

tonicity is unknown. By 10 days of oral 2 percent NaCl, vasopressin concentration in both the supraoptic nucleus and retrochiasmatic area was less (although only in the latter area was the decrease statistically significant), implying that the rate of transport of hormone away from these areas had exceeded synthesis.

Hypertonic saline ingestion was chosen as the dehydration stimulus because it is as potent as complete water deprivation in causing depletion of vasopressin and oxytocin biologic activity from the rat posterior pituitary (2). Hypertonic saline ingestion is probably less of a general stress to the animal than complete water deprivation and thus should be a more specific hypertonic stimulus. There was no significant difference in protein content of each microdissected area when tissue from dehydrated rats was compared with tissue from control rats. Thus, the differences reported here with hormone expressed as picograms per microgram of protein are due to changes in the content of hormone and not protein. Microdissection was confined to within nuclear areas so as not to include extraneous tissue, and therefore total hormone content of hypothalamic nuclear areas was not measured.

It is of interest that there was no significant change in vasopressin or oxytocin concentration in median eminence at times of significant changes in concentration of both hormones in the posterior pituitary and in various areas of the hypothalamus. There was also no significant change in concentration of either hormone in the supraoptic nucleus in response to oral hypertonic saline. Neurophysins, proteins that bind vasopressin and oxytocin, have been found by immunofluorescence in supraoptic, paraventricular (11), and supraoptic nuclei (12). There is also a recent report of neurophysin in the bovine arcuate nucleus (13).

The depletion of vasopressin from the arcuate nucleus after 3 days of oral hypertonic saline is presumably not due to changes in axons in passage through the nucleus, as vasopressin concentration in the retrochiasmatic area, which we assume to contain axons in passage, was increased after 3 days of oral hypertonic saline. The arcuate nucleus lies just above the median eminence, and it is possible that vasopressin and oxytocin are serving as neurotransmitters in this nuclear area and may be involved in control of anterior pituitary function (14).

The arcuate nucleus has not been thought to be part of the neurosecretion system for vasopressin or oxytocin, but from our findings here it appears to be in-

volved in the dehydration response. This is consistent with an earlier autoradiography study in which we found increased incorporation of [³H]uridine into RNA in response to oral hypertonic saline in the arcuate as well as the supraoptic nucleus but not in supraoptic or paraventricular nuclei (15). Evidently, in both supraoptic and arcuate nuclei, dehydration causes depletion of vasopressin and oxytocin and possibly synthesis of new proteins or polypeptide hormones.

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References and Notes

1. W. Bargmann and E. Scharer, *Am. Sci.* **39**, 255 (1951).
2. C. W. Jones and B. T. Pickering, *J. Physiol (London)* **203**, 499 (1969).
3. M. Palkovits, *Brain Res.* **59**, 499 (1973).
4. J. M. George and D. M. Jacobowitz, *ibid.* **93**, 363 (1975).
5. J. F. R. Konig and R. A. Klippel, *The Rat Brain* (Krieger, Huntington, N.Y., 1970).
6. O. H. Lowry, N. J. Rosebrough, A. L. Farr, R. J. Randall, *J. Biol. Chem.* **193**, 265 (1951).
7. J. M. George, C. C. Capen, A. S. Phillips, *J. Clin. Invest.* **51**, 141 (1972).
8. B. J. Winer, *Statistical Principles in Experimental Design* (McGraw-Hill, New York, ed. 2, 1971).
9. H. Sachs and Y. Takabatake, *Endocrinology* **75**, 43 (1964).
10. E. Arnaud, J. D. Vincent, J. J. Dreifuss, *Science* **185**, 535 (1974).
11. E. A. Zimmerman, A. G. Robinson, M. K. Husain, M. Acosta, A. G. Frantz, W. H. Sawyer, *Endocrinology* **95**, 931 (1974).
12. F. Vandesande, J. DeMey, K. Diericks, *Cell Tissue Res.* **151**, 187 (1974).
13. J. DeMey, K. Diericks, F. Vandesande, *ibid.* **161**, 219 (1975).
14. F. E. Yates, S. M. Russell, M. F. Dallman, G. A. Hedge, S. M. McCann, A. P. S. Dhariwal, *Endocrinology* **88**, 3 (1971).
15. J. M. George, *ibid.* **92**, 1550 (1973).
16. I thank Mrs. Margaret Penrose, Ms. Arlene McCoy, and Ms. Sharman Staples for expert technical assistance and Dr. Richard Lanese and the Biometrics Laboratory, Department of Preventive Medicine, for valuable statistical analysis. This study was supported in part by the Veterans Administration and General Clinical Research Centers grant RR-34, National Institutes of Health, Bethesda, Md.

