evidence exists from any insect other than *P. bicarinata* for resetting of critical sizes by JH during larval development. However, the known role of JH during embryogenesis in forming the program of JH secretion, which includes the original setting of critical size, makes JH a likely physiological tool for revising critical size during larval development.

Finally, in order to integrate this model of caste determination with the bionomics of an ant colony, we propose that nutritional state directly controls the endogenous titer of JH. The fact that *Pheidole* soldiers are produced only when larvae are fed a highly proteinaceous diet is well documented (*13*). The link between the larval endocrine system and the nutritional environment is likely to be a rate factor associated with diet. In honey bees, artificial diets with high sugar content enhance the feeding rate of larvae and induce queen development. A high feeding rate appears to produce abdominal stretch, which triggers an increased rate of JH synthesis and secretion (*14*).

The discovery of a JH-sensitive period for soldier determination provides a physiological basis for the decision points (*15*) along larval developmental pathways. A decision point is a time in development at which one or the other of two sets of growth patterns is acquired by the larva, after which the individual proceeds in its development toward one caste (or subcaste) or the other (*15*). In ants, previous examples of decision points have correlated a period of winter dormancy with a change in the developmental pathway (*16*). The mechanism of soldier determination in *P. bicarinata* is independent of season and thus may have wide applicability to the control of polymorphism in ants.

DIANA E. WHEELER
H. FREDERIK NIJHOUT
Department of Zoology,
Duke University,
Durham, North Carolina 27706

References and Notes

1. E. O. Wilson, *The Insect Societies* (Harvard Univ. Press, Cambridge, Mass., 1971).
2. L. Passera and J.-P. Suzzoni, *C.R. Acad. Sci. Ser. D* **286**, 615 (1978); *Insectes Soc.* **26**, 343 (1979).
3. We studied the subspecies *vinelandica* of the species *Pheidole bicarinata*.
4. D. E. Wheeler and H. F. Nijhout, *Int. J. Insect Morphol. Embryol.* **10**, 131 (1981).
5. From a single colony, at least ten third-instar larvae could be drawn from each 0.1-mm segment of the full size range (0.6 to 1.3 mm). Consequently, a 0.2-mm size class was required in order to acquire 20 larvae. Therefore, a single experiment entailed dividing larvae from a single colony into size classes of 0.6 to 0.8, 0.8 to 1.0, and 1.0 to 1.2 mm or 0.7 to 0.9, 0.9 to 1.1, and 1.1 to 1.3 mm. Within each size class, 20 larvae were selected so that the mean size was equal to the mode.
6. The volume of JHA applied per gram varied somewhat from individual to individual because of the size range of the larvae and the difficulty of controlling drop sizes, which were as small as 1 nl for the smallest larvae.
7. P. Wirtz, *Meded. Landbouwhogesch. Wageningen* **73-5**, 1 (1973); G. M. Copijn, J. Beetsma, P. Wirtz, *Proc. K. Ned. Akad. Wet. Ser. C* **82**, 29 (1978); A. Dietz, H. R. Hermann, M. S. Blum, *J. Insect Physiol.* **25**, 503 (1979).
8. H. F. Nijhout and D. E. Wheeler, *Q. Rev. Biol.*, in press.
9. H. F. Nijhout and C. M. Willians, *J. Exp. Biol.* **61**, 481 and 493 (1974).
10. F. Sehnal, in *The Juvenile Hormones*, L. I. Gilbert, Ed. (Plenum, New York, 1976), pp. 301–322.
11. L. M. Riddiford and J. W. Truman, *Nature (London)* **237**, 458 (1972).
12. P. Cassier, *Insectes Soc.* **13**, 17 (1966).
13. L. Passera, *ibid.* **21**, 71 (1974).
14. M. Asencot and Y. Lensky, *Life Sci.* **18**, 693 (1976); E. A. Goewie, *Meded. Landbouwhogesch. Wageningen* **78**, 1 (1978).
15. G. F. Oster and E. O. Wilson, *Caste and Ecology in the Social Insects* (Princeton Univ. Press, Princeton, N.J., 1978).
16. M. V. Brian, *Insectes Soc.* **2**, 1 (1955); L. Plateaux, *Ann. Sci. Nat. Zool. Biol. Anim.* **12**, 373 (1970); L. Passera, *C.R. Acad. Sci. Ser. D* **275**, 2013 (1972); B. Delage-Darchen, *Annee Biol.* **16**, 517 (1977); D. Dartigues and L. Passera, *Bull. Soc. Zool. Fr.* **102**, 197 (1979).
17. We thank M. Nijhout and J. Travis for critical reviews of the manuscript. The ZR-515 was a gift from G. B. Staal (Zoecon).

