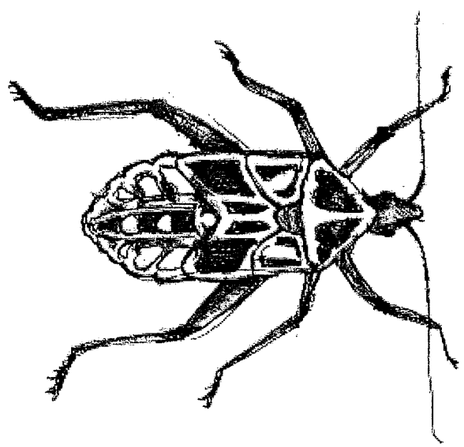
Literature Cited

Brown, A. C., J. S. Veysey, B. R. Arnold, and S. E Laplante. 2000. Sexual selection or wind dispersal? Alternate explanations for the evolution of gigantism in *Dahlia* sp. (Asteraceae). Pp. 71 - 74. *in* L. E. Aucoin, M. N. Conte and J. A. Macintosh, eds. Dartmouth Studies in Tropical Ecology. Dartmouth College, Hanover, NH.

Lief, G. M., S. E. Kopplin, A. C. Rutherford and A. M. Shumate. 1996. Gigantism as a product of sexual selection in *Senecio* sp. Pp. 62 - 64 *in* A. L. Mannan and D. S. Canny, eds. Dartmouth Studies in Tropical Ecology. Dartmouth College, Hanover, NH.



Social structure, parental care and communication in passalid beetles

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Abstract: Passalid beetles are reported to have some degree of sociality, but little is known about the role or degree of their social behavior. We studied social structure, parental care and communication in one species of Passalidae that occurs in the high elevation oak forests of Costa Rica. Groups, which appeared to be family units, varied in number from one to fourteen individuals, consisting of adults, larvae and callow adults. Larvae were never found alone. Both sexes were found with young and both sexes seemed capable of making stridulation sounds. Adults did not return to their larvae in a separation experiment, implying that passalids do not actively protect young. Adults did not respond to stridulation of other adults with any obvious directional movements, but they sometimes appeared to respond by stridulating themselves (apparently reciprocal communication). Many other species were associated with passalids in logs; passalids seem to accelerate decomposition processes and contribute to biodiversity.

Key Words: Coleoptera, keystone species, sociality, stridulation, subsocial, wood-borer

Introduction

Eusocial insects such as ants, wasps and termites are among the most numerous and diverse groups in the animal kingdom, suggesting that sociality confers ecological benefits. Sociality is rare among the Coleoptera, but one family, Passalidae, is known to live with and feed their young (Borror and DeLong 1964). Parental care is regarded as the most ancestral form of sociality, defining the subsocial insects (Choe 1989); the benefits for young may include increased protection, resource procurement and learning. However, the precise degree of sociality in passalids is unknown and may exceed simple parental care. Passalids stridulate when disturbed, and it has been suggested that stridulation in other insects is a form of communication (Borror and DeLong 1964). If so, passalid sociality may be more advanced than previously thought, with individuals sharing information about resources, danger or aggression. To elucidate the degree of sociality in passalids, we investigated family group structure, parental care and communication in a common species within the high elevation oak forests of Costa Rica.

We hypothesized that passalid sociality consists of two major components: parental care and communication through stridulation. We predicted that passalids would occur in family groups consisting of a few adults and dependent larvae, and that parental care would include guarding larvae and attempting to reunite with larvae when separated. Stridulation could be a recruitment call, and, if true, we would expect adults to move towards stridulation calls. Alternatively, stridulations could be a signal of intraspecific aggression or a predator alert. Stridulation calls could be individually specific (e.g., with unique frequency, amplitude and duration signatures), or content specific (e.g., with disturbed beetles having different calls than undisturbed beetles).

Methods

We studied a species of wood-boring beetle (Coleoptera: Passalidae) common in the high elevation oak-bamboo forest of Cuerici Biological Station, San Jose Province, Costa Rica. On 26 – 27 January 2002, we collected beetles from decaying logs along the Mirador trail. We measured the mass and length of each individual, and head capsule width for larvae. Adults with a reddish-colored, softer exoskeleton were classified as callow adults.

We examined the response of adult passalid beetles to separation from their larvae with a choice test experiment. In 15

trials, a leaf with a larva and a control leaf were placed 40 cm apart, and an adult passalid from the same family was placed between them, perpendicular to the axis. We placed a hollowed-out half-log over this configuration, waited 10 min, and then recorded the position of the adult along the axis between larva and control leaf. A movement towards or away from the larvae was analyzed as a choice for or against the larvae. We used a chi-square test to determine whether the direction of beetle movement was nonrandom.

The response of passalid beetles to stridulation calls was also measured with a choice test experiment. A 40 x 40 cm open cardboard box was filled with a thin layer of organic matter and separated into halves with an imaginary line along the diagonal axis from one corner to the opposite corner. In opposite corners we placed 3 x 3 cm open boxes, one to hold an adult beetle and one as an empty control. We were unable to control for family status of beetles because of small sample size. We disturbed the enclosed beetle by blowing or gently prodding to make it stridulate as often as possible during the experiment. In 14 trials, an adult was placed in the center of the box and observed for 5 min while the enclosed beetle stridulated. After 5 min, we recorded its location as on the control side of the box, the call side or still in the center (within 2 cm).

