in astigmatism, the interval between the focal lines is never in focus.

We have not found any nonastigmatic subjects who showed significant vertical-horizontal resolution differences. However, not all of our astigmatic subjects exhibited the substantial resolution imparities noted above. This is not surprising considering the nonstatic nature of the eye's effective refractive state. By virtue of accommodation or changes in observation distance, the eye can receive focused input over a considerable range of distance in visual space. In most cases of astigmatism, the meridian that is blurred by unaccommodated distant observation can be brought into focus by accommodation or by a change in viewing distance. The extent to which this will occur depends on the nature and amount of the astigmatism (*8*). These considerations suggest that, for astigmatic subjects with only the normal reduction in resolution of the oblique orientation, the frequency with which each meridian was brought into focus during development of the visual system was sufficient to prevent neural consequences.

Our supposition that ocular astigmatism can alter neuronal connections requires that the astigmatic condition was present during the "critical period" of the development of the visual system (*9*). Although we cannot be sure that this holds for our subjects, considerable clinical evidence makes the likelihood high (*10*). Even so, an alternate explanation could also account for meridional resolution differences. The differences could be explained if there were anomalous structural asymmetries in the retina or visual pathways of astigmatic eyes that developed totally independently of visual input. If this were the case, our findings would require that minimal resolution and maximal image blur occur along the same axis. While the possibility cannot be eliminated, we know of no evidence in its favor.

On the other hand, a number of investigations have shown that, if visual form is absent during development of the nervous system, the receptive fields and synaptic properties of cortical neurons and the morphology of lateral geniculate cells can be markedly altered (*9, 11*). At the cortical level, the physiological effect of monocular deprivation is considerable, but if both eyes are visually deprived the effect is minimal (*12*). This implies that consequences of deprivation depend on interactions between sets of afferents from both eyes. The experiments with a controlled visual environment, described earlier, suggest that meridional afferent interactions are also important (*13*). These studies, in conjunction with our findings, are consistent with the view that modifications in neural connections, induced by astigmatism, are responsible for meridional resolution anisotropies.

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5. The refractive errors for the subjects shown are as follows: D.A., −3.75 −3.75 × 170; D.M., +1.50 −2.75 × 180; H.F., +2.75 −4.25 × 2; and A.C., +4.50 −5.00 × 180.
6. For a review of studies on target orientation and visual resolution, see M. M. Taylor, *J. Opt. Soc. Amer.* **53**, 763 (1963).
7. The method was a modification of the technique described in (*3*). Modulation sensitivity is a measure of the ability to detect differences in contrast between alternate bars of a grating.
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14. We thank G. Haegerstrom for help with the experiments. Supported in part by NIH Biomedical Sciences Support grant FR-7006 to R.D.F. and National Research Council of Canada grant APA 7660 to D.E.M.

13 September 1971; revised 16 December 1971 ■

Sound Production in Scolytidae: Chemostimulus of Sonic Signal by the Douglas-Fir Beetle

Abstract. *Stridulation by male* Dendroctonus pseudotsugae *was recorded in response to the natural female attractant (frass) or to three synthetic components of the attractant (frontalin, 3-methyl-2-cyclohexen-1-one, and* trans-*verbenol). This stridulation was acoustically distinct from stress sound and correlated with known attraction behavior. The response of female* D. pseudotsugae *to male stridulation—negation of her attraction—was induced by playback of recorded attractant stridulation but not by that of stress sounds. Acoustic communication must be more important in scolytid behavior than it was heretofore believed to be.*

Although many bark and timber beetles (Scolytidae) stridulate, or produce sound by friction of body surfaces (*1, 2*), there are few behavioral studies of this phenomenon; research has centered on the strong chemical signals of these insects. Stridulatory organs have been recognized in only that sex that does not select the host tree (*1, 2*), and Barr proposed that the function of this sound is to announce the arrival of the stridulating sex to the host-finding, gallery-initiating sex (*1*). With two North American *Ips* species, stridulation is necessary for natural entrance into the gallery of the opposite sex (*1–3*).

In field studies with *Dendroctonus pseudotsugae*, Rudinsky (*4*) found that stridulation by the male beetle at the entrance of the gallery of an attractive female induced the female inside the bark to quickly and entirely negate her chemical attraction for flying beetles.