4 March 1981; revised 4 May 1981

Vibration Signal Transmission in Spider Orb Webs

Abstract. *Vibration transmission from the prey-catching region to the hub of the unloaded orb web of* Nuctenea sclopetaria *was measured by laser vibrometry. Compared to transverse or lateral vibrations, longitudinal vibration shows less attenuation and contains more directional information. It is transmitted well throughout the entire frequency range measured (1 to 10,000 hertz).*

A century ago, Boys (*1*) observed that a spider will attack a vibrating tuning fork touching its web. Since that time interest in vibration signals in spiders' webs has continued (*2–8*), and it has become clear that the web is not only a device for ensnaring prey but also a medium for transmitting information on the nature and position of the source of mechanical disturbances. Therefore, an understanding of vibration transmission through the web is central to understanding the use of vibration signals by web spinners. Despite a number of investigations (*4–8*), there has been no satisfactory means of measuring web vibrations that does not load the web at the point of measurement. The web's light construction—one spanning 500 cm^2 may weigh only 1 to 2 mg—requires a noncontact, and therefore optical, measurement technique, while the signal from entangled prey—expected to extend over a frequency range of about 1 to 10,000 Hz at amplitudes ranging from nanometers to millimeters—demands an instrument with extended frequency and amplitude response.

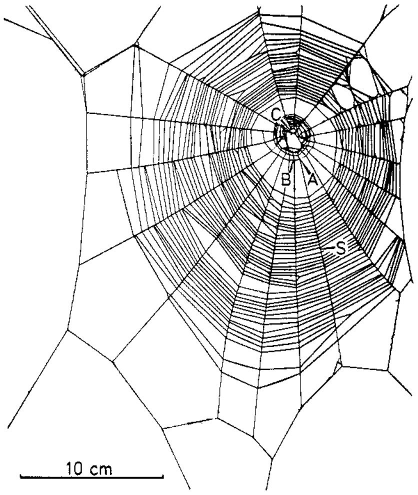

Fig. 1. A reversed-image photograph of the orb web from which the vibration measurements shown in Fig. 2a were made. The hub is the central area of dense meshwork surrounded by a spiral-free zone. Radial strands attach at their distal ends to the frame threads forming the web margin; these in turn are fixed directly, or else via supporting stays, to the wooden frame (not shown) in which the web was built. The web was stimulated at point S (or, in other webs, on any radius in the web's lower half) and the vibration measured at points A to C.

We now report on the differential transmission of three types of vibration signals through the unloaded web of *Nuctenea* (= *Araneus*) *sclopetaria* determined by laser Doppler vibrometry. Our results represent the first step in a program intended to describe the complete system composed of the spider, its web, and a vibration source (prey or mate, for example). It has now become possible to measure transmission over a very broad range of frequency (probably the whole range of interest to the spider), and the results show that there are several types of web vibration, not previously distinguished, each having different transmission properties, with perhaps different functions.