We dissected and sexed 4 adult passalid beetles, 2 that stridulated and 2 that did not. We used a bat detector (Pettersson D240X) and SonoBat software to analyze 4 sequences of stridulations from solitary disturbed (by prodding and blowing) individuals, one sequence of calls between 2 undisturbed individuals, and 3 call sequences between disturbed pairs. The duration, frequency and amplitude of stridulations were compared to examine differences in call complexity.

Results

We found 12 logs occupied by a total of 62 beetles: 23 adults, 3 callow adults and 36 larvae. Groups within a gallery (putative families) consisted of either adults or of adults with larvae, but never of larvae alone. Group size varied from 1 - 14 individuals, and one group also had 15 eggs (Table 1). Typically all the larvae in a group were clustered together in an area of soft, well-chewed wood, while the adult(s) were several centimeters away in harder, more solid wood (Fig. 1). Nearly all adults and some of the larger larvae carried mites. Other invertebrates such as arachnids, thysanurans, beetles, harvestmen, termites, centipedes and millipedes occupied the same galleries as the passalids.

Larvae within a family group varied in

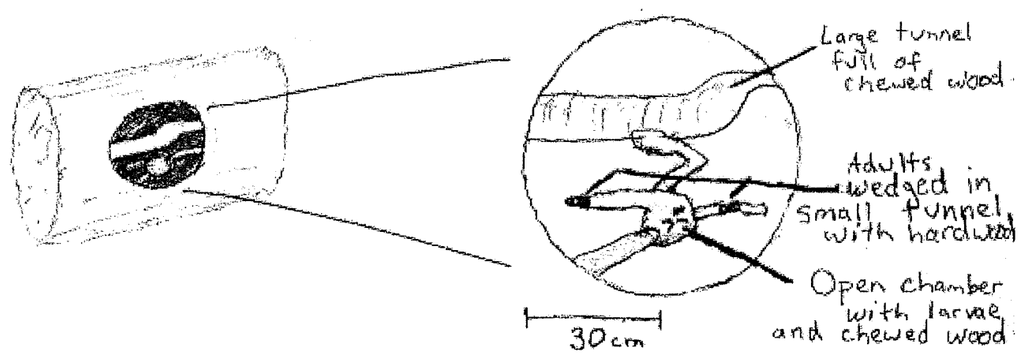

FIG. 1. Diagram of a typical passalid gallery within a decomposing log.

TABLE 1. Number of individuals by developmental stage within 12 groups (putative families) that were aggregated in galleries within 12 different logs.

Family	Adults	Callow adults	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Eggs	Total
A	1								1
B	1								1
C	2				1				3
D	1	2			1*				3
E	1					2			3
F	3								3
G	1				1		1		3
H	3								3
I	3				5	2			10
J	2		1	1	2	3			9
K	2			3	1	3			9
L	3	1	1	1	2	5	1	15	14
Totals	23	3	2	5	13	15	2		62
Mean head capsule width ± SE			0.5	1.34 ± 0.09	2.52 ± 0.06	3.34 ± 0.04	4.6 ± 0.1		

*larva lost before size class was determined.

size, indicating that several broods were being raised together. Larval head capsule width fell into five distinct classes, defining five larval instars (Fig. 2; Table 1). Larval mass (g) was related to larval length (mm) as mass = $0.00209 * (1.258)^{length}$; $r^2 = 0.94$. Larvae were unusual for Coleoptera in that their 2 hind legs are greatly reduced and have almost certainly lost their function in locomotion.

In the larval separation choice experiment, 9 of 12 adult beetles moved in the direction of their larva, but this result was not significant ($\chi^2 = 3$, df = 1, P = 0.08; excluding the 3 adults that did not move). The calling response experiment provided no evidence that movement of adult beetles is influenced by a calling adult in the vicinity: the test beetle moved towards the enclosed stridulating beetle 3 times, moved away 2 times and remained in the middle 9 times. We were unable to statistically analyze these results due to the small sample size. It appeared that the test beetles often responded to stridulation by stridulating themselves, but we were unable to quantify this behavior.

