sence of spikes does not, therefore, appear to be related to the morphological distance over which information must be conducted by an interneuron. A comparison of the roles of spiking and nonspiking local interneurons in local reflexes reveals further similarities. First, interneurons of both types have apparently direct synaptic effects on hind leg motor neurons. Second, interneurons of both types are excited by movements of the hind legs. For example, during movements of the femoral-tibial joint, a series of spikes or excitatory postsynaptic potentials (EPSP's) can be elicited in some spiking or nonspiking interneurons, respectively (*17*). When the joint is held flexed or extended some spiking local interneurons spike tonically, whereas some nonspiking interneurons show tonic shifts in their membrane potential (*18*). Third, interneurons of both types can cause either transient or sustained changes in the membrane potentials of postsynaptic motor neurons. Discrete synaptic potentials in motor neurons may be caused by single spikes in spiking local interneurons, or by single EPSP's in nonspiking local interneurons (*17*). Sustained postsynaptic changes may be caused by repetitive spikes in spiking local interneurons, or by sustained depolarization of nonspiking local interneurons (*18*). However, when the outputs and inputs of the two types of interneuron are compared, two differences emerge. First, spiking local neurons can, when stimulated individually, produce only a limited motor effect. By contrast, individual nonspiking local interneurons can cause vigorous and well-coordinated movements about several joints of a hind leg (*4–6*). Second, spiking local interneurons respond to more restricted sensory inputs than do nonspiking local interneurons. Further study may reveal differences between the two types of interneuron in the relative locations of input and output synapses, or in the electrotonic distances over which information must be transmitted intracellularly (*19*).

We do not yet know enough about the connections of local spiking interneurons to provide any general rationale for the presence of both spiking and nonspiking local interneurons. Nonetheless, the most reasonable assumption on which to base further experiments is that the use of particular types of local interneurons is related to their different functions in the behavior of the animal. For example, one role of spiking interneurons is to effect local reflexes in response to specific sensory inputs, and one role of nonspiking interneurons is to coordinate the output of groups of motor neurons. These functions may, in turn, account for the need to conduct a particular type of signal intracellularly, or the need to effect the release of transmitter in a particular way.

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1. Local interneurons are those in an anatomically restricted region of the nervous system [see (*2*)]. In the ventral nerve cord of arthropods, a local interneuron is confined to a segmental ganglion; in the brains of arthropods and vertebrates, the distinction is less easy to make.
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9. For example, for olfactory stimuli, see R. Selzer, *ibid.* **134**, 159 (1979); S. G. Matsumoto and J. G. Hildebrand, *Proc. R. Soc. London Ser. B* **213**, 249 (1981).
10. The methods are described in detail by G. Hoyle and M. Burrows [*J. Neurobiol.* **4**, 3 (1973)] and in (*4*). The femora of the hind legs were fixed and the tibiae moved by mechanical actuators controlled by a microprocessor. Microelectrodes were filled with either 2*M* potassium acetate (d-c resistances of 40 to 60 megohms) or with a cobaltous lysine complex made as described by F. Gallyas, L. Lenard, and G. Lazar [*Neurosci. Lett.* **9**, 213 (1978)]. The interneurons were stained with cobalt and silver, as described by R. M. Pitman, C. D. Tweedle, and M. J. Cohen [*Science* **176**, 412 (1972)] and J. P. Bacon and J. S. Altman [*Brain Res.* **138**, 359 (1977)]. Adult *Schistocerca americana gregaria* (Dirsh) of either sex were obtained from a crowded laboratory culture.
11. Spikes in the somata of the interneurons were typically 1 to 5 mV in amplitude and were of briefer duration than those recorded in the somata of leg motor neurons. The site of their initiation is unknown.
12. Two levator tarsi motor neurons were originally described, one fast and one slow, in M. Burrows and G. Hoyle [*J. Neurobiol.* **4**, 167 (1973)]. Present evidence indicates that there is usually only one excitatory motor neuron (M. V. S. Siegler, *J. Exp. Biol.*, in press).
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14. Passing current into the motor neuron reverses the polarity of these potentials at a membrane potential more negative than the normal resting one. The synaptic potentials are therefore both chemically mediated and inhibitory. The IPSP's often occur in a pattern that includes beats, indicating that they are derived from two sources. The larger IPSP class is mediated by the interneuron described here.
15. At the giant synapse of the squid, the synaptic delay is 1.2 msec at 15°C [A. Takeuchi and N. Takeuchi, *J. Gen. Physiol.* **45**, 1181 (1962)]. Our measurements made at 22°C are therefore consistent with the connection being monosynaptic, but physiological evidence alone cannot rule out the possibility of an interposed nonspiking interneuron.
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Force-Sensitive Interneurons in the Spinal Cord of the Cat