Normally, a spider sits either at the hub of its web (Fig. 1), the convergence point of all web radii, or hides nearby and monitors web vibration via a signal strand that runs to the hub. The radii appear to be the most important vibration-conducting elements of the web, since it is along them that the spider orients when trying to locate a vibration source (*3, 4*). We can distinguish several

0036-8075/81/0717-0363$00.50/0 Copyright © 1981 AAAS

types of radius vibration. *Transverse* vibration, as used here, occurs when each part of the radius undergoes motion perpendicular to the radius and perpendicular to the plane of the web. *Lateral* vibration is motion perpendicular to the radius in the plane of the web. *Longitudinal* vibration is motion along the axis of the radius (and therefore also in the plane of the web). In a normal situation, of course, the vibration of the radius is a combination of all three types of motion (*9*).

Vibration motion was measured with a commercially available laser Doppler vibrometer that detects the Doppler shift (proportional to target velocity) in the frequency of a laser beam reflected from the target (*10*). A lens focuses the laser beam onto the moving object (the spider web) and also collects the reflected light. Since only light scattered directly back from the object to the lens is captured by the instrument, only the vectoral component of the object's motion along the axis of the lens-laser system is measured—motion in other directions merely increases background noise. This directional selectivity permits independent measurement of any one of the three types of web vibration when the laser beam is arranged to strike the web from the appropriate direction (*11*).

To determine the vibration-transmitting characteristics of the web (*12*), we stimulated a radius (*13*) transversely, laterally, or longitudinally at known amplitudes at a point about in the middle of the prey-catching region (Fig. 1, point S). The vibration transmitted to several points in the hub, where the spider would normally be located, was compared with the input vibration over the frequency range 1 to 10,000 Hz (*14*). The resulting transmission curve, normalized to input vibration, is the transfer function connecting the point of stimulation with the point of measurement.

Transmission curves for longitudinal, transverse, and lateral vibrations (top to bottom) in one web are shown in Fig. 2a. In all three cases the response was measured on the stimulated radius where it attached to the hub (Fig. 1, point A)—about where the spider's tarsus would normally grasp the web. Distinct differences can be seen in the transmission curves. Longitudinal vibration ordinarily shows almost no attenuation over the range 1 to 3000 Hz (only 1 to 2 dB), and some amplification (sometimes up to 10 dB) above ~ 3 kHz. In contrast, over this same frequency range, transverse and lateral vibrations are attenuated at least 10 to 30 dB. The vibration transmission to the middle of the hub (Fig. 1, point C), near where the spider's signal thread would be attached, is generally similar in form to the curves shown in Fig. 2, but with more attenuation, particularly above ~ 1 kHz.

Although transmission may be altered by the presence of a spider or prey in the web (*15*), our results show that differences exist in the transmissibility of the three types of vibration. Since longitudinal vibration is the least attenuated, it could be the type of most importance to the spider, a proposition supported by Liesenfeld's (*4*) finding that a spider responds more readily to longitudinal than transverse vibrations of its signal thread. Unfortunately other studies of spiders' responses to web vibration have not distinguished among or considered separately the various vibration types.