Such an interaction of sonically and chemically induced behavior was not known in any species and was least expected in Coleoptera, since sound production in this order is generally considered to be rudimentary and to have evolved late (*5*). We have induced this behavior of *D. pseudotsugae* in the laboratory, in the first demonstration with insects of sonic response to chemical stimulus and consequent chemical response.

Since scolytids are known to stridulate in various situations, we looked for distinctive sounds by electronic recording techniques that are used especially with Orthoptera (*6*). Earlier, Allen *et al.* (*7*) recorded sounds inside the bark during gallery construction by *D. pseudotsugae*, and Wilkinson *et al.* (*3*) reported differences in the speed of stridulation during stress and courtship of *Ips calligraphus* (Germar).

Sounds were recorded with a condenser microphone, a low-noise preamplifier, and an instrumentation tape recorder (*8*). The microphone free-field response was rated flat within 1 db over the frequency range of 20 hz to 25 khz, and tests indicated useful response with negligible resonance to frequencies greater than 40 khz. The preamplifier bandwidth was set with a lower limit of 300 hz to minimize stray acoustic noise and an upper limit of 100 khz. The tape recorder was operated at 152 cm/sec in the frequency modulation mode to achieve maximum bandwidth yet permit time scaling for signal recovery. The recorder bandwidth under these conditions was 0 to 25 khz, and noticeable distortion in the form of ringing occurred for strong signal components with frequencies significantly greater than 25 khz. Although oscillograms indicated major signal energy at frequencies approaching 10 khz with harmonic components well above this range, we believe that the bandwidth limitations of the equipment did not significantly influence the waveform properties that we analyzed.

The amplifier gain setting ranged from 60 to 70 db, depending on the proximity of the specimen, to produce a peak output of about 1 volt. The microphone sensitivity was −60 db referenced to 1 volt/μbar, which indicates a peak sound pressure level of about 1 μbar at about 1 cm from the insect.

Oscillograms were recorded (*9*) by first establishing a cueing track on the tape to initiate a single oscilloscope sweep just before signal onset. Polaroid photographs of temporally distributed chirps were made at a tape speed of 19 cm/sec.

Beetles tested for both sound production and response came from naturally infested Douglas-fir logs from western Oregon, which were stored at 4°C and brought to beetle emergence temperature as described (*10*). At least three to five healthy individuals were recorded sequentially in each test situation. Stress stridulation was recorded while the beetle's head and thorax were held by the thumb and forefinger about 1 cm from the microphone. Premating stridulation was recorded both when the male was at the entrance of a female gallery inside the bark of a 50-cm log section (the microphone was 1 cm above the gallery entrance) and when the male was alone but was stimulated by natural and synthetic attractants in the olfactory walkway (*10*). This walkway, which was used for bioassay during pheromone identification studies (*11, 12*), was devised to simulate the gallery entrance of an attractive female (*10*). The walkway was 35 cm long and had a recessed, screened opening for a glass vial of the test compound, over which the male beetle would walk or would stop in the arrestment response (*13*). This response was known from field observation of male approach to the female gallery.

The arrested males that stridulated were counted without regard to differences in sounds, such as increases in

