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The effects of adult sex ratio and density on parental care in *Lethrus apterus* (Coleoptera, Geotrupidae)

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Theoretical models suggest that adult sex ratio (ASR) and population density are expected to influence parental roles by reducing the mating opportunities of the commoner sex and by changing the intensity of sperm competition, although experimental evidence for these predictions is sparse. In biparental species with a high risk of extrapair paternity and consecutive egg laying over the breeding period, males are expected to reduce their parental investment and to spend more time on mate guarding if male density is high, to maximize their fitness. We conducted a field experiment to test this hypothesis in *Lethrus apterus*, a flightless biparental beetle species from the Geotrupidae family. Using seminatural enclosures, we assigned individuals to nine treatment groups differing in adult sex ratio (three levels) and individual density (three levels) using a full factorial experimental design. Nest attendance and parental provisioning (i.e. collecting and transporting leaves to the nest) were recorded as well as the number, size and sex ratio of the offspring. We found that as the level of male–male competition increased, generated either by the increased density of individuals or by the male-biased sex ratio, pairs showed higher nest attendance and collected fewer leaves. Male-biased groups also produced fewer offspring under high and low densities indicating a possible conflict of interest between the sexes over paternity and brood size. These results support the increased paternity assurance hypothesis under a high level of intrasexual competition.

Parental care, defined by Smiseth, Kölliker, and Royle (2012, p. 7) as 'any parental trait that enhances the fitness of a parent's offspring, and that is likely to have originated and/or to be currently maintained for this function' is most commonly observed in females, especially among mammals (Kleiman & Malcolm, 1981) and invertebrates (Smiseth & Moore, 2004; Suzuki, 2013; Tallamy & Wood, 1986; Zeh & Smith, 1985). Even in biparental systems, where both parents care for the offspring, females in many species tend to invest more in parental activities than males (Kosztolányi, Nagy, Kovács, & Barta, 2015; Quinn, 1990). One explanation for this difference is that females have greater certainty of parentage than males, if sperm competition exists (Queller, 1997). Parents are expected to adjust their parental investment to the level of competition among males for females which is highly influenced by the population density (Manica & Johnstone, 2004) and the adult sex ratio (ASR, the proportion of males in the adult population; Houston & McNamara, 2002; Székely, Weissing, & Komdeur, 2014). There has been little previous work to investigate how the ASR affects mating behaviour (e.g. Le Galliard, Fitze, Cote, Massot, & Clobert, 2005; Vahl, Boiteau, de Heij, MacKinley, & Kokko, 2013), and most theoretical and empirical studies have focused on the effects of the operational sex ratio (OSR, ratio of sexually active males to females; e.g. Emlen & Oring, 1977; Forsgren, Amundsen, Borg, & Bjelvenmark, 2004; Pomfret & Knell, 2008). It is important, however, to distinguish between the two, since the ASR is based on the demographic properties of the population while the OSR depends also on the individual's decisions, and so their effects on mate choice and parental care cannot be equated (reviewed by Carmona-Isunza et al., 2017; Kokko & Jennions, 2008; Székely et al., 2014).

According to theory, a skewed ASR and high population density reduce the mating opportunities of the commoner sex and hence

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increase the level of intrasexual competition and sexual selection (Kokko & Jennions, 2008; Queller, 1997). When, for example, ASR is male-biased, males may not be able to reproduce faster than females, owing to their low chance of finding a new mate (Kokko & Jennions, 2008). In this context, many studies, using primarily birds as model systems, found that males should invest more in parental care to maximize their fitness (Burley & Calkins, 1999; Kokko & Jennions, 2012; Liker, Freckleton, & Székely, 2014, 2013; Remeš, Freckleton, Tökölyi, Liker, & Székely, 2015). However, in a surplus of males there is also a higher chance of extrapair copulations increasing the risk of sperm competition and reducing certainty of paternity. If paternity certainty is low, females may gain higher fitness benefits by caring than males (Alonzo, 2010; Simmons, 2014; Trivers, 1972); therefore, males are expected to desert (Kokko & Jennions, 2012) or to invest more in ensuring paternity (Fromhage, McNamara, & Houston, 2008; Yamamura, 1986) and less in caring (Alonzo, 2010; Fromhage & Jennions, 2016; Houston & McNamara, 2002; Neff, 2003; Westneat & Sherman, 1993). Desertion, however, may not be beneficial under a male-biased sex ratio if the chance of finding a new mate is low. Paternity assurance may be especially important in species where egg laying is continuous throughout the time of care causing the risk of sperm competition to spread over the entire breeding season. In these species, cues indicating reduced certainty of paternity (e.g. social competitive environment generated by high male ratio) may increase mate guarding while reducing the investment in actual paternal activities. High population density may further strengthen the effects of a biased ASR through the increased number of interactions between individuals resulting in even stronger intrasexual competition (Emlen, Marangelo, Ball, & Cunningham, 2005) and a higher risk of sperm competition. Indeed, several studies have demonstrated that changes solely in population density can also influence mating behaviour and reproductive success (e.g. Jirotkul, 1999; Spence & Smith, 2005; Warner & Hoffman, 1980).

