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Sexual dimorphism divergence between sister species is associated with a switch in habitat use and mating system in thorny devil stick insects

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ABSTRACT

The habitat and resource use of females critically affects their pattern of distribution and consequently their monopolisability by males and the mating system of a species. Shifts in habitat use are therefore likely to be associated with changes in mating system and sexual selection acting on males' phenotypes, consequently affecting patterns of sexual dimorphism. Although sexual dimorphism is often correlated with shifts in habitat use at the macroevolutionary scale, the underlying microevolutionary processes involved are typically unclear. Here, we used the New Guinean stick insect genus *Eurycantha* to investigate how changes in habitat use and mating system were associated with a change in sexual dimorphism seen specifically in the thorny devil stick insects (*Eurycantha calcarata* and *Eurycantha horrida*). Male thorny devils display sexually dimorphic and enlarged hindlegs endowed with a sharp spine. Sexual size dimorphism is also very reduced in these species relative to other phasmids. Using field observations, morphological measurements and radiotelemetry, we investigated changes in mating system associated with the reduction of sexual dimorphism and tested predictions from the hypothesis that sexual selection drove the evolution of this unusual male morphology. We found that thorny devils switched from solitary roosting in the canopy during the day to communal roosting inside cavities of a few host trees, shifting the distribution of females from scattered to clumped. Male thorny devils used their large hindlegs to fight with rivals for positions on the tree close to cavities containing females, and larger males were associated with cavities containing relatively more females. In contrast, the sister species, *Eurycantha insularis*, displays relatively small and unarmoured males (ancestral state). Adult female *E. insularis* were always scattered in the canopy, and this species displayed a scramble competition mating system typical of other phasmids, where mobility, rather than fighting ability, is probably critical to males' reproductive success. Overall, our study illustrates how a drastic change in sexual dimorphism can be associated with a switch from solitary to communal roosting and from a scramble competition to a defense-based polygyny mating system.

1. Introduction

Sexual dimorphism (*i.e.*, phenotypic differences between males and females) is widespread and widely variable across animals (Fairbairn et al., 2007). Dimorphism ultimately results from differential selection acting on traits that have sex-dependent benefits and costs, leading the same trait toward different optima in each sex (Blanckenhorn, 2005). Body size is typically sexually dimorphic as it influences multiple and potentially different aspects of fitness between the sexes (Blanckenhorn, 2000; Peters, 1986). Fecundity selection usually favors larger body sizes in females (Honěk, 1993; Pincheira-Donoso and Hunt, 2017; Preziosi et al., 1996), whereas sexual selection, when present, typically favors larger sizes in males (Andersson, 1994; Kokko et al., 2014). The ecology of females is a critical determinant of the mating system of a species and thus of the intensity and nature of competition between males for access to females (Emlen and Oring, 1977; Herberstein et al., 2017; Shuker and Simmons, 2014; Thornhill and Alcock, 1983). Female habitat use in particular is a key parameter of the *environmental potential for polygamy* (EPP) because it affects the economical defensibility and monopolisability of females by males (Emlen and Oring, 1977). Switches in female habitat and resource use are therefore likely to critically influence the strength and/or direction of sexual selection acting on male phenotypes.

At the macroevolutionary scale, shifts in the habitat use of a lineage (*e.g.*, from terrestriality to arboreality) are often associated with changes

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in sexual dimorphism (Lizards: Butler et al., 2007, 2000; Kaliontzopoulou et al., 2015; Turtles: Berry and Shine, 1980; Stephens and Wiens, 2009; Chameleons: Stuart-Fox and Moussalli, 2007; Snakes: Hendry et al., 2014; Bats: Wu et al., 2018; Grasshoppers: García-Navas et al., 2017; Spiders: Moya-Laraño et al., 2009 ; Ungulates: Pérez-Barbería et al., 2002). However, in many of these clades, the specific selective pressures driving the evolution of dimorphism remain unclear, since elucidating these microevolutionary processes requires precise information on mating system and sex-specific habitat and resource use. Such insights can be gained by studying the sex-specific ecology of very closely related species or conspecific populations differing in the direction or extent of sexual dimorphism (*e.g.*, Sepsis flies: Puniamoorthy et al., 2012; Rohner et al., 2016; Eye-lid geckos: Kratochvíl and Frynta, 2007; Side-blotched lizards: Corl et al., 2010; water striders: Toubiana and Khila, 2019; seed-feeding beetles: Fox et al., 2007). The in-depth study of such systems can illuminate specific ways that recent shifts in habitat use or behaviour may be associated with sex-specific phenotypic responses.

In this study, we studied how a recent shift in sexual dimorphism in thorny devil stick insects was associated with changes in habitat use and mating system. The New Guinean thorny devil stick insects (*Eurycantha calcarata* Lucas, 1869 and *Eurycantha horrida* Boisduval, 1835) and their close relatives, the oil palm stick insects (*Eurycantha insularis* Lucas, 1869) differ drastically in the extent of sexual dimorphism in body size and hindleg morphology. This genus of stick insects includes very large herbivorous, nocturnal and robust insects (Fig. 1, Bedford, 1976; Bradler and Buckley, 2018) that are major oil palm pests where they occur in Papua New Guinea (PNG) (Kimsey et al., 2013; Monteith and Dewhurst, 2011). In *E. calcarata* and *E. horrida*, adult males have enlarged hindlegs endowed with a sharp spine and males are very similar in body size to females (Figs. 1, 2A, Video S1), which is uncommon in the order Phasmatodea where sexual size dimorphism is usually extremely female-biased (Bedford, 1976; Bradler and Buckley, 2018; Buckley et al., 2009). This unusual “tree lobster” morphology seems to have evolved recently in the *Eurycantha* lineage as *E. insularis*, the sister species to *E. horrida* and *E. calcarata,* and *Eurycantha coronata* (Redtenbacher, 1908), a seemingly more basal lineage (Pacheco, 2018; Robertson et al., 2018), have relatively smaller males without enlarged hindlegs (Fig. 2A). We used *E. insularis* as a control of the ancestral state of this clade to investigate potential changes in habitat use and mating system that happened in the *E. calcarata/horrida* lineage that may be associated with the evolution of large male body and hindleg sizes.

Except for two brief field notes (Bedford, 1976; Monteith and Dewhurst, 2011) and a few lab studies (Gottardo et al., 2015; Hsiung, 1987; Hsiung and Panagopoulos, 1998) on *E. calcarata*, the natural history of *Eurycantha* spp. is largely unknown and therefore it is especially unclear

Fig. 1. *Eurycantha* spp. adults *in situ*. Adult female (A) and male (B) *E. calcarata* in threatening posture. *E. calcarata* adult female (C) and adult male (D), and *Eurycantha insularis* adult female (E) and adult male (F) with paint markings and equipped with radio transmitters. (G) Adult male *E. horrida* in resting posture. (H) Adult pair *E. insularis.* Photos by first author.

