DOOR CONSTRUCTION BEHAVIOR OF THE MYGALOMORPH
SPIDER FAMILY ANTRODIAETIDAE AND ONE MEMBER OF THE
FAMILY CTENIZIDAE (ARANEAE, MYGALOMORPHAE)

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by

Ann Burgess Mayo

Frederick A. Coyle, Director
Professor of Biology, Department of Biology

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Abstract

DOOR CONSTRUCTION OF THE MYGALOMORPH SPIDER FAMILY

ANTRODIAETIDAE AND ONE MEMBER OF THE FAMILY CTENIZIDAE

(ARANEAE, MYGALOMORPHAE)

Ann Burgess Mayo, M. S.

Western Carolina University, December 1988

Director: Dr. Frederick A. Coyle

The entrance construction behaviors of *Aliatypus thompsoni* and

Antrodiaetus unicolor (family Antrodiaetidae) and one member of the genus

Hebestatis (family Ctenizidae) are described from direct laboratory

observations of incomplete and complete construction sequences. These

descriptions were compared to test the hypotheses that the collar door of

Antrodiaetus is the primitive construct in the family Antrodiaetidae and that the

evolutionary shift from one entrance form to the other requires little genetic or

neurophysiological change.

The descriptions of construction behaviors demonstrate great similarity

in the form, timing, orientation, and sequence of these construction behaviors

and hence, their conservative evolutionary nature. Consequently, a primitive

nature for the collar construct in the family Antrodiaetidae could not be

established by these observations, but neither can this hypothesis be rejected.

The great similarity among the behavior patterns of these species

suggests the hypothesis that little neurophysiological, and hence little genetic,

change may be sufficient to change the entrance form. A change in the control of orientation for the units of behavior is the key difference in the construction of different entrance forms in the family Antrodiaetidae. A model of such a neurophysiological control system and a change in this system that would be sufficient to cause the production of the other entrance form is presented.

INTRODUCTION

Charles Darwin (1872) was the first to propose that animal behavior evolves in the same manner as morphological characters do. In his 1844 (1971 [1958]) essay he presented evidence, drawn from both domesticated and wild animals, that evolution has generated the variety of behaviors exhibited by related taxa, and he proposed possible evolutionary pathways for some behaviors. By the turn of this century, studies in animal behavior were becoming common. Among the most notable of these studies are Morgan's (1886) work on instinct and habit, Jenning's (1923) work on the behavior of unicellular organisms, and Huxley's (1922) studies on bird courtship and mating behaviors, which were the first studies to consider the effects of natural selection on reproductive behavior. Despite Darwin's proposal, it was not until Heinroth (1911), Whitman (1919), Lorenz (1937), and Nice (1937) proposed a genetic basis and control for behavioral characters that the means of evolution for behavioral characters and hence, their properties of homology, became apparent. Ethology, the comparative study of animal behavior, began in the 1930's with the increasing acceptance of behavioral homology.

Comparative descriptive studies of the behaviors of closely related taxa and genetic studies which attempt to produce individuals which perform hybrid or mutant behaviors can be used to estimate or reveal the number of gene loci responsible for specific behavioral differences (Bristowe 1930; Crane 1949;

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Lorenz 1937; Goodall 1971; Bentley and Hoy 1972; Maynard Smith 1978; Eberhard 1982;Richman 1982; Halliday and Slater 1983). Observations of stereotyped behaviors which are largely under genetic control have been particularly helpful in understanding phylogenetic relationships; behavioral characters are sometimes more useful than morphological characters (Huxley 1922; Lorenz 1937). For instance, observations of the stereotyped courtship and web building behaviors of many spiders have been useful in testing phylogenies because of the degree and consistency of this stereotypy at generic and familial levels (Peckham and Peckham 1889; Petrunkevitch 1926; Robinson 1975; Robinson and Robinson 1980; and Stratton and Uetz 1981, 1986). Studies of web building behavior have been particularly useful in clarifying relationships among the orb weaving spiders (Eberhard 1982, 1987a and b; Coddington 1986). These studies indicate that many details of web construction behaviors are quite conservative.

Literature on the behavior of nonaraneomorph spiders is sparse and the literature on entrance construction behavior of these "primitive" spiders consists primarily of descriptions and illustrations of burrow and entrance constructs with almost no mention of the construction behaviors involved (Atkinson 1886a, b, and c; Enock 1885, 1892; Main 1957a, 1978; Main and Mascord 1974; McCook 1888; Moggridge 1873, 1874; Poteat 1890; Rivers 1891; van Dam and Roberts 1917). Only a few papers provide details of actual construction behaviors. Beck (Passmore 1933) and Muma and Muma (1945) described portions of the burrow and door construction behavior in *Bothriocyrtum californicum* and *Sphodros rufipes* respectively, and Coyle (1971) described burrow construction behavior for *Antrodiaetus unicolor*. The

only complete description of door construction behavior has been given for one member of the ctenizid genus *Ummidia* (Coyle 1981).

Most nonaraneomorph spiders (Mesothelae and Mygalomorphae) excavate and live in burrows. Although some species build no door constructs, most species close their burrow entrances with either a trapdoor or collar door. The trapdoor consists of silk and soil shaped into a flap which is hinged to the uppermost sector of the entrance rim. The collar door is a more flexible collar-shaped, silk and soil extension of the burrow lining which extends around the entire circumference of the entrance.

The taxonomic distribution of nonaraneomorph entrance construct form can be summarized as follows: 1) The most common construct is the trapdoor, found as the primary construct in six of the 16 nonaraneomorph families (Actinopidae, Barychelidae, Ctenizidae, Idiopidae, Liphistiidae, and Migidae) and less commonly in the Antrodiaetidae, Cyrtaucheniidae, and Nemesiidae (Main 1957a and b, 1985; Raven 1985; Coyle 1986). 2) The collar is the most prevalent door construct in the family Antrodiaetidae, but also occurs in some members of the Atypidae, Cyrtaucheniidae, Idiopidae, and Theraphosidae (van Dam and Roberts 1917; Coyle 1971, 1981, 1986). 3) Within each of the families Antrodiaetidae, Barychelidae, Cyrtaucheniidae, and Idiopidae, there are species which construct trapdoors and species which construct collar doors. 4) There is much variety in trapdoor form within families.

The presence of both trapdoors and collar doors in the family Antrodiaetidae (trapdoor constructs are found in the 11 species of *Aliatypus*; collar constructs are found in the 16 species of *Antrodiaetus* and *Atypoides*) and the monophyletic nature of this family (Coyle 1971; Raven 1985) make it a

suitable taxon for studying the phylogeny of entrance construction behaviors. The genera *Antrodiaetus* and *Atypoides* construct collar doors and turrets (Coyle 1971) which are similar in form to the tubes and collars of the family Atypidae, the sister family of the antrodiaetids (Gertsch and Platnick 1980). A photograph of the entrance of a spider in the atypid genus *Calommata* (Platnick, in prep) indicates that this entrance closely resembles the collar door of *Antrodiaetus* . The antrodiaetid genus *Aliatypus*, however, constructs a trapdoor similar in appearance and orientation to the trapdoors of the Ctenizidae (Coyle 1974).

