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Factors Influencing Dominance Ranking in Paired Interactions Between Males of the Glowspot Cockroach *Lucihormetica verrucosa* (Blattodea, Blaberidae)

Das Dominanz-Ranking beeinflussende Faktoren bei Paarinteraktionen zwischen Männchen der Leuchtschabe *Lucihormetica verrucosa* (Blattodea, Blaberidae)

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Summary: Paired interactions were observed between adult males of the glowspot cockroach *Lucihormetica verrucosa,* a species in which males are characterised by two symmetrical pronotal spots, ranging in colour from white to yellow, orange and red. Adult males of this species are highly aggressive and perform numerous agonistic and submissive behaviours. Interactions were recorded as a series of bouts of fighting, each ending with one male (the „loser") retreating from the other („winning") male. The male that won the most interactions was ranked as the more dominant male. Various agonistic and submissive behaviours were observed, and their relative occurrence recorded in terms of the proportion of bouts they appeared in. The colours of their pronotal spots were also measured, in terms of RGB colour components. Based on these observations, two-sample t-tests found no statistically significant difference between the RGB colour values of the pronotal spots of the dominant individuals, and those of the subordinate individuals. On the other hand, it was found that there was a statistically significant positive correlation between the males that initiated the greater proportion of bouts (the most „aggressive" males), and those that won the greater proportion of bouts (the more „dominant" males). The implications of these results for the function of the pronotal spots are discussed.

Keywords: *Lucihormetica verrucosa*, Blaberidae, pronotal spots, dominance, aggression

Zusammenfassung: Zwischen Paaren erwachsener Männchen der Leuchtschabe *Lucihormetica verrucosa*, eine Art, bei der die Männchen durch zwei symmetrische Pronotalflecken gekennzeichnet sind, deren Farbe von Weiß bis Gelb, Orange und Rot reicht, wurden dyadische Interaktionen analysiert. Erwachsene Männchen dieser Art sind äußerst aggressiv und zeigen zahlreiche agonistische und submissive Verhaltensweisen. Die Interaktionen bestehen aus einer Abfolge von Kämpfen, die jeweils damit endeten, dass sich ein Männchen (der „Verlierer") von dem anderen Männchen (dem „Gewinner") zurückzog. Das Männchen, das die meisten Interaktionen gewann, wurde als das jeweils dominante Männchen eingestuft. Es wurden verschiedene agonistische und submissive Verhaltensweisen beobachtet und ihr relatives Auftreten entsprechend ihrem Anteil an den Kämpfen, in denen sie auftraten, erfasst. Auch die Farben der Pronotalflecken wurden gemessen, und zwar hinsichtlich der RGB-Farbkomponenten. Auf der Grundlage dieser Beobachtungen ergaben Zwei-Stichproben-t-Tests keinen statistisch signifikanten Unterschied zwischen den RGB-Farbwerten der Pronotalflecken der dominanten Individuen und denen der untergeordneten Individuen. Andererseits wurde festgestellt, dass es eine statistisch signifikante positive Korrelation zwischen den Männchen gab, die den größeren Anteil der Angriffe initiierten (die „aggressivsten" Männchen), und denjenigen, die den größeren Anteil der Kämpfe gewannen (die „dominanteren" Männchen). Die Folgerungen dieser Ergebnisse für die Funktion der Pronotalflecken werden diskutiert.

Schlüsselwörter: *Lucihormetica verrucosa*, Blaberidae, Pronotumflecken, Dominanz, Aggression

1. Introduction

Male cockroaches belonging to the family Blaberidae often exhibit aggressive intrasex interactions, such as those seen between males of the Madagascan hissing cockroach *Gromphadorhina portentosa* (CLARKE & MOORE 1994). The establishment of dominance hierarchies has been investigated in several species (GORTON et al. 1979; BELL et al. 2007). For example, in *G. portentosa* there exists dominance-based territoriality, with female mate choice based on dominance ranking (LEIBENSPERGER et al. 1985). During dyadic interactions between males of this species, size (BARTH 1968) and hissing sounds (NELSON & FRASER 1980) are predictive of „winning". Being the initiator of an interaction is also predictive of winning (BREED et al. 1981). This was also observed during intermale interactions in *Periplaneta americana,* although the reverse is true for longer interactions: the responder has the upper hand in such fights (BREED & RASMUSSEN 1980). However, in contrast to *G. portentosa*, in the blaberid roach *Nauphoeta cinerea,* size does not determine dominance ranking between males (SCHAL & BELL 1983). Therefore, a variety of factors may influence dominance ranking in Blaberidae.

