



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.

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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 m²; 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, & Székely, 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.

Behavioural Data

Plots within a group were observed on the same day, and groups were observed on consecutive days to collect data from each group at approximately the same time of the breeding season. Six groups were observed four times and one group only three times due to the abrupt end of the breeding season (marked by when individuals dig themselves deeper and stay underground until next spring). Above-ground activity in a plot was recorded using a webcam (Logitech C920) fixed on a purpose-built tripod above the plot. Two webcams were connected to a netbook computer (Acer Aspire V5) at a time, and a 2304 × 1296 pixels video was recorded at 1 fps frame rate. We used two netbooks simultaneously; hence we could record all four plots in a group at the same time. The netbooks were powered by a 12 V leisure battery (Banner Energy Bull 956) connected to a DC-AC inverter (e-ast CL300-12). We recorded the behaviour of the individuals for 8 h, between 1000 and 1800 hours on each recording day to be able to check whether the manipulations influenced the daily activity patterns of the beetles (see below). These recording hours coincide with the main above-ground activity time of the species during the breeding season. Recordings were sometimes paused or postponed in rainy weather conditions and the total daily recording times of the plots were 7.26 ± 0.14 h (mean \pm SE).

Video footage was analysed using the 'mwrap' video event recorder software (Bán, Földvári, Babits, & Barta, 2017). We recorded (1) time spent outside the burrow and (2) successful leaf-collecting events (defined as the moment when the individual brought a leaf inside the burrow). Individuals often spent a considerable amount of time walking along the wall, which may not be related to leaf collecting or mate-searching behaviour, but rather a thigmotactic tendency well known in many taxa (Blokland, Geraerts, & Been, 2004; Schütz & Dürr, 2011). Therefore, the time spent by the wall was excluded from the total observation time. Since individuals and sexes were often indistinguishable on the recordings, we recorded only the total activity for each plot. Videos were analysed by three observers. The results were not influenced by the identity of the observer, as adding observer (factor with three levels) as a random factor to the final statistical models (see below) did not significantly increase the model fits (all $P \geq 0.400$).

At the end of the breeding season we marked all burrows (i.e. nests) inside each experimental unit with a nail, to permit their later localization using a metal detector (Silver Star 3; F. Chrenkó, Szigetszentmiklós, Hungary). Then, between 2 and 25 September 2014, by which time larvae had become adults, we dug out all the marked nests to determine reproductive success. The number of offspring (both alive and dead) was recorded as well as offspring sex (based on the presence or absence of mandibular tusks). We measured weight to the nearest 0.01 g with a digital balance, and measured thorax width and tusk length to the nearest 0.1 mm with a calliper.

Statistical Analyses

All statistical analyses were performed in the R statistical environment (v. 3.3.2; R Development Core Team 2016). Since data were collected from each plot at approximately the same stage of the breeding period and same hours of the day, data for the 3 or 4 days (see above) were averaged for each plot. Behavioural variables were calculated for 8 h (for shorter recordings in adverse weather data were estimated for 8 h) and divided by the number of individuals in the plot. We had two behavioural response variables. Duration of time spent inside the burrow (nest attendance) was

calculated as the difference between the total active time (observation time minus time spent at the wall, see above) and the time spent outside the burrow. Frequency of parental provisioning was the observed number of leaf-collecting events during a day. The number of offspring was calculated as the number of offspring per female in the plot.

The behaviour of individuals within the plots may be influenced by the geographical positioning of the seven groups of plots in the field (e.g. different vegetation cover can influence time needed to collect suitable leaves for the food balls); therefore, linear mixed models (LMM) were used in the analyses from the lme4 package (v. 1.1–12; Bates et al., 2016) with group ID as a random effect. The behavioural response variables were natural log transformed to ensure the normality and homoscedasticity of residuals. Explanatory variables were sex ratio (fixed factor with three levels), density (fixed factor with three levels) and their interaction. Reported results are from likelihood ratio tests (LRTs) from model comparisons. Hour of the day was not used as an explanatory variable in the final analyses because the interaction between density, sex ratio and hour of the day was not significant in any of the behavioural response variables tested, i.e. the manipulations did not influence the daily activity pattern of the individuals (LMMs with plot ID within group ID random structure, LRTs for the three-way interaction, all $P \geq 0.174$; Appendix Fig. A1).

