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Antennal Depression as a Consummatory Response in the Madagascar Hissing Cockroach

by

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Abstract

Sign-tracking is a counterintuitive response that occurs when a signal stimulus is paired with reinforcement. Sign- and goal-tracking studies have been replicated across several species including pigeons, rats, quail, and cuttlefish. To date, no sign-tracking studies with the Madagascar Hissing Cockroach (MHC) are in the literature. Replicating sign-tracking studies with this new species is essential to an understanding how this counter-intuitive behavior occurs, particularly in invertebrate species like the MHC. To establish research on MHC sign- and goal-tracking, however, will first require ethological studies to identify potential dependent variables that indicate MHC responses to meaningful versus neutral stimuli. This study identifies the response topography of consummatory behavior in the MHC, for use with future studies.

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Chapter 1: Introduction and Literature Review

Organismic responding is sometimes counterintuitive. For example, Jenkins, Barrera, Ireland, and Woodside (1978) created an apparatus for dogs in which a light and a food hopper were placed on adjacent walls. They found that some dogs would interact with the light, which was illuminated prior to food delivery, even though doing so had no influence over the probability of getting fed. Even more difficult to explain is that the dog would continue to interact with the light after the food was delivered, thus losing the opportunity to eat. When organisms attend to, or *track* the stimulus that signals reinforcement is forthcoming, it is called *sign-tracking*. Its counterpart, *goal-tracking*, sees responding focused on the reinforcement.

The counterintuitive nature of sign-tracking stems from an issue of experimenter perspective. Specifically, experimental work focused on operant relations might miss respondent relations that hold more influence over responding. Said differently, while we often ask questions of control through response-reinforcer relations, sometimes it is the stimulus-response relation that has the most influence over behavior, and we may not account for these stimulus-response relations (see Hearst & Jenkins, 1974). To be sure, every operant must contain, at least in part, respondent relations (see Pear & Eldridge, 1984 for a discussion of the operant-respondent distinction).

In addition to concerns of respondent-operant overlap, experimenter perspective in terms of stimulus selection might prove to be equally troublesome for interpreting research. Let's take an example with a simple discrimination paradigm. Here, a rat presses a lever in the presence of a green light to receive food. In this case, we can easily identify some variables that might influence responding, like the lever, the light, and the food, but might miss other stimuli more salient to the rat, such as smell, orientation, time of day, or the predictable patterning of shadows prior to the green light when the experimenter passes by. If the organism does not respond to the conditions as expected, it might be the case that the experimenter has failed to account for the appropriate source(s) of control. Thus, in a given operant procedure, we are never completely certain what stimulus or particular stimulus combination gave rise to the response (Hearst & Jenkins, 1974).

Sign-tracking is further complicated with the understanding that different stimuli bring about different sign- and goal-tracking patterns within species, that the same stimulus arrangement can produce different effects between species, and what qualifies as sign- and goal-tracking itself can vary between species. I turn now to the sign- and goal-tracking literature to help shed light on these important differences.

Sign- and Goal-Tracking Responses

As early as Pavlov, behavioral researchers have reported response patterns in research that are inconsistent with what would be expected given those particular experimental arrangements. When Pavlov (1934) was working with his dogs, for example, he was looking to elicit salivation by presenting a light or a sound before presenting food. After repeated presentations he noticed that not only would the dogs salivate in the presence of the light or sound, but that they would also make responses towards the light or sound. For example, after repeated pairings of a light with food, when the light turned on the dogs would lick the lamp. When a sound was presented before the food, the dogs would chomp at the air when the sound was played. The dogs were responding to the lights and sound, or the conditioned stimuli, as if they were the food.

In an operant example, Breland and Breland (1961) found that when training animals through shaping procedures, the animals would behave in ways that could not be accounted for with the theories of learning available at the time. For example, Breland and Breland placed chickens inside a caged baseball field analogue in which the chickens were restricted from entering the outfield. They trained the chickens to pull a string which, in turn, would operate a mechanical baseball bat. The baseball bat was set to hit a small baseball. If the baseball was struck hard enough (dependent on the force of the string pull), it would travel to the back fence and food would then be delivered. However, when the fence was removed between the chicken and the outfield, the chickens no longer continually worked to swing the bat. Instead, the chickens chased after the baseball.

In the chickens-playing-baseball example, clearly something else was interfering with the previously-reinforced response patterns. Breland and Breland (1961) concluded that the chickens' responses were an example of "instinctive drift." For the chickens, when food was continually paired with the baseball, the baseball became the conditional stimulus that preceded food delivery. As such, the chickens responded to the baseball as they would to any food source when made freely available: they chased it. Similarly, Pavlov's dogs licking the bulbs and Jenkins et al.'s dogs begging the light are both behavioral patterns dogs routinely produce when presented with an opportunity to feed.

The mechanisms behind instinctive drift are likely those that result in the behavioral patterning known as *autoshaping*[1]. In autoshaping, an organism acquires a conventionally operant behavior without the use of shaping by successive approximations. Autoshaping suggests that there are relations in the environment that may make the chicken learn to chase the ball rather than pull the string. One possible explanation for autoshaping is that an organism comes to respond to some manipulandum that precedes reinforcement as though the

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[1] Autoshaping was traditionally explained as an artifact of superstitious pairing (e.g., Skinner, 1948), though later accounts debunked this as an explanation (Staddon & Simmelhag, 1971).

manipulandum were the reinforcement (e.g., Brown & Jenkins, 1968). For example, Brown and Jenkins (1968) brought about a key peck response in pigeons by presenting a lit key prior to delivering food, both on fixed time schedules. As a consequence of this pairing, pigeons started to respond to the key as though it were food by pecking at it when lit. Subsequent studies confirmed these observations by showing that response topography changed as a function of reinforcement type; pigeons tended to "eat" the key when it is paired with food and "drink" the key when paired with water (Jenkins & Moore, 1973).

The most counterintuitive responding in autoshaping is seen when behavior persists towards a signal stimulus despite the absence of any advantages for responding as such. Williams and Williams (1969) extended Brown and Jenkins (1968) by lighting a key prior to the delivery of grain, but arranged the conditions so that any peck of the keylight cancelled the delivery of grain. Williams and Williams demonstrated that pigeons continued to peck the key when lighted before the presentation of grain, even if pecking the key resulted in losing the opportunity to access grain, demonstrating that consequences did not maintain pecking behavior in autoshaping arrangements. The counterproductive responding in Williams and Williams prompted Hearst and Jenkins (1974) to conceptualize autoshaping as one instance of a larger class or responding; sign-tracking.

Hearst and Jenkins (1974), in a review of the autoshaping literature found that across studies, when a stimulus serves as a sign or a signal for the reinforcer, because it has repeatedly been paired with the reinforcer, behavior is directed towards that stimulus. The term *sign-tracking* emphasizes that when this stimulus-reinforcer relation has been established, some counterintuitive behavior occurs that does not appear to be maintained by consequences. Instead of a term that focuses on the emergence of a behavior without reinforcing successive approximations, as in autoshaping, Hearst and Jenkins reclassified autoshaping as sign-tracking, to classify counterintuitive responding as specific type of learning that occurs in the presence of signals.

The point is that in sign-tracking the stimulus-reinforcer relation exerts much more powerful effects on skeletal motor action than the contingencies in place. Whether the behavior is directed at or activates a standard manipulandum is not relevant (e.g., Peterson, Ackil, Frommer, & Hearst, 1972). What is common to all sign-tracking studies is the establishment of a stimulus-event relation, with the stimulus serving as a signal for the presence of the event (Hearst & Jenkins, 1974). The factors that influence whether an organism sign-tracks or goal-tracks are the result of the manipulation of variables outside of the establishment of a stimulus-reinforcer relation.

Within-Species Differences

Sign- and goal-tracking responses can vary within species. As Hearst and Jenkins (1974) noted in their monograph on the subject, sign-tracking occurs when a stimulus-reinforcer relation is established through repeated pairings. Several factors influence the response's topography and the whether an organism sign- or goal-tracks; establishing a signal-reinforcer relation, the signal stimulus used, the reinforcer used, and the physical distance between the reinforcer and the signal. Varying each of these three factors results in differing responses and topographies of behavior.

Signal-reinforcer relation. For sign tracking to occur, the signal stimulus must indicate that an event is more probable when the signal is present. A typical sign-tracking experiment involves presenting a signal stimulus prior to a reinforcing event, such as the presentation of food. The reinforcing event is typically presented regardless of the organism's responding, somewhat resembling a Pavlovian forward conditioning procedure. In contrast to Pavlovian conditioning, Gamzu and Williams (1971) demonstrated that sign-tracking can occur without reliably pairing the stimulus and reinforcement event on every trial. Instead, Gamzu and Williams demonstrated that sign-tracking occurs when the probability of reinforcement is more likely in the presence of a signal. They did this by comparing the performance of pigeons under conditions where the probability of grain delivery was higher when a keylight was lit versus when it was not lit, and conditions under which the probability for grain delivery was the same whether the light was on or off. Gamzu and Williams found that the pigeons only pecked the keylight when there was a higher probability of grain delivery only when the light was on. When the probability for grain delivery was the same when the keylight was lit and when it was not, the pigeons no longer pecked the keylight.

Signal selection. For sign tracking to occur, it is then important that the signal stimulus be salient from the rest of the environment. For example, if you are driving east in the early morning and the sun is in your eyes at a stoplight, it is difficult to tell whether the light has changed and you can pass through the intersection. We cannot produce the behaviors that occur in the presence of a signal if that signal is obscured by other variables, such as the sun in our eyes.

For example, Wasserman (1973) demonstrated that manipulating the stimulus features in a sign-tracking arrangement affected whether a pigeon pecked a keylight. Wasserman replicated the Brown and Jenkins (1968) autoshaping procedure, but varied conditions within subject by turning the houselight on or off. The houselight-on condition was essentially the same as the Brown and Jenkins forward pairing procedure. In contrast, during the houselight-off condition, the only illuminating light in the chamber was the keylight. In the houselight-off condition, the pigeon did not peck the keylight. Wasserman hypothesized that in the houselight-off condition, the pigeon did not need to look at the keylight to know that food was available as the keylight illuminated the entire chamber making it easy for the pigeon to determine that food was available without having to direct its behavior toward the light. If the organism does not have to attend directly to a signal stimulus and can wait for other cues (e.g., light shining on an opposing wall), it is more likely to goal-track and direct its behavior towards the reinforcer. Alternatively, if a signal stimulus does not produce additional cues, such as when the houselight is on, the organism is more likely to sign-track towards the signal stimulus.

Some signal stimuli, such as a sound, have diffuse properties that make it more likely for them to produce redundant cues than a visual stimulus like a light. Imagine trying to locate someone in a forest when he or she is flashing a mirror in the sun versus when they are calling your name. Their voice may echo across the forest, making it harder to locate the source of the sound, whereas a flashing mirror does not create other flashes. As auditory stimuli produce redundant cues regardless of experimental conditions, they are less desirable for use in sign-tracking arrangements.

Some researchers have hypothesized that the diffuse characteristics of auditory stimuli inhibit sign-tracking (Hearst & Jenkins, 1974). In fact, attempts to produce sign-tracking with auditory stimuli have typically resulted in goal-tracking (see Bilbrey & Winokur, 1973; Cleland & Davey, 1983). Cleland and Davey (1983) found that rats who previously sign-tracked when a visual stimulus was used would not sign-track towards an auditory stimulus even though they had demonstrated that the rats could discriminate the presentation of the auditory stimulus, had associated it with food, could localize the source of the stimulus, and would approach the auditory stimulus when this response was required for the delivery of food. Overwhelmingly, the rats in Cleland and Davey goal-tracked towards the food bin when an auditory signal stimulus was used. Cleland and Davey attributed the differential responding (goal-tracking) to the auditory signal stimulus because of their within-subject data that compared responding to the use of a visual stimulus, where the rats sign-tracked. There is evidence that some species do sign-track to auditory stimuli (e.g., cats in Grastyàn & Vereczkei, 1974); however, these studies are often flawed by including magazine training and pre-exposure to conditioning trials prior to exposure to sign-tracking arrangements.