Glowspot cockroaches of the genus *Lucihormetica* are characterised by an unusual sexual dimorphism: contrary to the females, males have two symmetrically arranged white, yellow or red spots on the pronotum (BECKERT et al. 2018). Recent studies, after reports from keepers, on *Lucihormetica verrucosa* have shown that the colour of these spots depends on the carotenoid content of the diet (FRITZSCHE 2013; BECKERT et al. 2017). Carotenoids are stored mainly in the epidermis below the transparent cuticle of the spots (BECKERT et al. 2018), instead of within the fat body as previously suggested (GREVEN & ZWANZIG 2013; BECKERT et al. 2017). Each spot is associated with a lateral tubercle; under SEM the cuticle of the spots shows irregularly arranged small knobs – each bearing a sensory bristle, which are likely mechanoreceptors (GREVEN & ZWANZIG 2013).

The function of these spots has been a matter of dispute. However, BECKERT et al. (2018) found that G and B colour values of the spots are negatively correlated with the "attractiveness" of a male to a conspecific female. Thus "redder" pronotal spots, with a higher carotenoid content, may confer an advantage in attracting a mate. To a female, this could reflect a healthier male (discussed in detail in GREVEN & ZWANZIG 2013).

It has also been remarked that the colour of a males' pronotal spots could play a role as a visual signal between males (GREVEN & ZWANZIG 2013). Perhaps an individual could convey information about its fitness to a conspecific rival. Hence, the colour of these pronotal spots would influence dominance hierarchy. The tubercles associated with these spots may also bare a resemblance to the pronotal horns possessed by other male roaches, such as *G. portentosa* (CLARK & MOORE 1994). Such processes of the pronotum may be used aggressively in the context of competition between males (summarised in BELL et al. 2007). Nevertheless, no study to date has assessed the intermale interactions of this species. Given the current understanding of the factors that influence dominance ranking in blaberid roaches, it would be interesting to see if pronotal spot colour plays a role (given that it is a characteristic unique to *Lucihormetica*). This study will investigate factors, including pronotal spot colour, that influence dominance hierarchy formation between paired adult males of *L. verrucosa*. Behaviours observed during these interactions will also be recorded.

2. Materials and Methods

2.1. Insect culture

24 individual *Lucihormetica verrucosa* males were received from a private breeder in Nuneaton,

United Kingdom. Males remained separated upon arrival, in isolated plastic containers (15 x 6 x 8 cm), for a month before experiments began. This procedure prevented males from learning about their competitive ability through interactions with other adult males, as in other blaberid roaches (Clarke & Moore 1994). Hence, when males were placed together, a dominance hierarchy would form based on whichever factors were of significance. Cockroaches were maintained at 26-28 °C on a 12:12 light:dark photoperiod, with small holes in the container for ventilation and 3 cm depth of moist coconut fibre as substrate. Specimens were fed either with a carotenoid-rich (carrots, courgette, kale) or carotenoid-poor (potatoes, parsnips, oats) diet leading to males with red spots and males with orange or yellow spots (Beckert et al. 2017). Both fresh water and food were provided *ad libitum*.

2.2. Experimental procedure

All interactions were observed under low light, during the first two hours of the dark phase of the photoperiod – since this is a nocturnal species (Greven & Zwanzig 2013). Males were assigned a partner to generate pairs. Prior to each experiment, the length (front margin of the pronotum to the genital opening) of each male was estimated in the millimetre range using a ruler, whilst the animal remained still in a "spi-pot". Care was taken to pair similarly sized males in the experiments – however, due to variation in pronotal spot colour, individuals in a pair were easily distinguished.