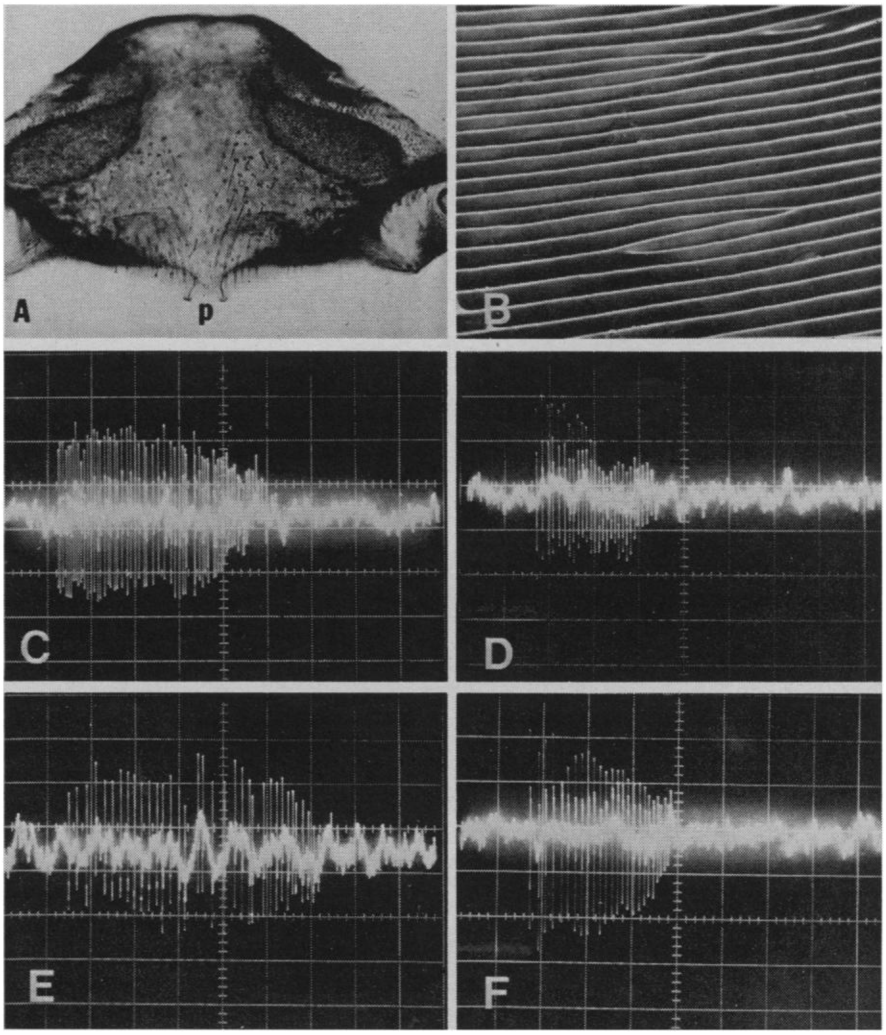

Fig. 1. Stridulatory organ of male *D. pseudotsugae* and oscillograms of stridulation. On the oscillograms (C–F), sound pressure is the ordinate and time (12.5 msec/division) is the abscissa. (A) Micrograph of the seventh abdominal tergite with paired processes (*p*) on the posterior margin which serve as the plectrum (× 62). (B) Scanning electron micrograph of the file of parallel, transverse ridges or teeth on the ventral surface toward the suture and apex of the left elytron. These teeth serve as the pars stridens (× 740). (C) A typical stress chirp of a male beetle held in hand (17 October 1970; 18°C). (D) A typical chirp of a male near attractive female frass (17 October 1970; 18°C). (E) A typical chirp of a male near a live female in attractive frass (13 March 1971; 18°C). (F) A typical chirp of a male near synthetic components of female's attractant (17 October 1970; 18°C).

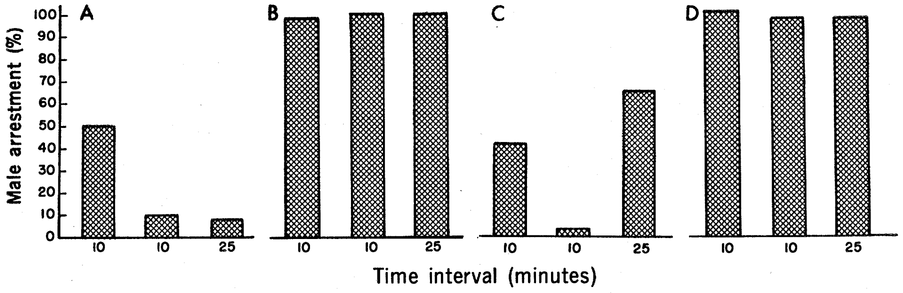

Fig. 2. Response of female *D. pseudotsugae* to male stridulation. This response, in which the female nullifies her attractiveness and that of the surrounding frass, is shown by the failure of male beetles to stop at her gallery entry in a log. The tests were run for 45 minutes; the bars show percentage of tested males that stopped at the gallery entrance in minutes 1 to 10, 11 to 20, and 21 to 45. (A) Normal males were used; their stridulation was the sound stimulus. (B) Silenced males were used; there was no sound stimulus. (C) Silenced males were used; playback of recorded sound made by normal males near a female's gallery was the sound stimulus. (D) Silenced males were used; sound stimulus was playback of stress sounds made by normal males when they were held. These experiments were repeated three times (four with the playback of male sound at the female gallery); each replicate used 40 to 60 fresh males and a new female.

volume or number of chirps before pauses. The number of responses is considered minimal since only naturally audible sounds were included, and control tests with earphones or an oscilloscope showed a general 7 to 8 percent increase in totals. Slow, gentle handling and separate testing of each beetle prevented confusion between stridulation caused by stress and that caused by female attractant, especially since only the latter was accompanied by the typical arrestment behavior. Beetles that fell on their backs and stridulated were not counted or were tested again later.