Reinforcement selection. The reinforcing event might influence the topography of the sign-tracking response. In general, the literature includes orienting, approach, and contact responses towards the signal stimulus in descriptions of sign-tracking responses. Peterson, Ackil, Frommer, and Hearst (1972) found that these orienting, approach, and contact responses occur even when the reinforcement is intracranial brain stimulation (i.e., a reinforcement which does not require the organism to approach its location to consume). Peterson and colleagues presented a lever prior to food delivery and brain-stimulation. They found that the rats approached and contacted the lever when it was paired with both food and brain stimulation. In other words, the reinforcer used did not affect whether the animals sign-tracked or goal-tracked. The rats reliably sign-tracked when both food and brain stimulation were presented after a lever was inserted into the chamber.

While sign-tracking was present in both reinforcement conditions, Peterson, Ackil, Frommer, and Hearst (1972) did notice a difference in the topography of responding when food was used as reinforcement from when brain stimulation was used as reinforcement. When the reinforcement was food, the rats gnawed and licked at the lever; when the reinforcement was brain stimulation, the rats engaged in “exploratory” behaviors such as sniffing and touching the lever lightly with their forepaws (Peterson et al., 1972). Peterson and colleagues were able to track these responses' features by video recording as well as enabling the lever to record any contact by the rats. Had they not made video recordings of their procedure, and only recorded lever contacts, their data would have been missing significant levels of sniffing behavior that was too sensitive for their data collection apparatus.

Reinforcement selection in sign-tracking arrangements then becomes significant because it influences data recording procedures. Jenkins and Moore (1973) used high-speed photography to observe sign-tracking behaviors when water was presented after lighting a keylight compared to grain presented after a lit keylight. Jenkins and Moore demonstrated that when water was used as a reinforcer the pigeons appeared to make “drinking” movements with their beaks and did not depress the keylight with very much force. When grain was presented with a keylight, the pigeons pecked the keylight much more vigorously, similar to pecking responses when eating.

Responding to a stimulus as if it were the reinforcer after repeated pairings, termed *stimulus substitution*, has many implications. However, the significance of stimulus substitution for this paper is two-fold; first, if reinforcement influences response topography, data collection procedures or devices should be calibrated to the anticipated response topography based on reinforcement selection. Second, that certain response topographies can be expected in sign-tracking arrangements given that we know the topography of the behaviors the organism exhibits in the presence of the reinforcer.

Distance between reinforcement and signal. Ronald Black was the first to use an unusually long chamber to show the persistence of keylight pecking by pigeons, up to a distance of 91 cm from the grain box (Jenkins, 1973 as cited in Burns & Domjan, 2000). The function of increasing the distance between the signal light and reinforcement is similar to removing access to reinforcement as previously described in Williams and Williams (1969) in that responding towards the signal stimulus effectively removes access to reinforcement. However, the longbox arrangement allows the experimenter to determine the persistence of sign-tracking over incremental increases in distance. The increased distance allows for the measurement of the persistence of orienting and approach as sign-tracking responses rather than requiring a response to a particular manipulandum, such as pecking a keylight, to remove access to reinforcement.

Burns and Domjan (2000) used a long box spatial arrangement of a signal stimulus and reinforcement in an experimental chamber to exaggerate the persistence of behavior directed towards the signal stimulus in a sign-tracking arrangement. Burns and Domjan noted that increasing the distance between the signal stimulus and the reinforcement has a detrimental effect on sign tracking across species. Across increasing distances, quails that served as subjects, were more likely to sign-track than to approach the reinforcer.

The distance between the signal stimulus and reinforcement can then serve as an experimental arrangement for determining the persistence of sign tracking behaviors, and also as an arrangement that can accommodate orienting and approach responses as dependent variables. This is important because requiring different responses for different species, as in a keypeck for a pigeon and a lever press for a rat, would confound replications across species. Thus, for replications of sign-tracking arrangements with novel species, orienting and approach responses are preferred because they are translatable between species and can be easily modified to a scale appropriate to an animal's size.

In addition, measuring orienting and approach responses to a reinforcer takes advantage of the behavior that every organism must produce when it consumes a reinforcing item; it must go near it. The fact that an organism will approach a signal stimulus more often and for longer periods than reinforcement is counterintuitive and worthy of study. In other words, to be deemed sign-tracking, it is not necessary for an organism to operate a manipulandum such as a keylight in addition to orienting, approach, or contact responses. Orienting, approach, and contact responses are overwhelmingly the dependent variables of concern in replications of sign-tracking experiments with different species (for a replication of sign-tracking with invertebrates using approach responses as a dependent variable, see Purdy, Roberts, & Garcia, 1999).

Between-Species Differences

In the study of sign-tracking, it is still unclear if the differences between species arise due to the stimuli used, or response under study (Burns & Domjan, 2000). It has been noted by researchers who have replicated sign-tracking experiments with different species that species-specific behaviors (e.g., unconditioned responses) elicited by the reinforcer exert strong effects on the strength and topography of sign-tracking behavior (Burns & Domjan, 2000). Given the factors previously discussed, the essential task for replicating a study with a novel species is to determine dependent variables that are appropriate for the behavioral repertoire of the species of concern, while still remaining relevant to the existing literature.

To determine whether behavioral processes are the same across species, it is essential to develop definitions of the behaviors of concern before experimentation. For example, a pigeon may peck at a stimulus that it is exploring, while a rat may gnaw at the same stimulus. An experimenter could easily mistake the rat's gnawing as a consummatory behavior, or the pigeon's pecking as aggression. Thus it is important for researchers to formalize the definitions of the behaviors of concern a priori. The study of identifying and formalizing definitions of animal behavior is called *ethology*.

Ethological method. Ethology is the study of animal behavior in the natural environment (Abramson, 1994). The product of ethology is the ethogram, which is produced by systematically observing animal behavior. An ethogram catalogs the topography of behaviors for a particular species by function; such as eating, mating, and aggression (Abramson, 1994). The ethogram can consist of a single member of a species or several members of a species, and describe a single behavior, a chain of behaviors, or multiple behaviors (Abramson, 1994). A famous example of a researcher creating an extensive ethogram is Jane Goodall's studies of chimpanzees. The complexity of ethograms ranges from comprehensive studies, such as Goodall's lifetime of work, to a single observation.

The interests of the researcher determine the complexity of an ethogram. However, there are several essential elements that must be taken into consideration, namely; decisions must be made on which behaviors to include and exclude in a definition, how to define and record an instance of behavior, and how to categorize behaviors in a manner that relates to categories established in the literature (Abramson, 1994). Deciding which behaviors to include in a definition is determined by observing an organism in a particular environmental arrangement across multiple observations. For example, recording the behaviors present when a domesticated dog eats prepared dog food may include sniffing, licking, and consuming food. When eating prepared dog food, the dog does not hunt or chase after the food bowl. Hunting and chasing behaviors would be excluded from an ethogram of eating behaviors in a domesticated dog. After observation, the eating behaviors would be categorized as either approach or consummatory behaviors. Perhaps, across observations the dog sniffed the food before putting its mouth in the bowl to grab food and chew it. In this case, sniffing is an approach response and the mouth in the bowl and chewing is a consummatory response. The approach and consummatory definitions can then be compared across species. Additional observations or a search of the literature could compare the ethogram of the dog's food approach and food consumption behaviors to another species, such as a wolf.

The domesticated dog example reveals that the ethogram must be standardized to the point where comparisons between and within species are possible. While attempts to create a standard ethogram across species have been made, (see Schleidt, Yakalis, Donnelly, & McGarry, 1984) researchers such as Abramson (1994), have instead recommend that ethograms be standardized to the point that they are reproducible across researchers, and valid representations of the behaviors of concern. Developing reproducible, valid ethograms is a function of repeated observations within a study, and between studies. The validity of an ethogram cannot be determined on an a priori basis. Instead, the validity of an ethogram is determined by its repeatability within a species across observations.

The reproducible results of an ethogram allow researchers to standardize their interpretations of behaviors. A pigeon's peck could be interpreted as aggression if we only observe once. However, if we repeatedly see that pigeon pecks only occur when a new object enters the environment, and does not peck, but instead flaps its wings when defending its young, we can determine the function of the behavior. The pigeon pecks new things to find out what they are, and the pigeon flaps its wings to scare off intruders. While these are not actual ethological findings, the point is that we cannot assume the function of a behavior until we have recorded its occurrence across observations. Only once we have determined the environmental conditions under which pecking reliably occurs can we classify pecking as exploratory or aggressive behavior.

Determining the function of behavior a priori is essential to designing and interpreting replications of experiments with a novel species. For example, if we used a novel stimulus, such as an aluminum can, as a signal stimulus in a sign-tracking arrangement with a pigeon, the pigeon would likely begin to peck the can. If we had not determined the function of the peck prior to the study we could potentially, and erroneously, conclude that the pigeon is sign-tracking. Instead, it is likely that the pigeon is exploring a novel stimulus in its environment, given what we know about when a pigeon pecks at objects from our ethological study. If we know the conditions under which a particular species exhibits particular behaviors we can use that information to construct and interpret replications of experimental arrangements with that species. Without that knowledge, we are working off of assumptions of the functions of behaviors, which can confound the interpretation of results.

Sign-tracking with a novel species. Purdy, Roberts, and Garcia (1999) replicated a sign-tracking arrangement with cuttlefish by first conducting an ethological study of cuttlefish approach and consuming behaviors. Purdy and colleagues then developed an ethogram of cuttlefish foraging behaviors to determine orienting, approach, and contact responses when capturing prey. Conducting an ethogram prior to creating and implementing a sign-tracking arrangement allowed Purdy and colleagues to track particular behaviors during the sign-tracking arrangement, which essentially took the guess work out of determining whether the animal was exhibiting an approach response.

Purdy, Roberts, and Garcia (1999) then implemented an alternating treatments design where one condition delivered food paired with a signal stimulus some distance away from the food, and another where the same stimulus was presented at random times relative to the presentation of food. Presenting the food and light at random times served as a control as to whether the cuttlefish was approaching the signal stimulus because it was paired with food, or if the cuttlefish approached the signal stimulus even though it was not paired with food. As discussed in the introduction, according to Gamzu and Williams (1971), the animal should be more likely to approach the signal stimulus when there is a higher correlation between the presence of the signal stimulus and reinforcement, and less likely to approach the signal when it is not paired with reinforcement. Purdy, Roberts, and Garcia (1999) found that in the paired condition, there were a higher percentage of approach responses to the signal stimulus than there were in the unpaired presentation.

The procedures in Purdy, Roberts, and Garcia (1999) can serve as a model in creating replications of sign-tracking studies with novel species. Purdy and colleagues took care to determine species-typical foraging behaviors prior to implementing the sign-tracking arrangement, and to demonstrate differential responding between paired stimulus-reinforcer conditions and unpaired stimulus-reinforcer conditions. Conducting an ethogram prior to the sign-tracking study allowed the researchers to anticipate species typical foraging responses a priori, and to determine experimental controls appropriate to their subjects. In order to do the same with the MHC, there are several variables that require specific consideration. Specifically, determining reinforcement and an appropriate signal stimulus require an investigation into the particular biology of the MHC.

The Madagascar Hissing Cockroach

Cross species replication is essential in basic behavioral research. To date, there have not been any replications of sign-tracking arrangements with MHC. A demonstration of sign tracking behaviors with the MHC would demonstrate the generality of this phenomenon across species.

Charles Abramson, a leading researcher in invertebrate behavior, has said that the first rule of basic behavior experimentation is to “know your animal” (Abramson, 1990, p. 2). What Abramson meant was that an experimental arrangement should consider and take advantage of the phylogenic history of an animal in its design and implementation (Abramson, 1990). The MHC is an endemic species that can only be found on the island of Madagascar, and MHCs have unique biological characteristics which differ from other species of cockroach; most notably its distinctive hiss and a lack of wings (Mulder, 2008). Atypical behavior patterns relative to other closely related cockroach species have been noted in ethological studies (e.g., Barth, 1968). In effect, decisions on the selection of materials and apparatus designs cannot be made based upon arrangements that were successful with similar species.