The sister group relationship of the families Antrodiaetidae and Atypidae (Coyle 1971; Gertsch and Platnick 1980; Raven 1985) and the presence of collars in both of these families suggests that the collar construct, rather than the trapdoor construct, is the ancestral entrance structure for the antrodiaetids (Coyle, pers. comm.). It follows from such a hypothesis that the trapdoor of *Aliatypus* is a derived structure and that similarities between this antrodiaetid trapdoor and those of the ctenizids are due to convergent evolution.

This research is the first study of entrance construction behaviors in the family Antrodiaetidae. The objectives of this project were: 1) to give detailed descriptions of the entrance construction behaviors of the antrodiaetids *Aliatypus thompsoni* and *Antrodiaetus unicolor* and one member of the ctenizid genus *Hebestatis*, 2) to compare these descriptions and that of one member of the ctenizid genus *Ummidia* (Coyle 1981), 3) to estimate the amount of behavioral change and therefore, in a general way, the amount of genetic change, required for the evolution of a trapdoor from a collar door or

vice versa, and 4) to test the hypothesis that the trapdoor construct is the derived entrance form in the family Antrodiaetidae.

In regard to objective 3, weak support for the hypothesis that relatively little behavioral (and, consequently, genetic) change is required during the evolution from the collar door to the trapdoor construction (or vice versa) comes from the observation that this evolutionary event has occurred at least once in each of four mygalomorph families (Antrodiaetidae, Barychelidae, Ctenizidae, and Cyrtaucheniidae). This hypothesis would be further supported if only minor behavioral differences (such as timing or orientation differences) were responsible for the construct differences between *Antrodiaetus* (collar door) and *Aliatypus* (trapdoor). Conversely, if these construct differences result from major differences in the form of some of the behavioral units, differences which likely result from major differences in the neural pathways, the hypothesis would be weakened.

Until the entrance construction behavior of the genera of the sister family, Atypidae, is described, the direction of the evolution of construction behaviors within the Antrodiaetidae (objective 4) will be difficult to establish. Great differences between the trapdoor construction behavior of *Aliatypus* and the ctenizids *Hebestatis* and *Ummidia* (Coyle 1981) would suggest that the *Aliatypus* trapdoor program has evolved independently and would consequently provide some support for the hypothesis that the collar is the primitive construct in the Antrodiaetidae. The absence of such fundamental behavioral differences would neither support nor weaken this hypothesis.

METHODS

Only adult female spiders and a few juveniles were used in this study.
Specimens of *Antrodiaetus unicolor* (Antrodiaetidae) were collected during
1985 - 86 from steep road and stream banks near Cullowhee, Jackson County,
North Carolina. *Aliatypus thompsoni* (Antrodiaetidae) and one member of the
genus *Hebestatis* (Ctenizidae) were collected on June 28 and October 23,
1985 from a steep stream bank, 1 mi. NW of Highway 27 on Old Toporga
Canyon Road, in the Santa Monica Mountains, Los Angeles County,
California. For brevity and clarity, only the generic name of each species will
be used throughout the remainder of this paper.

These spiders were initially kept in plastic cups with moistened paper
toweling in a laboratory from October 1985 through July 1986. The
photoperiod approximated that of the actual season at Jackson County.
Spiders were then placed in terraria, consisting of plastic sewer pipes cut to 20
cm long and 7 cm in diameter, stood on end, and filled to within 2 cm of their
upper edge with a somewhat sandy soil obtained from sites where
Antrodiaetus are abundant. These pipes were set in a 2-4 cm deep layer of
soil within rectangular, plastic containers, three pipes per container. One edge
of each plastic container was placed on a piece of plywood, so that the
substrate surface was sloped approximately 45 degrees. The soil in the
rectangular containers was kept moistened, providing moisture to the burrows

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within the pipes. The spiders were offered mealworm larvae (*Tenebrio*, Tenebrionidae) when they were in hunting postures.

Observations were made of rim and door construction behavior, performed in these terraria, of 21 specimens of *Aliatypus*, 36 specimens of *Antrodiaetus*, and four specimens of *Hebestatis*. Door construction behaviors are described from approximately 64 observation hours of 23 complete door construction sequences and 216 observation hours of incomplete door construction sequences performed by *Aliatypus*, 26 observation hours of 10 complete collar construction sequences and 106 observation hours of incomplete collar construction sequences performed by *Antrodiaetus* and 38 observation hours of 18 complete door construction sequences and 209 observation hours of incomplete door construction sequences performed by *Hebestatis*.

During construction, descriptions of behavior were written on paper and recorded verbally on mini-cassettes. Some behaviors were photographed with a 35 mm camera and electronic flash, sketches were made of spider activity immediately following observation, and final drawings were made using preserved specimens as models and the original sketches and photographs as guides to positioning. After the completion of door construction the spiders were removed from their burrows and placed in new terraria or their rim and door constructs were removed. Consequently, the construction behavior of most individuals was observed repeatedly.

RESULTS

The entrance construction behavior of each species is composed of stereotyped units of activity, such as digging and carrying. Summary descriptions of these units of behavior are given below, followed by a description of the complete construction sequence of these behavioral units for that species. Any noteworthy variation in these units of behavior or in the entire sequence is also described. A comparative summary of the construction behaviors of all three species is given in conclusion.

ALIATYPUS THOMPSONI

Descriptions of Units of Behavior

Digging: The chelicerae are elevated, extended and spread apart. As the cephalothorax moves towards the soil, the fangs and pedipalps are extended to the soil surface. The soil load is formed into a small, rounded clod by the flexion of the pedipalps and fangs, and is picked up by the flexion of the fangs, chelicerae and pedipalps and the lifting of the cephalothorax. This behavior was only observed during the initial stage of burrow construction and may differ inside the burrow.
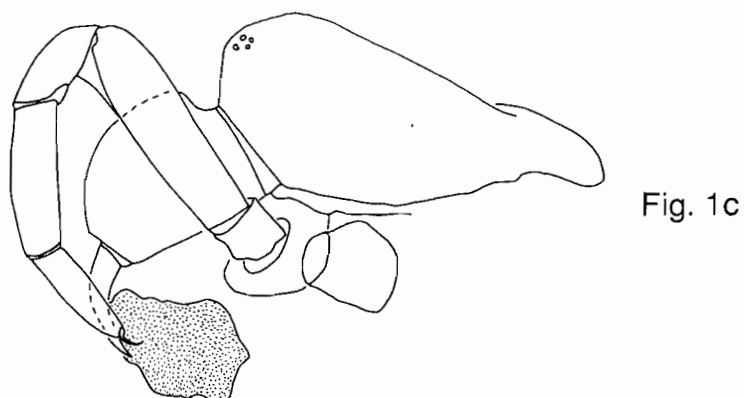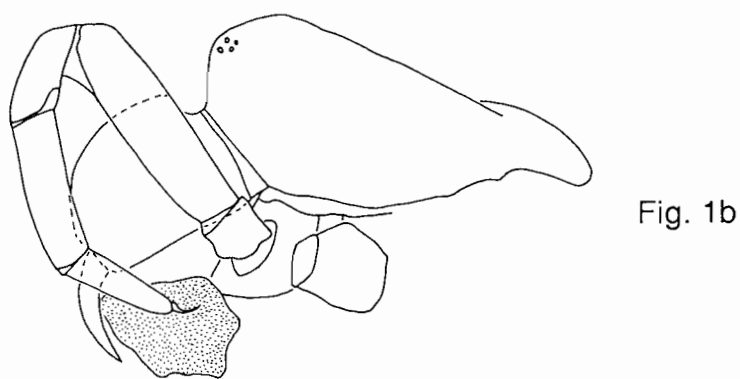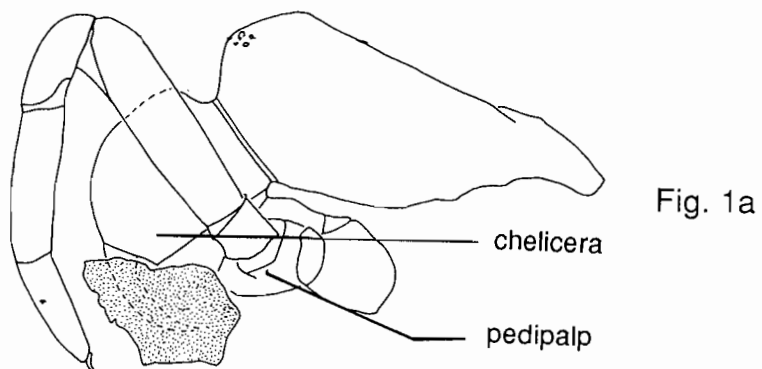
Figure 1. *Aliatypus* carrying and releasing.