Male pairs to be tested were introduced into a clear glass arena (diameter 14 cm, height 16 cm) and immediately observed for 20 min (N = 12 pairs). A preliminary trial showed that males were highly aggressive, and fights began as soon as males made contact for the first time (males showed no signs of thigmotactic stress); in several instances the difference in aggression was so significant that the subordinate male had to be removed prematurely for their own safety. Since no intermale behavioural observations have been published for this species, behaviours were classified as in Clarke & Moore (1994) (see Tab. 1). The highly aggressive nature of *L. verrucosa* males made some observations difficult - the preliminary trial also showed that counting the number of agonistic behaviours exhibited by a single male (for example, as in Breed et al. 1981) was not practical, since males spent the vast majority of their time in continuous bouts of head butting. These bouts ended when one male retreated, and started when one initiated a fight. Hence, for observational purposes, each experiment was divided into series of bouts (interactions), for which there was an initiator and a retreater. The retreater was considered the "loser", and the other male the "winner". The dominant male was described as the male who "won" most interactions in the test, whilst the subordinate male was the male which retreated in most interactions (as in Gorton et al. 1979). Thus, the prevalence of behaviours was given by the number of bouts that they appeared in, not by how many times they occurred in a test. This also meant that behavioural data could not be presented in transition matrices (as in Breed et al. 1981), since behaviours were not recorded as dyads.

2.3. Colour analysis of pronotal spots

As in Beckert et al. (2018), the colour of the pronotal spots of all males involved were analysed by means of RGB values, using single images from videos and the tool "colour pipette" (radius 4) of the image-editing programme GIMP 2.8.22 (GNU Image Manipulation Programme, www.gimp.org). The "arena" was divided into 5 subareas and one photo (from the video sequence) was taken from each male in each subarea resulting in five images per male. Care was taken that the males were aligned with the upper left corner of the arena in the direction of the

overhead light source. All videos were shot from above using an Iphone 8 on a tripod. From these photos, a mean value for the Red, Green and Blue colour components for the pronotal spots of an individual were found. Firstly, a mean for each spot was found using the 5 values per spot, and then a final mean was calculated, from those values, for each colour component, per individual male (hence each male had one R, one B and one G colour value).

2.4. Data analyses

Means are given with standard errors (mean ±SE). As discussed above, each individual had single mean Red, Green and Blue values for their pronotal spots. The difference between the means of the RGB values for dominant and subordinate individuals were analysed using two sample t-tests (one for each colour component) to determine whether there was a statistically significant difference between the colour values of dominant and subordinate individuals.
In addition to this, after preliminary trials, it was decided to test whether there was a correlation between the tendency of a male to initiate a bout, and its dominance ranking, as in BREED et al. (1981). The former was defined as the proportion of bouts initiated by an individual male in the test (bouts initiated by male /total bouts in test), and dominance was indicated, as above, by the proportion of bouts won by a given male (bouts won by male /total bouts in test). The tendency of a male to initiate a bout was regarded as an indication of how aggressive the male was. The correlation between these data was analysed using Spearman's rank correlation coefficient.

3. Results

3.1. Dominance determination

The dominant male was described as the male who won most bouts, whilst the subordinate male was the male which retreated in most bouts (see above). By this definition, there was an overall winner (and therefore clear dominant individual) in every experiment. All males who exhibited submissive behaviours were of the latter category, although not all subordinate males necessarily exhibited submissive behaviours. In addition, many males immediately retreated upon contact with the other roach and thus could be considered subordinate – it was clear that they avoided the dominant individual, especially if this retreat occurred multiple times in succession. One experiment only yielded a 14.3 % difference in the proportion of bouts won between males, but in this experiment the male who lost most bouts also exhibited multiple submissive behaviours, which identified him as the subordinate male. The mean difference in the proportion of bouts won between males in a pair was 81.47±7.93% (2.d.p).