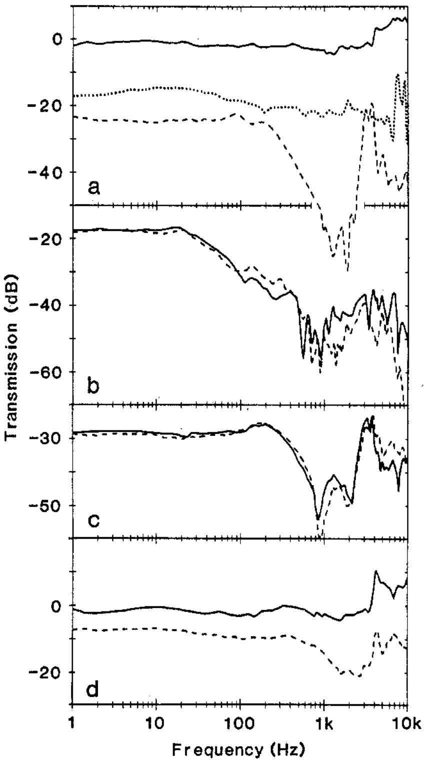

Fig. 2. (a) Longitudinal (solid), transverse (dotted), and lateral (dashed) vibration transmission between points S and A for the web shown in Fig. 1. (b) Transverse, (c) lateral, and (d) longitudinal vibration transmission for three different webs measured at the edge of the hub on the stimulated radius (solid) and an adjacent radius (dashed), corresponding to points A and B in Fig. 1. Longitudinal vibration [(a) upper curve; (d) solid curve] is characterized by good transmission to the hub at all frequencies. Transverse vibration [(a) middle curve; (b) solid curve] typically tends to drop gradually, although not always uniformly, with increasing frequency and often has sharp resonance peaks above about 1 kHz. Lateral vibration [(a) bottom curve; (c) solid curve] appears always to have a plateau region extending out to about 300 Hz, with increasing attenuation above the plateau and often, as illustrated, a well-defined resonance peak in the 3- to 4-kHz range.

Directionality of the signal transmitted by the web is important since vibration cues help the spider locate the prey in the web. When the spider is in the web, its legs [on which the principal vibration receptors are located (*16*)] normally contact the web in a nearly symmetrical pattern around the periphery of the hub. Therefore, by measuring the signal at different points on the edge of the hub, we can determine how strongly the leg nearest the vibrated strand will be stimulated compared to one further away, and, assuming the spider makes a similar comparison, determine how easily it can locate the vibrated radius. Two points on the edge of the hub were measured (Fig. 1, points A and B), the first on the stimulated radius and the second on an adjacent one. For transverse and lateral vibrations (Fig. 2, b and c), the curves overlap extensively indicating little signal directionality, but for longitudinal vibration (Fig. 2d) there is clear separation at all frequencies, with transmission measured on the adjacent radius attenuated by 5 to 15 dB relative to the stimulated radius. This means that longitudinal vibration provides a much better cue to the direction of the source of vibration than do the other two types (*17*).

The results presented here reveal the dependence of the web's conductive properties on the type of signal it is transmitting. They also raise the question of whether the spider might be relatively "deaf" to certain vibration types, whether it can "listen" selectively to longitudinal vibration, or whether it can distinguish different frequencies or merely different intensities.

Our findings may account in part for the following conflicting reports: (i) The signal transmitted by an insect trapped in an orb web does not exhibit energy above ~ 500 Hz (*6, 7, 18*); but (ii) the distal metatarsal lyriform organ (the most likely receptor of small web vibrations) is most sensitive above 1 kHz (*19*). Given that insects can produce high frequency vibrations (*20*) and that the web has now been shown to be capable of transmitting such frequencies, it seems likely that the signal produced by a snared insect can contain high frequency energy and therefore that the spider is not, maladaptively, best equipped to receive vibrations that its prey does not excite and that its web cannot transmit. While not previously observed, this does not mean that high frequencies are absent in prey-generated signals (*21*). It may even be, considering the spider's differential sensitivity, that higher frequency vibrations, despite their smaller amplitudes, are a more intense stimulus than lower frequency vibrations.

W. MITCHELL MASTERS
HUBERT MARKL

Fachbereich Biologie,
Universität Konstanz,
D-7750 Konstanz,
Federal Republic of Germany