Aliatypus a) carrying prior to release, b) flexing the pedipalps and extending the fangs at the beginning of release, and c) extending the pedipalps laterally along the chelicerae to release the soil load. Appendage portions hidden behind another are indicated by small dashes and the soil load is represented by stippling.

Carrying (figure 1a): The chelicerae remain spread apart while holding the soil

load. Distal to the femur the pedipalps are flexed, positioning the tarsi

slightly below the soil load but not against it. The pedipalps appear to

protect the soil load as it is transported. The spider then backs up the

· burrow, spinnerets first.

Pivoting: In order to reverse direction, the spider rotates around its dorsoventral

axis while flexing dorsoventrally at its pedicel. Pivoting occurs just within

the burrow entrance.

Releasing (figure 1b-c): The chelicerae and the fangs extend, releasing the soil

load, while the pedipalps are further flexed and raised above the

chelicerae and are then extended to pass on either side of the spread

chelicerae. The pedipalps may repeat this activity, thus removing

remaining pieces of the load.

Rim Molding (figure 2a-b): The soil load is pressed into the rim with the frontal

and dorsal surfaces of the chelicerae, while the ventral surfaces of the

tarsi of the pedipalps and first legs pull the soil inwards from outside the

entrance rim against the dorsal surfaces of the chelicerae. The

pedipalps, first legs, and chelicerae usually shift to the left and/or the right

and repeat this activity.

Silk Application: Silk is applied by raising and lowering the spinnerets in

synchrony or slightly out of phase with each other while moving the

abdomen towards and away from the area of silk application and flexing

at the pedicel. During each bout of silk application, the body is moved

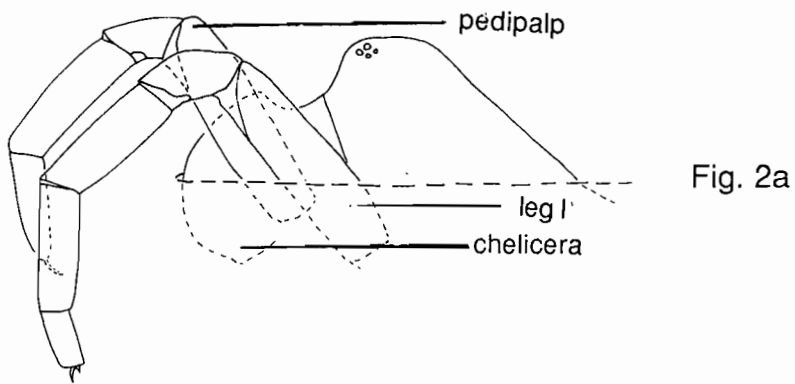both right and left so that silk is applied to 1/4 to 1/2 of the rim
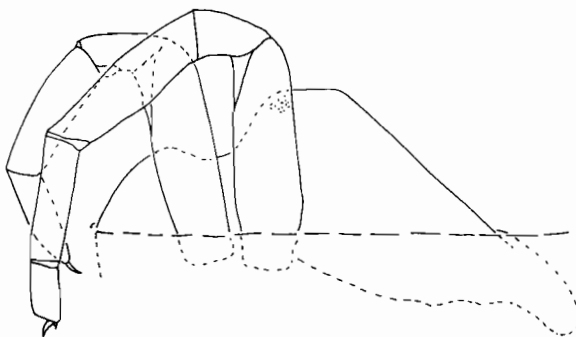
Figure 2. *Aliatypus* molding.

Aliatypus a) with the pedipalps and leg I extended and b) with the pedipalps and leg I flexed against the rim. The spider pushes against the inside portion of the rim with the chelicerae; note the change in their position from a) to that in b). The construct outline is indicated by the heavily dashed line.

circumference (although most of the silk is applied to the more limited
area of soil release).

Door Molding: Door molding is performed only at the door's edge. The
pedipalps and first legs flex, pushing the soil load into the door's edge,
. while the cephalothorax remains stationary. The chelicerae oppose the
force of the first legs and the pedipalps. This activity is also repeated to
the left and right of the area of soil release.

Door Shape Testing: While the spider positions itself at the uppermost portion of
the rim with the sternum against the undersurface of the trapdoor, the tips
of the tarsi of the pedipalps and first legs lightly tap the edge of the door
as they move along it. If the pedipalps and legs move over a notch, the
tapping concentrates there. The soil load will be placed in this notch.

Door Fit Testing: During construction, the door is periodically pulled downwards
to cover the burrow opening. This behavior usually begins when the
door's length is approximately half the diameter of the entrance. Often
the spider remains behind the door for several minutes to an hour.
During this time the spider may tap at the remaining opening with the
tarsi of the pedipalps and first legs.

Description of Entire Sequence of Door Construction

Door construction ($N = 11$) is completed within 2 to 12 hours of the
spider's placement in a terrarium. Initially one or more depressions are dug but
only one of these becomes a burrow. Soil is initially deposited immediately
outside the burrow entrance, which elevates this area, particularly downslope of

the opening. This elevated area of soil is occasionally compacted by rim molding.

Whenever rim molding occurs, it immediately follows soil release. Rim molding is infrequent in early stages of burrow construction, but becomes more frequent as construction continues. After this activity the spider pivots and often applies silk over the newly deposited soil. The spigots apply silk on top of the rim and to the inside surface of the rim and burrow. In the early stages of rim construction, releasing occurs 3 - 8 times for each silk application (N = 12, mean = 6); during later stages of rim construction silk application follows every bout of rim molding.