16 March 1976

Heart Rate in Spiders: Influence of Body Size and Foraging Energetics

Abstract. Resting heart rates in 18 species of spiders as determined by a cool laser transillumination technique range from 9 to 125 beats per minute. Cardiac frequencies obtained in this fashion may readily serve as a measure of standard rates of metabolism. A spider's resting heart rate is a function of body size and of foraging energetics.

Spiders are interesting to physiological ecologists because of their highly organized, yet relatively simple body plan and because they constitute a major link

as predators in most terrestrial food webs. Little is known about their energy budgets under natural conditions. Standard metabolic rates can be derived from

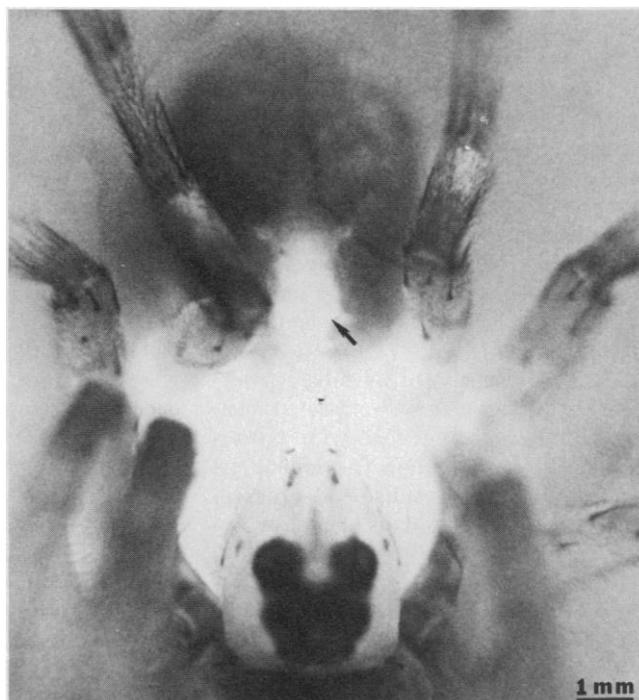


Fig. 1. Laser-illuminated wolf spider (*Lycosa ceratiola*). The tubular heart is visible as a pulsating oval spot on the dorsal surface of the abdomen (arrow) when the spider is irradiated from below by a cool He-Ne laser.

resting heart rates, which are easily measured in free-ranging vertebrates (1). However, techniques developed to monitor cardiac performance in large animals often are unsatisfactory for studies with arthropods. We now report on the detection and interpretation of heart rates in unrestrained spiders differing in body size and foraging strategy.

The spider heart is unusually sensitive to locomotory activity because blood serves a mechanical as well as a respiratory function. Spiders use blood as a hydrostatic fluid to extend their appendages (2). Correspondingly, some leg joints have flexor, but not extensor, muscles (3). Hence, the antagonistic musculature characteristic of insects, crustaceans, and vertebrates is incomplete in spiders. Normal leg extension is achieved by a moderate elevation of blood pressure, reaching 60 mm-Hg in the limbs of tarantulas (4). During a struggle or jump, there are dramatic surges in peripheral blood pressure, ranging from 450 to an estimated 1080 mm-Hg (2). When a spider becomes excited, blood pressure increases not only in its appendages but also to some degree in the prosoma and abdomen (4). This generalized rise in fluid pressure feeds back on the tubular heart, located mid-dorsally in the abdomen, and may produce a transient drop in the already elevated heart rate (5, 6). Spider heart beats are neurogenic (7). Therefore, it is possible that output from the central nervous system independently augments or opposes hydrostatic influences on cardiac function.