Lethrus apterus is one of the few known beetle species that shows biparental care. At the beginning of the breeding season in early spring, individuals dig a 10–20 cm deep underground tunnel for themselves which serves as a shelter before they find a partner. Paired beetles prepare a 50–90 cm deep burrow, terminating in six to eight brood chambers with a single egg developing in each (Clutton-Brock, 1991; Emich, 1884; Kosztolányi et al., 2015; Wilson, 1971). Eggs are laid sequentially. After an egg is laid, the parents gather leaves from near the burrow (i.e. an area of about 3.5 m^2; Frantsevich et al., 1977) that they bring back for the developing larvae. After collecting enough leaves, they close the chamber and start the next one. The decomposed leaf parts serve as the only food source for the larvae until the next year, when they finally leave their brood chambers. According to early studies (Emich, 1884; Schreiner, 1906) there is a clear division of labour between the sexes as males are responsible for collecting leaves, while females use them to form food balls inside the brood chambers. However, this division of duties, despite being frequently mentioned in the literature (e.g. Arrow, 1951; Clutton-Brock, 1991; Trumbo, 1996; Wilson, 1971), has been questioned in a recent study that reported predominant female leaf-collecting behaviour in a Hungarian *L. apterus* population (Kosztolányi et al., 2015). Further observations suggest that besides occasional leaf collection, males spend a considerable amount of time inside the burrow to guard it against intruders. This behaviour is also indicated by the presence of their sexually dimorphic mandibular processes, also called tusks (Wilson, 1971), which probably have a role in resolving intrasexual contests. Guarding males respond quickly when a rival approaches the burrow (Frantsevich et al., 1977). These intrusions occur frequently and fighting males can be seen almost everywhere during the breeding season. These fights can last for up to 15–30 min. Still, the effects of guarding on offspring survival are poorly known. Infanticide by intruders has been reported in various beetle species, for example the roundneck sexton beetle, *Nicrophorus orbicollis* (Scott, 1990) or the patent-leather beetle, *Odontotaenius disjunctus* (King & Fashing, 2007). However, there is no evidence for such behaviour in *L. apterus*. Presumably the function of burrow guarding in this species is to guard against extrapair copulations by females and to ensure paternity. This explanation is reasonable, since mating has very rarely been observed outside the burrows and there are ample opportunities for sperm competition as females lay eggs consecutively throughout the breeding season.

In this study, we investigated the effects of ASR and density of individuals on nest attendance (the time spent inside the burrow), parental provisioning (frequency of leaf collection) and reproductive success (number and quality of offspring) in *L. apterus* under seminatural conditions. According to our hypotheses, under a high level of intrasexual competition among males (i.e. under male-biased ASR or high population density), males should spend more time on mate guarding or copulate more frequently with their social partner because of the higher risk of extrapair copulations or the more frequent, time-consuming encounters with rivals. In this case, we predict an increase in the total time pairs spend inside the burrow where mate guarding and presumably also copulations take place. If females do not compensate perfectly for the lower investment of their mate (Harrison, Barta, Cuthill, & Szekely, 2009), then we also expect a reduction in leaf collection and fewer or smaller offspring. Otherwise, when ASR is female-biased, males are predicted to care more as a result of their higher confidence in paternity and/or the less time they spend fighting with intruders.

METHODS

Fieldwork

The field study was conducted near Dorogháza village, situated in the Mátra Mountains (47°59′29″N, 19°53′36″E) in northern Hungary. The study area was located on a sloping grazed grassland, which is inhabited by a large population of *L. apterus*. The experiment was carried out during the brief active period of the species between 23 April and 7 June 2014.

Experimental Design

To manipulate ASR and individual density, we established enclosures by fencing off plots of size 2 × 1 m, using plastic flower bed edges. The fences were approximately 0.15 m high, which was enough to keep these flightless beetles inside. Individuals were wild-caught after emergence, individually marked with a paint marker (Edding 751, Edding International GmbH or Uni-ball PX-21, Mitsubishi Pencil Co. Ltd.), and randomly assigned to one of the nine possible experimental treatments created by the full factorial combination of three ASR levels (proportion of males: 0.25, 0.5, 0.75) and three density levels (4, 8, 12 individuals). We had three replicates of each treatment combination totalling 27 plots containing 216 individuals. To ease the monitoring of the individuals' behaviour (see below), plots in the field were arranged in groups of four (six groups) or three (one group). The group of plots were located 225 ± 26.7 (mean ± SE) m apart and plots within a group always received different treatments.