The rim is greatly compacted, smoothed, and strengthened by rim molding activity prior to door construction. The concentration of silk application at the dorsal-most sector of the rim extends this rim to produce a hinge 3/4 the maximum diameter of the final door. Soil is added to this silken hinge extending it as a flap (the incipient door) perpendicular to the plane of the burrow entrance. Before releasing, the spider tests the shape of the door and releases the soil load in a notch on the door's edge. Molding behavior joins this load with the door's edge. As door construction proceeds, the spider holds onto the undersurface of the door with the tarsi of the second and third legs and onto the burrow wall with the tarsi of the fourth legs. The first legs, the pedipalps, and chelicerae are thus free for door molding and shape testing activities. Pivoting and silk application follow each door molding bout. During door construction, the duration of individual bouts of silk application and door molding is longer than during rim construction.

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Once the door spans 1/3 to 1/2 of the burrow opening, the spider closes the door and remains behind the door for several minutes. The spider then continues door construction and only infrequently performs bouts of releasing, molding and silk application at the rim. Door construction is interrupted by bouts of closing and opening the door and periods of apparent inactivity which last up to five minutes. Occasionally, while the door is closed, the spider pulls the lower sector of the rim in towards the edge of the trapdoor with the tarsi of the pedipalps. Silk application does not last longer as door construction continues. Soil is occasionally applied to the burrow wall below the entrance rim, usually at the lowest sector of the wall.

The normal sequence of behavior patterns during rim construction is digging, carrying, pivoting, pausing for several seconds, rim shape testing, releasing, rim molding, pivoting and silk application. The general sequence of behaviors for door construction is digging, carrying, pivoting, moving to the uppermost sector of rim, ascending door, door shape testing, releasing, door molding, descending to rim, pivoting, ascending to door, silk application, and descending into the burrow. During door construction, some individuals extend and flex their first legs and pedipalps for two to three seconds upon emergence from the burrow. This behavior is immediately followed by rim shape testing, but there is no release of soil. The function for this behavior is not obvious. The newly completed trapdoor is often thin and flimsy, but during the course of a few more days, becomes thicker and sturdier.

ANTRODIAETUS UNICOLOR

Descriptions of Units of Behavior

Digging: The same as for *Aliatypus.*

Carrying (figure 3a): The same as for *Aliatypus.*

Releasing (figure 3b-c): The soil load is released by the repeated extension and

flexion of the chelicerae and fangs, after which the soil is pressed into the

rim by the frontal and dorsal surface of the chelicerae.and fangs.

Rim Molding (figure 4a-b): The same as for *Aliatypus*, except that during

repetitions the chelicerae remain stationary while the pedipalps and first

legs extend and flex and there is no shifting of position along the rim.

Pivoting: The same as for *Aliatypus.*

Silk Application: The same as for *Aliatypus.*

Collar Molding: The same as rim molding behavior described earlier.

Collar Shape Testing: The same as door shape testing in *Aliatypus.*

Description of the Entire Sequence of Door Construction

The specific behavior patterns involved in collar construction are

identical to those involved in rim construction. Molding (N = 3) is repeated 3 - 4

times in each bout of rim or collar molding; however, there is no shifting to the

left or right. After molding, the spider pivots before silk application and digging.

Silk is applied primarily to the interior of the burrow, rim, and collar and only

rarely outside of the rim. The spider commonly digs within the burrow while

pedipalp
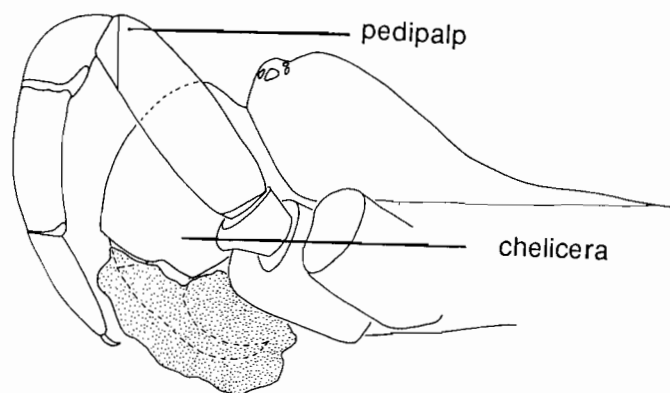
Fig. 3a
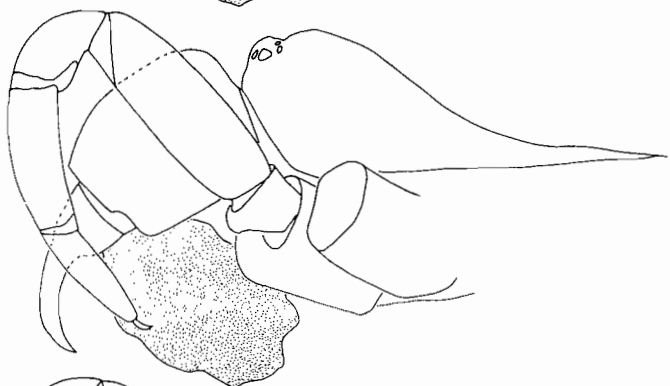
chelicera

Fig. 3b
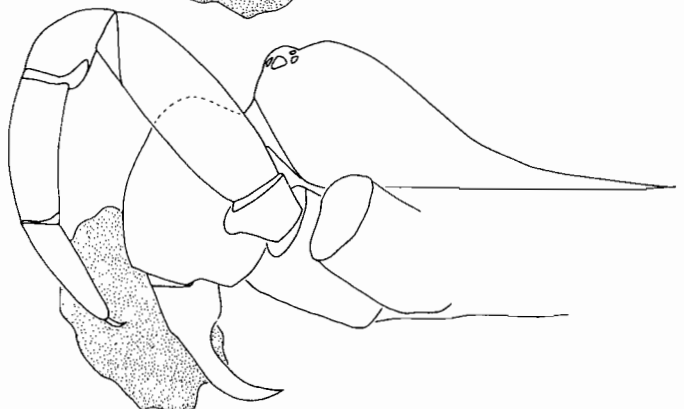
Fig. 3c

Figure 3. *Antrodiaetus* carrying and releasing.

Antrodiaetus a) carrying , b) releasing by flexing the pedipalps and extending the chelicerae and fangs, and c) extending the pedipalps at the end of release. Appendages which pass behind another are outlined with small dashed lines and the soil load is indicated by stippling.
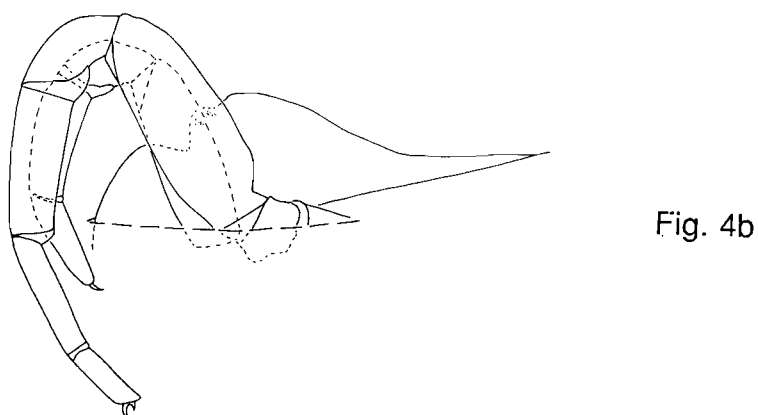
Figure 4. *Antrodiaetus* molding.