Offspring number and sizes (offspring weight, thorax width, tusk length averaged for each plot) were analysed using LMMs with the same random structure and explanatory variables as the behavioural variables. To ensure the normal distribution of the model residuals, offspring number was natural log transformed in the analyses. For offspring sex ratio, a generalized linear mixed-effect model (GLMER) was used with binomial error structure.

Nonsignificant interaction terms (LRTs, all $P \geq 0.065$) are not reported in the results and were removed from the models before testing the main effects. For the number of offspring, the significant density*ASR interaction was further investigated by contrasting the male-biased treatment with the other two sex ratios (contrast: -1, -1, 2 for ASR 0.25, 0.5, 0.75, respectively) within each density treatment separately using general linear hypotheses tests (GLHT) from the multcomp package (v. 1.4–6; Hothorn et al., 2016).

Ethical Note

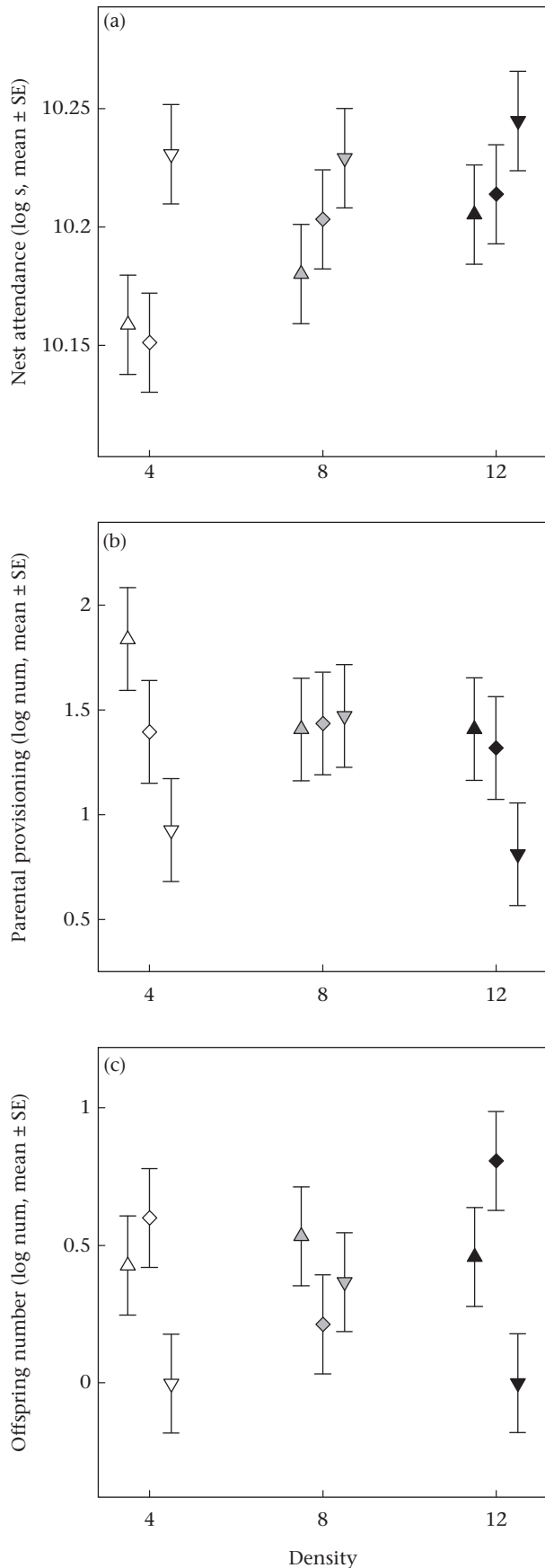
Lethrus apterus has been protected by Hungarian law since 2012 and this research was permitted by the Middle-Danube-Valley Inspectorate for Environmental Protection, Nature Conservation and Water Management (approval number: KTVF: 5866-4/2013). The study was designed to minimize the number of individuals used in the experiment and all animals were handled carefully without removing them from their natural habitat.

