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SHORT COMMUNICATION

Differential movement and activity patterns of sexes in a biparental beetle during the reproductive season

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Abstract. 1. Biparental care is stabilised if parents perform different tasks during care. Specialised parental roles may require different time and energy budgets that in turn are expected to influence the activity and space use of sexes.

2. Here we investigate movement patterns of the biparental *Lethrus apterus* beetle using a grid of pitfall traps in their natural habitat.

3. Sexes of the burrow building *L. apterus* perform different roles during caregiving, as females collect most of the leaves, which serve as food for the offspring while paired males stay mostly in the burrow. We hypothesised that sex differences in mate search and parental activities are reflected in movement patterns.

4. We found that females frequently travelled short distances, whereas males were detected less often but when detected, they travelled significantly longer distances than females.

5. Our results are consistent with the notion that efficient parental food provisioning requires more localised movement and activity patterns. Furthermore, the long distance movements of some males may indicate active mate searching behaviour.

Key words. Biparental care, Geotrupidae, insect, movement activity, sex role.

Introduction

Biparental care can be expected (i) if it is more beneficial for males to stay with their current mate and provide care than to desert and search for new mates, and (ii) if two parents are better than one at improving offspring survival by care (Gilbert & Manica, 2015). Biparental care is often associated with division of labour and task specialisation as the ability of one parent to provide all types of care may be limited (Barta *et al.*, 2014). These sexual differences in care behaviour are frequently correlated with sexual differences in other traits, such as morphology, movement, and activity (Trumbo, 2012; Šklíba *et al.*, 2016).

Intersexual differences are well-studied in dung beetles (*Onthophagus* spp.) where sexes usually differ in body morphology, and take part differently in parental care (Hunt & Simmons, 2002a; Simmons & Ridsdill-Smith, 2011). Typically, males wear horns that are used as weapons during nest guarding against intruders (Simmons & Ridsdill-Smith, 2011). Furthermore, males and females of onthophagine beetles perform different steps of dung collection to provision the larvae and this task specialisation is also reflected in the different above ground movement and activity patterns of the sexes (Hunt & Simmons, 2002a,b): Onthophagine males play an important part by collecting dung above ground thus travel more frequently between the dung pad and the nest, while females spend more time in the nest underground to form dung balls for each larva. Although parental task specialisation and hence sexually different movement and activity patterns are well-studied in dung beetles, the literature about earth-boring beetles that are also known to show biparental care (Lukas, 2013) is scarce.

In the earth-boring beetle *Lethrus apterus* (Laxmann 1770, Coleoptera: Geotrupidae), reproduction lasts from March until June in Hungary. At the beginning of this period, males search for tunnels occupied by females (Frantsevich *et al.*, 1977). After pair formation, the female and the male cooperate in preparing and provisioning a nest underground where the female lays 6–8 eggs and the hatched larvae develop in brood chambers and

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feed on leaf-balls prepared by parents (Emich, 1884). Unlike in dung beetles, Kosztolányi *et al.* (2015) observed that females in this species collect significantly more food for the offspring than males. This study along with Rosa *et al.* (2017) suggests that similarly to other burrow building species (Scott, 1998; Trumbo, 2012), the role of males may be more restricted to the defence of the burrow.

Considering the differences between sexes in mating and care behaviour, different movement patterns and activities of sexes in *L. apterus* are also expected, nevertheless are not yet described. In this study, we investigate the movement of individuals by pitfall traps during the reproductive season with particular attention to potential differences between the sexes. We predict that females, as a result of their more frequent involvement in plant collection around the nest, would be more likely to get recaptured and be seen more frequently and for longer periods of time above ground than nest-guarding males. Longer movements by some males may also be expected if they are not paired with a female or have recently been displaced by a rival male.