Ethological studies begin by exploring the particular biology of a species. In sign-tracking studies, reinforcer selection, apparatus design, and the signal stimulus must be adapted to the biology of the MHC. This section highlights research on the sensory capabilities and typical responses of the MHC under particular environmental arrangements. This research helps us to better orient to our subject matter and decisions in construction a sign-tracking arrangement.

Feeding behaviors and diet. It is hypothesized that MHCs are opportunistic feeders that scavenge the forest floor in a tropical climate and are mostly herbivorous, but are known to be omnivorous (Mulder, 2008). In lab settings they eat most forms of dry pelleted food that is occasionally supplemented by fresh fruit or vegetables. However, they do not require frequent feeding. They have an especially slow digestive system that may take up to one month to completely void food (Davis, Gamble, & Matheson, 2008). Research has also shown that MHCs are sensitive to nutritional deficits in their preference for food, and that preference may differ by sex (Carrel & Tanner, 2002). However, very little is known about their feeding habits. Identifying the latency to approach and consume food is essential to the design of a sign-tracking apparatus as it informs the schedule of food delivery in an experimental arrangement. Factors such as dominance, sex, and levels of food deprivation should also be taken into consideration to determine if subjects differ within species in their feeding habits.

Hydrophilia and water conserving behaviors. MHCs can tolerate up to 28% weight loss due to dehydration (Yoder & Grojean, 1997). To conserve water, MHCs huddle together, which helps them to tolerate extremely dry conditions for long durations (Yoder & Grojean, 1997). Given the low tolerance for dehydration in dry conditions, it is here suggested that water deprivation may serve as a motivating operation for foraging for water, perhaps more effectively than food deprivation.

Sight. The eyes of the MHC closely resemble those of the American Cockroach (Mishra & Meyer-Rochow, 2008). According to Mishra and Meyer-Rochow (2008), MHCs and American Cockroahes have an ability to detect linearly polarized light, and also have green and UV receptors in their eyes. The ability to see polarized light is advantageous in dark habitats where animals with color vision, such as humans, struggle to see movement when little light is available to bounce off of objects in the environment. The MHC's natural habitat is the forest floor, where there is very little light. On the forest floor, animals that can see polarized sight have a greater advantage in that even minimal light bouncing off of detritus on the forest floor is contrasted in polarization from light bouncing off of moving animals (Mishra & Meyer-Rochow, 2008).

While creating the conditions to produce polarized light are simple (e.g., shining a light through a thin slit in a piece of cardstock), it is also possible that a simpler stimulus (e.g., a green

LED that emits green light) is detectable by the MHC. American Cockroaches demonstrated conditioned antennal movements in a Pavlovian conditioning procedure with a green LED as the CS (Lent & Kwon, 2004). Given that MHC's eyes are similar to the American cockroach, they will likely respond likewise to the same stimulus.

Hearing and hiss. MHCs are named for their distinctive hiss, which is produced when air is forced through the same spiracles, or holes in their sides, through which they breathe (Mishra & Meyer-Rochow, 2008). Clark and Moore (1995), in a study of the topography of the MHC hiss, found that of the 200 males that were tested, only about 60% ever made a hiss during observations. What they found was that the MHC's hiss only occurs when specific conditions are present, which then correspond to the topography of the hiss.

There is a positive genetic and phenotypic correlation between the duration of the MHCs hiss when aggressing and the weight of a MHC male (Clark & Moore, 1995). Males that are more aggressive have a lower frequency hiss and longer hisses (Clark & Moore, 1995). Termed *honest signaling*, because the topography of a hiss directly correlates to a MHC's size, a hiss will allow smaller males to avoid fights with larger males, because they can determine from a hiss whether the other male is larger than them (Clark & Moore, 1995). Additionally, studies show that the courtship hiss is a necessary part of the mating ritual in that males whose spiracle was blocked with glue were unable to successfully mate with a female (Clark & Moore, 1995). The necessity of the hiss in mating and dominance rituals suggests that MHCs are able to discriminate between stimulus gradients of the hiss by other roaches, or a lack thereof.

***Sound as a signaling stimulus*.** Some species have been known to sign-track with an auditory stimulus (e.g., cats in Grastyán & Vereczkei, 1974). However, sign-tracking responses with auditory stimuli vary from species to species (e.g., Cleland & Davey, 1983). Given the inconsistent results in the literature, an auditory signal stimulus is not ideal for the purposes of this study. Also, given that sound has diffuse characteristics, it would be difficult to tell if an auditory stimulus creates redundant cues that inhibit sign-tracking (see previous discussion of signal stimulus selection). For these reasons, auditory stimuli are not likely to be successful in a sign-tracking arrangement with the MHC.

As the MHC has demonstrated differential responding to subtle variations in topography across auditory stimuli (e.g., Clark & Moore, 1995), it is possible that environmental noises may overshadow programmed stimuli in an experimental arrangement. However, differential responding has only been demonstrated with respect to a specific auditory stimulus, the MHC hiss. While it is not known how sensitive MHCs are to auditory stmuli as a whole, given that auditory stimuli are unlikely to influence sign-tracking, and the fact that only auditory stimuli are significant to the MHC under specific conditions, environmental noises are unlikely to affect dependent variables significantly.

Scent. Previous studies (e.g., Balderrama 1980; Watanabe, Kobayashi, Sakura, Matsumoto, & Mizunami, 2003; Watanabe & Mizunami 2006) have demonstrated that several species of cockroaches are capable of signal learning in a discriminatory conditioning procedure. Harri-Dennis, Heys, & Witts (2015) demonstrated differential conditioning of preferred stimuli with non-preferred scents using MHCs as subjects. When responses were averaged, there was an increased allocation of responding towards a non-preferred scent. However, individual responding was highly variable. No ethological studies of responding to scent have, as of yet, been published.

Experimental Considerations for the Madagascar Hissing Cockroach

Sign-tracking is brought about under conditions where a signal stimulus reliably indicates that reinforcement is available (Hearst & Franklin, 1977). To demonstrate that a signal stimulus has control over responding, a control condition, where the signal stimulus is not paired with reinforcement, is contrasted with an experimental condition where the signal stimulus is presented just before reinforcement (e.g., Gamzu & Williams, 1971). Several considerations are essential for the design of a sign-tracking apparatus: reinforcement selection, signal stimulus selection, apparatus design, and experimental controls. Each of these considerations must be tailored to the particular phylogenetic history of the subject. Addressing each of these factors allows us to determine whether sign-tracking and goal-tracking responding are due to the experimental arrangements and not due to extraneous factors.

Response selection. Determining whether the MHC sign- or goal-tracks can be determined by whether the MHC approaches or contacts the signal stimulus or reinforcement (Burns & Domjan, 2000). If the MHC approaches the signal stimulus on the majority of opportunities, it is sign-tracking. If the MHC approaches reinforcement on the majority of opportunities, it is goal tracking. It is not necessary for the organism to operate a manipulandum.

Before approach and contact responses are recorded, they must be defined. To define the behaviors of concern we must know what the MHC does when it is foraging for food or water. It is then necessary that an ethogram relevant to foraging behavior must be conducted with the MHC prior to sign-tracking experimentation. An ethogram is a tool for coding and sequencing species typical behaviors. The process of creating an ethogram is similar to a descriptive assessment in that there are no particular responses that are necessarily part of an ethogram. Rather, the relation of responses to other events determines the responses of concern. For example, the movement of antennae just before the MHC consumes a piece of banana can be a part of a foraging response. If across several observations the antennae always move in the same direction before the MHC eats, pointing the antennae is likely a part of a foraging response. If across several observations the direction and movement of antennae vary before the MHC eats, antennae movement and direction are not indicative of foraging behavior. Identifying the chain of behaviors that reliably correlates with consuming food or water allows us to differentiate when the MHC is approaching a stimulus versus when it may just be moving around.

To know whether a behavior is indeed an appetitive foraging behavior, its link to the consummatory behaviors must be empirically demonstrated. The use of statistical analyses in descriptive assessments to determine a correlational relation between behaviors has been demonstrated in the applied literature by the use of a conditional probability analysis (e.g., Fritz, Iwata, Hammond, & Bloom, 2013). To determine the precursors to self-injurious behaviors, Fritz, Iwata, Hammond, and Bloom (2013) presented discrete trials similar to the attention and demand conditions of a functional analysis of problem behavior. Fritz and colleagues identified seven categories of behavior topographies present in taped observations. From these categories, potential precursor behaviors were identified and defined. After precursor behaviors were defined, the tapes were again reviewed and each trial was scored as having the occurrence of precursor behaviors, or the non-occurrence of precursor behaviors. After the precursor behaviors were scored, several conditional probability analyses were calculated and compared for each potential precursor. The conditional probabilities were as follows: the conditional probability of the target behavior given the precursor, conditional probability of the target given the absence of the precursor, the unconditional probability of the target, the conditional probability of the precursor given the target, conditional probability of the precursor given the absence of the target, and the unconditional probability of the target.

A similar arrangement can be used to define and determine orienting, approach, and contact responses in the MHC by setting up an analogue foraging arrangement where food is introduced into an apparatus after the MHC has been allowed to acclimate to the apparatus for several minutes. The target behavior would be the consummatory response. Behaviors that occur before and after food is introduced into the apparatus can be logged and categorized. Then, once defined, the behaviors can be scored as occurring before a consummatory response or non-occurring before a consummatory response. Conditional probability analyses can be calculated for the behaviors scored. Behaviors that are more likely to occur prior to consuming a food item can be identified as orienting and approach responses.

This process results in creating an ethogram in that through repeated observations, behaviors that consistently occur before eating are identified as foraging responses. The specific topography of each behavior is noted and coded over several observations to ensure that the chain of behaviors observed before consuming food is consistent.

The behaviors identified in an ethogram as described can determine whether the MHC is exhibiting foraging behaviors in the presence of the signal stimulus. Having the specific knowledge of what behaviors the MHC exhibits when foraging is also essential to designing the apparatus and experimental arrangement. If the MHC always touches the banana with its antennae before eating it, but never touches the light with its antennae, touching something with its antennae is likely an approach response. If after several pairings with food the MHC begins to touch the light with its antennae, this could then be an indication of sign-tracking.

The behaviors of concern for the ethogram are then foraging behaviors and behaviors that occur in the presence of the signal stimuli. The ethogram then serves as a descriptive assessment to determine which responses will serve as dependent variables in future research, such as with sign- and goal-tracking preparations.

Reinforcement selection. As MHCs are opportunistic feeders, their biology supports long periods without food. While food is the most frequently used in sign-tracking research, additional studies have used water, heat, and sexual reinforcement (e.g., Burns & Domjan, 2000). Recent studies with MHCs have found that fruit and fruit-based foods (e.g., juice) are highly preferred (e.g., Harri-Dennis, Hayes, & Witts, 2015). However, it is essential to quantify the effect that any reinforcers have on MHC behavior by determining the reliability of MHCs to approach items when they are placed in the environment. For example, if an MHC only eats a banana on 5 out of 10 opportunities, it is not clear if the organism is not eating the banana because it is not hungry, or because it is simply not a preferred food. In contrast, if the MHC eats the banana on 9 out of 10 opportunities, it is less likely that preference or satiety influenced responding. Reliability of approach and contact responses are essential to determining the schedule of delivery in the sign-tracking apparatus.

Signal stimulus selection. Previous sign-tracking studies demonstrated that the signal stimulus must be localizable, but should not create redundant cues in the experimental environment (e.g., Wasserman, 1973). This study will evaluate light as a putative signal stimuli.

An ethogram that describes approach and contact responses, if any, to a light when introduced into an apparatus is essential in ensuring that the light is indeed a neutral stimulus. If the MHC has a similar topography of behaviors when a light is turned on as when searching for food, it will be difficult to tell whether the light is producing the behavior or the reinforcement.

However, if when the light is introduced the MHC has markedly different topographies of approach and contact behaviors from when a banana is introduced, any changes in topography during experimentation can be contributed to the stimulus that produces those behaviors. Evidence of sign-tracking would be seen when the roach then responds to the light as it would to the banana, assuming topographically-distinct response patterns to these two stimuli.

Previous studies with American Cockroaches, who have a similar eye structure to MHCs, demonstrated associative learning with a green LED as the CS (Lent & Kwon, 2004). It is likely that a similar signal stimulus would be successful in a sign-tracking arrangement with Madagascar Hissing Cockroaches, but it is not guaranteed.