For statistical analysis of variance in the properties of male stridulation, ten photographs each for stridulation caused by hand pressure, female frass, synthetic attractants, and a live female in a log were selected at random from more than 4000 chirps recorded on tapes. These four kinds of stridulation were then analyzed by number of tooth-strikes per chirp, duration of chirp, and number of tooth strikes per second. Other characteristics were not analyzed; instead, behavior tests were used to determine whether the different sounds functioned as signals.

In the stridulatory organ of male *D. pseudotsugae* (Fig. 1, A and B), two processes on the median posterior margin of the seventh abdominal tergite strike a file of ridges or teeth on the left elytron (*14*). Teeth were counted on the files of 20 beetles; the number of teeth per file was 87 to 137 and the average was 110. When the beetle was held by the head and thorax and observed at ×90 magnification, the stridulatory movement appeared to be slightly upward, back, and downward as the processes struck the file. Sound occurs only on the downward push, not on the retraction of the abdominal segment, and one movement corresponds to one chirp.

When oscillograms of typical sounds evoked by stress (Fig. 1C) and by the frass of an attractive female (Fig. 1D) are compared, significant differences in the sound properties are seen (*15*).

Table 1. Response of 60 unfed male *D. pseudotsugae* to synthetic attractants in the olfactory walkway. Attractant components are: A, 99.5 percent frontalin; B, 3-methyl-2-cyclohexen-1-one (technical grade); C, 95 percent *trans*-verbenol; fresh Douglas-fir resin; and camphene (technical grade). All substances were diluted to indicated percentages in 95 percent ethanol.

Attractant components	Number of beetles that:	
	Stopped	Stridulated
Complete attractant (♀ frass)	60	59
Resin, A, B, and C	49	37
Camphene, A, B, and C	26	15
Resin, A, and B	43	35
Resin, A, and C	42	26
Resin, B, and C	14	4
Camphene, A, and B	32	21
Camphene, A, and C	45	40
Camphene, B, and C	5	0
A, B, and C	29	16
A and B	28	14
A and C	24	4
B and C	2	1
Resin and A	34	13
Resin and B	30	15
Resin and C	19	5
Camphene and A	30	10
Camphene and B	22	11
Camphene and C	5	0
Resin, 0.01 percent	17	3
Camphene, 0.001 percent	15	1
A, 0.01 percent	17	1
B, 0.001 percent	15	5
C, 0.001 percent	13	1
Ethanol (control)	0	0

The distinctiveness of the sound response of the male to female attractant supports the earlier belief that stridulation is a critical part of male attraction behavior (*4*). Therefore we attempted to duplicate the sound with synthetic attractants. Scolytid pheromones often comprise several substances, and in *D. pseudotsugae* there are at least five (*11*). The three identified components are 1,5-dimethyl-6,8-dioxabicyclo[3.2.1]octane (frontalin) (*11*, *16*), 3-methyl-2-cyclohexen-1-one (*11*), and *trans*-verbenol (*12*). We used these three components and the monoterpene camphene, a known host attractant (*17*, *18*), to evoke male stridulation (Fig. 1F). For the properties tested there were no significant differences (that is, differences for which $P > .01$) between stridulation evoked by these substances and that evoked by the natural attractant, female frass. However, when the male was stridulating over a live female in attractive frass (Fig. 1E), significantly more teeth were struck and the chirp was longer, but the rate was the same. This difference may reflect some unidentified chemical not in the frass, tactile stimulus of the log compared to that of the smooth walkway, or a nonchemical interaction between male and female.

Further evidence that this male sound is not an incidental response to the female's attractant is the fact that it occurred with almost 100 percent of the males arrested at attractive frass and up to 88 percent of males arrested at various incomplete combinations of synthetic attractants (Table 1). The difference between totals for arrestment and stridulations might have resulted from the absence of unidentified components or of the tactile stimuli or other stimuli of the entry hole in bark. All established characteristics of the response of bark beetles to attractants are reflected in the stridulation data (at the statistical confidence level of .05), especially the synergism of multicomponent attractants (*19*) and of host substances. Extensive field tests of these same compounds confirm our results, especially the strong response to frontalin in all combinations, the synergistic effect of *trans*-verbenol and camphene with frontalin, and the low response to most combinations without frontalin (*20*). It had seemed likely that only one component or a single combination of components would evoke sound. However, if male stridulation announces the male presence to the female inside the bark [as Barr suggested (*1*)], there is survival value in variability of the chemical stimulus, since both the female beetle and the host tree show individual variations in the quantities of attractants that they release.