Methods

Field procedures

Fieldwork took place in the foothills of the Mátra Mountain near the village of Dorogháza (47°59′29″N, 19°53′36″E), Hungary, between 24 April and 2 June in 2015. We used a square grid of 11×11 pitfall traps covering a square area of $100\,m^2$ of the field. The traps (400 ml plastic cups) in the grid were 1 m away from each other, as individuals forage about 1 m from their nests (Frantsevich *et al.*, 1977). We used a separate set of 400 ml cups filled with sand to close the traps when they were not in use. As *L. apterus* is diurnal and active only in sunny weather (Frantsevich *et al.*, 1977; and personal observations by JK, AK and ZN), traps were open between 08:00 and 19:00 on 16 days for a total of 88 h (on average 5.5 h a day, as weather permitted). We checked the traps hourly, marked any unmarked individuals caught and noted the date, the position of trap in the grid, and number and IDs of caught individuals. During peak season, between 11–13 May, we recorded newly captured individuals only from the inner 5×5 traps of the grid to reduce capture volume to a manageable level while recaptures were continuously recorded from all traps.

At first capture, we measured the width of the individuals' pronotum with calipers. We determined sex based on the presence or absence of the 'tusks' (ventral mandibular processes). Each beetle was uniquely marked with a paint marker (Marabu Brilliant, Bietigheim-Bissingen, Germany or Marvy Uchida DecoColor, Tokyo, Japan), which made individual identification possible upon later encounters.

Data analyses

All statistical analyses were performed using R (version 3.5.1, R Core Team, 2018). To explore differences between males and females in activity and movement patterns, we investigated the following response variables: (i) the number of times an individual was (re)captured over the study period, (ii) the time interval (in days) between the first and last captures of an individual on the study area, (iii) the total distance an individual travelled during the study calculated as the sum of distances between successive pitfall traps where the individual was caught. Body size may influence movement behaviour (Fountain-Jones *et al.*, 2015); therefore, we controlled in all analyses for individual pronotum width (a good predictor of body size, Rosa *et al.*, 2019). As there is sex difference in pronotum width (Rosa *et al.*, 2019), pronotum width was standardised within sexes.

To test differences between males and females in (i) the number of (re)captures, we used Negative Binomial Generalised Linear Model (further on NBGLM by using 'glm.nb' function in MASS package; Venables & Ripley, 2002) to handle over-dispersed count data. In the full model, we included body size as covariate, sex as factor as well as their interaction as the explanatory terms.

To test whether there are differences between sexes in (ii) the time interval (in days) between the first and last captures, an NBGLM was used. To investigate differences between males and females in (iii) total distance the individuals travelled, we used a linear model where the response variable was log-transformed. In the latter two full models we used sex as factor, body size, number of recaptures as covariates, and all possible two- and three-way interactions (to explore the potential synergistic effects of combined predictors) as explanatory variables.

We conducted backward variable selection by removing the least significant interaction at each step until none met the criterion $P > 0.05$. The significance of retained predictors was tested using 'drop1' function, with likelihood ratio tests in case of NBGLMs, and with F-tests in case of linear models. During the model selection, all interaction terms were dropped from all models (all $P \geq 0.098$). As we expected a priori that main effects may have an effect, they were retained in the final models independently of their significance. Where the number of recaptures was used as an explanatory variable, individuals captured only once were excluded from the analyses.

Results and Discussion

We found that sex had a significant effect on both the number of (re)captures (NBGLM, $\chi^2_1 = 10.974$, $P < 0.001$) and on the time interval between the first and last captures of beetles (NBGLM, $\chi^2_1 = 4.787$, $P = 0.028$), as females were recaptured more frequently and were seen for significantly longer period of time in the season than males (Fig. 1a,b). In the case of total distance travelled (Fig. 2a), we found that sex and number of recaptures had significant effects (linear model, sex: $F_{1,59} = 4.194$, $P = 0.045$; number of recaptures: $F_{1,59} = 19.093$, $P < 0.001$): males travelled significantly greater distances than females did when controlling for number of recaptures (Fig. 2b). Body size had no significant effect on any response variable (all $P \geq 0.203$).