Subject selection. While differences in food preference between male and female MHCs have been noted in the literature (e.g., Carrel & Tanner, 2002), it is not clear if there is a difference in orienting, approach and contact responses between male and female MHCs. Ethological studies can determine whether males or females have differences in reliably approaching and contacting food and water sources. It is possible that orienting, approach, and contact responses may have different topographies between sexes as well. Within sex ethograms between dominant and non-dominant males have not been conducted in the literature. An ethogram of foraging behavior should include dominant male, non-dominant male, female, and juvenile subjects to ensure replicable responding within the species.

Apparatus design. In sign-tracking arrangements, the signal stimulus and reinforcer are made available on fixed schedules independent of the organism’s responding. Ethological studies in the proceeding section will determine the frequency of presentation that is likely to lead to signal learning. Additionally, MHCs do not necessarily move quickly (see Harri-Dennis, Heys, & Witts, 2015). While slow responding can be a function of motivation as well as species-specific factors, these issues must be addressed as a part of an ethological assessment. If ethological studies reveal that longer ITIs are necessary for reliable responding, this finding can influence the design of a sign-tracking arrangement. As previously noted, it is not known how often MHCs feed, but data collection on eating behavior during an ethological assessment can provide data to make any necessary future iterations of an apparatus more successful.

Experimental controls. In sign-tracking arrangements, the specific response towards a signal stimulus does not need to be known a priori. The response of concern is simply any directed action towards a signal stimulus. Thus, it is not necessary for us to know whether the MHC will touch the signal stimulus with its antennae or mandibles for sign tracking to occur; it is the approach response that is of concern. However, ethological studies prior to implementing a sign-tracking arrangement can reveal whether subtle behavior patterns (e.g., antennae position) occur when approaching the signal stimulus. This can give us additional evidence of changes in responding if other variables (e.g., latency to response) are not appropriate to the MHC.

The purpose of the study was to determine the behaviors highly correlated with approach and consummatory behaviors. Identifying these behaviors will support any data that the MHC is approaching and contacting the signal stimulus in a sign-tracking arrangement, and not simply in proximity of the signal stimulus. This is because, if reinforcement is found to influence response topography, data collection procedures can be calibrated to the anticipated response topography and use the response topography as a dependent variable. Creating an ethogram to determine the orienting, approach, and consummatory responses typically seen in the MHC thus identifies dependent variables for sign-tracking work. It was also demonstrated that those responses were not seen with signal stimuli. To date, no investigations of approach or consummatory responses have been conducted in the MHC. Ethological studies are then necessary inform data collection for future studies, such as sign-tracking experimentation. Determining an approach and consummatory response will also support whether the MHC will sign-track under conditions that are similar to sign-tracking arrangements with other species.

Chapter 2: Method

Subjects

Two separate colonies, one male and one female, were kept in a lab, a room that was not used for other purposes at the time of the experiment. Nymphs were kept in both colonies until they could be sexed. The lab had one north-facing window that had the shades drawn, or lights turned on, to keep a 12-hour night/day cycle. Night and day cycles were not reversed as sessions were conducted in evening hours. Each habitat, male and female, were kept at a temperature of 25°C, which was maintained by an adjustable heat lamp. The habitats were separate terrariums, where substrate in each colony was terrarium carpet and woodchips. Food in the form of commercial dry dog food was available in each colony at all times, except during the banana assessment. Water was sprayed on the walls and on a water dish one time per day, except during the water assessment. Three structures were provided in the male colony where dominant males could establish territory. Hiding structures were provided in the female colony.

For this study, three dominant male roaches, three non-dominant male roaches, three female roaches, and three juveniles were selected from the lab source colony. The three roaches that were found the most frequently on top of structures in the colony for two observations per day for one week were selected as the dominant male roaches. Three non-dominant males were selected as the three males that were not observed on top of any structure for two observations a day after one week. Three juvenile nymphs were selected at random from the male and female colonies. Three females were selected at random from the female colony.

Apparatus

A white plastic 11-quart dishpan was used for all observations (see Figure 1). A piece of white standard letter paper was placed at the bottom of the dishpan for each observation, and changed out for each subsequent observation. A grid of one-centimeter squares was printed on the paper to assist with measuring the distance of the MHC relative to the substance placed in the apparatus. The walls of the apparatus were coated with a thin layer of Vaseline© beginning at 3 cm above the base of the dishpan. All observations were recorded with the camera app on an iPhone® attached to a stand that was not attached to the apparatus, positioned to record an overhead view of the apparatus. A stopwatch timer was used to measure latency data to approach and contact, and the duration of the trial.

Putative reinforcers, water and bananas, were placed in the apparatus on 1 cm^2 plastic Plexiglas® squares. Bananas were cut into approximately 2 mm^3 cubes before being placed on the plastic squares. Water was placed on the plastic squares two drops at a time from a marinade injector syringe.

For the signal-stimulus ethological assessment, the apparatus was the same as the putative reinforcer assessment. However, instead of banana or water placed in the apparatus, a 5 mm green LED was placed through a hole in the tub glued to the bottom of the apparatus. The light was turned on by a switch that could be operated without disturbing the apparatus.

Pilot Study

Before the assessments were conducted, a pilot study of the discrete behaviors that reliably occurred in the 10 seconds before and after drinking was completed. Each subject was placed in the apparatus, after the subjects was allowed to acclimate for two minutes, two drops of water were placed in the apparatus on a plastic square 10 cm away from the head of the subject. If the MHC drank the water, the experimenter waited two minutes before removing the MHC from the apparatus. If after five minutes the MHC did not drink the water, it was removed from the apparatus. Each trial was videotaped, and later reviewed with a second observer.

The experimenter and the second observer reviewed the videotapes at the same time. Discrete behaviors were identified and operationally defined by both observers first independently identifying any potential discrete behaviors. The lists were compared and an operational definition was developed for each discrete behavior that was agreed upon by both observers. If certain behaviors had similar topographies, they were grouped together (e.g., climbing and sticking stationary to walls) and were given one definition and defined as the same behavior. The discrete behaviors included: several iterations of antennal position and movement, climbing, touching with antennae, touching with mandibles, eating or drinking, antennal depression, grooming, freezing, and head rearing (for operational definitions, see Appendix B).

These definitions were used to code for the occurrence and non-occurrence of behaviors in the video assessment (see Video Assessment below). However, it became clear during the first scoring session that the only reliable response with predictive utility was the antennal depression. Given that the occurrence of the target behaviors was scored in the pilot study using video, and the video assessments were scored using still shots, many of the discrete behaviors identified in the pilot study could not be scored in the video assessment. Specifically, operational definitions that included movement (e.g., scanning, turning), could not be reliably scored in the video assessment. Also, other behaviors that could be reliably scored (e.g., climbing) were not scored at all by the end of the first scoring session. In contrast, *antennal depression*, defined as: both antennae, or one antenna if only antenna was intact, pushed into the floor of the apparatus in a stationary position, or at least the tips or more of the antennae are touching the floor of the apparatus while stationary, was scored in the video assessment for each subject. This narrowed the focus to assessing whether antennal depressing was more likely to occur during approach and consummatory behaviors in the following procedure and video assessment.

Procedure

Banana and water ethological assessments. The assessments for water occurred first and were completed in their entirety before the assessments for banana began. Assessments were conducted one time per day with each subject. All observations were recorded for their duration. Each observation session was conducted with one MHC at a time, for a maximum of 5 minutes excluding an acclimation period of two minutes. Prior to each observation session, a new piece of paper was placed in the bottom of the apparatus and then the roach was placed in the apparatus, a timer was started, and the subject was allowed to acclimate for two minutes. After two minutes passed, the experimenter placed either a 1 cm^2 plastic square with banana or water in the apparatus 10 cm away from the MHC. Whether the roach ate or drank, and the latency to eat or drink were recorded on a data sheet for each trial (see Appendix A).

Once the banana or water was placed in the apparatus, the MHC remained in the apparatus for up to 5 minutes. If after 5 minutes the roach had not consumed whichever substance was placed, it was be returned to the colony. If the MHC consumed the substance, the experimenter waited for two minutes after the MHC finished consuming the item before returning the roach to the colony. Waiting two minutes after consumption was necessary to prevent accidental punishment for consumption if handling was aversive (see Davis & Heslop, 2004).

Subject selection criteria. Each of the banana and water assessments for each MHC ended after 10 trials if the roach met the criteria for consuming the banana or water respectively on 8 out of 10 trials in a row on each assessment. If the roach was ineligible to meet the criteria on 8 out of 10 trials in a row, the assessments for banana and water respectively were ended after 10 trials. The assessment continued past 10 trials if the roach was eligible to meet the eight out if 10 consecutive trial criteria. However, a maximum number of 15 trials were allowed to meet the 8 out of 10 trial criteria.

MHCs that did not consume the item on 8 out of 10 consecutive opportunities were eliminated from the study. In other words, if female subject one drank the water on 9 out of 10 consecutive opportunities within 10 trials, and dominant male subject two drank the water on 5 out of 10 opportunities within 10 trials, dominant male subject two was eliminated from the study.

Light assessment. The assessments for light were completed after both the banana and water assessments were conducted in order to demonstrate that antennal depressions did not occur in the presence of non-consumable stimuli. Light assessments were conducted only with MHCs that met the subject selection criteria. Presentations of the light occurred once per day using similar procedures to the banana and water foraging ethological assessment in that a two minute acclimation period began the trial, before a 5 mm green LED glued to the bottom of the apparatus was switched on. Light trials, differed in that they lasted for 5 minutes before the MHC was returned to the colony on all trials, without any response criteria. Only 10 trials of the light assessment were conducted for each MHC that met the subject selection criteria.

Video Assessment and Recording

After the assessments were completed, a still shot was created for each of the 10 seconds before the water or banana was placed in the apparatus, the ten seconds before the MHC consumed the item, and the ten seconds after eating or drinking began. Only the videos of trials where drinking or eating occurred were made into still shots and scored. For the light assessment, only videos where the subject’s head came within 1 cm of the light were scored. The first second that eating or drinking began was defined as the first second where the outer mandibles touched the banana or water. The second before the water or banana was placed was defined as the last second during the acclimation period before the water or banana came in to the frame of the videotape.

Each still shot was then scored for the occurrence or non-occurrence of antennal depression defined as both antennae touching the floor of the apparatus at least at the tips. Antennae may be bent at the tips, but must not be moving (i.e., not blurry in the still shot). If the MHC had antennae that were not intact or missing, antennal depression was scored for the intact antenna. If antennal depression occurred during a particular still shot, a “1” was scored, if it did not occur a “0” was recorded (see Appendix C for an example data sheet). Each of the water, banana, and light assessments were scored separately for each subject that met selection criteria.

Inter-Observer Agreement

Inter-observer agreement (IOA) was scored on 30% of trials (i.e. the before, approach, and the consummatory or near phase of each assessment on one day) for each subject. Training was conducted prior to the second observer scoring still shots for both the antennae intact group and the antennae not intact group. A random number generator selected the trials for the IOA assessment by the date of the trial. This was done by having the number generator select the number of dates that corresponded to 30% of the total number of trials for each subject.

Antennae intact group. A second observer was trained first by reviewing the operational definition as written (see Appendix B for operational definition). Next, a demonstration of antennal depression was conducted by reviewing still shots that served as examples and non-examples.

After the definition was reviewed, both observers simultaneously scored trials for Non-Dominant Male 2 and Dominant Male 1 that were not selected by the number generator. For the first trial, both observers ensured that they agreed on each occurrence of antennal depression in each still shot in which it occurred. After the first trial, each observer scored a trial separately and then met to calculate agreement after the trial was completely scored.

Exact agreement IOA was calculated by scoring agreement or disagreement for each still shot in the trial. The number of still shots with agreements was divided by the number of agreements plus disagreements to calculate a percentage. During training, any disagreements were reviewed after scoring. Training continued until the observers completed three trials with 90% agreement or above. After training, all trials with antennae intact subjects selected by the number generator, for all three assessments, were scored by the second observer.