Only 2 of 23 adults were never observed stridulating. We determined through dissection that the two non-stridulating adults were a male and a female (distinguishable by observing the reproductive structure within the abdomen - male identifiable by large aedeagus and dark colored connective [tuning fork-like structure]; female identifiable by short ovipositor and small white ovaries.) Both of the stridulating beetles we dissected were males. Stridulation calls of 4 individuals, analyzed using SonoBat, were all between 15 and 18 kHz in frequency and 250 – 400 msec in duration (sound files have been archived on the course computer as Passalid.stridulate.wav.). We saw no consistent difference in call frequency or duration between natural calls

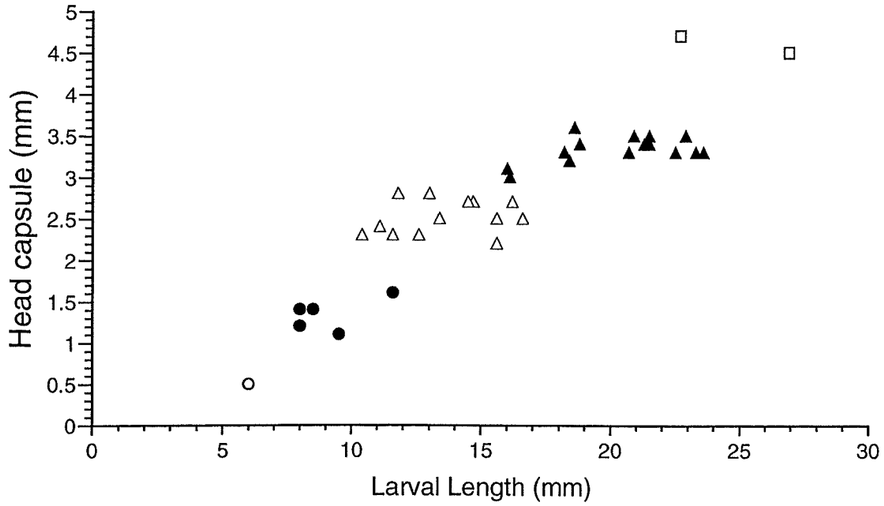

FIG. 2. Larval length versus head capsule width in a species of passalid beetle. Clustering around head capsule lengths indicates the five putative instars.

and calls in response to human disturbance. Individuals were not recognizable by call frequency or duration, but alternating calls between individuals (appearing to be reciprocal communication) were distinguishable by duration and amplitude.

Discussion

The make-up of passalid groups was consistent with the structure of an immediate family. Most groups had multiple age classes of larvae associated with 1 - 3 adults in a gallery. It is possible that groups consist of more than one family or that larvae occurring together have only one common parent; bringing tissue samples to the lab would permit tests of relatedness. Although we never observed adults feeding young, the apparent obligate association of larvae with adults and the low mobility of larvae (due in part to greatly reduced hindlegs) supports the parental care hypothesis. Callow adults were also found with larvae. This suggests that older siblings could be feeding young, an advanced social behavior that is more characteristic of the eusocial insects (Wilson 1971). However, sociality for passalids may not include protection of young. Adults did not obviously tend to move towards their stranded and presumably vulnerable larvae. The costs of protection may outweigh the benefits, especially if only one larva, as in our experiment, is at risk. If passalids are long-lived, then an adult with high reproductive value might not exhibit a great degree of protection. Alternatively, passalids may lack the sensory and/or behavioral repertoire to aid separated larvae even though it would enhance their fitness if they could. It is also possible that larvae in nature never become separated from their group, in which case there would be no selection for adults to aid separated larvae.

Adult beetles appeared to interact (communicate) via reciprocal stridulating, which would support the hypothesis that sociality in passalids extends beyond feeding the young. Unfortunately, we were unable to quantify this behavior or develop a statistical test of the hypothesis that the calls coincided only by chance. Apparently, both sexes stridulate, as 21 of 23 beetles stridulated; however, more beetles must be sexed to substantiate this claim. We were unable to acquire evidence that the calls function in recruitment or aggression, perhaps because they do not perform

such functions or because the beetles were too removed from their natural settings.

Passalids, including our focal species and a second, larger species, were the most commonly observed Coleoptera in decomposing logs in the high elevation oak forest, suggesting that they play a significant role in the decomposition of coarse woody debris. In the 12 logs that we examined closely, passalids were also the only beetle that formed extensive galleries in the xylem. These galleries appeared to greatly increase the rate of decomposition, both through direct chewing by the passalids and by indirectly enabling fungi and other animals to penetrate and colonize the wood. Logs colonized by passalids and their associated organisms might follow a different decomposition trajectory, with different rates of carbon flux and nutrient release, than logs without passalids. Furthermore, passalids appear to create habitat for many other species of insects, mites and other invertebrates; they might be legitimately regarded as keystone species.

Our results raise some new questions about passalid sociality. Studies of whether parents would feed young of another family and whether siblings may feed larvae, would provide insights into the nature of passalid social systems. Future studies could also compare responses to the calls of family and non-family beetles and determine whether communication by stridulation is restricted to adults or also occurs between adults and larvae. Passalids provide a unique opportunity for studying the evolution of sociality in a group where it has arisen independently of the Hymenoptera and Isoptera that have been the subject of most research into insect sociality.

Literature Cited

Borror, D. J. and D. M. DeLong. 1964. Family Passalidae Pp. 309 - 310 *in* An introduction to the study of insects. New York, NY: Holt, Rinehart and Winston.

Choe, J. C. 1989. Maternal care in *Labidomera suturella chevrolat* (Coleoptera: Chrysomelidae: Chrysomelinae) from Costa Rica. *Psyche* 96: 63 - 67.

Wilson, E. O. 1971. *The Insect Societies*. Cambridge, MA: Harvard University Press.