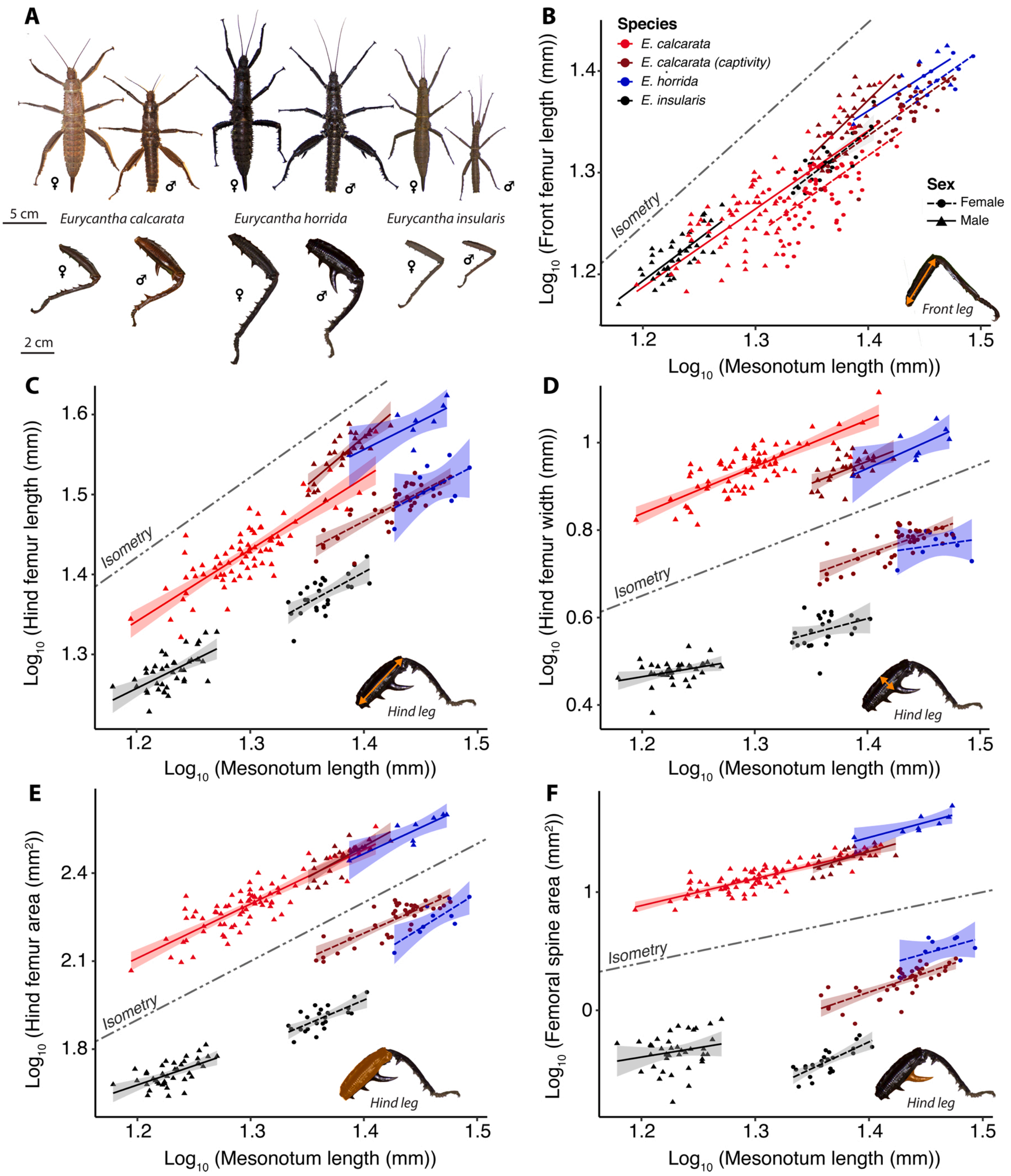

Fig. 2. Sexual dimorphism and scaling relationships between body size and front or hind leg size across *Eurycantha* species. (A) Photographs in dorsal view of adult pairs of *E. calcarata*, *E. horrida* and *E. insularis*. Side views of their respective hindlegs are shown below. Scaling relationships between front femur length (B), hind femur length (C), hind femur width (D), hind femur area (E) and hind femoral spine area (F) and mesonotum length (~body size) for males and females of each species. Leg photographs in the bottom right corner illustrate the variable measured. The grey dashed line represents an isometric slope (intercept = arbitrary). Shaded areas represent 95 % confidence intervals. They are not represented in (B) for clarity.

why species within this genus vary so drastically in sexual dimorphism, and what the primary function of male thorny devils' exaggerated hindlegs is. Remarkably, *E. calcarata* have been documented to be ground dwellers and gregarious cavity nesters (Bedford, 1976), unlike most phasmids that are solitary canopy dwellers (Bradler and Buckley, 2018). However, the relationship between sexual dimorphism, habitat use and mating system within this clade is unresolved. We hypothesized that these behavioural and habitat use differences may be associated with changes in mating system and patterns of sexual dimorphism in this group. Indeed, the social behaviour and pattern of distribution of females is likely to affect their monopolisability by males and the relative importance of fighting success for male fitness (Emlen and Oring, 1977; Thornhill and Alcock, 1983). Specically, we predicted that clumped and gregarious females would be associated with a female-defense mating system favouring large and strong males, while scattered and solitary females would be associated with a scramble competition mating system, favouring small and endurant males (Herberstein et al., 2017). In this context, sexual selection could explain the evolution large body sizes and enlarged hindlegs in *E. horrida* and *E. calcarata* ("sexual selection hypothesis") (Andersson, 1994; Emlen, 2008; Rico-Guevara and Hurme, 2018; Shuker and Simmons, 2014). Males of these species may use their hindlegs to fight against rivals and defend groups of females inside diurnal cavities or near these cavities (Emlen, 2014). In many animals, such sexually selected weapons are typically hypervariable and disproportionately large in larger individuals ('positive allometry hypothesis' reviewed in O'Brien et al., 2018). While this positive allometry is not always true for all weapons (Bonduriansky, 2007; Fea and Holwell, 2018), recent studies suggest that it particularly applies to those that function as visual threat signals of individual body size (Eberhard et al., 2018; O'Brien et al., 2018). The allometry of hindleg size with body size in thorny devil stick insects could therefore offer insights into the function of these legs.

To provide a first critical test of the "sexual selection hypothesis", we investigated whether changes in sexual size dimorphism were associated with changes in the mating system of these insects. We characterized the sex-specific habitat use and mating systems of these phasmid species in the field in relation to their pattern of sexual dimorphism in body and hindleg size. We used natural history observations, morphological scaling relationships and radiotelemetry to uncover intersexual differences in habitat use and interspecific differences in mating system. In *E. calcarata* and *E. horrida*, we specifically tested (1) whether the male hindlegs displayed a positively allometric scaling relationship with body size, (2) whether the movement patterns of males and females were consistent with a female-defence mating system (*i.e.*, show aggregation of males around groups of females), (3) whether males used their hindlegs to fight against other males in the field, and (4) whether males with larger hindlegs were associated with larger groups of females. In contrast, we predicted a scramble competition mating system in *E. insularis*, where males would search for solitary females across the landscape (Herberstein et al., 2017), as is typically found in stick insects (Kelly, 2014; Myers et al., 2015). In such context, male mobility is likely to be critical for their reproductive success and may favour males with relatively smaller sizes and longer legs (Herberstein et al., 2017; Kelly et al., 2008). Consequently, using our observations and radiotelemetry data, we tested (1) whether females of *E. insularis* were solitary and scattered across the landscape, (2) whether males were more mobile than females, and (3) whether small males were more mobile than larger ones.

2. Materials and methods

2.1. Study populations

We observed populations of *E. calcarata* near Kimbe, West New Britain, Papua New Guinea (PNG) and populations of *E. insularis* and *E. horrida* near Popondetta, Northern (Oro) Province, PNG, in October/November 2018. We surveyed tree cavities and vegetation during the daytime in search for phasmids at four field sites near Kimbe: Dami palm plantations (S5° 31.846′ E150° 20.221′), Dami rainforest (S5° 31.129′ E150° 20.077′), Tamabu palm plantations (S5° 19.757′ E150° 01.212′), Gabuna rainforest (S5°26.787′ E150°03.102′); and two sites near Popondetta: Koropata palm plantations (S8° 50.556′ E148° 00.998′), and Tunana palm plantations (S8° 49.008′ E148° 02.236′). To find *E. calcarata* and *E. horrida*, we visually searched for suitable trunk cavities and looked for piles of stick insect frass on the ground around trunks to potentially locate hidden cavities. At the same time, we visually searched for *E. insularis* in the canopy of trees and bushes as none were found inside cavities.

2.2. Morphology

We photographed adult males and females of each species in dorsal view and a side view of one of their hindlegs. Pronotum width, mesonotum length and width, front femur length, hind femur length, width and area, were then measured using ImageJ (v 1.51, Schneider et al., 2012, Figure S1). *E. calcarata* individuals were photographed in the field, marked with quick drying silver paint markers (©Pilot, medium point) and then released back to their cavity (n = 73 males, n = 71 females). *E. horrida* (n = 9 females, n = 8 males) and *E. insularis* (n = 40 males, n = 25 females) individuals were brought to the entomology laboratory of the Higaturu PNGOPRA sub-centre for photographing and were added to the Oil Palm Research Association (OPRA) captive populations. *E. calcarata* females' hindlegs were unfortunately not photographed in the field due to time constraints and security concerns (we had to work quickly, and our priority was relating male hindleg size with the number of females inside each cavity). Also, the defensive posture of both sexes of *E. calcarata* made it impossible to measure body length from pictures in the field as their abdomen could not be flattened. Morphological measurements for an additional 28 adult males and 40 adult females of *E. calcarata* were also obtained from individuals bred in captivity (Missoula, MT, USA) and fed maple leaves *ad libitum*. The initial population was provided by the Missoula Insectarium (MT, USA) but the exact origin of this culture is unknown.

All statistical analyses in this study were carried out using R version 3.3.1 (R Core Team, 2016), and for all linear models, we systematically checked for normal distributions of the residuals and the absence of any specific patterns in their distribution. For each species, body size measurements (*i.e.*, pronotum width, mesonotum width and length, and body length) for both sexes were used to run a principal component analysis in order to find the best linear proxy for body size (*function*: 'R package'; *prcomp*:'stats', R Core Team, 2016). We determined mesothorax length to be the best proxy for body size as it was the main variable contributing to PC1 in all species (Figure S2). We then tested how the extent of sexual size dimorphism differed between species by building a linear mixed model (LMM, *lmer*:'lme4', Bates et al., 2015) with $\log_{10}$ mesonotum length as the response variable and species, sex and their interaction as main fixed effects. Collection site was added as a random factor.