Unlike previous cardiac techniques, our method attempts to minimize hydrostatic as well as nervous perturbations of the heart in intact, resting spiders. Nothing is attached to an animal, and it is able to move freely in two dimensions on a solid surface or its web (8). When a cool helium-neon laser is focused onto the ventral surface of a spider near its pedicel, the pulsating heart becomes apparent when viewed from above (Fig. 1). The superficial heart is visible because it is more translucent than other abdominal tissues. As the heart contracts, the amount of red light emitted from the abdominal cuticle overlying it correspondingly decreases. To facilitate observation and recording of heart beats and to eliminate disturbances that could alter them, the preparation is mounted on a vibration-free stand, isolated in a dimly lighted (20 lux) chamber, and monitored remotely with closed-circuit television. Usually spiders do not move noticeably for many minutes after an initial period of adjustment to the experimental situa-

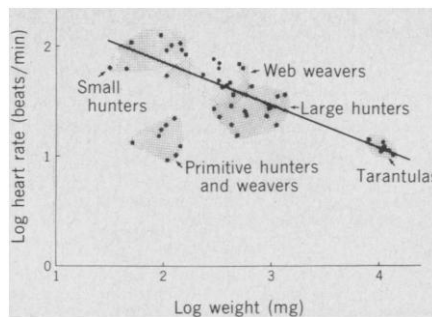


Fig. 2. Heart rate (H) in spiders as a function of body weight (W). A regression line, $H = 423 W^{0.409}$ ($r = .84$; $P < .001$), is indicated for all spiders but the primitive hunters and weavers.

tion (9). Heart rates are determined at 10-minute intervals until stable resting values are obtained. If a spider becomes active while determinations are in progress, the experimenter waits until it is quiescent, realigns the laser beam, if necessary, and then resumes counting as before.

Forty-eight adult female spiders representing 18 species and 11 families (Table 1) were collected in the summer of 1974 and 1975 in Missouri, Florida, and Arizona. Because metabolic rates in spiders vary according to levels of hunger and activity (10), a strict feeding and experimental schedule was maintained (11).

Heart rates in spiders, as measured by this technique, ranged from 9 to 125 beat/min. Generally, these values are less than one-half of those reported for re-

strained or postoperative spiders (4, 5). Cardiac frequencies comparable to those reported here have been found in untethered spiders (6, 12).

Resting heart rate of spiders is primarily a function of body size (Table 1 and Fig. 2), as it is in other animals (13). With the exception of primitive hunters and weavers, there is a highly significant ($r = .84$; $P < .001$) negative relation between body weight and heart rate. The same size relation was also observed in metabolic studies (14). Because the exponentials in both regression equations are identical, it is possible to cancel out body weight as a variable. Thus, the standard metabolic rate of a spider is estimated to be approximately 2.5 times its resting heart rate. These results confirm the idea that cardiac frequencies may readily serve as a measure of standard rates of metabolism in spiders.

The exceptions to this heart rate-body size rule are important because they reflect fundamental differences in foraging strategies among spiders. The brown recluse and the spitting spiders deviate significantly from the regression shown in Fig. 2. These primitive hunters and weavers weigh as much as jumping spiders, yet their resting heart rates are as low as a tarantula's. We suggest that this is an energy-conserving adaptation of spiders that invest little effort in prey capture and, consequently, feed only occasionally. Unlike salticids and thomisids, which are small, free-ranging, and more

Table 1. Taxonomic relationships of spiders studied. Families are listed in order according to magnitude of resting heart rates (average number of beats per minute) for individual adult female spiders.

Foraging style	Family (common name)	Species	Number studied
Tarantulas	Theraphosidae (typical tarantulas)	<i>Aphonopelma chalcodes</i>	3
		<i>Dugesia hentzi</i>	
Primitive hunters and weavers	Scytodidae (spitting spiders)	<i>Scytodes</i> sp.	3
		<i>Loxosceles reclusa</i>	
Large hunters	Pisauridae (nursery-web spiders)	<i>Dolomedes tenebrosus</i>	2
		<i>Lycosa ceratiola</i>	
	Lycosidae (wolf spiders)	<i>Lycosa osceola</i>	2
		<i>Pardosa</i> sp.	
	Sparassidae (giant crab spiders)	<i>Heteropoda venatoria</i>	2
		<i>Filistata hibernalis</i>	
Web weavers	Filistatidae (snare weavers)	<i>Argiope aurantia</i>	3
		<i>Eriophora</i> sp.	
	Araneidae (orb weavers)	<i>Neoscona arabesca</i>	2
		<i>Agelenopsis pennsylvanica</i>	
Small hunters	Thomisidae (crab spiders)	<i>Misumenops asperatus</i>	2
		<i>Misumenoides formosipes</i>	
	Salticidae (jumping spiders)	<i>Metacryba</i> sp.	2
		<i>Phidippus audax</i>	