The findings that females were recaptured more frequently, travelled shorter distances and were seen longer during the

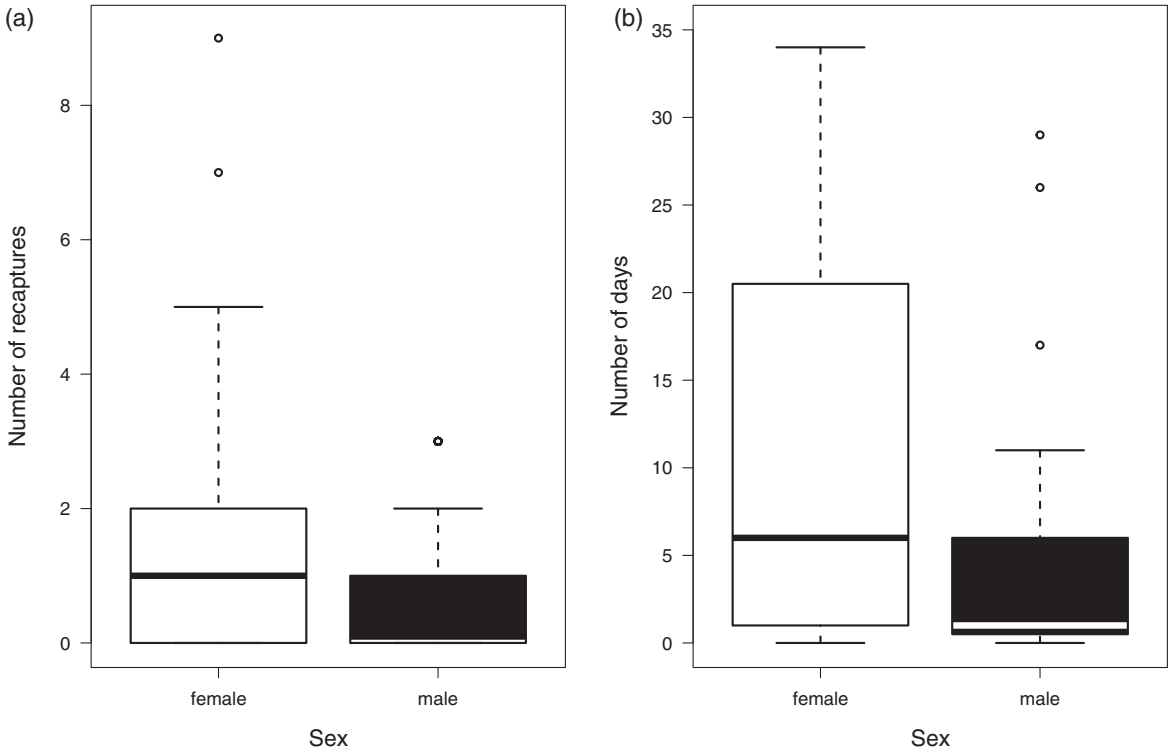

Fig 1. Box plot diagrams of (a) number of (re)captures in female ($n = 58$, white box) and male ($n = 86$, black box) and (b) number of days in female ($n = 32$, white box) and male ($n = 31$, black box) *Lethrus apterus* between the first and last capture on the study area. (Only recaptured individuals are presented on panel (b)). The bottom and top edges of the box indicate the interquartile range (IQR). Bands inside the boxes indicate the median values, whiskers indicate 1.5 times the IQR from the first and third quartiles. Small circles indicate outliers.