We then tested for sex and species differences in the scaling relationships between body size and front leg size or hind leg size. On a log scale, a steeper, and typically higher than one, slope between hindleg and body size in males than in females could be indicative of a sexually selected weapon serving as an intraspecific threat signal (O'Brien et al., 2018). The allometry of the putatively unspecialized front legs – used as a reference trait – with body size was compared to that of the hindlegs to potentially detect a unique scaling pattern in the hindlegs. We considered the scaling relationships of various hindleg measurements – *i.e.*, femur length, femur width, femur area and femoral spine area – as only some aspects of hindleg morphology may show sex and/or species differences. We built five LMM (*lmer*:'lme4') including either $\log_{10}$ front femur length, $\log_{10}$ hind femur length, $\log_{10}$ hind femur width, $\log_{10}$ hind femur area or $\log_{10}$ hind femoral spine area as response variable and $\log_{10}$ mesonotum length, sex and species as predictor variables, as well as all two-way and three-way interactions. Collection site was also added as a random factor. Captive and wild *E. calcarata* populations were considered as different species in these analyses. AIC-based model selection was used to identify the best model. Only the fixed effects from the best models are included in the final analyses to provide the most accurate parameter estimates. Significance of the fixed effects was assessed using type III ANOVAs and the Satterthwaite's method to estimate degrees of freedom (*anova*:'lmerTest'; Kuznetsova et al., 2017). Pairwise *post hoc* tests using estimated marginal means with Tukey contrasts were performed to further investigate interspecific and intersexual differences in these scaling relationships (*emmeans* and *emtrends*:'emmeans'; Lenth, 2019). We tested for departure from isometry (null expectation) between each leg measurement and mesonotum length (*i.e.*, a linear measurement of body size) using 95 % confidence intervals around the estimated regression slopes. In the case of front femur length, hind femur length and width (*i.e.*, linear measurements), isometry corresponds to a slope of 1 and in the case of hind femur and spine area (*i.e.*, surface measurements) it corresponds to a slope of 2.

2.3. Roosting behaviour

When a group of *E. calcarata* or *E. horrida* was found inside a cavity, we manually removed every individual and counted the number of adult males and females. In total, we found 87 adult female and 77 adult male *E. calcarata* in 44 different cavities; 9 adult female and 8 adult male *E. horrida* in 11 different cavities; 27 adult female and 40 adult male *E. insularis* that were never found in a cavity. Each cavity and tree was only sampled once to assess group size and sex ratio. We then tested the prediction that male *E. calcarata* with larger hindlegs would be associated with more females (*i.e.*, found in more female-biased groups). We built a generalized linear mixed-effects model (*glmer*:'lme4′, Bates et al., 2015) with binomial errors including male-female proportion as the response variable, and $\log_{10}$ group-averaged male hind femur area as fixed effect. Tree ID and field site were included as random factors. Significance was assessed using a Wald chisquare test (*Anova*:'car', Fox and Weisberg, 2019).

2.4. Movement patterns and mobility

We used radiotelemetry to assess the habitat use and movement patterns of *E. calcarata* and *E. insularis* in smallholder oil palm blocks respectively near the Dami OPRA Station (Kimbe, West New Britain, PNG; S5° 31.846′ E150° 20.221′), and at Ambogo New Britain Palm Oil (NBPOL) Plantation near the Higaturu PNGOPRA Sub-centre (Popondetta, Northern (Oro) Province, PNG; S8°44.468' E148°11.985'). The block in Dami contained 8−10 m oil palms (*Elaeis guineensis* Jacq.*)* and *Kleinhovia hospita* L. trees (Malvaceae) offering suitable trunk cavities where high densities of *E. calcarata* have been found as well as low vegetation covering the ground (see picture in Fig. 4A). The plantation near Popondetta was chosen for security reasons because it was close to the Higaturu centre, and had oil palms measuring 5−6 m in height allowing accurate localization of the insects in the canopy and contact between tree canopies (see picture in Fig. 4B). Adult *E. calcarata* were collected inside different tree cavities at the study site and released on the same tree. Adult *E. insularis* were captured in smallholder oil palm blocks near the Tunana site, mostly in the canopies of oil palm trees, and transferred on the same day to the study site (Higaturu), 24 km away, which was safer to survey at night. The collection plantations were very similar to the survey plantation and unlike *E. calcarata*, adult *E. insularis* are never found inside cavities, hiding instead in the canopy. Therefore, *E. insularis* individuals were unlikely to be affected by this re-location.

We glued 0.5 g transmitters (ATS, Model A2415, battery life: 12–24 days) onto the mesonotum of a total of 9 adult *E. calcarata* females, 9 *E. calcarata* males, 9 *E. insularis* females and 8 *E. insularis* males using cyanoacrylate glue (Loctite® Super Glue Gel Control™) (Fig. 1C-F). To maximize sample size, the same transmitters were first glued onto *E. calcarata* individuals and were then transferred to *E. insularis* individuals. Transmitters represented on average 1.9 % of a *E. calcarata* female's mass, 2.7 % of a male's mass, 5.7 % of a *E. insularis* female's mass and 15 % of a male's mass. Radio-tagged individuals appeared to feed, mate and walk normally (Video S2). Radio transmitters had unique frequencies ranging from 150.341 to 150.621 Hz (pulse rate: 27 ppm, pulse width: 15 ms). Radio signals were detected using a three-element Yagi antenna connected to a portable scanning receiver (ATS, R410). We searched for the radio-tagged individuals once during the day (around 16:00 h) and once during the night (around midnight) in both locations for three consecutive days. When an individual was located, we recorded its position with a global positioning system (Garmin GPSMAP 64S, accuracy ∼5 m). The position of each individual was marked with orange flag tape and the ground (*i.e.,* horizontal) distance travelled since the previous sighting was measured using a 50 m measuring tape. Because the phasmids are mostly inactive and hiding during the daytime, the distances measured at midnight should reflect distances travelled during the first half of the night (18:00 – 0:00) while the distances measured in the afternoon should reflect distances travelled during the second half (0:00 – 6:00). Patterns of individual movements were visualized using ArcGIS Desktop (v. 10.7, Esri, Redlands, CA). GPS coordinates and individual trajectories were projected on the corresponding satellite map (2019; Bing, Microsoft corporation, Redmond, WA; Digitalglobe, Westminster, CO). Five male and five female *E. insularis* lost their radiotransmitter at some point during the survey period. Observations for which the transmitter was observed detached from the insect were not included in the analyses.

To examine whether sex-differences in mobility differed by mating system, we built LMMs (*mixed*:'afex', Singmann et al., 2019) for both species separately including distance travelled as the response variable. Sex, time of day (day- or nightime) and their interaction were included as fixed effects while body size ($\log_{10}$ mesonotum length) and front leg size ($\log_{10}$ front femur length) were also included as covariates that we allowed to interact with sex. Individual ID, date and trunk ID where the individual was collected and released (for *E. calcarata* only) were finally added as random factors. We included body and leg size in the models as these variables are known to affect mobility in walking insects (Herberstein et al., 2017; Kelly, 2014; Kelly et al., 2008). All interactions including sex were included to potentially uncover sex differences in the effect of time, body or leg size. Significance for fixed effects was determined using type III Likelihood Ratio Tests (LRT, *anova:*'afex'). The LMM for *E. insularis* found a significant effect of the interaction terms between sex and body size and between sex and leg size. To investigate in details these sex-specific effects of body and leg size on distance travelled, beyond simply comparing slopes between sexes, we built additional LMMs for males and females separately including distance as the response variable, $\log_{10}$ mesonotum length and $\log_{10}$ front femur length as fixed effects, and individual ID and date as random factors.