These results demonstrate that the male *D. pseudotsugae* stridulates in response to the chemostimulus of the female attractant, but the male sound cannot be called a signal unless communication occurs. For proof that the female responds, we induced the effect, known from field tests (*4*), in which the stridulation of male beetles over the screened entries of female galleries in the bark caused the female to nullify or mask her attractiveness to flying beetles (*21*).

The female's response to various sounds, live and recorded, was inferred from the behavior of a series of males, each of which either passed by the entrance to her gallery or stopped by it. Each female was tested separately in a log section, and each was checked for attractiveness and the ability to nullify or mask her attraction. In tests in which playback of male sound was used, the males were silenced by excision of their sound organs (*4*) so that they could not evoke or maintain the mask by their own stridulation. A ceramic disk (*22*), 5.1 cm in diameter and 0.6 cm thick, was used as a transducer. The disk was excited, in the thickness expander mode, to a peak voltage of 10 to 15 volts by a power-supply amplifier (*23*). During playback the disk was mounted in a groove in the bark adjacent to the gallery, its axis perpendicular to the log to allow observation of the male beetles.

The fidelity of sound reproduction at the location of the female in the gallery was not determined. However, the frequency response of the transducer was characterized by the de-emphasis of low frequencies and by resonances throughout the audio spectrum, which varied according to the details of mounting, with the major resonance near 40 khz. The oscilloscope displays and direct auditory monitoring of playback both indicated signal parameters consistent with those used for statistical comparison. Therefore, that the female's response was phonokinesis instead of natural behavior seemed unlikely.

The female's response was induced first by the actual stridulations (not recorded) of normal male beetles nearby, but was not induced by silenced males that were similarly arrested. When the attractant was masked, males showed no repellancy behavior (that is, they did not turn back toward the release point), and they frequently hesitated briefly at the attractant before passing on. No "digging" or klinotaxis occurred. The same behavior was induced by playback of the recorded sounds of a male beetle over the gallery of an attractive female but not by playback of recorded male stress sounds (Fig. 2). Exact time trials were not made, but when stridulation was almost continuous for 2 to 3 minutes the female's lack of attraction became evident a few minutes later (the next males passed without stopping). As was found in field studies (*4*) male sound stimulus appeared to be necessary to maintain the female response as well as to evoke it when the male was kept outside the gallery. After the playback ended, no arrestment occurred for the first 9 to 14 minutes of silence, but then the female apparently stopped the mask. Normal males occasionally stopped and stridulated throughout the tests, presumably because of individual variation in response threshold. Such occasional sound may have served to maintain the female response through the otherwise silent period, since the mask continued longer than it did in experiments with playback and silenced males. Tests were run only 45 minutes, and sound stimulus alone might not suffice to maintain the female response for longer periods.

In nature the male was found to enter the gallery and reach the female fairly soon, and also to stridulate inside the gallery (*7*). Repeated tests confirm the report (*4*) that the female response can occur without stridulation when a silenced male is allowed to contact the female in the gallery.

Two implications of these studies may be clear. (i) Stridulation could be a criterion of olfactory response in bioassay of scolytid attractants and might shed light upon differences between aggregative and sexual aspects of these attractants, which so far are scarcely distinguished. (ii) The soft sounds produced in Scolytidae are short-range signals, and the only long-range signals that are effective in forest terrain must be the chemical ones. However, control and regulation of the attractants—including the duration of their production or release or both, as well as the triggering of masks, inhibitors, or repellants—occur within the aggregated population, where short-range acoustic signals are effective. Busnel (*24*) has called attention to both (i) the likelihood that a repertoire of low-intensity sound signals will evolve wherever high population density gives them survival value and (ii) the relative importance that acoustic signals have in the hierarchy of animal communication because of their speed, their equidistant transmission in all directions from the source, their impermanence unless repeated, and their relatively great codification. Like chemical signals they may be "primers" as well as "releasers" and may therefore explain certain physiological puzzles inherent to attempts to explain scolytid aggregation wholly as a series of olfactory mechanisms (*25*). The severe environmental damage caused by destructive scolytid beetles dictates that we intensify our study of sonic signals in their aggregation and colonization behavior (*26*).