Antrodiaetus a) with the pedipalps and leg I extended at the onset of molding, and b) flexed, pressing against the outer surface of the collar. The construct is indicated by the heavily dashed line.

applying silk, as evidenced by her bringing up a soil load immediately upon finishing silk application.

The collar is built by extending the rim with the addition of soil and silk, and there is no distinct change in construction behavior in the transition from rim to collar construction. The first pair of legs is only occasionally involved in collar molding behavior. Silk is applied mostly to the edge of the rim and the inside of the collar and burrow, and is infrequently applied to the outside of the rim. Despite the molding activity, the texture of the outer surface of the collar remains coarse.

Antrodiaetus does not perform door fit testing behavior on its collar door. When the collar is completed during the light period (N = 4), the spider closes the collar by pulling inwards two opposite, lateral, sides of the collar. When the collar is completed during the dark period, the spider assumes a hunting posture after completion, waiting alertly at the rim, within the open collar door (N = 6). Such spiders, when presented with *Tenebrio* larvae, readily seize the prey and retreat into their burrows.

HEBESTATIS

Descriptions of Units of Behavior

Digging: The same as in *Aliatypus* and *Antrodiaetus.*
Carrying (figure 5a): The same as in *Aliatypus* and *Antrodiaetus.*
Releasing (figure 5b-c): The same as for *Aliatypus.*
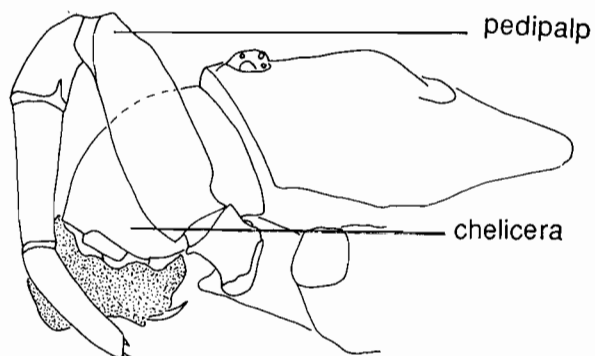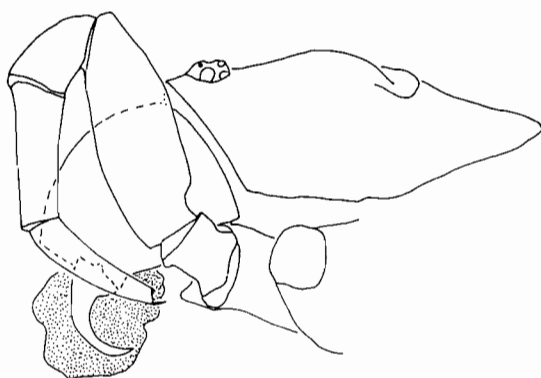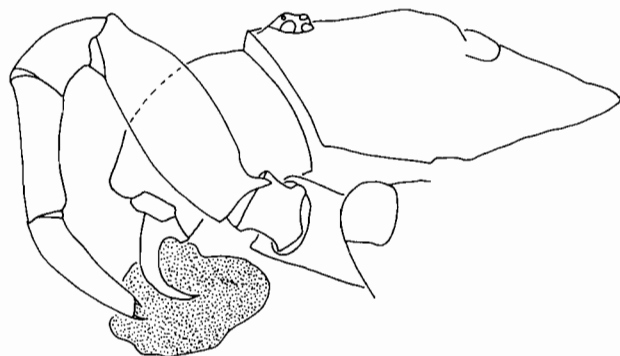
Figure 5. *Hebestatis* carrying and releasing.*Hebestatis* a) carrying the soil load, b) beginning to release with pedipalps flexed while the chelicerae extend, and c) extending the pedipalps and guiding the soil load from the chelicerae. Appendages which pass behind another are outlined by small dashes and the soil load is indicated by stippling.
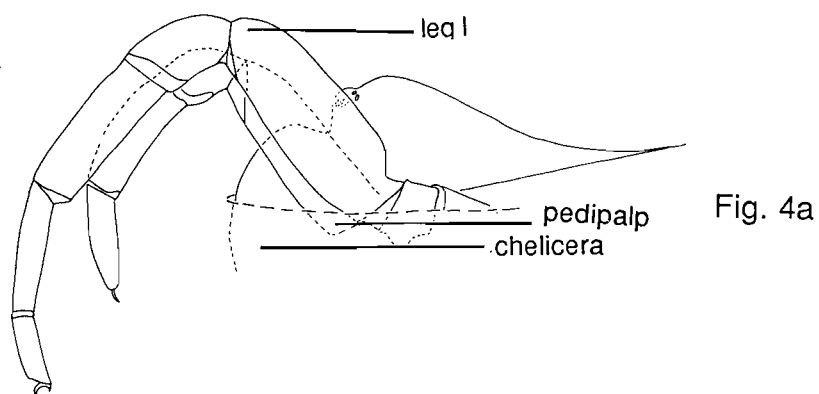
pedipalp

leg I

chelicera
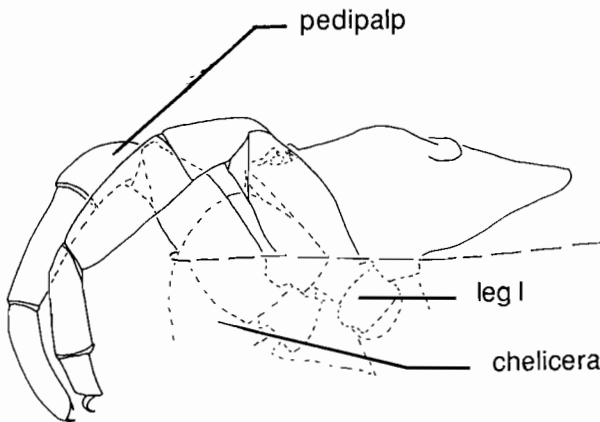
Fig. 6a
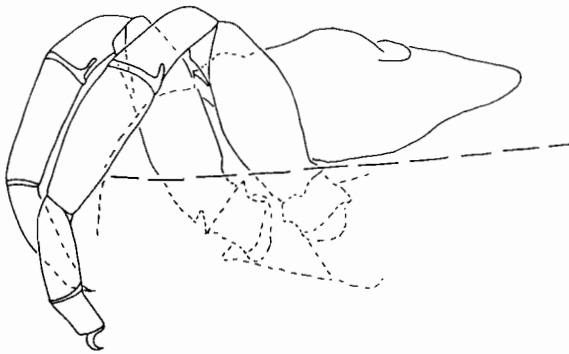
Fig. 6b

Figure 6. *Hebestatis* molding.

Hebestatis with pedipalps and leg I a) extended and b) flexed to compact the soil against the construct. The construct is indicated by the heavy dashed line.

Rim Molding: (figure 6a and b): The same as in *Aliatypus* and *Antrodiaetus.*

Pivoting: The same as for *Aliatypus* and *Antrodiaetus.*

Silk Application: The same as for *Aliatypus* and *Antrodiaetus.*

Door Molding: The cephalothorax moves the chelicerae and fangs into contact
· with the door's edge, while the legs and pedipalps remain stationary. Molding behavior occurs in the area of releasing and is then repeated to the left and right.