2.5. Nightly activities

To explore the nocturnal behaviours of *E. calcarata* around cavities at night and further characterize their mating system, we placed two video cameras in time lapse mode (GoPro HERO 4©, interval: 0.5 s) to film the trunk of a *Kleinhovia hospita* tree bearing 12 different cavities containing *E. calcarata* groups near the Dami research station (Kimbe, West New Britain, PNG) during four different nights in October and November 2018. We collected and marked some individuals ($n = 12$ females and 19 males) with a silver paint marker on the night prior to the first night of recording. Recordings were made under red illumination as red light did not interfere with the nocturnal behaviour of captive animals (RB, personal observation). The red lamps and the cameras were powered by 12 V 12AH SLA batteries placed inside dry bags. Recordings lasted from 4 P M to 8AM. Sunrise was around 5:30AM and sunset around 5:50PM. Using the event logging software BORIS (v. 7.5.3, Friard and Gamba, 2016), we recorded the time after sunset when an identifiable individual would leave or enter a cavity, move to or return from the canopy of the tree to the trunk or move to or return from the ground. When a marked individual was observed both leaving and entering a cavity during the same night, we calculated the time it had spent outside. We compared the time of occurrence of each of these nocturnal behaviours and the duration spent outside cavities between males and females using LMMs (*mixed*:'afex') with time (or duration) as the response variable, sex as fixed effect and date and individual ID as random factors. Significance of the fixed effect was assessed using LRT (*anova*:'afex'). The onset of copulations and male aggressive interactions was also recorded along with the duration of these copulations. Aggressive interactions between two males ranged from antennal contacts followed by one male walking away from the other, to kicks, pushes, mounting behaviours and hindleg squeezes (Video S3, S4). Finally, the predictability of female's behaviour in leaving or returning to cavities can have implications as to what mating behaviour males should adopt throughout the night. Thus, we compared the variance of the times when marked females left cavities at the beginning of the night and the variance of the times they re-entered them at the end of the night (combining the four nights) using a paired

Pitman-Morgan test (*Var.test*:'PairedData', Champely, 2018).

In addition, the number of adult males and females visible on the trunk (marked or unmarked) was counted every 15 min from sunset for the whole night to evaluate how adult densities and sex ratios on the trunk changed over the course of a night. The temporal dynamic of male and female numbers was visualized by fitting a cubic smoothing spline to the data of all four nights combined ($df = 10$, *smooth.spline*:'stats'). We built a GLMM (family = Poisson, *mixed*: 'afex') including the number of individuals visible on the trunk as the response variable, sex and time post sunset as fixed effects and date as a random effect. A quadratic term, time^2, was also added to account for the non-linearity of the effect of time. The interactions sex:time and sex:time^2 were also included to uncover sex-specific effects of time on the number of individuals present on the trunk. Significance of fixed effects was assessed using Type III LRT (*anova*:'afex').

Finally, we examined the changes of male reproductive behaviours in relation to temporal changes in female number and sex ratio throughout the night. For each of the 15 min time points, we also categorized whether each of the visible males present on the trunk was guarding – *i.e.*, immobile and likely defending a territory – or searching – *i.e.*, walking and potentially searching for females or food. The temporal dynamic of the relative proportion of guarding and searching males was also visualized by fitting a cubic smoothing spline to the data of all four nights combined ($df = 10$, *smooth.spline*:'stats'). To formally test how this proportion changed across time, we ran a GLMM with binomial errors including male guarding/searching ratio as the response variable, time post sunset as a fixed effect and date as a random factor (*glmer*:'lme4′). Significance was assessed using a Wald chisquare test (*Anova*:'car').

3. Results

3.1. Morphology

We first tested if species and sexes differed in body size (Table S1). We found a significant effect of species ($F_{3,2.2} = 155.7$, $p = 0.004$), sex ($F_{1,282.5} = 243.6$, $p < 0.0001$) and their interaction ($F_{3,282.6} = 34.6$, $p < 0.0001$) on mesonotum length. *Post hoc* tests revealed that mesonotum length differed significantly between males and females in all species ($p \leq 0.001$), except for *E. horrida* ($p = 0.82$). Therefore, *E. horrida* was the only species to be non-size dimorphic.

We then explored the differences in scaling relationships between mesonotum length and front femur length between sexes and species, which were very similar overall across the three species (Fig. 2B). The best linear model (*i.e.,* with the lowest AIC) showed that the small interspecific differences were not significant, but that males and females differed significantly in intercept in all species (Table 1). Specifically, males consistently had longer front femurs for a given mesonotum length than females ($p < 0.0001$, Table 1, Fig. 2B). The slope of this scaling relationship did not differ significantly across species or sexes and was overall estimated as hypoallometric (*i.e.,* isometric slope = 1: $\beta = 0.82 \pm 0.04$, 95 % CI: $0.75 < \beta < 0.90$; table S2; Fig. 2B).

Similarly, we investigated the differences in scaling relationships between mesonotum length and hind leg size between sexes and species (Fig. 2A, C–E, table S1). We found that the scaling relationships between mesonotum length and hind femur length, width and area differed between species and sexes in intercept but not in slope, as none of the interaction terms involving mesonotum length was informative and included in the best models (Table 1). For all of the hindleg measurements, the effect of sex was dependent on the species (species:sex, $p < 0.001$, Table 1). In *E. insularis*, the differences in intercepts between males and females were relatively small and not significant (Fig. 2C-E; *post hoc* tests, $p > 0.1$). In *E. horrida* and *E. calcarata* (captive), the differences in intercepts between males and females for hind femur length, width and area were much more pronounced (Fig. 2C-E) and all were highly significant (*post hoc* tests, $p < 0.001$). Males of these two species had longer, thicker and consequently larger hind femurs than their respective females for a given body size. The slope of the scaling relationship between mesonotum length and hind femur length did not differ significantly across species or sexes and was, as with the allometry of front leg length, significantly hypoallometric (isometric slope = 1: $\beta = 0.82 \pm 0.05$, 95 % CI: $0.76 < \beta < 0.94$; table S2; Fig. 2C). Similarly, the slope of the scaling relationship between hind femur area and mesonotum length was overall hypoallometric (isometric slope = 2: $\beta = 1.79 \pm 0.09$, 95 % CI: $1.62 < \beta < 1.97$; table S2; Fig. 2E). Finally, the slope of the scaling relationship between hind femur width and mesonotum length did not differ significantly from isometry (isometric slope = 1: $\beta = 0.96 \pm 0.07$, 95 % CI: $0.83 < \beta < 1.09$; table S2; Fig. 2D).

We found the same significant effects for the scaling relationship between femoral spine area and mesonotum length (Table 1, Fig. 2F), with spines being much larger in male than in female *E. calcarata* (*post hoc* test, captive population, $p < 0.001$) and *E. horrida* ($p < 0.001$), and somewhat larger in male *E. insularis* than in females ($p < 0.001$). We also found a significant effect of the interaction between mesonotum length

Table 1

Results of type III analyses of variance (using the Satterthwaite's method) from linear mixed models contrasting the differences between sexes and species in terms of scaling relationships between body size (mesonotum length) and front leg size (front femur length) or hindleg size (hind femur length, width, area or femoral spine area). Only the best mixed models selected by AIC are presented.

Response variable	N	Explanatory variables	F	df1	df2	P
Log$_{10}$(front femur length)	294	log$_{10}$(mesonotum length)	447.3	1	71.3	<0.0001
		species	9.32	3	2.0	0.10
		sex	48.0	1	188.7	<0.0001
Log$_{10}$(hind femur length)	222	log$_{10}$(mesonotum length)	272.7	1	181.7	<0.0001
		species	36.3	3	2.0	0.03
		sex	187.5	1	215.0	<0.0001
		species:sex	48.5	2	209.5	<0.0001
Log$_{10}$(hind femur width)	222	log$_{10}$(mesonotum length)	199.6	1	214	<0.0001
		species	1016.1	3	214	<0.0001
		sex	481.8	1	214	<0.0001
		species:sex	122.2	2	214	<0.0001
Log$_{10}$(hind femur area)	222	log$_{10}$(mesonotum length)	387.4	1	82.1	<0.0001
		species	650.5	3	2.0	0.0015
		sex	516.3	1	173.8	<0.0001
		species:sex	125.8	2	185.0	<0.0001
Log$_{10}$(femoral spine area)	222	log$_{10}$(mesonotum length)	160.6	1	213	<0.0001
		species	994.7	3	213	<0.0001
		sex	12.6	1	213	0.0005
		species:sex	132.1	2	213	<0.0001
		log$_{10}$(mesonotum length):sex	4.31	1	213	0.04

and sex: despite having smaller spines, females in all three species display a steeper slope between spine area and body size than males ($p = 0.04$, Table 1 and S2). However, slopes of all of the scaling relationships were not different from isometry (*i.e.,* slope = 2) except for captive *E. calcarata* females which displayed a hyperallometric slope ($\beta = 3.27 \pm 0.47$, 95 % CI: $2.33 < \beta < 4.21$, table S2; Fig. 2F).