Abstract. *The input-output properties of interneurons mediating spinal reflexes were investigated by extracellularly recording the response of interneurons to excitation from muscle receptors in the ankle extensor muscles of decerebrated, spinal cats. A population of interneurons in the intermediate region of the spinal cord is potently excited by increases in muscle force. Unlike the discharge of Golgi tendon organs, which accurately encodes moment-to-moment variations in the force of a single muscle, the discharge of these interneurons depends in a dynamic and usually nonlinear way on the force in several muscles. Powerful input from unidentified mechanoreceptors in muscle, presumably free nerve endings, is at least partly responsible for these properties. These force-sensitive interneurons are more likely to mediate clasp knife–type inhibition than simple negative force feedback.*

Golgi tendon organs, sensory receptors located at the musculotendinous junction in vertebrate muscle, are accurate force transducers (*1*). Since electrical stimulation of muscle nerves at strengths sufficient to excite Golgi tendon organ afferents (Ib) inhibits homonymous motoneurons (*2*), the Ib pathway may provide negative force feedback. This feedback would act to oppose changes in muscle force, such as those associated with stretch, fatigue, or the length-regulating actions of spindle afferent pathways. Although several investigators report that the strength, or gain, of force feedback in decerebrated cats is small or negligible (*3*), their findings may be peculiar to the decerebrated preparation. Because measurement of reflex gain in alternative preparations is technically difficult, we chose to investigate directly the processing of force information in the spinal cord by extracellularly recording the response of spinal inter-

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neurons to changes in muscle force. We report that in the spinal cord of the cat there are force-sensitive interneurons whose discharge rate varies with muscle force. Golgi tendon organs, however, are not exclusively responsible for this force dependence. Rather, unidentified mechanoreceptors in muscle—presumably free nerve endings—strongly excite the force-sensitive interneurons. The powerful excitation of these interneurons by unidentified mechanoreceptors, marked dynamics, and usually nonlinear dependence on muscle force suggest that force-sensitive interneurons are more likely to mediate clasp knife–type inhibition than simple negative force feedback.

We anesthetized 33 adult cats with a mixture of Fluothane, nitrous oxide, and oxygen and removed the laminae of vertebrae L4 through L6. The triceps surae and plantaris muscles were separated and attached to an electromagnetic muscle puller with rigid metal hooks, and the muscle nerves were dissected for electrical stimulation. Other muscle and cutaneous nerves of the hind limb were sectioned. We then withdrew gaseous anesthesia and decerebrated 21 cats at the level of the superior colliculus and sectioned the spinal cord at T12. Eight cats were decerebrated and the dorsal half of the spinal cord was sectioned at T12. The remaining four cats were anesthetized with chloralose. These preparations were chosen because the Ib pathway may not be suppressed to the same extent as in cats that have only been decerebrated (*4*). The animals with hemisectioned spinal cords and occasionally the spinal animals exhibited weak stretch reflexes and a pronounced clasp knife reflex, which is an abrupt and sustained inhibition of muscle force occurring when an active muscle is stretched beyond a certain length (*5*).

Muscle length was varied with an electromagnetic muscle puller. Muscle force was varied by (i) changing the rate or intensity of muscle nerve stimulation at a constant muscle length, (ii) changing muscle length during muscle nerve stimulation at a constant rate, (iii) inducing bipolar intramuscular stimulation of motoneuronal axons with insulated, stainless steel wires (50 μm in diameter), (iv) stretching the passive muscle, (v) longitudinally vibrating the tendons to elicit reflex responses, and (vi) evoking the crossed extensor reflex by manipulating the contralateral hind limb. The responses of single interneurons in vertebral segments L5 through S1 were extracellularly recorded with fine, high-impedance (4 to 10 megohms), tungsten microelectrodes. Since recording stability was often poor due to movement of the animal, analysis of many interneurons was incomplete. Interneurons were distinguished from tract cells by their failure to respond antidromically to spinal cord stimulation at T12, from motoneurons by their failure to respond antidromically to stimulation of motoneuronal efferents in the muscle nerves, and from primary sensory afferents by their pattern of sensory input, response latency, and location.