Door Shape Testing: The same as for *Aliatypus* and *Antrodiaetus.*

Door Fit Testing: The same as for *Aliatypus*, except that the door is forcefully pulled into the rim.

Soil Ejection: The spider facing outwards from the burrow entrance, forcefully ejects a soil load out of the burrow. The load is thrown out by the quick flexion followed by extension of the pedipalps, as the chelicerae and fangs extend releasing the load. This behavior, while not an integral part of door construction, did occur during the door construction sequence.

Description of the Entire Sequence of Door Construction:

Initial burrow construction usually begins quickly, often within 20 minutes of the spider's placement in a terrarium. The soil is released at the burrow entrance and is then pressed into the rim. After soil deposition, the spider pivots, exposing the spinnerets. Silk is applied to the area of previous soil release and the adjacent inside portion of the burrow by sweeping movements of the abdomen. During silk application digging sometimes takes place, such

that immediately upon the cessation of silk application the spider pivots and is holding soil in her chelicerae. As rim construction continues, the duration of silk application and rim molding increases. During each bout of rim molding, the molding act is repeated many times in the same place and several times to the left and right of the previously released soil. These repetitions make the rim compact and smooth and keep it flush with the substrate surface.

Door construction begins with the concentration of silk and soil on the uppermost portion of the rim. Soil is added to the rim and later the door by pressing the soil load into the construct using the fangs and the dorsal surfaces of the chelicerae. Then the construct is molded, after which silk is applied as in *Aliatypus.* The construction of a trapdoor consists of as many as 17 door molding bouts of 3 - 6 compactings each.

As the door lengthens the duration of each silk application bout increases from 15 seconds to 2 minutes. *Hebestatis*, like *Aliatypus*, positions itself against the undersurface of the lengthening door by holding it with the tarsi of the second legs and holding the burrow wall with the tarsi of the fourth legs. When the door spans 1/2 of the entrance area, the spider pulls it down over the entrance with the tarsi of the pedipalps and first legs. Rim molding often occurs after this activity. After a period of time, the door is opened and door construction is resumed for a while before it is closed again and so on. This final period of rim molding and shape testing activity produces a bevelled rim and a door which fits snugly into this rim.

Comparative Summary of Door Construction Behaviors:

There are many similarities and few differences between the collar construction of *Antrodiaetus* and the trapdoor construction of *Aliatypus*. There are four categories of differences: form, timing, orientation, and sequence (a summary of all behavioral differences is given in tables 1, 2, and 3). The form of each individual unit of behavior is identical except for differences in releasing and door fit testing (the latter is performed only by *Aliatypus*) which have no discernable effect on door form (see table 1). Timing differences (see table 2) are observed in the number of repetitions per bout of rim molding, *Aliatypus* performing three times as many repetitions in one bout of molding, on average, as *Antrodiaetus*. Orientation differences (see table 3) are observed in the location of releasing and door molding. As entrance construction progresses in *Aliatypus*, releasing (and the linked units of shape testing, molding and silk application) is most often directed to the upper-most sector and the door's edge (which develops from that sector), although some soil is occasionally released at the lower sectors of the rim.

The general sequence for entrance construction for both antrodiaetid genera studied is: digging, carrying, pivoting, door shape testing, releasing, rim or door molding, pivoting, and silk application. This sequence is repeated to complete door construction. However, *Aliatypus* often inserts door fit testing between silk application and digging and occasionally releases soil at a lower sector of the entrance.

The trapdoor construction of *Aliatypus* differs from that of the trapdoor constructing ctenizids *Hebestatis* and *Ummidia* (Coyle 1981) in the form and

Table 1. Summary of Form Differences. *Ummidia* data from Coyle´ (1981).

	Antrodiaetus	*Aliatypus*	*Hebestatis*	*Ummidia*
Releasing	pedipalps not involved	pedipalps push and guide soil by passing on either side of the chelicerae	pedipalps push and guide soil by passing on either side of the chelicerae	pedipalps push and guide soil by passing on either side of the chelicerae
	no pressing of soil load	no pressing of soil load	after release, the soil load is pressed into the construct by the dorsal edge of the flexed chelicerae	after release, the soil load is pressed into the construct by the dorsal edge of the flexed chelicerae
Rim/Door Molding	flexion of pedipalps and legs; cephalothorax remains stationary	flexion of pedipalps and legs; cephalothorax remains stationary	pedipalps and legs remain stationary; cephalothorax presses against construct	–
Door Fit Testing	no such activity	door is pulled shut by tarsi of legs I and II, the pedipalps tap along the door and rim edge	door is pulled shut by tarsi of legs I and II, the pedipalps tap along the door and rim edge	–
Silk Application	spinnerets move in synchrony	spinnerets move in synchrony	spinnerets move in synchrony	spinnerets move out of synchrony

Table 2. Summary of Timing Differences. *Ummidia* data from Coyle (1981). Mean, standard deviation, and sample size are given in parentheses. Number for rim and door molding represent the number of times the molding act is repeated per bout of molding.

	Antrodiaetus	*Aliatypus*	*Hebestatis*	*Ummidia*
Rim Molding	2 - 3 (2 ± 1, N = 17)	3 - 12 (6 ± 2, N = 12)	3 - 17 (8 ± 4, N = 17)	–
Door Molding	2 - 3 (2 ± 1, N = 8)	–	1 - 22 (13 ± 5, N = 17)	3 - 10
Silk Application (in seconds)	5 - 45s (21 ± 13, N = 7)	5 - 30s (4 ± 9, N = 6)	–	62 - 172s per construction (122 ± 14)

Table 3. Summary of Orientation Differences

	Antrodiaetus	*Aliatypus*	*Hebestatis*	*Ummidia*
Rim/Door Molding	performed only where soil load is released	also performed in areas adjacent to soil release	also performed in areas adjacent to soil release	also performed in areas adjacent to soil release
Release and Molding	activity is equally distributed to all sectors of the entrance	activity is concentrated at the dorsal sector of the entrance	activity is concentrated at the dorsal sector of the entrance	activity is concentrated at the dorsal sector of the entrance
Silk Application	covers 1/4 -1/2 of the entrance circumference	covers 1/4 -1/2 of the entrance circumference	covers the area of molding only	–

timing of some of the behavioral units (see tables 1 and 2), but shows the identical orientation for release and molding(see table 3) and great similarity in the sequence of these units. In door fit testing, *Hebestatis* appears to pull the door inwards with a great force, as evidenced by the slight bending of the door, while *Aliatypus* pulls its door downwards covering the entrance but not into the rim. *Aliatypus* and *Hebestatis* are similar in the form and timing of silk application but *Ummidia* (Coyle 1981) applies silk with asynchronous movements of its spinnerets, and silk application is longer in duration than in the former two species.

Door construction duration varies greatly within the same species due to periods of apparent inactivity lasting from 2 seconds to more than 24 hours. Construction durations, not including these periods of inactivity, were similar among the genera and lasted 1 to 1.5 hours, and are referred to as durations of active construction.