3.2. Roosting behaviour

Aggregations of *E. calcarata* were typically found inside vertical tree cavities, especially inside live *K. hospita*, where they are especially hard to reach (Fig. 3A,B). The largest group was composed of 26 individuals and the average group size was 5.29 ± 0.94 (mean ± SE) if ignoring solitary individuals, 3.73 ± 0.67 otherwise (Fig. 3C). Average sex ratio (= number of females / number of adults) inside the 44 sampled cavities was 0.39 ± 0.05 and 0.51 ± 0.05 when only considering the 28 groups with at least two individuals (Fig. 3D). Group sex ratio was positively correlated with the log-transformed mean male hind femur area of the group (Fig. 3E, GLMM, $n = 38$ groups, Wald $\chi^2 = 8.89$, $df = 1$, $p = 0.003$), such that males with larger hindlegs were found in relatively more female-biased groups.

For *E. horrida*, population density at our field sites near Popondetta was much lower than that of *E. calcarata* near Kimbe, and we mostly found solitary individuals (six males and five females) hiding inside cavities of living tree trunks (*Pterocarpus indicus* and *Gliricidia sepium* (Fabaceae)) or on the side of rotten logs (Fig. 1G), but also two groups inside cavities (one male with one female and one male with three females) confirming the gregarious behaviour of this species.

In contrast, adult *E. insularis* were only found living in the canopies of diverse tree species, including oil palms (Fig. 1H), sometimes in the exact same tree that would host *E. horrida* inside trunk cavities. They were all solitary (25 females and 38 males) except for two mating pairs.

3.3. Movement patterns and mobility

Radiotelemetry further confirmed that *E. calcarata* adult individuals mostly hide in groups inside tree cavities during the daytime. Relatively few *E. calcarata* were found out of a cavity during the day (11/49 sightings), and when that happened they were solitary and hiding under objects on the ground. *E. calcarata* seemed very faithful to a given cavity-bearing tree, hereafter referred to as “host tree” (Fig. 4A). Only one male and one female (out of nine each) changed host tree during the 3-days survey period. Relatively few individuals were found venturing away from their host tree for more than 24 h during the survey period (1/9 males, 2/9 females) (Fig. 4A). These moving individuals were consistently found on or very close to the ground, suggesting dispersal on the ground rather than through the canopy. At night, adult males and females mostly fed on the canopy of their host tree (*K. hospita*) and that of neighbouring trees (<20 m away), including oil palms, and females could be observed egg laying in the direct vicinity of the host tree. The maximum recorded ground distance travelled in half a night was 19.6 m for males (mean = 1.29 ± 0.57 m), 30 m for females (mean = 2.19 ± 0.78 m). Overall the movements of *E. calcarata* individuals on the landscape appeared centred around their host tree as they aggregate in and on these cavity-bearing trees (Fig. 4A). A LMM revealed that the effects of sex, body size, and time of day on distance travelled were non-significant ($p > 0.2$, Table 2). There was therefore no evidence that males and females differed in their mobility. However, we found that individuals with longer legs travelled longer distances ($p = 0.04$, Table 2).

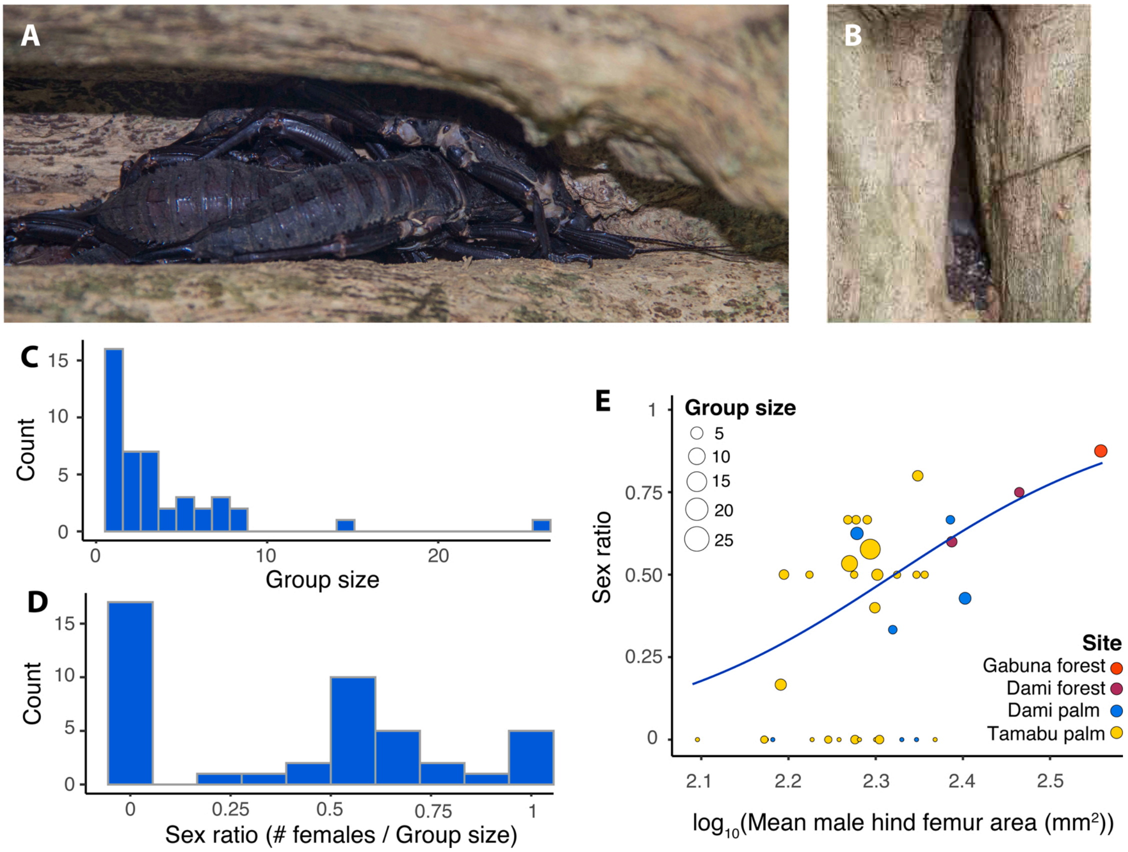

Fig. 3. *E. calcarata* group composition inside cavities. (A) Group of adults inside a cavity. (B) Cavity entrance (photographs by first author). (C) Distribution of group sizes in the field. (D) Distribution of group sex ratios. (E) Binomial GLMM showing the relationship between group sex ratio and the average size of male hind femurs inside the group ($p = 0.003$). Field sites are distinguished by color and group size is indicated by the size of each circle.

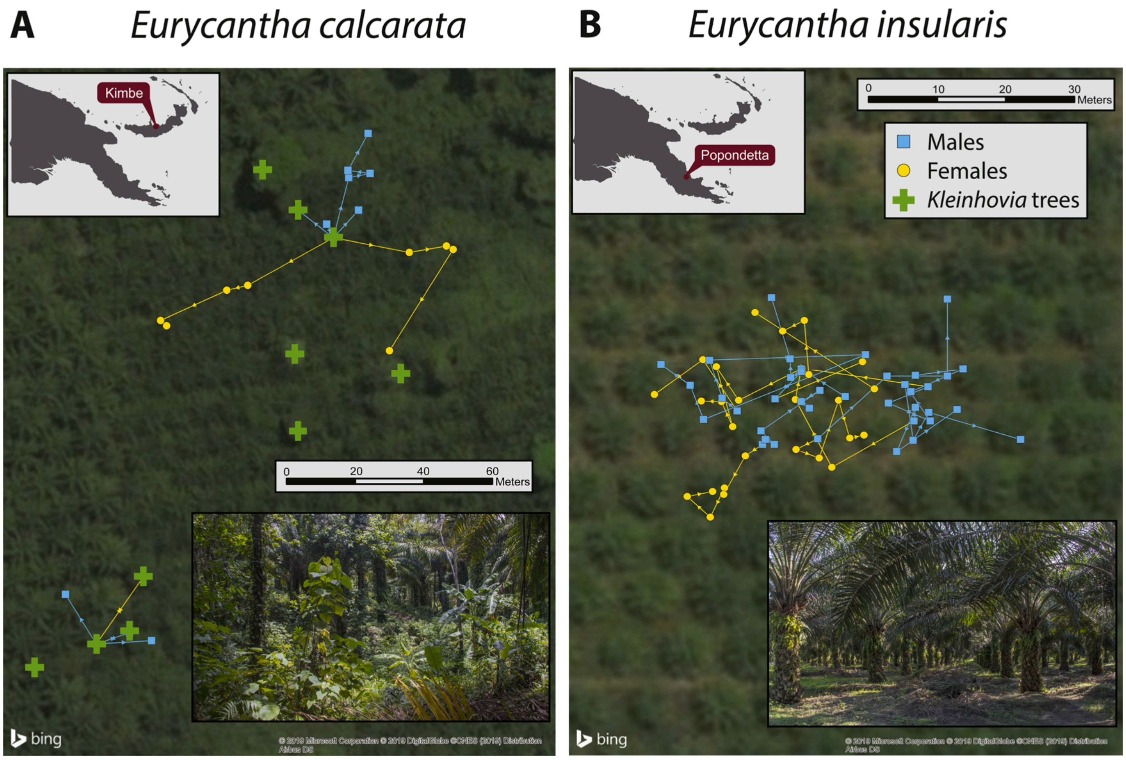

Fig. 4. Horizontal movement patterns of the mobile *E. calcarata* individuals (A) and all the *E. insularis* individuals followed (B). Points represent the position of an individual after each half day period. Green crosses represent the position of potentially suitable cavity-bearing host trees. Positions of *E. calcarata* individuals that stayed inside or directly outside a *Kleinhovia* trunk are not represented. Trajectories are drawn on top of a satellite view of the study areas. Maps on the top left corners show the location of the two study areas. Pictures show the two study sites. Photos by first author.