RESULTS

Behaviour

The duration of nest attendance increased significantly with the increasing proportion of males (LRT: $\chi^2_2 = 12.111$ $P < 0.001$; Fig. 1a) and with the density of the individuals ($\chi^2_2 = 6.866$, $P = 0.032$).

Parental provisioning (leaf collecting) tended to decrease with the increasing proportion of males ($\chi^2_2 = 5.591$, $P = 0.061$; Fig. 1b); however, the effect of density ($\chi^2_2 = 2.432$, $P = 0.296$) was not significant.



Reproductive Success

In total 72 offspring were counted in the 27 plots, including alive (70) and dead offspring (2). On average, 2.67 offspring per plot were produced (range 0–13). Nine plots contained no offspring, with seven of them belonging to the male-biased ASR treatment (78% of the plots with this treatment), one to the female-biased (11%) and one to the even ASR treatment (11%).

For offspring number, the interaction between ASR and density was significant ($\chi^2_4 = 10.307$, $P = 0.036$; Fig. 1c). The number of offspring tended to be lower at the male-biased ASR at the low density (GLHT contrast: $-1, -1, 2$ for ASR 0.25, 0.5 and 0.75, $Z = -2.351$, $P = 0.055$) and at the high density ($Z = -2.885$, $P = 0.012$), while there was no significant difference at the moderate density ($Z = -0.031$, $P = 1.000$).

Of the 72 juveniles, 37 were female and 35 were male. Neither density nor ASR influenced offspring sex ratio in the plots (density: $\chi^2_2 = 1.332$, $P = 0.514$; ASR: $\chi^2_2 = 2.007$, $P = 0.367$). Adult sex ratio, density of individuals or their interaction did not have any effect on offspring weight, thorax width or, in the case of male offspring, tusk size ($N = 34$ male and 33 female offspring; LRTs: all $P \geq 0.164$).

DISCUSSION

In this study, we investigated how ASR and individual density affect parental behaviour and reproductive success in a biparental insect species. Our results support the predictions of the paternity assurance hypothesis: as the sex ratio became more male-biased, individuals spent more time inside their tunnels. Nest attendance also increased with individual density. The resulting decline of the above-ground activity in the male-biased groups was mirrored in the reduced number of leaf-collecting events and of offspring; however, the latter was only significant at low and high densities. Offspring size and sex ratio were not affected by the treatments.

Studies have shown that when ASR is male-biased, nests are more exposed to threats by intruders; therefore, males are expected to spend more time on mate guarding or copulate more frequently with their mate, to avoid extrapair copulations and to ensure paternity (Takeshita & Henmi, 2010; Wada, Tanaka, & Goshima, 1999). Our results indicate that guarding under intense male–male competition is, in some cases, inversely related to brood size. This can be explained by the reduced time parents spent on food collection. Mate guarding or multiple mating are both time consuming; hence food collection might be traded off against these activities. It is also possible that females are able to adjust the number of offspring to the level of paternal care or at least to the amount of resources provided by the parents. For example, females might not start a new brood chamber until they have provided enough food for the current offspring. This could also explain why we did not find any effects of the treatments on offspring size. However, missing effects could also have been caused by the low number of offspring (only three) in the male-biased plots, where we expected the largest effect on offspring size. These results are in good agreement with other studies that have shown a conflict between the parents over paternity and offspring number or