DISCUSSION

The entrance construction behavior patterns of the antrodiaetids
Aliatypus and *Antrodiaetus* and the ctenizids *Hebestatis* and *Ummidia* (Coyle
1981) are nearly identical in form and sequence, but there are some important
differences in timing and orientation (Tables 1, 2, and 3), which are
responsible for differences in door form.

Some behavior pattern differences among these taxa produce
relatively minor, but noticeable, differences in the form and function of the
entrance constructs. For example, the number of repetitions of molding per
bout is greater in the trapdoor constructing species. This increased number of
repetitions observed in trapdoor construction increases the sturdiness of a
door unit which, unlike a collar, has to span the entire entrance opening from a
limited hinge site. Similarly, differences between the trapdoor taxa in the
intensity of door fit testing and in the quantity of soil added to the door create
differences in the degree to which the trapdoor edge and the entrance rim are
bevelled. Unlike *Aliatypus*, the ctenizids have taken door fit testing to an
extreme; they greatly bevel both the trapdoor and rim by pulling the door into
the rim with great force, as evidenced by the slight bending of the trapdoor and
rim during door fit testing. More numerous additions of soil and, perhaps silk,
to the undersurface of the ctenizid trapdoor increase the thickness of the
trapdoor and probably increases the amount of bevelling. The ctenizid

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bevelling behavior probably functions in securing the door against adverse climatic conditions and renders the entrance less visible and more difficult to open by providing no free edges or prominent gaps between the door edge and rim. The bevelling and thickness of the door render the burrow both water-tight and drought resistant (Main 1957a and b, 1985, 1986).

The one behavioral difference responsible for the striking difference between the form and function of the antrodiaetid collar door (*Antrodiaetus*) and the antrodiaetid trapdoor (*Aliatypus*) is simply a difference in the orientation of soil release which occur after the transition from the rim construction phase to the door construction phase. In collar construction, soil releases are distributed about equally among all sectors of the entrance rim; in trapdoor construction, soil releases are directed almost exclusively to the uppermost sectors.

It is well documented that phylogenetically related organisms (like *Aliatypus* and *Antrodiaetus)* often share many behavioral patterns, while exhibiting some important differences, which may result from small neurophysiological and genetic differences (Bastock 1956; Rothenbuhler 1964; Evans 1966; Bentley and Hoy 1972 and 1974; Eckert and Naitoh 1972; Benzer 1973; Kung et al 1975; Koshland 1977). Bastock (1956) found that the gene mutation resulting in the yellow mutant of *Drosophila melanogaster* also causes changes in the timing of the wing display of males during courtship. Normal males repeat their wing display several times during short intervals, while the yellow mutant males repeat their wing display fewer times at longer intervals. Normal females are stimulated less by the display of yellow mutant males than by that of normal males, reducing mating success of yellow mutant

males with normal females. Thus, a change in one gene can bring about a behavioral change great enough to effect individual fitness, and thereby effect the course of evolution for the population.

Bentley and Hoy(1972, 1974), using a variety of methods including microelectrode techniques and hybridization, studied the neuronal mechanisms and genetic basis of song in the cricket genera *Teleogryllus* and *Gryllus* . They proposed two different neural mechanisms to explain the rhythms of the distinctly different songs of *Gryllus campestris* and *Gryllus armatus* (1972). The rhythm of the song of *G. campestris* is produced by the combined effect of two resonant-type oscillator neurons with strong inherent rhythms. Only when input from both of these oscillators reaches the motor neurons is song produced. The rhythm for the song of *G. armatus* is produced by a single generator neuron which has a burst of activity followed by an inactive period, another burst of activity, and so forth.

A simple modification in the neurophysiological mechanism controlling the orientation of entrance construction behavior might be sufficient to account for the large structural and functional differences between the *Aliatypus* trapdoor and the *Antrodiaetus* collar. In order to envision what kind of neurophysiological changes might have been involved it is useful to present a model for the control of orientation for each of the antrodiaetid species. Such a model is useful in at least two ways. It can be experimentally tested and discarded or modified, and it may provide some indication of the magnitude of the genetic change necessary to produce the behavioral change and hence, provide some information about the evolutionary nature and history of these behavior patterns (Wilson and Waldron 1968; Bentley and Hoy 1972).

Two orientation pattern observations in both *Aliatypus* and *Antrodiaetus* give some insight into the possible mode of control for orientation during rim, collar, and trapdoor construction. First, the general orientation to the entrance sector that will be shape tested appears to be set prior to pivoting. Upon emergence from the burrow, the spider is oriented toward one sector and does not turn to examine other sectors. There appear to be consistent limits on the radius of the entrance circumference included in a sector; i.e., shape testing only occurs along a limited portion (approximately 60 degrees) of the construct. Second, the specific location of soil release and subsequent molding and silk application within that sector is chosen on the basis of shape testing.

A neural control center for orientation is proposed that would distribute testing-releasing-molding bouts equally around the entrance circumference (figure 7). There appears to be no rigid distribution pattern for these bouts. For example, construction sometimes occurs in the same sector (but not at the same point) as the previous release. Detection of great unevenness in the rim during the previous bout of shape testing probably initiates such a repeat of construction within the same sector. If there are no large notches within the sector, the control center directs the subsequent construction bout to another sector. In other words, feedback from this shape testing may act as a deciding input for inhibiting or initiating a repeat release in the same sector. It is postulated that the sector for the next release is chosen on the basis of the location of past releases, such that sectors in which fewer releases have occurred will tend to be chosen. This sector choice can be accomplished by selective inhibition of the neurons triggering orientation toward sectors in
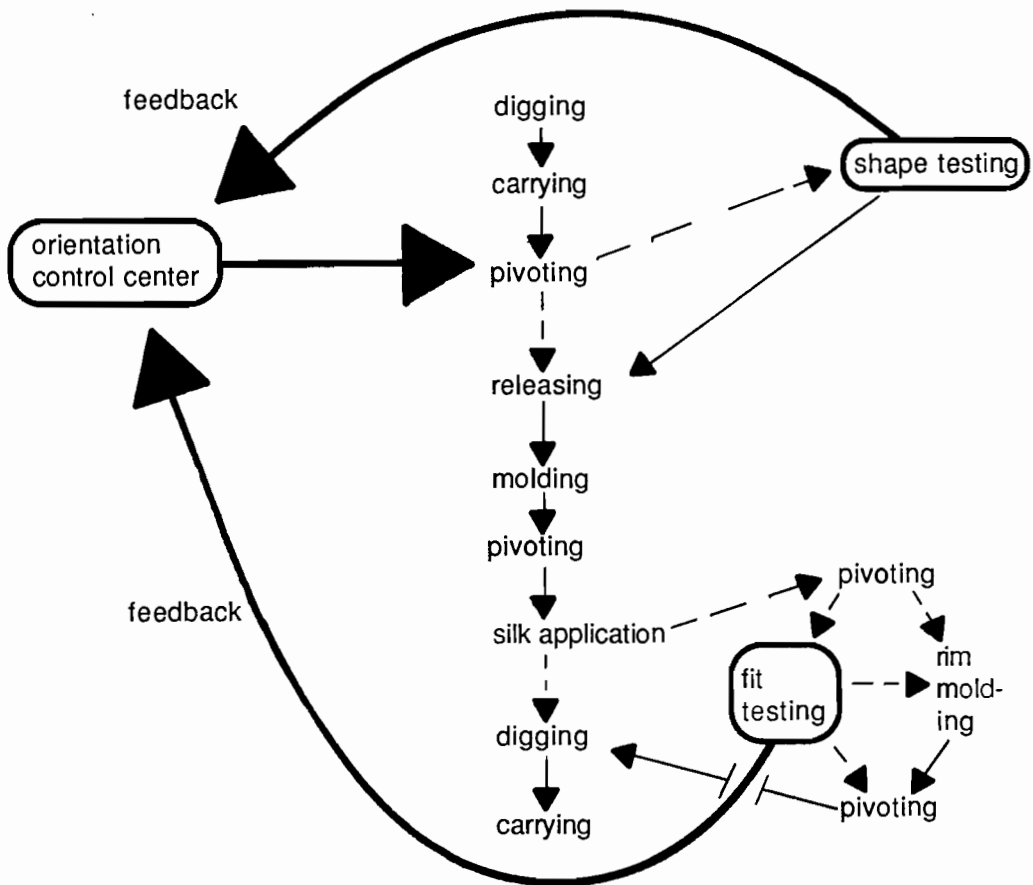
Figure 7 A general flow diagram depicting the behavioral sequence of trapdoor construction and the role an orientation neuron may play. Solid arrows show the sequence of behavioral units which always occur one after the other throughout the entire construction pattern; dashed arrows indicate alternate pathways within one pattern. Thicker arrows indicate the pathways of neural control and feedback. Feedback from the structure of a completed or nearly completed rim switches the control center activity from an all-sector mode to an upper-sector mode.