Antennae not intact group. The IOA for the antennae not intact group was conducted after the antennae intact group was completed. The operational definition was again reviewed with the following exceptions: if only one antennae was intact, only the antennae that was intact was scored according to the definition; and if antennae were too short to touch the floor while eating, antennal depression was scored if the ends of the antennae were pointed towards the floor. Examples and non-examples were reviewed with the second observer after the definition was reviewed.

Training was then conducted in a similar manner to the antennae intact group except, trials were not scored simultaneously, and only two trials needed to be scored separately at 90% agreement to end training. After training, the second observer scored the trials selected by the number generator independently.

Exact agreement IOA was calculated by scoring agreement or disagreement for each still shot in the trial. The number of still shots with agreements was divided by the number of agreements plus disagreements to calculate a percentage.

Conditional Probability Analysis

Once the still shots were scored, a conditional probability analysis was conducted to determine the probability of antennal depression given the presence of banana or water, and given that the MHC is eating or drinking. The total number of still shots scored with antennal depressions and the total number of still shots for each phase were calculated separately for each subject (see Appendix D for conditional probability analysis data sheet). Once totaled, the conditional probability of antennal depression was calculated for the water and banana assessments separately.

The conditional probability analysis included the following calculations: the conditional probability of antennal depression given consuming, the conditional probability of antennal depression given the absence of consuming, the unconditional probability of antennal depression, the conditional probability of the MHC consuming given antennal depression, the conditional probability of consuming given no antennal depression, and the unconditional probability of consuming (for formulas see Figure 2). The same calculations were run for the presence of the banana or water (see Figure 2). Antennal depression was then calculated to be a probable approach or consumption behavior if the conditional probability of antennal depression given consumption or presence of a consumable was higher than both the conditional probability of antennal depression given the absence of consumption or the presence of consumption, and the unconditional probability of antennal depression (see Appendix D for examples of calculations). The conditional probability of consuming or consumable presence given antennal depression also must be higher than the conditional probability of consuming or presence of consumable given the absence of antennal depression, as well as the unconditional probability of consuming or the presence of the consumable for antennal depression to be a probable approach or consumption behavior.

After each of these probabilities were calculated to ensure that the conditional probability of antennal depression given drinking, and the conditional probability of drinking given antennal depression were higher than the other four probabilities that were calculated. If so, it was determined that antennal depression is a likely consummatory response.

Chapter 3: Results

Subject Selection

In the water assessment 6 of the 12 subjects met the criteria of drinking on 8 out of 10 consecutive trials. Specifically, Dominant Male 1, Dominant Male 2, Dominant Male 3, Non-Dominant Male 2, Non-Dominant Male 3, and Nymph 3 met the criteria. No female MHCs met the criteria during the water assessment. Nymph 3, which met the criteria, was housed in the male habitat, while the two nymphs that were housed in the female habitat (i.e., Nymph 1 and Nymph 2) also did not meet the criteria. The average latency to drinking after the water was placed in the apparatus was 59.5 s, with the shortest latency at 3.0 s, and the longest latency at 4 min 56.0 s.

In the banana assessment, 7 of the 12 subjects met the criteria on eating on 8 out of 10 consecutive trials. Specifically, Female 1, Female 3, Nymph 3, Non-Dominant Male 2, Non-Dominant Male 3, Dominant Male 1, and Dominant Male 2 met the criteria. Dominant Male 3 met the criteria for the water assessment, but did not meet the criteria for the banana assessment. Female 1 and Female 2 met the criteria for the banana assessment, whereas no females met the criteria for the water assessment. The average latency to eating after banana was placed in the apparatus was 54.4 s, with the shortest latency at 2.0 s, and the longest latency at 5 min 0.0 s. The subjects that met the criteria for either the banana or water assessment were also selected to participate in the light assessment.

Water Assessment Results

The results for the water assessment are displayed in Figure 3 and Figure 4. Figure 3 shows the cumulative number of antennal depressions for subjects with antennae fully intact. Figure 4 shows the cumulative number of antennal depressions for subjects with antennae missing or partially intact. Results are separated by antennae intact and antennae not intact groups because, as described below, a between groups effect was seen in the data.

Before water phase. The before water phase consisted of the 10 still shots taken, one per second, before water was placed in the apparatus. In the antennae intact group; Non-Dominant Male 2 had 3 cumulative antennal depressions across all still shots in each trial, Dominant Male 1 had 2 cumulative antennal depressions, and Nymph 3 had 0 cumulative antennal depressions. In the antennae not intact group; Dominant Male 3 had the highest number of cumulative antennal depressions across all still shots in each trial at 12, Non-Dominant Male 3 had 5 cumulative antennal depressions, and Dominant Male 2 had 0 cumulative antennal depressions. Between groups results for the before slide phase show that the subjects with antennae intact had fewer cumulative responses than the antennae not intact group.

Water present, approach phase. The water present approach phase consisted of the 10 still shots taken, one per second, before drinking. More antennal depressions were recorded in this phase across subjects than in the before water phase. In the antennae intact group; Nymph 3 had 17 cumulative antennal depressions across all still shots in each trial, Non-Dominant Male 2 had 12 cumulative antennal depressions, and Dominant Male 1 had 9 cumulative antennal depressions. In the antennae not intact group; Dominant Male 3 had the highest number of cumulative antennal depressions across all still shots in each trial at 24, Non-Dominant Male 3 had 20 cumulative antennal depressions, and Dominant Male 2 had 7 cumulative antennal depressions. Between groups results for the approach phase show that the subjects with antennae intact had fewer cumulative responses than the antennae not intact group.

Water present, drinking phase. The drinking phase was the 10 still shots that were scored beginning with the first frame in which the MHC began drinking. Within subject, the cumulative number of antennal depressions for each subject was higher in the drinking phase than in both the before water phase, and the approach phase. In the antennae intact group; Dominant Male 1 had the highest number of antennal depressions in this phase with 76 cumulative antennal depressions across all still shots in each trial, Non-Dominant Male 2 had 52 cumulative antennal depressions, and Nymph 3 had 48 cumulative antennal depressions. In the antennae not intact group; Dominant Male 3 had 60 cumulative antennal depressions across all still shots in each trial, Dominant Male 2 had 29 cumulative antennal depressions, and Non-Dominant Male 3 had 26 cumulative antennal depressions. Contrary to previous phases, in the drinking phase, the antennae intact group had a higher number of cumulative responses than the antennae not intact group.

Banana Assessment Results

The results for the banana assessment are displayed in Figure 5 and Figure 6. Figure 5 shows the cumulative number of antennal depressions for subjects with antennae fully intact. Figure 6 shows the cumulative number of antennal depressions for subjects with antennae missing or partially intact.

Before banana phase. The before banana phase consisted of the 10 still shots taken, one per second, before banana was placed in the apparatus. Similar to the water assessment, in the before banana phase, few antennal depressions were recorded with each subject. In the antennae intact group; Non-Dominant Male 2 had 2 cumulative antennal depressions across all still shots in each trial, Dominant Male 1 had 1 cumulative antennal depression, Nymph 3 had 2 cumulative antennal depressions, and Female 1 had 0 cumulative antennal depressions. In the antennae not intact group; Non-Dominant Male 3 had the highest cumulative number of antennal depressions across all still shots in each trial at 9, Female 3 had 7 cumulative antennal depressions, and Dominant Male 2 had 2 cumulative antennal depressions.

Banana present, approach. The banana present approach phase consisted of the 10 still shots, one for each second, before each subject began eating. More antennal depressions occurred across subjects in the approach phase than in the before banana phase. In the antennae intact group; Female 1 had 14 cumulative antennal depressions across all still shots in each trial, Dominant Male 1 had 9 cumulative antennal depressions, Nymph 3 had 4 cumulative antennal depressions, and Non-Dominant Male 2 had 3 cumulative antennal depressions. In the antennae not intact group; Female 3 had 17 cumulative antennal depressions across all still shots in each trial, Non-Dominant Male 3 had 9 antennal depressions, and Dominant Male 2 had 5 cumulative antennal depressions. Female 3, of the antennae not intact group, had the highest number of cumulative antennal depressions at 17. Similar to the water assessment, when analyzed within subject, the number of antennal depressions in the approach phase was higher than in the before banana phase for each subject.

Banana present, eating. For each subject in the eating phase, the cumulative number of antennal depressions was higher than that of the before banana and approach phases. In the antennae intact group; Female 1 had 45 cumulative antennal depressions across all still shots in each trial, Dominant Male 1 had 42 cumulative antennal depressions, Nymph 3 had 32 cumulative antennal depressions, and Non-Dominant Male 2 had 19 cumulative antennal depressions. In the antennae not intact group; Female 3 had 35 cumulative antennal depressions across all still shots in each trial, Non-Dominant Male 3 had 29 antennal depressions, and Dominant Male 2 had 12 cumulative antennal depressions. Female 1 of the antennae intact group had the highest cumulative number of antennal depressions at 45. In the antennae not intact group Female 3 had the highest cumulative number of antennal depressions at 35. Overall the cumulative number of still shots scored for antennal depression was lower than in the water assessment with the exception of Non-Dominant Male 3.

Again, similar to the water assessment, between subjects results for the before banana phase show that the subjects with antennae intact had fewer cumulative responses than the antennae not intact group, and likewise for the approach phase. Also similar to the water assessment, in the eating phase, the antennae intact group had a higher number of cumulative responses than the antennae not intact group.

Light Assessment Results

All subjects that met criteria for either the water or banana assessment were used in the light assessment. Very low responding was noted in all phases with few approaches to the light and very few antennal depressions throughout each of the phases (see figures 7 and 8). Only trials where the subject's head came within 1 cm of the light were scored. In comparison to the banana and water assessments, fewer approaches occurred for each subject in the light assessment.

Before light phase. The before light phase consisted of the 10 still shots, one per second, before the light was turned on in the apparatus in each trial. In the antennae intact group; Nymph 3 had 1 cumulative antennal depression across all still shots in each trial, Dominant Male 1 had 0 cumulative antennal depressions, Female 1 had 0 cumulative antennal depressions, and Non-Dominant Male 2 had 0 cumulative antennal depressions. In the antennae not intact group; Non-Dominant Male 3 had 5 antennal depressions across all still shots in each trial, Female 3 had 1 cumulative antennal depression, Dominant Male 2 had 1 cumulative antennal depression, and Dominant Male 3 had 1 cumulative antennal depression.

Light on, approach phase. The approach phase was the 10 still shots, one per second, before the subject's head was within 1 cm of the light when it was turned on. In the antennae intact group; Non-Dominant Male 2 had 1 cumulative antennal depression across all still shots in each trial, Dominant Male 1 had 1 cumulative antennal depression, Female 1 had 1 cumulative antennal depression, and Nymph 3 had 0 cumulative antennal depressions. In the antennae not intact group; Non-Dominant Male 3 had 7 antennal depressions across all still shots in each trial, Female 3 had 5 cumulative antennal depressions, Dominant Male 2 had 1 cumulative antennal depression, and Dominant Male 3 had 1 cumulative antennal depression. Overall, a greater number of cumulative antennal depressions were recorded than in the before light phase. However, the cumulative number of antennal depressions in this phase was lower than the cumulative number of antennal depressions in both the banana and water approach phases.

Light on, near light. The near light phase consisted of the 10 still shots, one per second, after the subject's head came within 1cm of the light when it was turned on. In the antennae intact group; Non-Dominant Male 2 had 1 cumulative antennal depression across all still shots in each trial, Female 1 had 1 cumulative antennal depression, Dominant Male 1 had 0 cumulative antennal depressions, and Nymph 3 had 0 cumulative antennal depressions. In the antennae not intact group; Non-Dominant Male 3 had 3 antennal depressions across all still shots in each trial, Female 3 had 4 cumulative antennal depressions, Dominant Male 2 had 0 cumulative antennal depressions, and Dominant Male 3 had 0 cumulative antennal depressions. There were fewer antennal depressions in the near light condition than in the approach light condition for each subject. In comparison to the banana and water assessments, there were significantly fewer cumulative antennal depressions in the light assessment.

Inter-Observer Agreement

IOA was calculated by comparing whether there was agreement in each still shot as to whether antennal depression occurred or did not occur in each still shot. Exact IOA was calculated for 30% of all trials.