Figure 1. The effects of density and adult sex ratio (ASR) treatments on (a) nest attendance (the duration of time individuals spent inside their burrows), (b) parental provisioning (the frequency of successful leaf-collecting events), and (c) the number of offspring per female (predicted values and standard errors were calculated based on the fixed-effects of the LMMs containing the ASR × Density interaction, see Methods). The proportions of males were 0.25 (upward-pointing triangles), 0.5 (diamonds) or 0.75 (downward-pointing triangles). Symbols in the same shade belong to the same density treatment.

quality (Hopwood, Moore, Tregenza, & Royle, 2015; Jormalainen, Merilaita, & Riihimäki, 2001; Takeshita, Lombardo, Wada, & Henmi, 2011; but see Rodríguez-Muñoz, Bretman, & Tregenza, 2011). Note, however, that at present we are unable to exclude that guarding by males can be successful also against brood parasites and predators and more experiments are needed to fully understand the role of the males.

Our findings contrast with many studies which suggest more intense male parental care under strong intrasexual competition due to the limited number of mating opportunities (Balshine-Earn & Earn, 1998; Burley & Calkins, 1999; Kokko & Jennions, 2008, 2012; Liker, Freckleton, & Székely, 2013; but see ; Fromhage & Jennions, 2016). Many of these studies, however, focused on bird model systems where parental care usually starts after the end of sperm competition, and there is little work on insects with more diverse reproductive systems (Hunt & House, 2011). For example, in species like *L. apterus*, where the risk of extrapair copulations extends until the end of parental care, an increased amount of care may not be beneficial under strong competition and, rather, males should invest more in ensuring paternity.

One weakness of our study is that males and females were indistinguishable on the recordings and we have no data about the different activity patterns of the sexes. It is possible, for example, that females can compensate for low paternal effort by providing more care. However, compensation in biparental species is expected to be only partial because otherwise the biparental system would not be evolutionarily stable (McNamara, Houston, Barta, & Osorno, 2003; Simmons & Ridsdill-Smith, 2011; Trumbo, 2012). Thus, female compensation typically reduces, but does not eliminate, the effect of ASR on paternal care. Therefore, our study should be interpreted as a conservative estimate of the manipulation of paternal investment. Also note that with the current data we cannot investigate whether decreased leaf collection was caused by higher competition between the males or by fewer offspring needing leaves. However, since pairs collect leaves for one offspring at a time, the total number of offspring does not necessarily affect provisioning effort on a given day of observation. The high percentage of plots without offspring under male-biased ASR may also influence our results as we have no information about the underground behaviour of the beetles without offspring. Furthermore, we assumed that nest attendance indicates paternity assurance, although some forms of parental behaviour (e.g. digging and forming food balls) also take place underground. However, according to our results individuals that spent more time inside also collected fewer leaves and produced fewer offspring. Therefore, the observed increase in nest attendance under high intrasexual competition is best explained by increased mate guarding and not by more parental care. Additionally, staying inside the tunnel might also be important in predator avoidance; however, we did not observe predation of adults. Another limitation of our study is that the fenced areas provided a seminatural environment and the walls of the plots distracted many individuals as they were often engaged in wall-following behaviour. Since all plots were under similar conditions and because time spent at the wall was excluded from the total observation time, however, this may not severely bias our results. We believe that our study has a great advantage over laboratory experiments for being conducted in the natural habitat of the individuals. Finally, we cannot exclude the possibility of any successful take-over attempts by rivals during the experiment (we know that mate changes can occur in natural populations, A. Kosztolányi, personal observation). According to resident–intruder game theory models (Maynard Smith, 1982), owners are expected to win most of the encounters, but the fenced environment may increase the aggressiveness of lower quality males as they have

little to lose. This increased ‘desperado effect’ (Grafen, 1987) can give an alternative explanation of our results as it might be higher in male-biased groups, and it can alter the observed residents’ behaviour by lowering their motivation in provisioning the offspring of an already mated female.