References and Notes

1. C. V. Boys, *Nature (London)* **23**, 149 (1880).
2. H. Frings and M. Frings, *Ecology* **47**, 578 (1966); A. A. Grünbaum, *Psychol. Forsch.* **9**, 275 (1927); G. W. Peckham and E. G. Peckham, *J. Morphol.* **1**, 383 (1887).
3. W. M. Barrows, *Biol. Bull. (Woods Hole)* **29**, 316 (1915); H. Peters, *Z. Vergl. Physiol.* **15**, 45 (1931); M. H. Robinson and J. Olazarri, *Smithson. Contrib. Zool.* **65**, 1 (1971); P. N. Witt, *Biosci. Commun.* **1**, 7 (1975).
4. F. J. Liesenfeld, *Z. Vergl. Physiol.* **38**, 563 (1956).
5. A. Finck, G. M. Stewart, C. F. Reed, *J. Acoust. Soc. Am.* **57**, 753 (1975); B. Krafft, *Symp. Zool. Soc. Lond.* **42**, 59 (1978); D. A. Parry, *J. Exp. Biol.* **43**, 185 (1965); E. Tretzel, *Z. Morphol. Ökol. Tiere* **50**, 375 (1961); F. Vollrath, *Science* **205**, 1149 (1979).
6. K. Graeser, thesis, University of Frankfurt (1973).
7. R. B. Suter, *Behav. Ecol. Sociobiol.* **3**, 283 (1978).
8. J. W. Burgess, *Anim. Behav.* **27**, 157 (1979); C. Walcott, *J. Exp. Biol.* **40**, 595 (1963).
9. A fourth vibration type, tortional motion of the radius, is also possible, but we have as yet no way of measuring it and must neglect it here.
10. For a more complete discussion of laser vibrometry, see P. Buchhave, *DISA Inform.* **18**, 15 (1975); A. Michelsen and O. N. Larsen, *J. Comp. Physiol.* **123**, 193 (1978).
11. It is not always possible to position the laser beam precisely along the correct path for optimal detection in a chosen direction, especially when measuring longitudinal vibration where the optimal path is then directly along the axis of the strand, but so long as the angle between the correct path and the actual path is $< 30°$ (in practice, $< 15°$ was always attainable), the underestimate of the true vibration amplitude will be < 1 dB.
12. Adult female spiders collected near Konstanz, Federal Republic of Germany, were kept (22° to 27°C, 13 hours of light and 11 hours of darkness) in wooden frames (45 by 45 by 6 cm) covered with removable plastic foil, in which they readily built webs. They were given water almost daily and fed flies of ~ 40 mg every 2 to 3 days. Measurements were made on freshly spun (< 24 hours) empty webs at 22° to 27°C, and at relative humidity of 40 to 60 percent.
13. The tip of the vibrator, a ceramic bimorph from a phonograph cartridge, was attached to the radius with beeswax without changing the equilibrium position of the strand. Orientation of the vibrator determined the type of vibration excited. The amplitude of the vibrator tip [0.1 to 30 μm (root-mean-square) depending on frequency], measured with the vibrometer (DISA Elektronik A/S, DK-2740, Skovlunde, Denmark) served as reference (0 dB) for the web transmission curves. Stability of the reference vibration was better than ± 1 dB throughout the session, which could last up to 10 hours.
14. A spectrum analyzer (Nicolet Scientific Corp., Northvale, N.J., model 446A) operating in the peak storage mode measured the output of the vibrometer; it served as a narrow-band filter to improve the signal-to-noise ratio of measurements and provided digital readout of frequency and amplitude. Between 40 and 100 measurements of signal amplitude over the range 1 to 10,000 Hz were made at a given point in the web, compared to the input (*13*) vibration at the corresponding frequency, and plotted against frequency (Fig. 2). To ensure that the vibrometer worked on spider webs, we measured the motion of the vibrator and the web adjacent to it. Readings agreed within ± 2 dB. Measurements of one or more vibration types were made on 18 webs spun by 11 spiders. Transversal vibration was measured eight times, lateral nine times, and longitudinal six times, at two to four points for each type.
15. R. M. Langer [*Am. Zool.* **9**, 81 (1969)] discusses the physics of spider webs.
16. F. G. Barth, in *The Insect Integument*, H. R. Hepburn, Ed. (Elsevier, Amsterdam, 1976), p. 445.
17. We do not know whether the spider can distinguish longitudinal from transverse and lateral vibration, nor can we infer from our results that the spider should be able to do so in order to locate prey. If the spider were equally sensitive to all three types and the prey produced equal-amplitude vibration in all three directions, the better transmissibility of longitudinal vibration would ensure its domination in the total (combined) signal, thus providing directional information.
18. Higher frequency vibrations have been reported in sheet webs and cobwebs (*8*).
19. F. J. Liesenfeld, *Biol. Zentralbl.* **80**, 465 (1961); C. Walcott and W. G. van der Kloot, *J. Exp. Zool.* **141**, 191 (1959).
20. B. Dumortier, in *Acoustic Behavior of Animals*, R.-G. Busnel, Ed. (Elsevier, Amsterdam, 1963), p. 346; H. Esch and D. Wilson, *Z. Vergl. Physiol.* **54**, 256 (1967); W. M. Masters, *J. Comp. Physiol.* **135**, 259 (1980).
21. Our preliminary measurements show that at least some trapped insects produce vibrations in the kilohertz range.
22. We thank A. Moffat for her many contributions to this work, A. Michelsen for discussions on laser vibrometry, K. Thaler for identifying the spiders, and T. Eisner and J. Tautz for comments on the manuscript. Supported by a NATO Postdoctoral Fellowship (to W.M.M.) and by Deutsche Forschungsgemeinschaft grants Ma 374/13 and Ma 374/15-2 (to H.M.).