3.2. Observations of paired interactions

A total of 57 bouts was observed over 12 tests. All males exhibited agonistic behaviours at some point during a test. Only "subordinate" males exhibited submissive behaviours. Amongst agonistic behaviours (as indicated in Tab. 1), head butts (characterised by a lowering of the pronotom, accompanied by a rapid lunge/drive forward towards the opponent) were the most common behaviour, and occurred in 92.98% of all bouts. Climbing over the opponent occurred in 14.04% of all bouts. Biting was observed, but was difficult to identify, and thus the percentage occurrence is unclear. Some dominant males were also observed performing a "stilt" posture accompanied by abdomen flicks and short jumps. This unusual behaviour was observed in 12.28% of bouts. This was typically performed as the opponent was retreating (perhaps as a display of dominance), and was never exhibited by a subordinate individual. By comparison, sub-

missive behaviours included crouching (often accompanied by the dominant male clambering on top), which occurred in 12.28% of bouts. All bouts ended with one individual retreating, and began after antennation or direct bodily contact by the initiating roach. In 19.3% of the bouts, an individual was flipped over onto its back by the head butts of the other male. Interestingly, males that are flipped over continue to be attacked by the other males. Hence, a bout can only be "won" by forcing the opponent into a retreat. Given that bouts are initiated by antennation, and end when one male moves away from the other (when males are no longer in direct contact), it may be that touch is the primary stimulus for fighting, which explains why flipped over, struggling males continue to be attacked by their opponents, as long as they are still in contact.

Fig. 1: Agonistic interaction between adult males of *Lucihormetica verrucosa* . One adult male (below) head butts the other (above) (Photo: J. M. Beckert).
Abb. 1: Agonistische Interaktion zwischen erwachsenen Männchen von *Lucihormetica verrucosa* . Ein erwachsenes Männchen (unten) gibt dem anderen (oben) einen Kopfstoß (Foto: J. M. Beckert).

Tab. 1: Occurrences of behaviours observed in intermale interactions. Agonistic behaviours indicated in bold. All other behaviours are submissive. All data are from this study.
Tab. 1: Auftreten von Verhaltensweisen, die bei Interaktionen zwischen beobachtet wurden. Agonistische Verhaltensweisen fett gedruckt. Alle anderen Verhaltensweisen sind submissiv.

Behaviour	Number of bouts observed in	Proportion of bouts observed in / %
Head butt and drive forward	53	92.98
Climb over	8	14.04
Stilt posture with abdomen flicks	7	12.28
Crouch	7	12.28
Retreat	57	100
Flipped over	11	19.3
Total number of bouts = 57		

3.3. Correlation between initiation and winning

It was observed that males who were more aggressive were often the winners. These males actively moved around the arena, and thus initiated most interactions. Therefore, a test was conducted to determine whether or not there was a statistically significant correlation between the males who were most likely to initiate a bout of fighting and the males who were most likely to win a bout of fighting (the more "dominant" males). For this Spearman's rank correlation coefficient was used. It was found that there was a statistically significant positive correlation ($r = 0.797$, $p<0.001$ when $n=24$) between the proportion of bouts initiated by a male, and the proportion of bouts which that male won (as in BREED et al. 1981). It is worth noting that these data were taken irrespective of bout length – which in other blaberids has been shown to influence the advantage conferred by initiating the bout (BREED & RASMUSSEN 1980), discussed later in more detail (see Tab. 2 and Fig. 2 for data).

3.4. Colour

As in BECKERT et al. (2018), the results showed that the „Red" component always had the highest value in all males (see Tab. 3 for data). Hence, it was unlikely that a statistically significant difference between dominant and subordinate males would occur for Red values. "Red" spots reveal high Red values, but low Blue and Green values. "Yellow" spots show high Red values as well as relatively high Blue and Green values. "Orange" show intermediate Green values, but relatively high Red and Blue values. Hence, the redder the spot, the lower the Green and Blue values. The difference in spot colour between dominant and subordinate individuals in a pair was analysed using two-sample t-tests. None of the tests revealed a statistically significant difference in colour components between dominant and subordinate males (R: $t = -1.85$, $p = 0.079$; B: $t = -1.19$, $p = 0.248$; G: $t = -0.90$, $p = 0.377$). This is in line with observations during the experiments that interactions