To sum up, our study gives a new example of the importance of ASR and individual density in reproductive biology. We showed that under high levels of intrasexual competition among males, individuals stayed in their burrows more, resulting in a reduction in parental investment and brood size in *L. apterus*, as expected from the paternity assurance hypothesis. We also found a significant interaction between sex ratio and density with respect to offspring number, implying a more complex relationship between ASR and density. In most biparental insect species the main role of the males is the protection of the nest (Suzuki, 2013). However, we suggest that the presence of males in the nest should be interpreted more carefully, and more work is needed to separate a biparental social condition (‘the presence of two potential parents’; Parker et al., 2015) from biparental care.

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APPENDIX

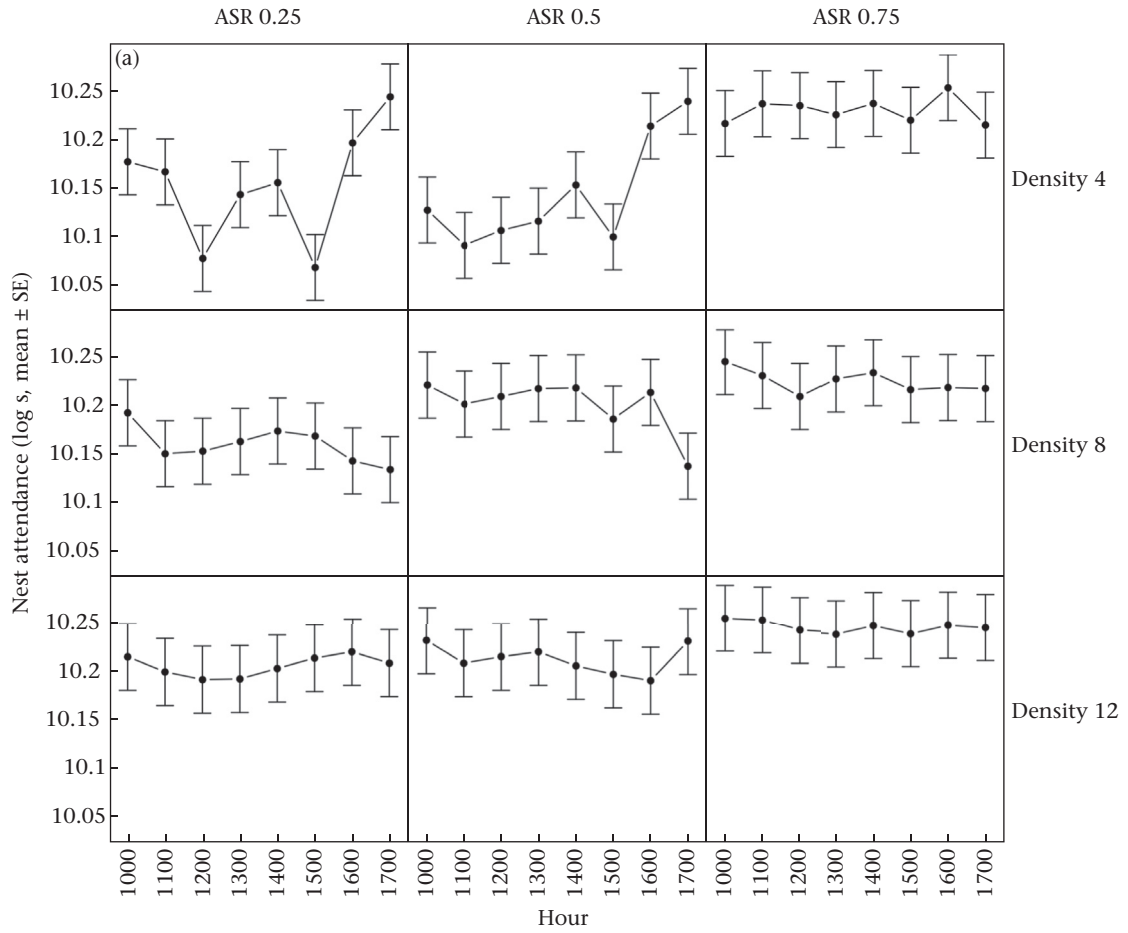


Figure A1. Hourly pattern of behaviour during the observation time: model-predicted values and standard errors of (a) nest attendance (time spent inside the burrow) and (b) parental provisioning (frequency of leaf-collecting events) in all nine treatment combinations of adult sex ratio (ASR) and density.