Table 2
Analyses of the effects of body size, leg size and sex on ground distance travelled.

Species	Sample size	Explanatory variables	β	SE	χ^2	*P*
E. calcarata	110 observations	(Intercept)	−207.8	96.2		
	18 individuals	Log_{10} (Mesonotum length)	79.4	63.6	1.48	0.22
		Log_{10} (Front femur length)	**78.1**	**36.3**	**4.18**	**0.04**
		Sex (Contrast Male : Female)	127.8	106.9	1.38	0.24
		Time (Contrast Night : Day)	0.31	1.13	0.07	0.79
		Sex × $\log_{10}$(Mesonotum length)	−52.4	78.4	0.44	0.51
		Sex × $\log_{10}$(Front femur length)	−42.3	49.5	0.72	0.40
		Sex × Time	0.34	1.59	0.04	0.83
E. insularis	59 observations	(Intercept)	−15.4	94.1		
	15 individuals	Log_{10} (Mesonotum length)	−5.25	87.9	0.004	0.95
		Log_{10} (Front femur length)	21.1	67.5	0.097	0.75
		Sex (Contrast Male : Female)	**451.3**	**140.7**	**9.45**	**0.002**
		Time (Contrast Night : Day)	1.16	1.62	0.40	0.53
		Sex × $\log_{10}$(Mesonotum length)	**−645.8**	**182.8**	**10.71**	**0.001**
		Sex × $\log_{10}$(Front femur length)	**286.0**	**110.6**	**6.15**	**0.01**
		Sex × Time	−3.19	2.29	1.90	0.17

Summary of linear mixed effect model outputs investigating the association between the distance travelled (in meters) by each radio tracked individual between each sighting and body size, front leg size, sex and time at sighting (daytime or nighttime). The output includes the estimated parameter value for each continuous fixed effect and the difference between levels (treatment contrasts) of each categorical fixed effect, and the standard error. Chi-square statistics and associated p-values were obtained from type III Likelihood Ratio Tests. Explanatory variables that were found to have a significant effect ($p < 0.05$) are bolded.

In contrast, radiotelemetry showed that adult *E. insularis* exclusively hide in tree canopies during the day and do not aggregate, as we never found any individual roosting with others. Reconstruction of their trajectories from GPS coordinates over the course of the 3-day survey period revealed that the movements of both sexes on the landscape appeared very chaotic, and that individuals do not aggregate in specific locations (Fig. 4B). We never found any individual on the ground, suggesting that they moved mostly by walking through the canopy instead of walking on the ground. The maximum horizontal distance travelled during half a night was 25.6 m for males (mean = 6.59 ± 1.01 m), 19.3 m for females (mean = 5.57 ± 0.88 m). A LMM showed a significant effect of sex ($p = 0.002$, Table 2), of the interactions between sex and body size ($p = 0.001$) and between sex and leg size ($p = 0.01$) on distance travelled. All other fixed effects were not significant ($p > 0.17$, Table 2). Body size more negatively affected distance travelled by males than by females, and relative leg length more positively affected the distance travelled by males than by females (Table 2). A LMM only including males further showed that smaller males (LMM: $\log_{10}$(Mesonotum length), $\chi^2_{5,1} = 11.51$, $p < 0.001$) with relatively longer front legs (LMM: $\log_{10}$(Front femur length), $\chi^2_{5,1} = 9.51$, $p = 0.002$) walked significantly longer distances. In contrast, in females, we did not find any evidence that distance travelled was affected by mesonotum length (LMM: $\chi^2_{5,1} = 0.04$, $p = 0.85$) or front femur length (LMM: $\chi^2_{5,1} = 0.24$, $p = 0.63$).

3.4. *Nightly activities*

Males were estimated to leave the cavities on average 1h3min earlier than females at the beginning of the night ($\chi^2 = 11.33$, $p < 0.001$, Fig. 5A). No other significant difference between sexes in time of occurrence of other behaviours was found: going to the canopy ($\chi^2 = 0.08$, $p = 0.78$), going to the ground ($\chi^2 = 1.50$, $p = 0.22$), returning from the canopy ($\chi^2 = 0.004$, $p = 0.95$), returning from the ground ($\chi^2 = 1.36$, $p = 0.24$) or entering a cavity ($\chi^2 = 0.99$, $p = 0.32$). The time when females exited cavities at the beginning of the night exhibited a lower variance, and was therefore relatively more predictable, than the time when the females returned to them at the end of the night ($t = -2.2$, $df = 16$, $p = 0.046$). Males spent on average 1h42 min longer outside cavities than females (5h23 min *vs* 3h41 min, $\chi^2 = 6.80$, $p = 0.009$). So males spent 46 % more time outside cavities than females.

We found a significant effect of sex ($\chi^2 = 30.9$, $p < 0.0001$), time ($\chi^2 = 25.7$, $p < 0.0001$) and time^2 ($\chi^2 = 34.4$, $p < 0.0001$) on the number of individuals visible on the trunk (Fig. 5B). The interactions between sex and time ($\chi^2 = 2.8$, $p = 0.09$), and sex and time^2 ($\chi^2 = 0.23$, $p = 0.23$) were not significant. These results indicate that the overall temporal dynamic of individual densities on the trunk did not differ between males and females except that males were consistently more numerous. The sex ratio (number of females/ total number of individuals) on the trunk was consistently and largely male biased throughout the night with an average of 0.19 ± 0.02. The proportion of guarding males relative to searching ones decreased significantly throughout the night (GLMM, $\chi^2 = 63.0$, $p < 0.0001$) revealing a switch in overall male mating behaviour during the night (Fig. 5C).

After leaving their cavities at the beginning of the night, males typically stayed stationary at a specific location, such as the vicinity of cavity entrances or the base of large branches (Fig. 5D, Video S4). They could be observed actively guarding these territories and/or fighting with rivals over direct access to females using kicks, pushes, mounting and hind leg squeezes (Video S3, S4). Additionally, scars of punctures, most likely caused by the femoral spine of another male, could be observed on the side of the hind femurs of three males (Fig. 5E). Males would intercept and copulate with females as they left their cavities, and/or as they walked either to the canopy or the ground (Video S5). Females were never observed resisting male copulation attempts. Upon contact with a male, females typically froze and the male initiated copulation rapidly by positioning itself on the side of the female (Video S3, S5), wrapping her abdomen with one hindleg and reaching her genitalia from underneath (Video S3). Copulations lasted on average 3.29 ± 0.19 min (n = 64). Finally, males could be observed actively preventing other males from entering a cavity at the end of the night (Video S6).