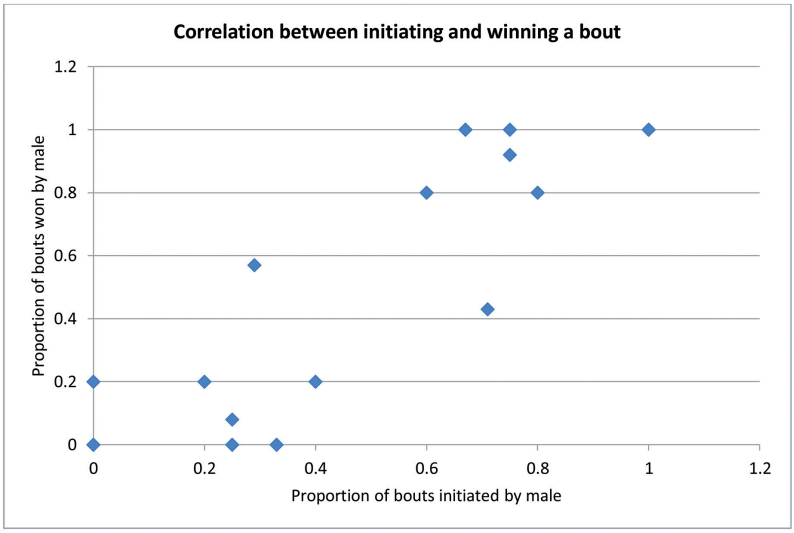

Fig. 2: Graph plotting correlation between initiating and winning a bout during the paired intermale interactions of *Lucihormetica verrucosa*.

Abb. 2: Graphische Darstellung der Korrelation zwischen dem Auslösen und dem Gewinnen eines Kampfes während der Interaktionen zweier Männchen von *Lucihormetica verrucosa*.

Tab. 2: Statistical analysis of relationship between the proportion of bouts initiated by a male, and the proportion of bouts won by a male, according to Spearman's rank correlation, where $p<0.05$ = significant.
Tab. 2: Statistische Analyse (Spearman'sche Rangkorrelation) des Verhältnisses zwischen dem Anteil der Kämpfe, die von einem Männchen begonnen wurden, und dem Anteil der Kämpfe, die von einem Männchen gewonnen wurden, mit $p<0,05$ = signifikant.

Male	Proportion of bouts initiated (1)	Proportion of bouts won (2)	Rank (1)	Rank (2)
I	0	0.2	2.5	10
II	0.67	1	15	21
III	0.67	1	15	21
IV	0.33	0	10	4
V	0.25	0	6.5	4
VI	0	0	2.5	4
VII	0.33	0	10	4
VIII	0	0	2.5	4
IX	0.4	0.2	12	10
X	1	0.8	22.5	14
XI	0.71	0.43	17	12
XII	0.75	0.92	18.5	17
XIII	0.29	0.57	8	13
XIV	1	1	22.5	21
XV	0	0	2.5	4
XVI	0.67	1	15	21
XVII	0.75	1	18.5	21
XVIII	0.25	0.08	6.5	8
XIX	0.6	0.8	13	15
XX	0.8	0.8	20	15
XXI	1	1	22.5	21
XXII	0.33	0	10	4
XXIII	0.2	0.2	5	10
XXIV	1	1	22.5	21
df = 22			r=0.797, p<0.01	

always start after antennation, rather than at a distance by visual cues. Had colour been a primary factor in determining dominance ranking, subordinate colour males may have exhibited submissive behaviours upon viewing a more „dominant-coloured" male. Instead, submissive behaviours were only performed after combat (see above). See Tab. 4 for data.
It is worth noting that the Red t-test results appear closer to a statistically significant value. However, since Red values are similarly high for all pronotal spot colours (there is a confidence limit overlap between the mean R values for subjective "orange", "yellow" and "red" spots, see Tab. 3) this is likely due to chance – particularly considering that this species may lack Red type photoreceptors (summarised in Beckert et al. 2018). The results obtained from G and B values (which vary with the "redness" of the spot) confirm that a statistically significant difference in colour is not present.

4. Discussion

This research into paired interactions provides insights into the behaviours presented by adult males of *Lucihormetica verrucosa,* as well as providing evidence for the role (or lack thereof) of factors, including pronotal spot colour, on dominance ranking. The adult males of this species are highly aggressive. This study suggests that domi-

Tab. 3: RGB-values of 24 males. Brackets indicate the colour of pronotal spots after the subjective impression of the observer. Colour data from male VIII was ignored as this male died prematurely.
Tab. 3: RGB-Werte von 24 Männchen. In Klammern ist die Farbe der Pronotum-Flecken nach dem subjektiven Eindruck des Beobachters angegeben. Die Farbdaten von Männchen VIII wurden ignoriert, da dieses Männchen vorzeitig starb.