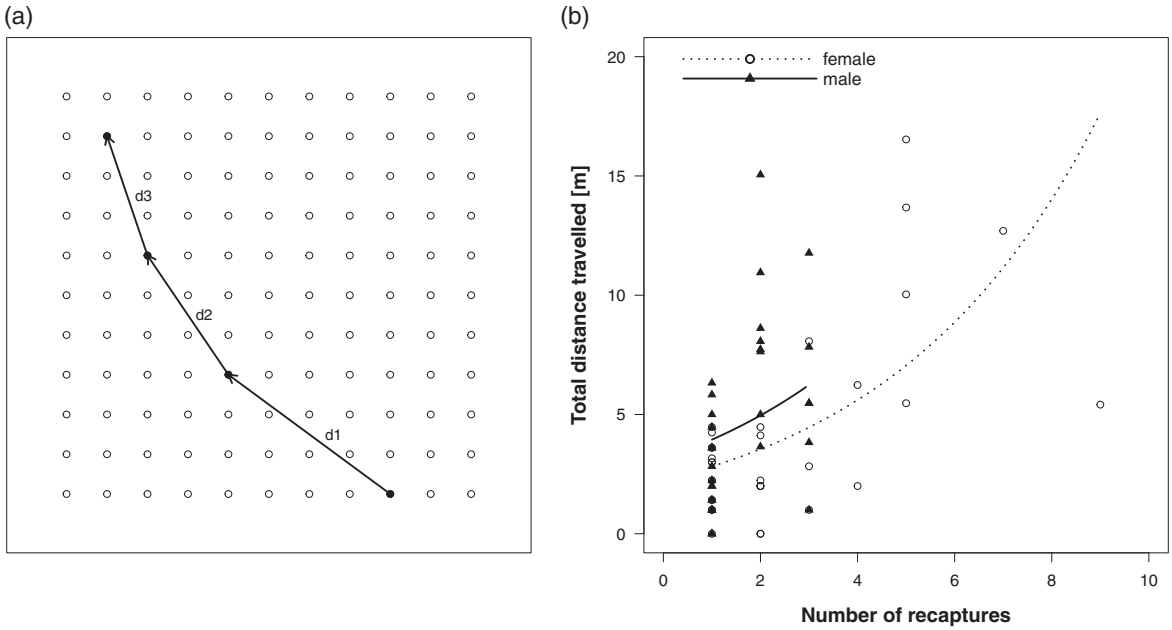

Fig 2. (a) Illustration of calculating travelled distances of *Lethrus apterus* individuals. Here the movement of a male recaptured three times is presented, and the total distance this individual travelled during the study is calculated as d1 + d2 + d3. (b) Relation between number of recaptures and total distance travelled by female ($n = 32$, circle) and male ($n = 31$, black triangle) *L. apterus*. Fitted lines for males (solid) and females (dotted) are predicted by a linear model.

reproductive season are likely the consequences of females playing a more active role in collecting plant materials for the offspring (Kosztolányi *et al.*, 2015). Each leaf-ball, which is prepared for a larva, is produced from at least two dozen leaves or shoots (personal observation, JK).

Our results that males were seen for shorter periods and less frequently in the study area are consistent with the hypothesis that their main task is to guard the burrow. Consequently, males stay close to or in the entrance of burrows and invest less in food collection. As successful guarding behaviour leads to increased confidence in paternity (mating seems to occur only in or at the entrance of burrows, Frantsevich *et al.*, 1977; and personal observations, JK) and enhanced reproductive success; by high investment in guarding paired males can reduce the chance of cuckoldry (Hunt & Simmons, 2002a,b; Simmons & Ridsdill-Smith, 2011) and offer more protection for the offspring against predators and parasites (Rodríguez-Muñoz *et al.*, 2011). Our finding that males travelled significantly longer distances but were recaptured proportionally less compared to females may be explained by the effort of males actively searching for potential mates. Resident males are expected to have a higher motivation to keep their position in a nest, which is supported by the finding that resident *L. apterus* males usually have a higher success and winning rate in contests compared to the intruders at the burrows (Rosa *et al.*, 2018). Thus, abandoning mate guarding and seeking another partner may only be beneficial for males after losing contest against an intruder male or when the guarded female is resisting to remate (Harts & Kokko, 2013).

In conclusion, our results are consistent with the observation that the female-biased provisioning behaviour in *L. apterus* results in more frequent above ground movements by females. Furthermore, our results support the notion that differences in mate search and care behaviour of the sexes are reflected in different movement and activity patterns.

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Author contribution

ZN, AK, and ZB conceived and designed research; ZN performed research; ZB and JK analysed data; and JK wrote the manuscript with input from all authors.

Data availability statement

The data generated and analyzed and complete analysis code (in the form of R script) during the current study are available through GitHub data repository at https://github.com/hannakiss/l.a.movement.pattern.

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