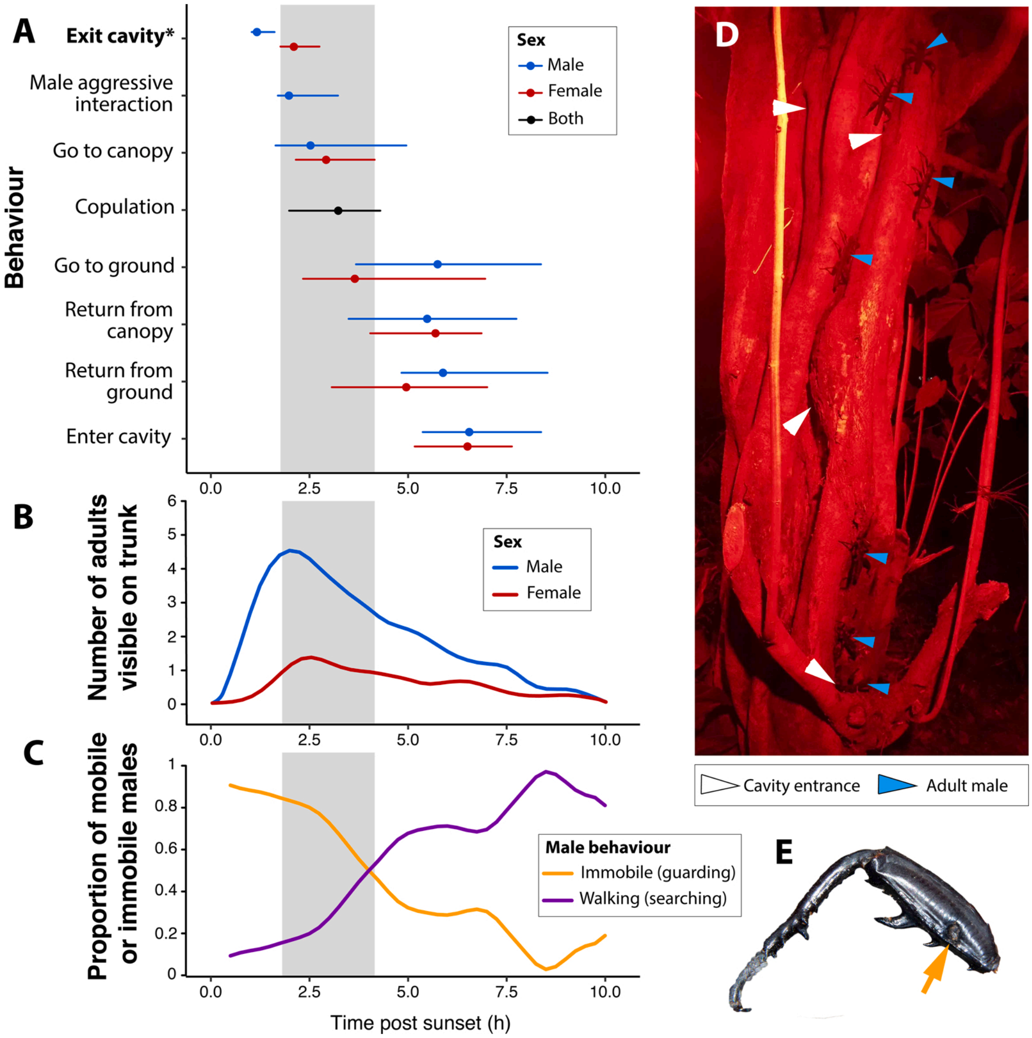

Fig. 5. Timeline of *E. calcarata* adult males and females' behaviours, obtained by combining behavioural data from the four nights of recording. (A) Time post-sunset of sex-specific behaviours, copulations, and male-male aggressive interactions. Points represent median times. Horizontal bars represent interquartile ranges. The grey box only serves illustrative purposes and highlights the period encompassing the interquartile ranges of females exiting cavities and females going to the canopy. It is during this period that most male aggressive interactions occur as well as most copulations. The asterisk and bold font indicate a significant difference between males and females ($p < 0.001$, see result section). (B, C) Cubic smoothing splines showing the number of males and females visible on the trunk (B) and the relative proportion of immobile/guarding males relative to walking/searching males (C) as a function of time post-sunset. (D) Snapshot of one side of a host trunk, 2 h post sunset: many males have already left their cavity but no females yet. Males are guarding and fighting over strategic locations close to cavity entrances that enable them to intercept females on their way to forage in the canopy. (E) Injury on a male hindleg likely caused by the femoral spine of a rival male.

4. Discussion

In this study, we show that the evolution of large armoured males in thorny devil stick insects (*E. calcarata* and *E. horrida*) is associated with a switch in habit use and mating system. In most studied stick insects including *E. insularis*, solitary females are scattered across the vegetation (Kelly, 2014; Myers et al., 2015). Males are relatively small and display a scramble competition mating system as they actively search for dispersed females. In contrast with *E. insularis,* both of the thorny devil species roost in groups inside trunk cavities, and this change in habitat use and social behaviour appears to be associated with a switch in mating system. We show that male thorny devil stick insects employ a defence -based polygyny mating system, with males actively fighting over direct control of clumped females or territories adjacent to roosting cavity entrances on the host tree trunk. Our data offer preliminary support for the hypothesis that sexual selection, rather than predator defence or sexual conflict, drove the evolution of large body and hindleg sizes in thorny devils: males use their enlarged and armoured hindlegs during fights with rival males to squeeze and potentially puncture their opponent, and large males with the largest hindlegs are associated with relatively more females inside roosting cavities.

Our radiotelemetry data revealed that in *E. insularis,* which displays relatively small and unarmoured males (*i.e.*, the ancestral state of the *Eurycantha* clade), females remained dispersed in tree canopies foraging at night and hiding in the leaves during the day. As with other studied stick insects, males employed a scramble competition mating system in the form of a prolonged searching polygyny (Herberstein et al., 2017; Kelly, 2014; Myers et al., 2015). Both sexes were highly mobile in the canopy of palm trees and did not seem to associate for extended periods of time. We found that smaller males with relatively longer legs travelled longer distances at night than larger males. Mobility advantages to smaller males with relatively longer legs have also been found in other walking arthropods with a similar mating system (*e.g.*, Cook Strait giant wētās: Kelly et al., 2008; crab spiders: Legrand and Morse, 2000). Mobility is expected to be critical in such mating systems as it increases the probability of encountering females (reviewed in Herberstein et al., 2017). We can therefore speculate that smaller *E. insularis* males are probably advantaged in this context because of increased mobility (the “mobility hypothesis”, Kelly et al., 2008), which may help explain the strong female-biased sexual size dimorphism in this species (Blanckenhorn, 2005, 2000; Corcobado et al., 2010; Fairbairn et al., 2007; Kelly et al., 2008). A more comprehensive understanding of other selective forces potentially acting on male size, as well as characterization of the selective forces acting on female size, will be needed to fully explain the pattern of sexual dimorphism seen in this species.

In contrast, in both *E. calcarata* and *E. horrida*, females descended from canopies before sunrise and took shelter inside cavities in the trunks of a small number of host trees. These animals collected in dense aggregations of mixed sex, suggesting the use of aggregation pheromones as is common in other insects (Wertheim et al., 2005). In *E. calcarata*, our primary focus of field observations, adult females aggregated inside these cavities and larger males with larger hindlegs were more often found roosting with relatively more females than smaller males. At dusk, males exited cavities earlier than the females and subsequently fought over direct access to these females as they left their cavities, or over control of strategic locations on the trunk for intercepting females, such as the vicinity of cavity entrances or the base of large branches. As females exited their cavities to forage, they were likely to walk past these locations and be intercepted by territory-guarding males. Interestingly, males only fought over territories at the beginning of the night. Later, after the majority of females had left the trunk, we observed a switch in male mating strategy from territory defence to scattering and active searching, with consequently fewer encounters between males. During the second half of the night, males found and copulated with females either on the ground or higher up in the canopy. Males never followed a female after copulation and therefore did not display any post-copulatory female guarding behaviours, unlike many other male phasmids known to spend extended periods of time *in copula* or on the female’s back as a post-insemination mate guarding strategy (Bedford, 1978; Kelly, 2015; Sivinski, 1979). Males did not resume territory defence at the end of the night, which was consistent with the time of return of the females to a cavity being more variable, and therefore less predictable, than the time when they leave cavities. Thus, territory guarding is likely more beneficial at the beginning than at the end of the night as females are more likely to pass by these territories more frequently early in the night. The absence of post-copulatory mate guarding behaviours and the occurrence of male fights mainly at the beginning of the night when the females exit the cavities could also be consistent with a first male sperm precedence (Simmons and Simmons, 2014, 2001). However patterns of sperm precedence are still unknown in this insect lineage.

We clearly observed male *E. calcarata* using their hindlegs to fend off rivals and potentially injure them, as witnessed by the stereotypical puncture wounds found on several males’ cuticles. Males consistently fought in three contexts: (1) over direct access to a nearby female with some males even stealing mates; (2) when defending strategic locations on the trunk where females are likely to walk by when leaving their cavity; and (3) to prevent rivals from entering a cavity. In context 1, the benefit of winning a fight is clear as victors earn direct access to mating. In context 2, males successfully keeping rivals away from the likely path of females should also lead to increased mating opportunities. These males would typically rush at trespassing rival males and often fought to repel them. Successful males immediately mounted any females that passed by. The benefits of preventing rivals from entering a cavity (context 3) are less clear. Individuals are tightly packed one on top of the other inside these cavities, and mating in such crowded conditions is likely difficult. In our captive (Montana) *E. calcarata* population, for example, despite hundreds of hours of observation we have yet to observe even a single copulation inside our artificial cavities (which have a transparent side), even though males and females aggregate together for many hours each day and readily copulate outside these cavities. If the same is true in the field, then this may explain why males tolerate other males inside their cavities, with most groups containing several males, sometimes more than females.