Males	**R**	**G**	**B**
I (Red)	64.8	34.6	19
II (Red)	61.1	31.1	19.3
III (Red)	62.9	32.4	15.5
IV (Red)	74.2	41.6	17.6
V (Orange)	60.9	37.4	18.9
VI (Red)	65.5	36.4	21.9
VII (No data)			
VIII (Red)	71.3	35.4	21.3
IX (Orange)	70	39.4	21.4
X (Yellow)	63.7	39.3	23.3
XI (Yellow)	62	37.2	19.6
XII (Red)	66.6	36	21.2
XIII (Red)	67.7	34.7	19.6
XIV (Orange)	71.4	39.7	17.5
XV (Red)	65.3	34.7	20.2
XVI (Orange)	59.5	33.9	17.6
XVII (Red)	59.9	33.7	18.7
XVIII (Yellow)	73.8	52.5	31.8
XIX (Yellow)	63.3	37.6	20.2
XX (Yellow)	62.4	41.1	21.2
XXI (Yellow)	61.3	40.2	22.9
XXII (Yellow)	61.8	36.3	23.1
XXIII (Red)	69.7	35.2	18.5
XXIV (Yellow)	66.3	41.6	11.8

Tab. 4: Statistical analysis of the difference between the RGB-values of dominant and subordinate individuals in a pair, according to two sample t-tests.
Tab.4: Statistische Analyse des Unterschieds zwischen den RGB-Werten der dominanten und der untergeordneten Individuen eines Paares mit Hilfe eines Zwei-Stichproben-t-Tests .

	Pairs		Red		Blue		Green	
	Dominant	Subordinate	Dominant	Subordinate	Dominant	Subordinate	Dominant	Subordinate
1	XVI	XXII	56.46	61.79	17.57	23.11	33.89	36.28
2	XIII	XI	67.73	62.02	19.63	19.64	24.7	37.16
3	XVII	V	59.94	60.86	18.71	18.91	33.72	37.43
4	XX	XXIII	62.36	69.65	21.2	18.47	41.12	35.16
5	XIX	IX	63.33	70.04	20.19	21.38	37.64	39.41
6	X	I	63.7	64.81	23.25	18.97	39.3	34.6
7	XXIV	VI	66.28	65.5	11.84	21.85	41.58	36.44
8	II	IV	61.07	74.16	19.29	17.55	31.14	41.64
9	XXI	XV	61.31	65.28	22.945	20.15	40.17	34.72
10	XII	XVIII	66.63	73.76	21.18	31.79	35.97	52.47
11	XIV	VIII	71.4	71.33	17.53	21.25	39.68	35.4
12	*III*	*VII*						
			t=-1.85, p=0.079		t=-1.19, p=0.248		t=-0.90, p=0.377	

nance ranking in this species is not influenced by pronotal spot colour, yet is correlated with the tendency of an individual to initiate agonistic interactions – i.e. how aggressive a male is.

Males exhibit a number of agonistic behaviours seen in other blaberid roaches, including head butting. The high occurrence of head butting (relative to other agonistic behaviours) may be linked to the horn-like tubercles associated with the pronotal spots – which possess many sensory hairs, likely mechanoreceptors (Greven & Zwanzig 2013). As summarised in Bell et al. (2007), many roaches exhibit similar processes, used as arms in aggressive interactions – the tubercles of *L. verrucosa* certainly bare a resemblance to the horns of *Gromphadorhina portentosa* (Clarke & Moore 1994). However, whether or not the pronotal tubercles (or the spots themselves) are intended for this purpose cannot be concluded from these data. Many dominant individuals also exhibited a stance which is similar to the "stilt posture" observed in other studies (Clarke & Moore 1994). Many subordinate males also exhibit submissive behaviours, although both dominant and subordinate individuals exhibit agonistic behaviours. Hence, this species exhibits a repertoire of behaviours that have already been recorded in other blaberids.