Antennae intact group. The antennae intact group for the water assessment was Dominant Male 1, Non-Dominant Male 2, and Nymph 3. Exact agreement IOA for the water assessment for the antennae intact group was 88.59%. The antennae intact group for the banana assessment was Dominant Male 1, Non-Dominant Male 2, Nymph 3, and Female 1. Exact agreement IOA for the banana assessment was 91.62%. The antennae intact group for the light assessment was Dominant Male 1, Non-Dominant Male 2, Nymph 3, and Female 1. Exact agreement IOA for the light assessment was 99.58%.

Antennae not intact group. The antennae not intact group for the water assessment was Dominant Male 2, Dominant Male 3, and Non-Dominant Male 3. Exact agreement IOA for the water assessment for the antennae not intact group was 88.06%. The antennae not intact group for the banana assessment was Dominant Male 2, Non-Dominant Male 3, and Female 3. Exact agreement IOA for the banana assessment was 89.26%. The antennae not intact group for the light assessment was Dominant Male 2, Dominant Male 3, Non-Dominant Male 3, and Female 3. Exact agreement IOA for the light assessment was 98.15%.

Conditional Probability Assessment

In the conditional probability assessment the conditional probability of antennal depression when consumables were present was compared to the conditional probability of antennal depression when consuming.

Water assessment. Results for the conditional probability of antennal depression in the water assessment are shown in the table in Figure 9. The values for the conditional probability of antennal depression given drinking and water [p(T|Pn)] are shaded in the table. The conditional probability of drinking and water present given antennal depression [p(Pn|T)] are also shaded in the table. Both conditional probabilities [p(T|Pn) and p(Pn|T)] were greater for still shots where drinking occurred for each subject, and were not for when water was present.

Banana assessment. Results for the conditional probability of antennal depression in the banana assessment are shown in the table in Figure 10. The values for the conditional probability of antennal depression given eating and banana present [p(T|Pn)] are shaded in the table. The conditional probability of eating and banana present given antennal depression [p(Pn|T)] are also shaded in the table. Both conditional probabilities [p(T|Pn) and p(Pn|T)] were greater for still shots where eating occurred for each subject, and were not for when banana was present.

Chapter 4: Discussion

The purpose of this study was to identify whether reinforcement influenced response topography. If so, data collection procedures can be calibrated to the anticipated response topography, and use the response topography as a dependent variable. Based on the results of a visual analysis of the ethological assessment, and the statistical results of the conditional probability assessment, antennal depression is a likely consummatory behavior in MHCs. Antennal depression is a behavior that can signal to the experimenter that the MHC is engaging in consummatory behavior. This becomes important in the design and interpretation of experimental arrangements with the MHC, specifically sign-tracking arrangements, in that; if antennal depression occurs in the presence of non-consumables, it is likely the result of conditioning and not a behavior that the MHC exhibits when interacting with non-consumable stimuli in the natural environment.

Confirming that antennal depression is a consummatory behavior gives support to future studies, sign-tracking or otherwise, that are based in operant and respondent conditioning of consummatory behavior. In other words, identifying the response topography of consummatory behaviors can eliminate instances of experimenter bias in determining whether the MHC is engaging in consummatory behavior. Defining the topography of consummatory responding in the MHC ensures that consuming behaviors are defined according to the species of study and not according to similarity of responding to other species.

Continued descriptive assessments also provide validity to existing descriptive assessments. This assessment confirmed the results of Yoder and Grojean (1997) in that female MHCs may conserve water by huddling together in the natural environment, whereas males do not engage in this behavior. In this study it was shown that females did not drink water on as many opportunities as the male subjects. No female subjects met the criteria for the water assessment, but two females met the criteria for the banana assessment. This is one instance of where an ethological assessment can be designed to address a single question about a species, but may in fact confirm multiple questions. Future descriptive assessments should continue to ensure that individual MHC characteristics such as sex, dominance, and age are recorded for each subject so that within species differences can be confirmed across studies.

In regards to sign-tracking, this study will inform several experimental design decisions. First, since the MHCs did not allocate behavior towards the 5 mm LED light on as many opportunities as the banana and water, the LED could be a putative signal stimulus. In contrast, when presented with consumables one time per day, roughly half of subjects responded at criteria level, with responding not clearly drawn along sex, age, or dominance status except in the case of females and water. All subjects had a similar low number of responses in approaching to, and engaging in antennal responding toward the light. If MHCs were shown to increase their responding toward the light on more opportunities after presentations of light and food or water, it would be likely that sign-tracking had occurred.

Also, the average latency to consume for the banana and water assessment was around one minute for both the water and banana assessment (i.e. 59.5 s and 54.4 s respectively). This suggests that longer presentations of light and consumables may be necessary for sign-tracking arrangements with the MHC. If it takes around one minute for the MHC to orient to stimuli that is within 10 cm of its head, the ITI of the presentation of the light and the consumable will be more successful with longer durations (e.g. 30 s of light before the presentation of food), than shorter durations (e.g. 3 s of light before the presentation of food).

Additionally, with such wide ranges of variability in responding, descriptive assessments may be integral to continued studies of MHC behavior in that, a subject selection phase may be necessary. In the case of this study, a higher cumulative number of antennal depressions was more likely influenced by whether or not the subject had intact antennae, than by any other ontogenetic or phylogenic factor. Until more is known about the MHC, the ethogram will continue to inform future behavioral study of this endemic species.

However, no functional relation between antennal depression and consummatory behavior has been demonstrated in this study. This may be unnecessary given that we are not intending to demonstrate that antennal depression is functionally related to eating or drinking. Instead, the purpose of this study was to define the topography of consummatory behavior. Future studies can show behaviors that are functionally related to eating or drinking once these behaviors are defined.

Another limitation is that the animal was moved from its habitat in order to study its natural behaviors. Here the decision was made that the controlled environment was necessary in order to isolate consummatory behaviors that would be difficult to measure in the animal's natural environment. In addition, the purpose of the ethological assessment was to isolate consummatory behaviors to bolster analyses in experimental designs. And so, while the controlled environment could have influenced responding, the arrangement of the ethological assessment conducted here is likely to be more similar to that of the experimental arrangement that is of concern, rather than behaviors in the natural environment which are not of concern to the study of sign-tracking behaviors specifically.

Descriptive assessments, such as the ethological assessment demonstrated here, are valuable to a scientific approach to the experimental analysis of behavior in that they can answer many questions about experimental design without the need for trial and error. Descriptive assessments can be designed in such a way that a lot of information can be gained from a single study if sufficient individual data is taken with respect to the age, sex, dominance, and other ontogenetic and phylogenic factors. Future studies with the MHC should continue with descriptive assessments as a cornerstone of the research.

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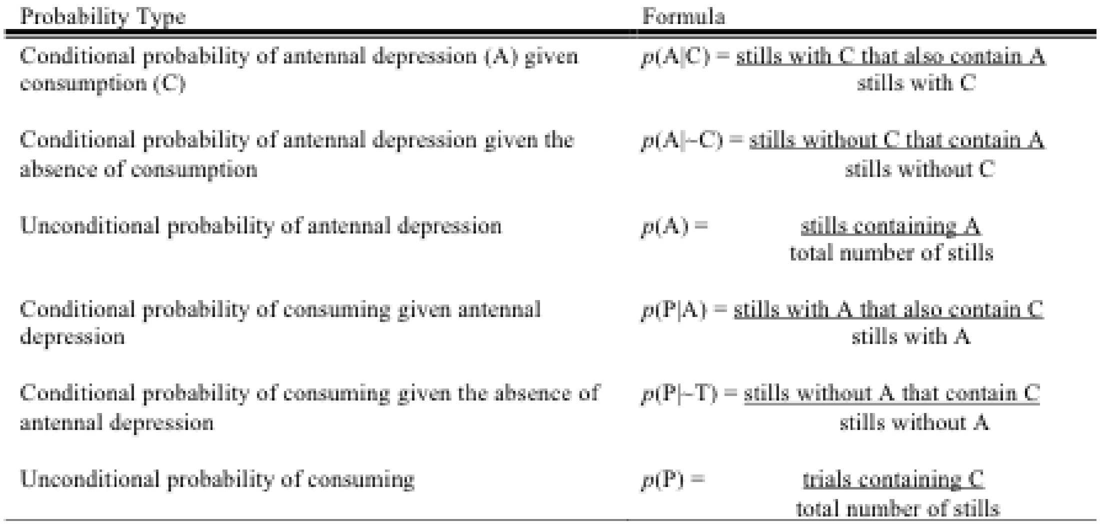
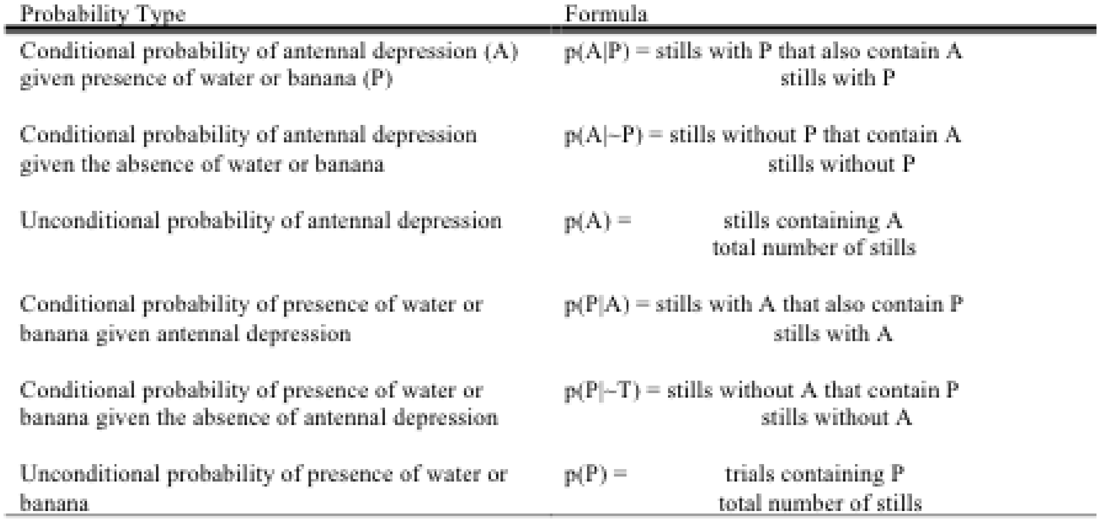
Appendix A: Figures

Figure 1. Ethological assessment apparatus. This apparatus included an 11-quart laundry tub lined with standard letter paper marked with 1cm grid squares. The squares were used to track movement using the location of the subject's head. During light trials, a second laundry tub with a 5 mm green LED light glued underneath the tub was used. The light was turned on with a switch not attached to the apparatus, so as to not move or disturb the apparatus during trials.



Probability Type	Formula
Conditional probability of antennal depression (A) given consumption (C)	$p(\text{A}\vert\text{C}) = \frac{\text{stills with C that also contain A}}{\text{stills with C}}$
Conditional probability of antennal depression given the absence of consumption	$p(\text{A}\vert\sim\text{C}) = \frac{\text{stills without C that contain A}}{\text{stills without C}}$
Unconditional probability of antennal depression	$p(\text{A}) = \frac{\text{stills containing A}}{\text{total number of stills}}$
Conditional probability of consuming given antennal depression	$p(\text{P}\vert\text{A}) = \frac{\text{stills with A that also contain C}}{\text{stills with A}}$
Conditional probability of consuming given the absence of antennal depression	$p(\text{P}\vert\sim\text{T}) = \frac{\text{stills without A that contain C}}{\text{stills without A}}$
Unconditional probability of consuming	$p(\text{P}) = \frac{\text{trials containing C}}{\text{total number of stills}}$



Probability Type	Formula
Conditional probability of antennal depression (A) given presence of water or banana (P)	$\text{p}(\text{A}\vert\text{P}) = \frac{\text{stills with P that also contain A}}{\text{stills with P}}$
Conditional probability of antennal depression given the absence of water or banana	$\text{p}(\text{A}\vert\sim\text{P}) = \frac{\text{stills without P that contain A}}{\text{stills without P}}$
Unconditional probability of antennal depression	$\text{p}(\text{A}) = \frac{\text{stills containing A}}{\text{total number of stills}}$
Conditional probability of presence of water or banana given antennal depression	$\text{p}(\text{P}\vert\text{A}) = \frac{\text{stills with A that also contain P}}{\text{stills with A}}$
Conditional probability of presence of water or banana given the absence of antennal depression	$\text{p}(\text{P}\vert\sim\text{T}) = \frac{\text{stills without A that contain P}}{\text{stills without A}}$
Unconditional probability of presence of water or banana	$\text{p}(\text{P}) = \frac{\text{trials containing P}}{\text{total number of stills}}$

Figure 2. Conditional probability analysis formulas. These formulas were used to calculate the conditional probability that antennal depression occurred in the presence of consuming and the presence of food and water. Formulae are adapted from Fritz, Iwata, Hammond, and Bloom (2013).