In some ways the *E. calcarata* mating system appears similar to that of the Wellington tree wētā (*Hemideina crassidens,* order Orthoptera), for which males use their exaggerated mandibles to drive rivals away from groups of females who also reside inside tree cavities (Kelly, 2004, 2006a, 2006b, 2006c, 2007). However, in tree wētās, males do not tolerate other males inside cavities (Kelly, 2004, 2006d). This is consistent with tree wētās copulating inside these cavities, and rarely outside (Kelly, 2006a). In contrast, copulation in thorny devils readily occurs directly outside the cavities, on the tree trunk, and probably only rarely inside cavities. This may reduce the benefit to males of fighting for exclusive control of harems inside cavities, and help explain why fights so often occurred just outside cavity entrances and along the trunks of host trees. Nevertheless, males could still be observed actively preventing some rivals from entering a cavity and large males were found inside cavities containing relatively more females. This behaviour may reduce competition for the next night or guarantee large males a better spot right outside the cavity entrance after the next sunset to intercept females as they leave. However, these explanations are speculative and further experiments and observations are needed to test them.

Exaggeration of the male hind legs in thorny devils (*E. calcarata* and *E. horrida*) is the result of an increase in the intercept of the otherwise hypoallometric scaling relationship between hind leg size and body size. Front leg size, that we used as a reference trait, similarly scaled hypoallometrically with body size. In addition, the allometric slopes for our different metrics of hindleg size did not differ between males and females. Sexually selected traits often display steeper and positive static allometry in males, but this is not universal (Bonduriansky, 2007) and our findings for *E. calcarata* and *E. horrida* add to our knowledge of those few species where exaggerated and potentially sexually selected male traits do not scale hyperallometrically (Bonduriansky, 2007; Fea and Holwell, 2018). Recent studies have proposed that hyperallometry – *i.e.*, disproportionate trait size in large individuals – is mostly expected when morphological traits function as intraspecific visual signals, as it can amplify individual differences in body size (Eberhard et al., 2018; O'Brien et al., 2018). Therefore, our finding suggests that the enlarged legs of thorny devils may function primarily as tools of combat rather than as intraspecific signalling displays, which is consistent with the fact that we never observed males sizing each other using their hindlegs or waving these legs at rival males. In the context of intrasexual fights, hind legs only appeared to be used to deliver powerful squeezes to the opponent and potentially injuring it by puncturing its cuticle with their sharp femoral spines. Hypoallometry may be remarkably advantageous in such context from a mechanical stand-point as lever components will stay in proportion, guaranteeing a conservation of mechanical advantage and avoiding the need for a compensatory investment in costly muscles (Levinton and Allen, 2005; O'Brien and Boisseau, 2018). Notably, the hindlegs of *E. calcarata* have already be shown to bear a significant energetic cost driven by muscle mass (O'Brien et al., 2019). Future studies will be needed to look at how hindleg size affects fighting success, how squeezing strength scales with hindleg size in this species, as well as assessment strategies during fights to shed further light on how these legs might function as tools *versus* signals during combat (McCullough et al., 2016).

Previous authors have repeatedly hypothesized that the enlargement of the hindlegs displayed by adult male *E. calcarata* was primarily driven by their function as antipredator defences used in threat displays and active counterattacks (Bedford, 1976; Buckley et al., 2009; Carlberg, 1989). This idea stemmed from the observation that male and female *E. calcarata* and *E. horrida* aggressively wave their hindlegs when approached by a predator or a person (Bedford, 1976; Carlberg, 1989): when threatened, they adopt a spectacular startle posture, reaching out with their spiny hindlegs poised to strike them together (Fig. 1A,B; Bedford, 1976; Carlberg, 1989). Upon further stimulation, these insects then rapidly swing these hindlegs together attempting to grasp imprudent attackers (Video S1). This defensive behaviour has been observed in several large phasmid species (Bedford, 1978) and we also observed it in female *E. insularis*. Thus, defence against predators is likely an ancestral function of the spiny hindlegs in this group, in both males and females. It is possible that predators might have also selected for hind femora that are larger in males than in females ("antipredator hypothesis"). Data on sex-specific predation risk and on the effect of hindleg size on survival and predator deterrence efficiency would be required to test this hypothesis. Nevertheless, this defensive function likely adds to the benefits of having enlarged hindlegs for males in addition to winning fights against rivals. Such dual benefits of a sexually selected weapon have also been found in fiddler crabs and elk, where males have been shown to benefit from their enlarged claw or antlers as it reduces predation risk (Bildstein et al., 1989; McLain et al., 2003; Metz et al., 2018).

A third hypothesis for the evolution of enlarged male hindlegs in thorny devils could be that males may use their hindlegs to overcome female resistance to copulation attempts (the "sexual conflict hypothesis"), as is found in other insects with sexually dimorphic hindlegs (*e.g.,* thick-legged flower beetles: Burrows, 2020; camel crickets: Haley and Gray, 2012; water striders: Rowe et al., 2006). In another phasmid species, the spiny leaf insect *Extatosoma tiaratum*, facultatively asexual females were observed readily resisting males, especially to avoid switching from parthenogenesis to sexual reproduction (Burke et al., 2015). In *E. calcarata*, females are also capable of facultative thelytokous parthenogenesis, raising the possibility that they might benefit from resisting male advances, especially if switching to sexual reproduction is costly or if parthenogenesis offers higher short-term fitness benefits. However, we never observed females resisting males, which was largely inconsistent with the hypothesis that males might have used their hindlegs primarily to overcome female resistance. Females always froze when approached by a male and were never observed kicking, shaking their abdomen or trying to walk away. We could speculate that this may be associated with higher benefits of sexual reproduction relative to parthenogenesis. Alternatively, given that, in thorny devils and contrary to most other phasmids, males occur in high densities around females, successively resisting many copulation attempts from several suitors may be extremely costly for the females and outweigh the cost of mating and thus favour sexual receptivity ("convenience polyandry") (Arnqvist and Rowe, 2005; Cordero and Andrés, 2002; Rowe, 1992).

Large armoured males are glaring exceptions among stick insects but occur in the New Guinean thorny devils, *E. calcarata* and *E. horrida* (Buckley et al., 2009). New Guinean insects generally, and *Eurycantha* species in particular, are poorly understood as few studies have ever observed these animals in the wild. Our field study characterized and compared aspects of the natural histories of *E. calcarata*, *E. horrida* and *E. insularis* for the first time. Our data notably suggest that the evolutionary increase in body and relative hindleg size seen in the thorny devils is associated with a shift in habitat use and roosting behaviour of the females. This association is however unresolved as the reduction of sexual size dimorphism could be both the cause or the consequence of this ecological shift in habitat use (Fryxell et al., 2019). Unlike most stick insects and unlike their sister species *E. insularis*, female *E. calcarata* and *E. horrida* descend from the canopy to roost in aggregate within cavities in the trunks of their host trees during the day. Males also collect in these cavities, but the huge size of these insects combined with the cramped space inside the cavities means that copulations are generally not possible within the cavities themselves. Instead, communal roosting may have increased the potential for polygyny in this lineage by concentrating multiple females within one location, and synchronizing their movements as females emerged each evening and began to walk up or down the trunk. We suspect that males benefitted from being "at the right place at the right time", intercepting and mating quickly with females as they emerged from cavities, and the resulting contests that ensued selected for increases in male body and weapon size. Interestingly, once females are no longer concentrated – *i.e.*, after the majority have dispersed to the canopy or on the ground – males appear to revert to what presumably was their ancestral mating behaviour, abandoning their territories for the remainder of each night and instead searching for females in the vicinity of their host trunk (*e.g.*, on the ground or in the canopy). In contrast with the ancestral scramble competition mating system found in *E. insularis*, the reproductive success of *E. calcarata* and *E. horrida* males may primarily be determined by weapon size and relative fighting success, rather than or in addition to mobility. Although our data offers preliminary support for the sexual selection hypothesis, further work relating male body and weapon size to fighting and mating success is required to fully test it.

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CRediT authorship contribution statement

Romain P. Boisseau: Conceptualization, Data curation, Formal analysis, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Validation, Visualization, Writing - original draft, Writing - review & editing. **Mark M. Ero:** Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Writing - review & editing. **Simon Makai:** Investigation, Methodology, Validation. **Luc J.G. Bonneau:** Funding acquisition, Project administration, Resources, Supervision, Validation. **Douglas J. Emlen:** Conceptualization, Funding acquisition, Resources, Validation, Writing - review & editing.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.beproc.2020.104263.

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