Analysis of pronotal spot colour components produced similar results to those found in Beckert et al. (2018). It was previously proposed that the pronotal spots of adult males may serve roles in both intersex and intrasex communication (Greven & Zwanzig 2013). The findings of Beckert et al. (2018) show that pronotal spot colour may influence mate choice in this species. When taking the time a female needed to climb the male for the first time as a measure of attractiveness, males with redder spots (due to a diet with a higher carotenoid content) were favoured by females – perhaps since higher carotenoid content reflects a healthier male (Greven & Zwanzig 2013). However, when analysed with two sample t-tests, no statistically significant difference between any of the colour values of dominant and subordinate males was found. Hence, it is likely that pronotal spot colour is not a significant factor in determining male dominance rank in this species. This is also supported by observations of intermale interactions, in that every bout of fighting between conspecific males is initiated by either antennation or by other bodily contact, suggesting that visual cues do not play a large role in stimulating an interaction. Males that exhibited submissive behaviours performed them during, or after, interactions (see results). No males were observed to act "submissive" upon viewing a redder spot colour (or vice versa) from a distance. This was confirmed by the results of the t-test (see above).

This study also found that there was a statistically significant positive correlation between the proportion of bouts that an individual initiated, and the proportion of bouts that an individual won – as found for *G. portentosa* in Breed et al. (1981) and for *Periplaneta americana* in Breed & Rasmussen (1980). An individual that initiates a large proportion of bouts may be regarded as more aggressive. Since the dominant individuals in this experiment are considered those with the highest proportion of wins in a test, this suggests that dominance ranking is influenced by how aggressive the individual is (more exactly, how likely that individual is to initiate an interaction with an opponent). This appears in agreement with the highly aggressive nature of the males. Both studies mentioned above (Breed et al. 1981; Breed & Rasmussen 1980) also noted that as the number of dyads (length) of a bout increases, the advantage conferred by initiating the bout is reversed – so that the advantage is held by the responder in longer bouts (bouts with a greater number of dyads). Due to the continuous aggressive fighting during the

bouts in this species, it was not possible to record results as a series of dyadic interactions (see method), and so it is worth noting that the values for the correlation between initiating a bout and winning the bout are taken irrespective of the bout length. It is also worth noting that a limitation of this study is that the effect of male size is not investigated. Whether or not dominance ranking influences mating success, or influences access to resources such as food or shelter, is not known for this species. Hence, although it is clear that the interactions between adult males of *L. verrucosa* involve behaviours described in other species of roaches, and that their dominance hierarchy is likely not influenced by pronotal spot colour, but by the initiating male (as in other blaberids), how these factors ultimately impact the lives of adult males is unknown, and will require further study. Studies on similarly aggressive blaberid roaches, such as *G. portentosa*, have shown that females can show a preference for more dominant males via chemical cues (LEIBENSPERGER et al. 1985). Dominant adult males of *Eublaberus posticus* have been shown to exhibit territoriality and control refugia (GORTON et al. 1979). It is possible that, belonging to the same family and being highly aggressive, dominance ranking in *L. verrucosa* could also confer such advantages. Hence a more aggressive male might be able to increase its chances of mating or gain better access to food. However, this cannot be concluded from these data.

Furthermore, in this study pairs of interactions, rather than interactions within groups, were studied. This meant that suitable t-tests could be conducted to assess the role of pronotal spot colour in paired interactions. Although it is unlikely that pronotal spot colour will affect dominance ranking differently at higher male densities, this cannot be concluded from these data. Smaller groups may also be insufficient to establish a stable hierarchy, and types of agonistic interactions may change as stable dominance hierarchies are established (BELL & GORTON 1978). In other blaberid roaches, increasing group density may increase the frequency of certain agonistic behaviours, but not others (CLARKE & MOORE 1994). The group interactions of *L. verrucosa* have not been formally studied in a natural environment, nor have stable dominance hierarchies in large groups been studied in captivity. It is unknown whether males control refugia. Other blaberid roaches may control refugia, becoming increasingly site specific with increasing group densities (GORTON et al. 1979). In larger groups, there may be disproportionally higher costs for aggressiveness – for example, in E. *posticus* a trade off between control of refugia and mating privileges exists at higher densities (GORTON et al. 1979). To study agonistic behaviours in *L. verrucosa* within a natural context, intermale interactions in larger groups should be studied, in a more natural environment.

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