Interneurons were identified as force-sensitive if their discharge rate monotonically increased with increasing muscle force. We identified 104 force-sensitive interneurons within 1 mm of the midline and 1.7 to 2.8 mm beneath the dorsal surface of the spinal cord (presumably Rexed's laminae V to VII). Seventy-nine were in the decerebrated cats with sectioned spinal cords, 16 in the decerebrated cats with hemisectioned cords, and nine in the chloralose-anesthetized cats.

The dependence of interneuronal discharge rate on maintained, or static, force is shown in Fig. 1A for a series of three tetanic contractions. Force was varied in this instance by stimulating motoneuronal axons with different combinations of four pairs of intramuscular electrodes, thereby recruiting different numbers of motor units. The relations between static muscle force and interneuronal discharge rate were obtained by first averaging the rate during the 500 msec preceding the stimulus and the

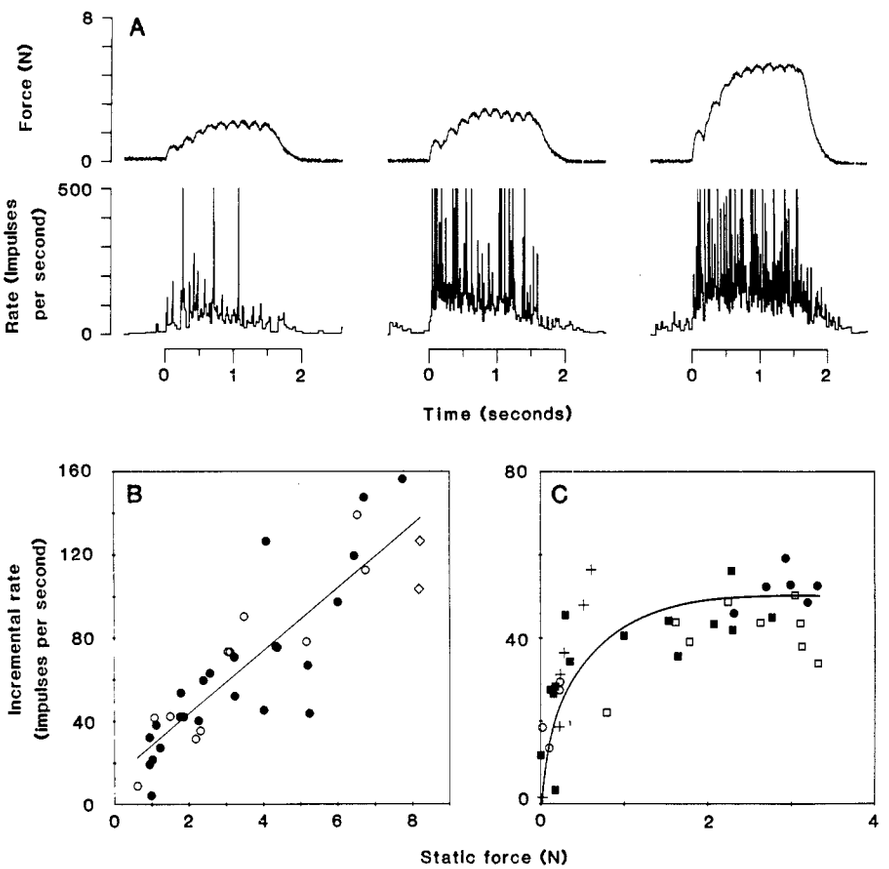

Fig. 1. Dependence of discharge rate of force-sensitive interneurons on static muscle force. (A) Increasing the force of isometric contractions of the soleus muscle produces increasing excitation of the force-sensitive interneurons. Muscle force was varied by stimulating motoneuronal axons with different combinations of four pairs of intramuscular electrodes. Interneuronal discharge rate was truncated at 500 impulses per second. (B) Force-rate relation for the force-sensitive interneuron represented in (A). Force was varied by stretching the passive muscle (◇), changing the intensity of intramuscular stimulation (○), and changing combinations of the four intramuscular electrodes (●). The line drawn through the points (slope, 15.2 impulses per second per Newton; *y*-intercept, 13.0 N; correlation coefficient, .87) was fitted by least-squares regression. (C) A different force-sensitive interneuron exhibits a nonlinear, saturating force-rate relation. The force of the soleus muscle was varied by changing the rate of muscle nerve stimulation (□), changing muscle length during muscle nerve stimulation at a constant rate (●), changing the intensity of muscle nerve stimulation (■), stretching the passive muscle (○), and longitudinally vibrating the tendons to elicit reflex responses (+). The output of force and length transducers was sampled on-line at 100 Hz and stored on diskettes by a PDP 11/03 microcomputer. Extracellularly recorded action potentials were stored on diskettes as interspike intervals and are displayed as instantaneous rate.

force and rate during the last 750 msec of the plateau phase and then graphing the change in rate versus force (Fig. 1, B and C). Of 38 interneurons analyzed in this way, nine showed a linear static force–rate relation (Fig. 1B) and 16 a nonlinear, saturating static force–rate relation (Fig. 1C). The remaining 13 were equally consistent with a linear or nonlinear relation. Force-sensitive interneurons with nonlinear relations and force-sensitive interneurons with linear relations are probably not different populations. Rather, the form of the force-rate relation seems to depend on the technique used to vary muscle force and the specific muscles involved. For instance, the best linear relations were obtained by using intramuscular stimulation, which may simulate motor unit recruitment more accurately than the other forms of stimulation. Although the remaining 66 interneurons were also force-sensitive, they were not held long enough for their force-rate relations to be completely characterized.