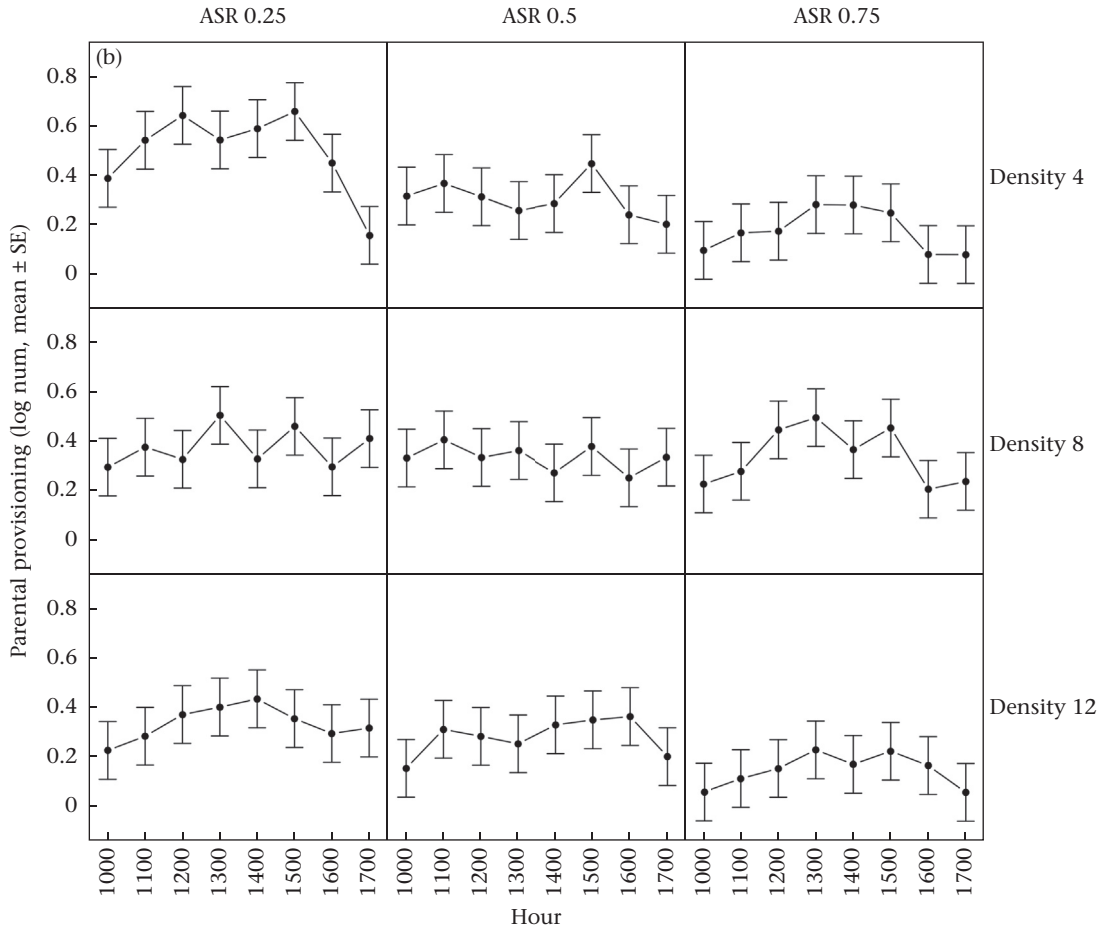


Figure A1. (continued).