active hunters (15), nearsighted loxoscelids and scytodids wait until prey becomes entangled in their crude snares before they use venom or a zigzag squirt of oral glue to subdue it. It is commonly known that the brown recluse can survive indoors for months or even years without food and water. Perhaps members of these families, more so than other spiders (10), can rapidly raise and depress their general metabolism to adjust to a particular situation (16).

Although there was no significant difference ($P > .05$) in body weights of large (230 to 630 mg) web weavers and hunters, the former group had significantly greater ($P < .001$; Student's t -test) heart rates (Fig. 2). Both types of female spiders use silk on some occasions during their lives (for example, to encase their eggs), but the degree to which they rely on it is different (15). Large hunters, typified by wolf spiders, ambush almost any small animal moving near them and attempt to overcome it by force. In contrast, web-building species are characterized by a sedentary existence, becoming so committed to a life on webbing that their delicate limbs and pendulous abdomens make locomotion awkward on a smooth, horizontal surface. We suggest that the superficially apparent sedentary nature of web-weaving spiders is deceptive. If the energy expended for silk production and utilization were added to predation energy budgets, it might show that orb weavers expend as much or more energy as active predators like lycosids. Hence, the ecological efficiency of web species could be much lower than predicted (17).

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References and Notes

1. S. F. Johnson and J. A. Gessaman, *Utah State Univ. Monogr.* **20**, 44 (1973).
2. D. A. Parry and R. H. J. Brown, *J. Exp. Biol.* **36**, 423 (1959); *ibid.*, p. 654.
3. C. H. Ellis, *Biol. Bull.* **86**, 41 (1944).
4. D. M. Stewart and A. W. Martin, *J. Comp. Physiol.* **88**, 141 (1974).
5. R. S. Wilson, *J. Insect Physiol.* **13**, 1309 (1967).
6. R. G. Sherman and R. A. Pax, *Comp. Biochem. Physiol.* **26**, 529 (1968).
7. C. R. Bursey and R. G. Sherman, *Comp. Gen. Pharmacol.* **1**, 160 (1970).
8. Spiders were individually enclosed in clear plastic culture dishes with small holes for ventilation, or in cardboard boxes modified for web building [P. N. Witt, *BioScience* **21**, 23 (1971)]. Both containers could be oriented either horizontally or vertically, whichever position is characteristic of the species. This arrangement permitted spiders to assume a typical resting posture. After addition of distilled water to prevent desiccation, the dish or box was clamped to a micromanipulator and positioned over a He-Ne continuous wave laser (Metrologic Instrument) with a wavelength of 632.7 nm and a power output of about 1 mw.
9. Monochromatic red light emitted by a low-intensity He-Ne laser probably causes little neural

excitation and virtually no heating or tissue damage in spiders. Spiders did not move when the laser beam was pointed at their eyes or other body parts. Furthermore, after a spider had rested for 1 hour or longer, neither continuous nor intermittent transillumination evoked a noticeable change in its heart rate. The elevation of body temperature in an anesthetized *Lycosa ceratiola* (1 g) after 1 hour of continuous illumination was 0.1°C above background temperature, as detected by a thermocouple inserted in the abdomen beside the heart.