The time course of interneuronal discharge did not usually parallel the time course of muscle force development. Of 88 force-sensitive interneurons, 77 showed an initial, transient overshoot in rate, and in 36 of 75 the response persisted for 0.5 to 5.0 seconds beyond the cessation of increased muscle force. In only four interneurons did the entire time course of interneuronal discharge closely parallel that of muscle force.

Golgi tendon organ afferent input was demonstrated (i) if the force-sensitive interneuron could be excited by electrical stimulation of the muscle nerve at strengths sufficient to excite group I muscle afferents but below threshold for group II muscle afferents (*6*) and (ii) if the force-sensitive interneuron did not receive vibration-induced Ia input (this occurred in two instances). Since Golgi tendon organs were expected to be responsible for the force dependence of force-sensitive interneurons, we were surprised to find that only 10 of 39 force-sensitive interneurons could be shown to receive electrically induced Ib input. However, this is probably a low estimate of the number of interneurons receiving Ib input, since interneurons receiving weak monosynaptic or polysynaptic Ib input may not be excited by a single, synchronous, afferent volley. Although it is conceivable that repetitive electrical stimulation of Ib muscle afferents may have contributed to the observed rate increases, no sustained rate augmentation occurred during electrical stimulation when force output was eliminated by succinylcholine (two interneurons) or by muscle activation at short lengths.

The most potent methods of exciting force-sensitive interneurons proved to be mechanical manipulations that were unlikely to have driven spindle receptors or Golgi tendon organs but which apparently excited other types of muscle mechanoreceptors, such as free nerve endings and Pacinian and paciniform corpuscles (*7*). We used light stroking of the muscle surface and tendon squeezing to excite subpopulations of these unidentified mechanoreceptors. Figure 2A shows a typical response to two squeezes of the soleus tendon with a pair of fine forceps. Absence of significant effects of these stimuli on spindle afferents or Golgi tendon organs was verified in control experiments by directly recording from six primary spindle and four Golgi tendon organ afferents. We found that 30 of 33 force-sensitive interneurons investigated with these stimuli responded to light stroking and tendon squeezing (Fig. 2A) and that 26 of these received input from more than one muscle. The potency of unidentified mechanoreceptor input was remarkable. Peak rates during surface stroking or tendon squeezing often exceeded 700 impulses per second. Input from unidentified mechanoreceptors was demonstrated in all three preparations, indicating that these effects were not peculiar to a specific preparation. Of the eight force-sensitive interneurons that satisfied our criteria for Ib input, all seven that were tested also received unidentified mechanoreceptor input.

