoperiod of 14:10 h light:dark for later bioassay in the laboratory. All beetles were kept in the laboratory until they died.

Male Mate Selection and Fitness Assay

Field observations

Field trapping and excavations of galleries were conducted in 2010 to compare body sizes of beetles that were in flight versus those with established galleries. We used body weight to evaluate size since weight is positively correlated with length and width in *D. valens* (see the Appendix and Fig. A1). Field trapping was conducted in the same stand of *P. tabuliformis* mentioned above. Beetles trapped alive (1023 females and 1047 males) were sexed and weighed on an electronic balance (accuracy 0.1 mg) on the day they were collected. Field excavations were conducted in the same area. Three stumps freshly infested with *D. valens* were randomly selected and all galleries were excavated with chisel and hammer. When pairs of beetles were found in a gallery (37 pairs), they were put in centrifuge tubes (1 pair/tube) and taken to the laboratory. Beetles were sexed and then weighed on an electronic balance. We compared body sizes of trapped and excavated beetles of both sexes to test whether males choose to mate with large females.

Two complementary experiments provided background information for our main experiments. The first showed that females of various sizes are equally likely to establish galleries under bark (see the Appendix and Fig. A2). The second showed that females and males increase their body weight by approximately the same amount after 3 days (see the Appendix and Fig. A3).

Mate selection behaviour

We tested whether males preferentially select a larger female over a smaller one, and whether their choice varies with male size. Based on the field observations, we tested this possibility in the laboratory under controlled conditions. In a dual mate choice experiment, a male had to choose between a large and a small female, based on body weight. Males were also classed as either large (30 mg or more) or small (ca. 20 mg or less). To simulate beetles colonizing trees in a natural environment, we randomly selected and felled uninfested mature trees with a DBH (diameter at breast height) of 30 cm, sectioned them into bolts from the bottom (ca. 60 cm long each), and transported them to the laboratory. The bolts were placed in a 20 °C temperature-controlled room with natural light, and their cut ends were coated with melted wax to reduce moisture loss. One large and one small (differing by approximately 20 mg) female beetles obtained from the traps were introduced freely into the same predrilled hole (diameter 1.0 cm) on the bolt with a 1.0 cm diameter cork borer. The hole was then secured with wire mesh (2 × 2 mm). The predrilled holes were checked twice daily to see whether any beetles had bored into the bark. Twenty-