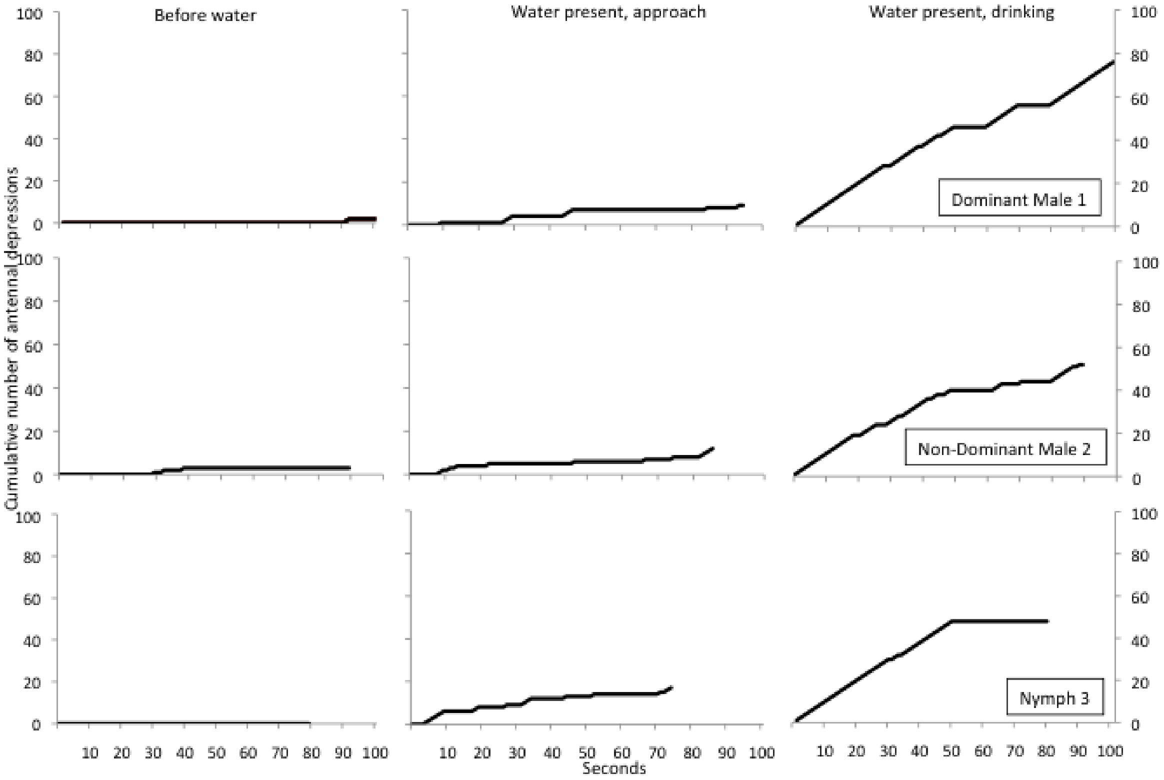


Figure 3. Cumulative number of antennal depressions during water assessment, antennae intact group. This graph represents the cumulative number of stills that were scored for antennal depression separated by the phases; before water was placed in the apparatus, water present 10 seconds before drinking, and water present and drinking.

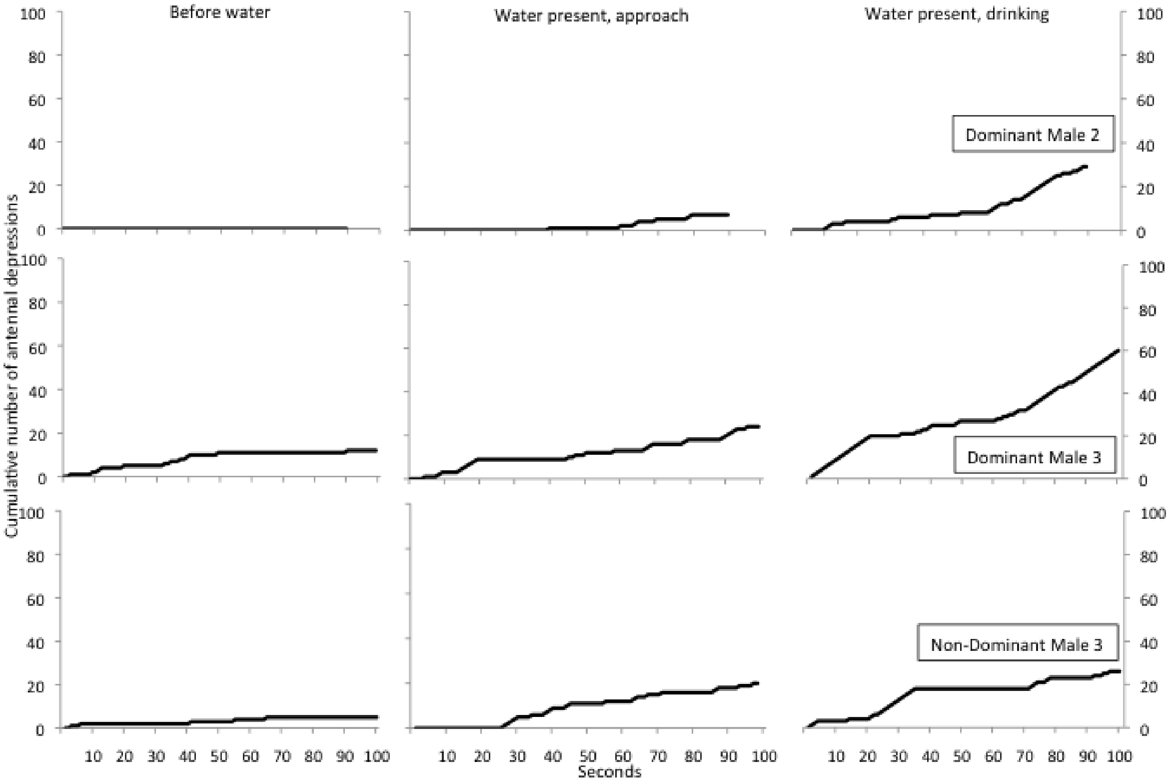


Figure 4. Cumulative number of antennal depressions during water assessment, antennae not intact group. This graph represents the cumulative number of stills that were scored for antennal depression separated by the phases; before water was placed in the apparatus, water present 10 seconds before drinking, and water present and drinking.

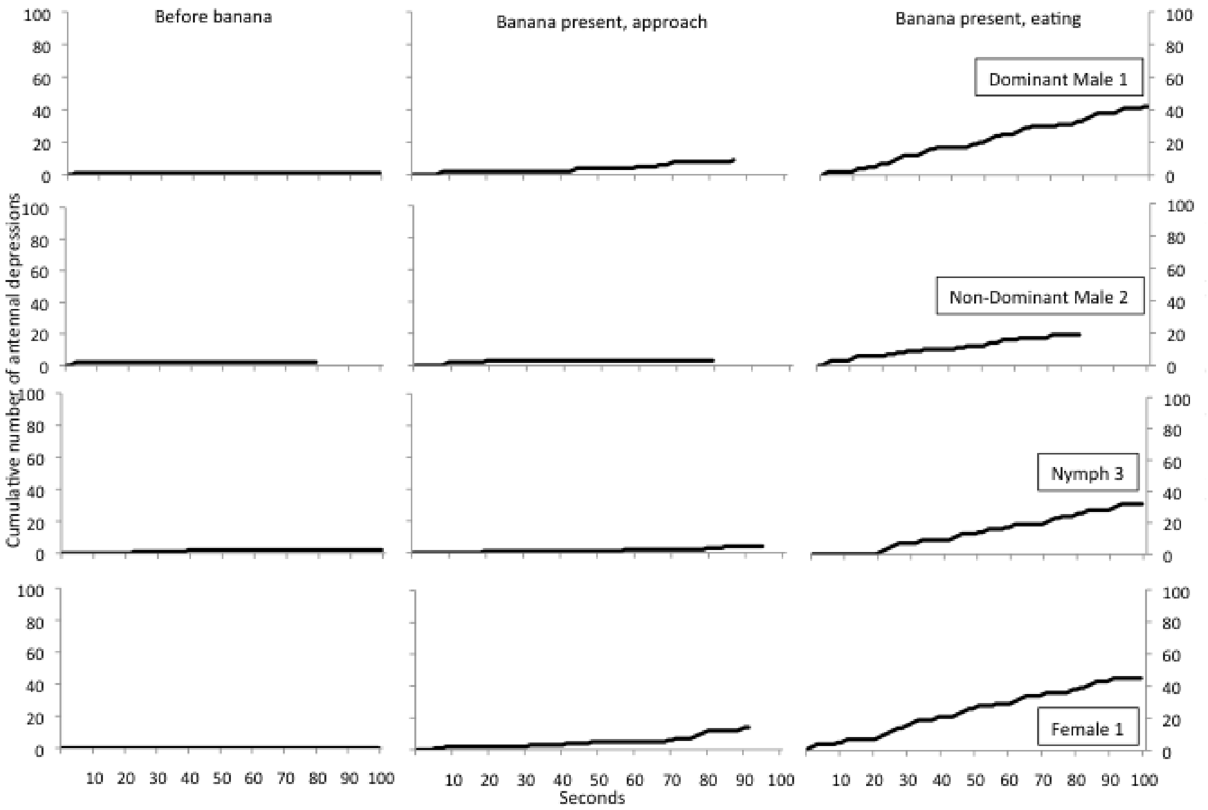


Figure 5. Cumulative number of antennal depressions during banana assessment, antennae intact group. This graph represents the cumulative number of stills that were scored for antennal depression separated by the phases; before banana was placed in the apparatus, banana present 10 seconds before eating, and banana present and eating.

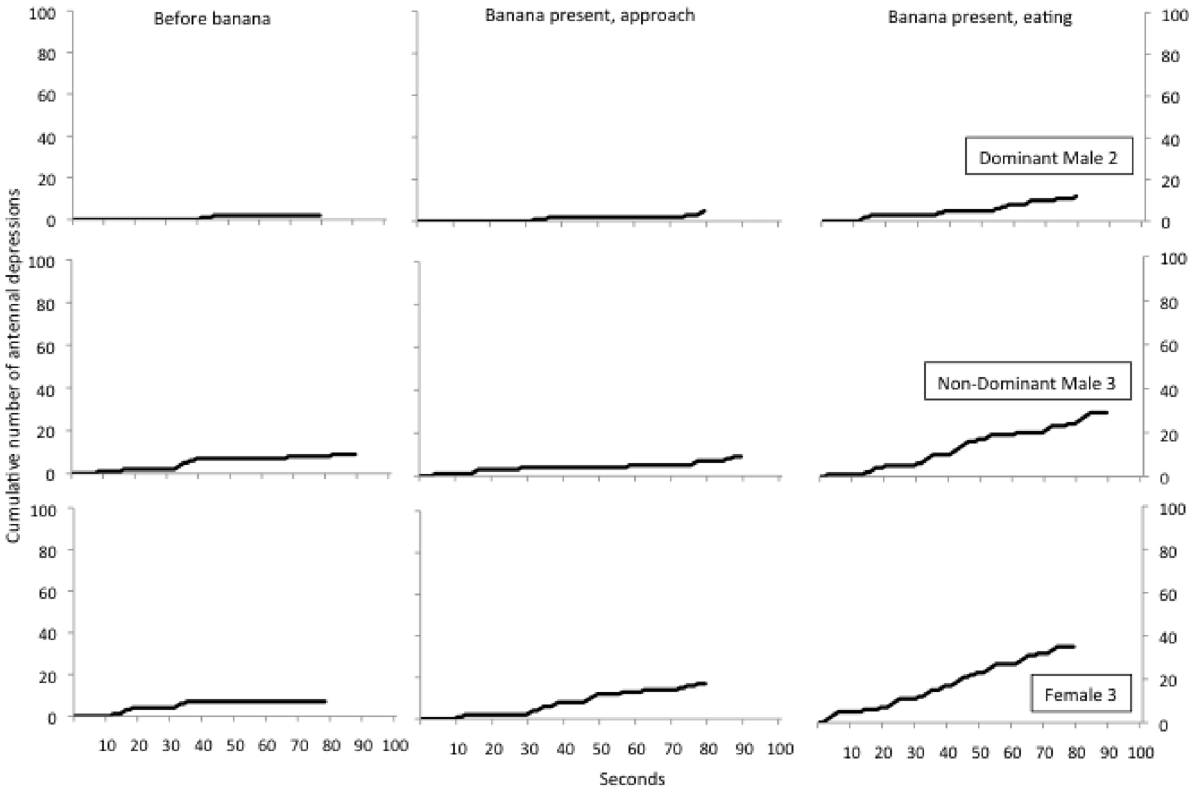


Figure 6. Cumulative number of antennal depressions during banana assessment, antennae not intact group. This graph represents the cumulative number of stills that were scored for antennal depression separated by the phases; before banana was placed in the apparatus, banana present 10 seconds before eating, and banana present and eating.