Primary spindle afferent input was investigated by using longitudinal tendon vibration (frequency, 160 Hz; amplitude, 100 μm) to selectively excite Ia afferents (*8*). A large majority of force-sensitive interneurons, 84 of 100, did not respond (Fig. 2B), and, in 8 of the 16 that did, the increase in discharge rate could be attributed to the force produced by the tendon vibration reflex rather than to primary spindle afferent input. Figure 2B shows that the same interneuron that was shown to respond to unidentified mechanoreceptor input in Fig. 2A did not respond to vibration.

Secondary spindle afferent input was assessed by stretching the passive muscle from short initial lengths to lengths insufficient to significantly increase passive muscle force. Provided the force-sensitive interneurons did not receive primary spindle afferent input, the absence of a maintained response to

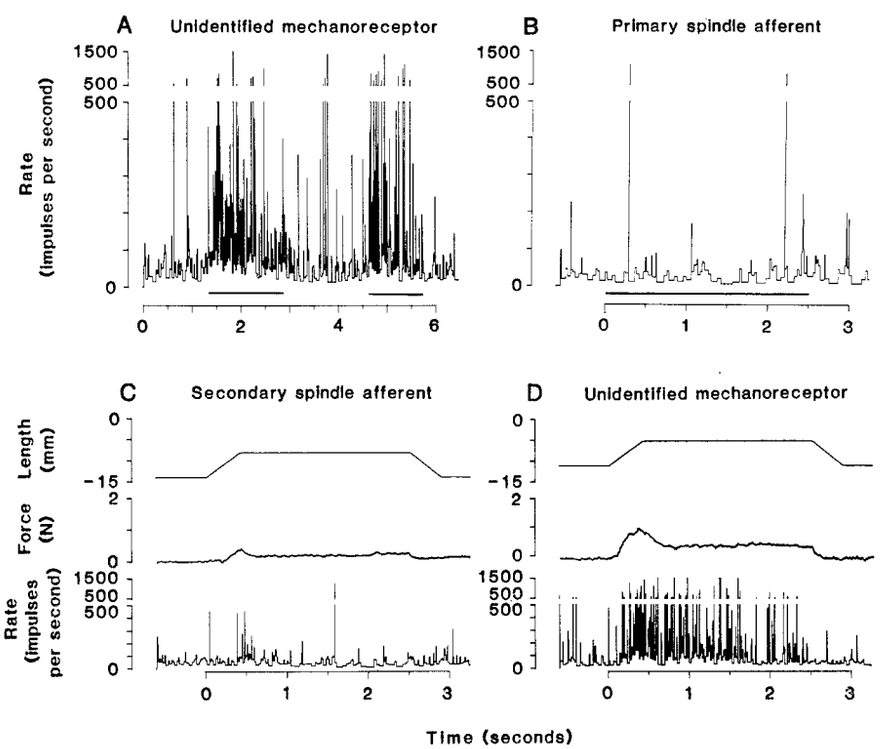

Fig. 2. Muscle receptor input to a single force-sensitive interneuron. (A) Localized squeezing of the soleus tendon (duration is indicated by the two horizontal lines) strongly excites the force-sensitive interneuron. (B) Vibration of the soleus tendon longitudinally (frequency, 160 Hz, amplitude, 100 μm) does not influence discharge rate. (C) Stretching the soleus, probably sufficient to excite secondary spindle afferents but insufficient to increase passive muscle force, is also ineffective. (D) Muscle stretching to greater lengths, which produces passive muscle force, excites the force-sensitive interneuron. Excitation presumably is mediated by unidentified mechanoreceptors. The force records in (C) and (D) were redrawn.

stretching suggests the absence of secondary spindle input (Fig. 2C). Of 36 force-sensitive interneurons, 31 did not respond under these conditions. In the remaining 68 force-sensitive interneurons, stretching excited the interneuron but also produced significant passive muscle force (Fig. 2D). Since increases in muscle force excite unidentified mechanoreceptors and since most of the force-sensitive interneurons were strongly influenced by unidentified mechanoreceptors, the response at long muscle lengths (Fig. 2D) may be due to input from unidentified mechanoreceptors rather than secondary spindle afferents.