which release most recently occurred. Such a control pattern would persist in *Antrodiaetus* for both rim and collar construction, but a small change in the activity of this proposed orientation control center would trigger a shift from rim to trapdoor construction in *Aliatypus*.

- In *Aliatypus* trapdoor construction, the concentration of construction bouts at the uppermost sector is the only clue to the onset of door construction. This concentration enlarges the upper sector rim into a flap and eventually a complete trapdoor. The orientation control center would effect this change in orientational mode from an all-sector mode (rim construction) to an upper-sector-only mode by inhibiting construction bouts in the lower sectors. The cue for initiating hinge and trapdoor construction probably arises from information about the development of the rim, its shape and sturdiness, since these qualities effect the ability of the rim to support a trapdoor.

Shape testing provides information for soil release within a sector as in rim construction, but information from door fit testing also influences to which upper (door) sector the soil load will be released. Occasionally, soil will be released to the rim at a lower sector after door fit testing. This occurrence suggests that inhibition of the rim construction orientation center is not absolute.

Until more is known about the neural systems involved in these behaviors, it will be difficult to postulate confidently about what kind of neural changes are necessary to account for these important orientation differences. However, on the basis of other studies (Spieth 1954; Bastock 1956; Bentley and Hoy 1972), it seems likely that these orientation changes that are responsible for the drastic differences in door form and function between

Antrodiaetus and *Aliatypus* could be caused by a simple change in the connections of neural pathways and/or differences in the controlling neurons themselves. Such changes could effect the sensitivity to certain neural networks that feed into the orientation control centers and could be brought about by a change in as few as one gene (Bastock 1956).

The greater similarity between the door construction behaviors of the two antrodiaetid genera than exists between that of *Aliatypus* and that of the ctenizids provides only weak support for the hypothesis that the trapdoor evolved from the collar door in the Antrodiaetidae. To more fully investigate the possible derived nature of the trapdoor, a complete description of the construction behavior of the collar-like entrance of the atypid spider *Calommata* and, possibly, of entrances of other members of the family Atypidae, the sister family to the Antrodiaetidae, is most appropriate. Great similarity between the construction behavior of *Calommata* and *Antrodiaetus* would provide support for the idea that the collar construct is ancestral in the family Antrodiaetidae.

Studies of the function of various entrance constructs suggest that natural selection acts upon the forms of these structures (and consequently upon the genes controlling construction behaviors) through the actions of climate, prey detection and capture efficiency, and predators. The preferences of most *Antrodiaetus* species for relatively mesic habitats and of most *Aliatypus* species for relatively arid habitats (Coyle 1971) are consistent with the hypothesis that climatic conditions have exerted important selective pressures in the evolution of entrance forms. A trapdoor entrance should improve fitness in dry environs by sealing out heat and flood waters while

maintaining humidity within the burrow better than a collar entrance. Coyle (1986) demonstrated that *Aliatypus* has a more restricted prey detection and capture area than *Antrodiaetus* because the hinge area of the trapdoor restricts the spiders' ability to catch prey at the upper-most sector. These observations suggest the hypothesis that in mesic environs, a collar entrance may increase fitness because of its beneficial effect on prey capture area. Natural selection may act upon these entrances in other ways as well.

The multiplicity of door forms in most of the nonaraneomorph families poses the same questions of evolutionary history and of the adaptive significance of entrance constructs as it does in the Antrodiaetidae. Much evidence (Bristowe 1930; Gertsch 1979; and Raven 1985) indicates that the trapdoor has evolved independently several times among the Mygalomorphae, which might lead to the expectation of great differences in the entrance construction behaviors of different taxa. However, this study has revealed that drastic changes in door form may result from relatively minor evolutionary changes in behavior. This apparent relative homogeneity of entrance construction behaviors in mygalomorph taxa, unlike some araneomorph web constructing behaviors (Eberhard 1982 and 1987a and b; Coddington 1986), may diminish their usefulness in testing phylogenies. (My preliminary observations of retreat construction by *Sphodros abboti* (Atypidae) show that its construction behaviors are also nearly identical in form to those described). The obscurity of the evolution of entrance constructs in the nonaraneomorph spiders may persist because of the many factors affecting entrance form, the near universal nature of some of the solutions, and the

ease with which simple changes in the behavior program may cause striking construct changes.

It will be interesting to discover if other burrowing mygalomorph spiders also exhibit great similarity in their entrance construction behaviors, particularly in families containing both trapdoor and collar door constructing species, such as the Barychelidae, Cyrtrauchenidae, and Idiopidae. Because descriptions of trapdoor construction are available for a member of each of the ctenizid genera *Hebestatis* and *Ummidia* (Coyle 1981) and because Main (1957a and b, 1985, 1986) has studied the adaptive nature of entrance form and body design of some members of the Idiopidae, an intensive study and comparison of their entrance construction behaviors is appropriate. The major questions to be addressed in such investigations concern the amount of similarity in the construction behaviors, the genetic basis of these behaviors, the selective pressures which act upon these behaviors, and the usefulness of construction behaviors in answering phylogenetic questions. A hypothesis arising from the present study, Coyle's *Ummidia* study (1981), and my preliminary observations of *Sphodros abboti* is that a majority of entrance construction behavior units are conserved among mygalomorph spiders, particularly digging, carrying, pivoting, and releasing, since these units are an integral part of burrow construction as well. Differences in these spiders' construction behaviors will probably be found in the sequence, timing, and orientation of these units in their entrance construction patterns.

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