10. J. F. Anderson, *Comp. Biochem. Physiol.* **33**, 51 (1970); *Ecology* **55**, 576 (1974).
11. Spiders were kept individually at room temperature (23° to 26°C) under constant fluorescent illumination (about 200 lux) either in clear plastic containers partially filled with moist sand or in special boxes (8). Water was supplied daily for drinking and humidification. Spiders were fed live mealworms (*Tenebrio molitor*) or cockroaches (*Nauphoeta cinerea*) weekly in numbers sufficient to keep their body weights relatively constant. Animals were acclimated for 3 to 4 weeks to these conditions. All measurements were made 2 to 6 days after a meal, usually between 1000 and 1400 hours CDST., although readings taken at other times of the day in two individuals of five species (*Aphonopelma chalcodes*, *Loxosceles reclusa*, *Lycosa ceratiola*, *Argiope aurantia*, and *Misumenoides formosipes*) were not significantly different ($P > .1$; Student's t -test). The heart rate of each spider was determined on three or more separate occasions spanning several weeks.
12. W. S. Bristowe and J. Millot, *Proc. Zool. Soc. (London)* **103**, 1015 (1933); I. Mikulska and W. Kokocinski, *Bull. Acad. Pol. Sci. Cl. 2 Sér. Sci. Biol.* **13**, 533 (1965).

13. C. L. Prosser, *Comparative Animal Physiology* (Saunders, Philadelphia, 1973), p. 837.
14. With the use of the data of Anderson (10) for adult female spiders, the relation between standard metabolic rate (M) (microliters of O_2 per gram per hour) and body weight (W) (milligrams) is $M = 947 W^{0.608}$ ($r = .91$; $P < .001$). This exponential is equal to the one in the heart rate (H)—body weight (W) regression of Fig. 2. It follows the $M/H = 2.25$. However, because these respiration rates were obtained at 4°C less than our heart rates, we estimate the isothermal ratio to be about 2.5.
15. W. J. Gertsch, *American Spiders* (Van Nostrand, New York, 1949).
16. If spiders are in a depressed metabolic state, an arousal period should be necessary for them to respond to a disturbance. We frequently have observed in the laboratory and at home that quiescent brown recluse spiders do not respond immediately when prodded, whereas their recently active cohorts do. Similar observations have been made with some wolf spiders of the genus *Lycosa*.
17. F. Enders, *Am. Nat.* **109**, 737 (1975), and references therein.
18. We thank R. Bunn, C. Higgenbotham, and S. Hata for technical assistance, and W. R. Enns, W. J. Gertsch, and H. K. Wallace for identification of spiders; the director and staff of the Archbold Biological Station, Lake Placid, Florida, for assistance and hospitality; and S. B. Chaplin for reading the manuscript. Supported in part by the Bache Fund of the National Academy of Sciences.

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20 February 1976; revised 22 April 1976

Intraclonal Histocompatibility in a Parthenogenetic Lizard: Evidence of Genetic Homogeneity

Abstract. A total of 175 skin grafts were transplanted among 20 individuals belonging to two separate populations of the parthenogenetic lizard *Cnemidophorus uniparens*. Of these, 98.8 percent were permanently accepted, which indicates that all individuals of each population may be genetically identical. These results further suggest that large populations or the entire species may consist of one clone derived from a single individual.

It is generally assumed with regard to parthenogenetic species that individuals within a clone are genetically identical, although the extent of genetic uniformity has not been clearly ascertained experimentally. Support for this assumption has been obtained by various tissue-grafting studies showing that allografts exchanged among conspecific individuals are not rejected (1–4). The majority of these studies, however, have involved a limited number of individuals from any one single population. For instance, in the case of the unisexual fish *Poecilia formosa*, some of the transplantation experiments involved the descendants of one or two individuals (2). In other studies in which allografts were exchanged among substantial numbers within a population (3, 4), the grafts were exchanged only between pairs, so that each individual received and donated one graft. Only Maslin (3) has intergrafted among several individuals to test for potential histoincompatible clones within a single natural parthenogenetic population. Using an elaborate transplantation scheme, he in-

tergrafted among six parthenogenetic lizards, each donating to and receiving grafts from the other five. A total of 30 grafts were transplanted and all were permanently retained.

These data do not, of course, rule out the possibility that occasional histoincompatible individuals may exist within single clones, but their detection is made difficult by inherent limitations in the existing surgical techniques employed to excise the grafts. For instance, in the case of *P. formosa*, whole organs, such as fins or hearts, are transplanted, which often requires killing the donors. In the case of parthenogenetic lizards, the use of skin grafts is more practical since donors need not be killed, and several grafts can be transplanted on one individual. Nevertheless, present techniques require conventional surgery, which is not only tedious but also imposes a limit on the size of the graft and therefore on the total number that may be transplanted to one individual. If genetic differences exist within clones, their detection will be maximized in pro-