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5 October 1971

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Altruistic Behavior in a Sphecid Wasp: Support for Kin-Selection Theory

Abstract. Trigonopsis cameronii *females often work in groups of up to four individuals on single nests, and because of inbreeding and a tendency to return to the mother nest, nestmates are likely to be highly related. The altruistic behavior associated with group living, most notably the failure to steal prey from nestmates, can thus be explained by kin-selection theory.*

Sociality has evolved independently at least 11 times in the order Hymenoptera (*1*, *2*), but the only known social species in the family Sphecidae is in the genus *Microstigmus* (Pemphredoninae) (*2*). In this report the behavior of a second, apparently independently social sphecid, *Trigonopsis cameronii* Kohl (Sphecinae) (*3*), is described, and it is shown that, as predicted by Hamilton's kin-selection theory (*4*), altruistic behavior associated with sociality is maintained in this species within groups of highly related individuals.

A *T. cameronii* female spends from about ½ to 1½ days building or renovating a cylindrical mud cell (renovation was always shorter than construction). She then captures and paralyzes a cockroach and carries it to her nest, lays an egg on it, places it in the cell, and closes the cell with a mud cap. After spending 1 to 3 relatively inactive days on the nest, she opens the cell, and over the next 1 to 7 days she adds more paralyzed roaches. Foraging for roaches occurs only from about 8 a.m. to 3 p.m. (the "work day"), and the wasp closes the cell at the end of each day's foraging, to open it at the beginning of the next work day. When the cell is sufficiently full (the number of roaches varied with their size, and was usually between 7 and 14), the female closes it and begins another. The egg in the cell hatches about 2 days after it is laid, and the larva consumes the roaches provided by its mother, pupates, and emerges as an adult about 50 days after the original oviposition. Males rest on groups of cells during the work day and mate with females as they emerge.

Nests occurred in sheltered, at least somewhat humid sites, such as under overhanging boulders at the edges of streams, and contained up to 130 cells. From one to four females were found working on cells in a given nest. The females almost always concentrated their building and foraging efforts on their own cells, but in certain situations they performed relatively minor behavior benefiting nestmates. They actively repelled ants on or near the nest (males also chased ants from nests). Females which had constructed new cells often added mud to the sides and back of the nest during the work days between oviposition and provisioning, and although most of this material was added to the wasp's own cell, some was added to others. Holes in cells containing pupae, occasionally caused by a female taking dirt from such a cell to close or renovate her own, were closed, sometimes by the female which caused the damage and sometimes by others.

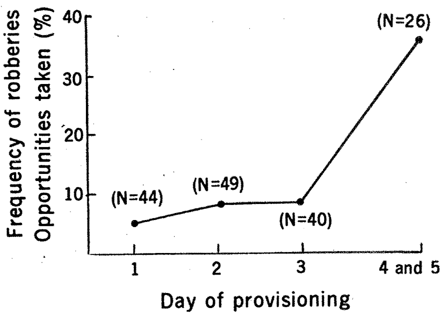

Fig. 1. Rates of stealing at various stages of provisioning (*N* is the number of observations).

The most striking altruistic behavior of *T. cameronii* involved the stealing of roaches captured by nestmates. Every time a female provisioning a cell arrived at the nest while a nestmate's cell was open and partially filled with roaches, she had the opportunity to steal them and put them in her own cell. Although apparently all females were capable of robbing (10 of 11 individuals observed for extended periods committed robberies), stealing was the exception rather than the rule (Fig. 1). Also, in no case did a female steal all the roaches available in a nestmate's cell, and usually (16 of 18 cases) she stole only one. In addition, cell owners very seldom made any attempt to prevent robberies. Although females often entered nestmates' open cells, I witnessed only one aggressive interaction apparently occasioned by one female attempting to enter another's cell, and I saw three robberies committed while the second female was present but she offered no resistance.

There are indications that robberies tend to occur in times of "need," that is, poor hunting success. They were more common during the last days of provisioning, especially when the wasp was unable to finish within 3 days [(*5*); Fig. 1]. All the robberies that did occur in the first 2 days of provisioning (five observations) happened in the last half of the work day and, in four cases, after especially unsuccessful hunting activity. The single aggressive interaction involving entry into a cell occurred between two females, each of which had had poor hunting success and had already robbed from the other; one was in her fourth day of provisioning and the other in her third.

The tendency to rob probably did not involve danger of the larva starving. Eggs hatched about 2 days after being laid (usually about the time provisioning started), and the new