23 September 1980; revised 28 January 1981

Age at Menarche: A Misunderstanding

Abstract. *Through a misinterpretation of historical data, the age of menarche in the 19th century is erroneously taken to have been 17 years. This error has resulted in unwarranted beliefs about change in female sexual maturation in the United States.*

Until recently, historical data about the age of menarche were probably of interest only to a few specialists. Much of the current publicity about the historical age of menarche has to do with the belief that in American girls menarcheal age has dropped from 17 years in the 19th century to 12.5 years today. This supposed trend has been regarded as the most significant factor in increasing teenage sexuality and the "growing problem of teenage pregnancy" (*1*). Stories about it have appeared in almost every kind of popular journal from *Newsweek* to *The Nation*, and in scholarly literature of anthropology, psychology, child development, nursing, and other fields. It apparently has even entered into predictions of demographic trends. Notions about the magnitude of the change in menarcheal age are based upon misinformation. There has been some change, but very much less than has been assumed.

In the United States in the present day the mean age at normal menarche is estimated to be 12.3 years (some would say 12.5 or 12.6) and the range from 9 to 17 years. Individual differences are attributed to differences in general health and nutrition, heredity, psychosocial development, and a number of other factors. Pediatricians would normally do a diagnostic work-up for girls who have not begun menstruating by 16 (*2*). It is important to emphasize the broad range of menarcheal age, because in the past each clinician contributing to the subject did so, with a few exceptions, on the basis of a very small sample, and historical data can be skewed because of this.

The informed guesses and best estimates of the past can be tested against age at first pregnancy, age at marriage, and other factors traditionally dependent upon menarche. Roman law, for example, assumed that females were mature at the age of 12, and classical writers described menarche as taking place sometime between the ages of 12 and 14 (*3*). Medieval authorities tended to agree. Much of our information comes from the later Middle Ages. One of the best indicators of medieval assumptions is in the gynecological text *De passionibus mulierum*, attributed to Dame Trotula, extant copies of which date from the 13th century. There are numerous copies of the English provenance, 18 at Oxford alone. In 12 of the English manuscripts there are tables on menarche, and the ages appear to vary according to the scribe's personal knowledge. Most of the Oxford copies put menarche at age 14; the most common other age given is 13 (*4*). Other medieval writers set it within the same range, 13 or 14 (*5*). In Islamic countries it was a criminal act to have sexual relations with a woman before she had menstruated. Before a marriage could be consummated women were to examine the girl to see that she was physically prepared, and Arabic law set a range of ages for this examination between 12 and 13 (*6*).

Some of the 19th- and early 20th-century data put menarche slightly later than classical or medieval authorities do. J. Whitehead, writing in the 1840's, put the average for Manchester workingwomen at 15 years 7 months and for "educated ladies" at 14 years 6 months (*7*). E. W. Murphy reported that obstet-

0036-8075/81/0717-0365$00.50/0