To the best of our knowledge, no previous descriptions of spinal neurons that respond to increases in muscle force have been published. Except for a single early study (*9*), preceding investigations of proprioceptive spinal reflexes based on recordings from spinal interneurons have been concerned with connectivity (*10*) and cellular properties (*11*). Although we anticipated that force dependence would be due to Golgi tendon organ input, our finding that unidentified mechanoreceptors potently excite force-sensitive interneurons, together with the results of others showing that group III and IV afferents are excited by increases in muscle force (*12*), indicate that unidentified mechanoreceptors may be at least partly responsible for the force dependence of force-sensitive interneurons. This conclusion is supported by our finding that only 10 of 39 force-sensitive interneurons could be shown to receive electrically induced Ib afferent input.

The response patterns of force-sensitive interneurons are unlike those required for simple force feedback. The discharge of interneurons mediating simple force feedback might be expected to be influenced significantly only by input from Golgi tendon organs, to vary linearly with static muscle force, and to exhibit a time course of discharge closely paralleling muscle force. Instead, we found that force-sensitive interneurons are influenced by unidentified mechanoreceptors [some of which can be excited by muscle stretching and mechanical pressure as well as by muscle force (*12*)] and usually show nonlinear force-rate relations. Finally, the early, transient overshoot in discharge rate and prolonged afterdischarge are also inconsistent with simple force feedback. In contrast, the clasp knife reflex has properties similar to those of force-sensitive interneurons. Muscle stretching excites force-sensitive interneurons and induces the clasp knife reflex only at long muscle lengths. At short lengths, neither motoneurons nor force-sensitive interneurons are influenced. The sustained afterdischarge of force-sensitive interneurons is matched by the sustained inhibition of the clasp knife reflex. Finally, lightly stroking the muscle surface, which potently excites force-sensitive interneurons also produces an abrupt and prolonged inhibition of motoneuronal output. Therefore, provided force-sensitive interneurons inhibit homonymous motoneurons, these interneurons most likely mediate the clasp knife reflex. Although the clasp knife reflex has only been demonstrated in decerebrated cats with dorsally hemisectioned spinal cords and in spastic human patients, the central pathways responsible may still influence motoneurons under normal conditions.

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Spatial Learning as an Adaptation in Hummingbirds

Abstract. *An ecological approach based on food distribution suggests that hummingbirds should more easily learn to visit a flower in a new location than to learn to return to a flower in a position just visited, for a food reward. Experimental results support this hypothesis as well as the general view that differences in learning within and among species represent adaptations.*

Learning is a mechanism by which animals modify their behavior to respond more efficiently to their environments. Like other adaptations, learning has evolved as the result of the interactions that occur between animals and their environments. From this perspective, the characteristics of learning should vary because the ecological and social conditions in which animals learn are varied. With sufficient information on the ecology of animals it should be possible to make a priori predictions about learning. We tested predictions about the ability of hummingbirds to learn different spatial patterns of food availability from individual flowers.

Hummingbirds obtain most of their energy from floral nectar, present in individual flowers in small, slowly renewed amounts (*1*). The small size of hummingbirds and their hovering flight while feeding make them dependent on short-term supplies of energy, requiring visits to many flowers (*2*). Their foraging efficiency depends on the difference between the rates of gain and expenditure of energy. Several experiments indicate that animals often approach maximum rates of net energy gain when they feed (*3*). Although learning may enhance energy returns, only a few experiments have examined the impact of learning (*4*).

In their natural environment, hummingbirds returning to a recently emptied flower would have a lower rate of net energy gain than birds going to a flower that contains nectar. We hypothesized that a hummingbird reinforced for visiting a flower location should more easily learn to choose a different location during a subsequent foraging effort than learn to return to the same location.

We studied four female *Archilochus alexandri* (black-chinned hummingbird; 3 to 4 g), two male *Eugenes fulgens* (Rivoli's hummingbird; 8 to 10 g), and two male *Lampornis clemenciae* (blue-throated hummingbird; 8 to 9 g) captured wild in southeastern Arizona (*5*). They were maintained individually in 1-m^3

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