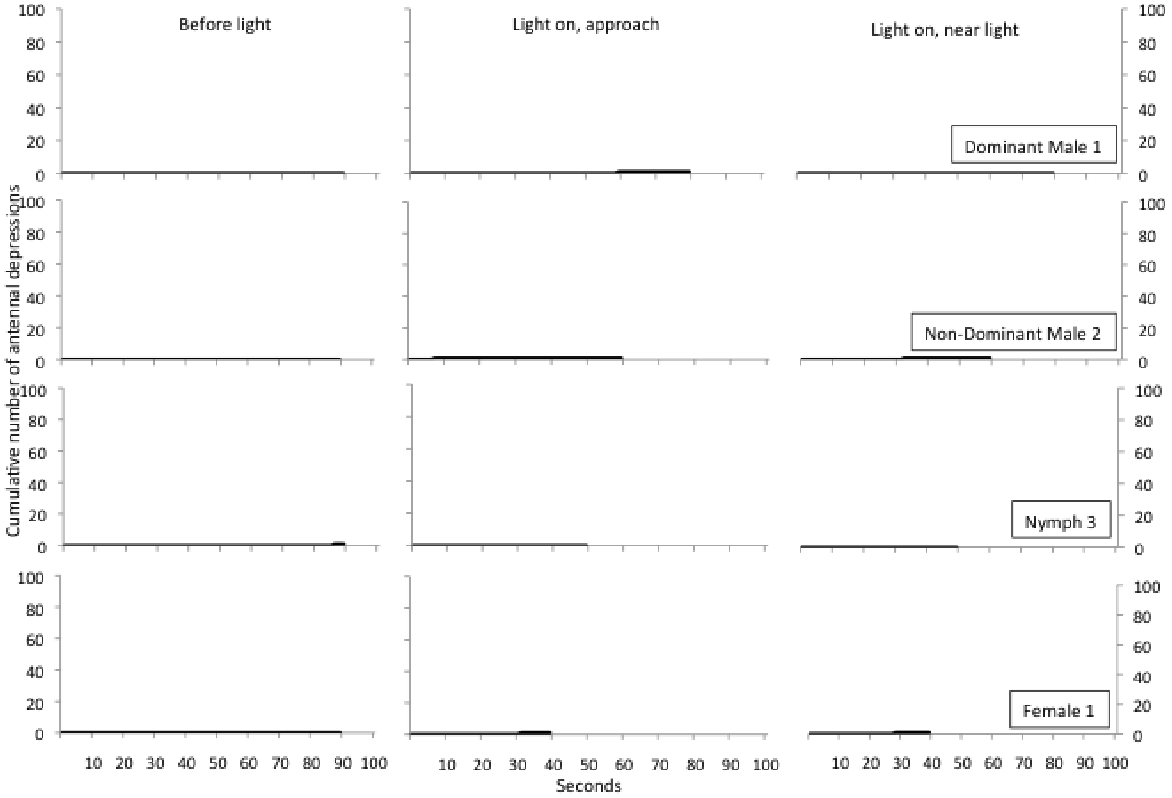


Figure 7. Cumulative number of antennal depressions during light assessment, antennae intact group. This graph represents the cumulative number of stills that were scored for antennal depression separated by the phases; before light was turned on, light on 10 s before going near light, and 10 s after going within 1 cm of the light.

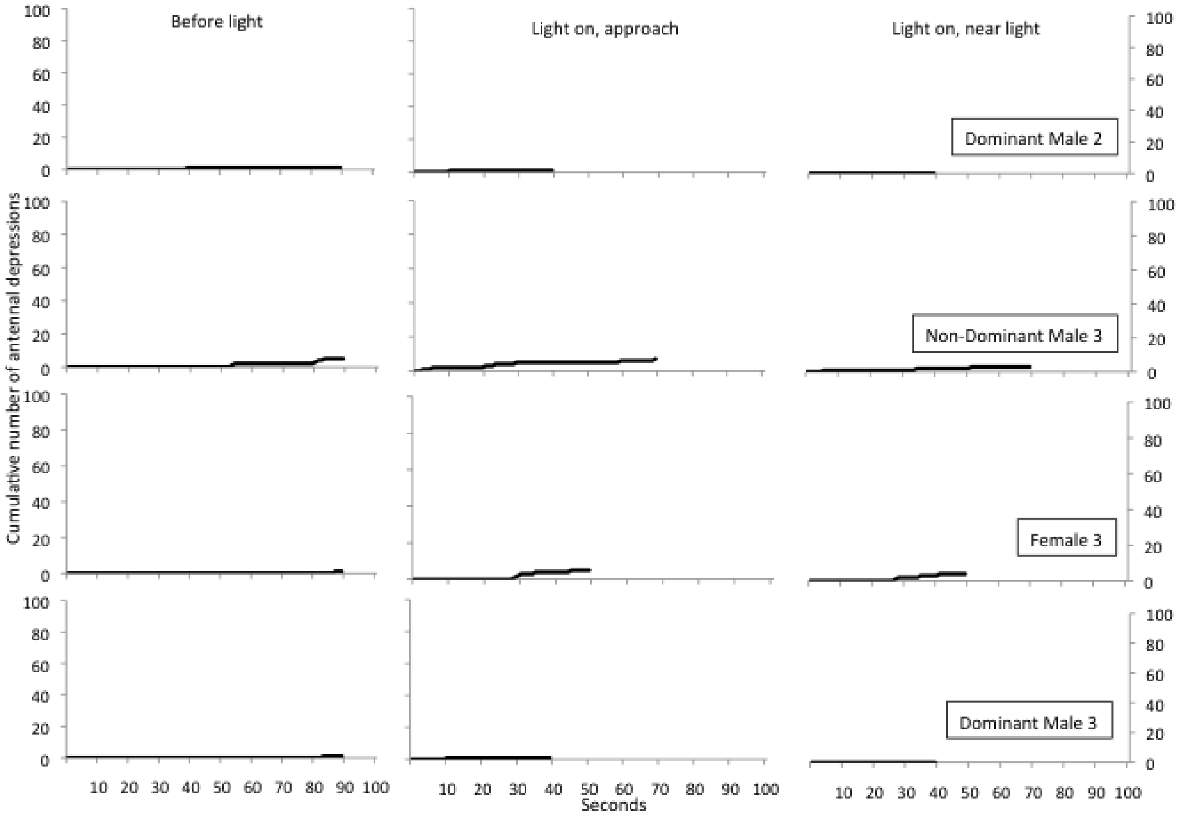
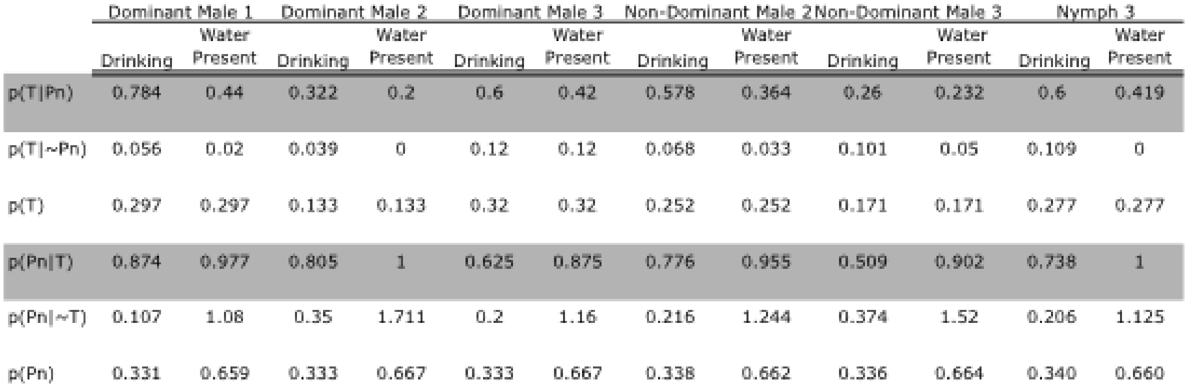
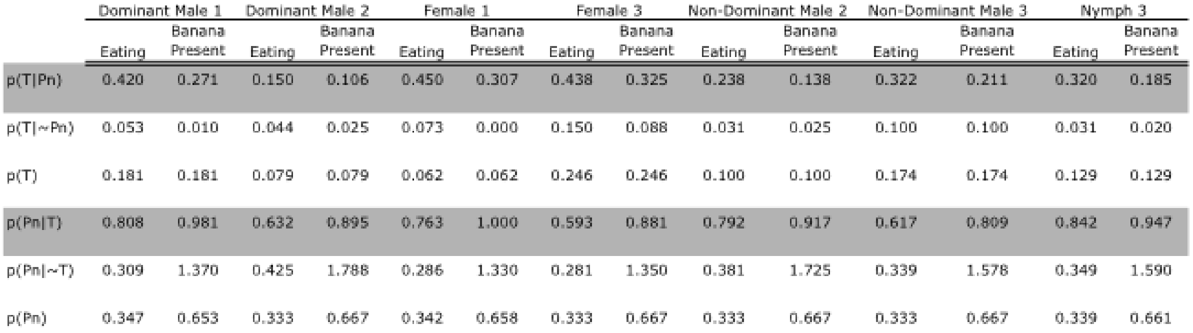


Figure 8. Cumulative number of antennal depressions during light assessment, antennae not intact group. This graph represents the cumulative number of stills that were scored for antennal depression separated by the phases; before light was turned on, light on 10 s before going near light, and 10 s after going within 1 cm of the light.



	Dominant Male 1		Dominant Male 2		Dominant Male 3		Non-Dominant Male 2		Non-Dominant Male 3		Nymph 3	
	Drinking	Water Present	Drinking	Water Present	Drinking	Water Present	Drinking	Water Present	Drinking	Water Present	Drinking	Water Present
p(T|Pn)	0.784	0.44	0.322	0.2	0.6	0.42	0.578	0.364	0.26	0.232	0.6	0.419
p(T|~Pn)	0.056	0.02	0.039	0	0.12	0.12	0.068	0.033	0.101	0.05	0.109	0
p(T)	0.297	0.297	0.133	0.133	0.32	0.32	0.252	0.252	0.171	0.171	0.277	0.277
p(Pn|T)	0.874	0.977	0.805	1	0.625	0.875	0.776	0.955	0.509	0.902	0.738	1
p(Pn|~T)	0.107	1.08	0.35	1.711	0.2	1.16	0.216	1.244	0.374	1.52	0.206	1.125
p(Pn)	0.331	0.659	0.333	0.667	0.333	0.667	0.338	0.662	0.336	0.664	0.340	0.660

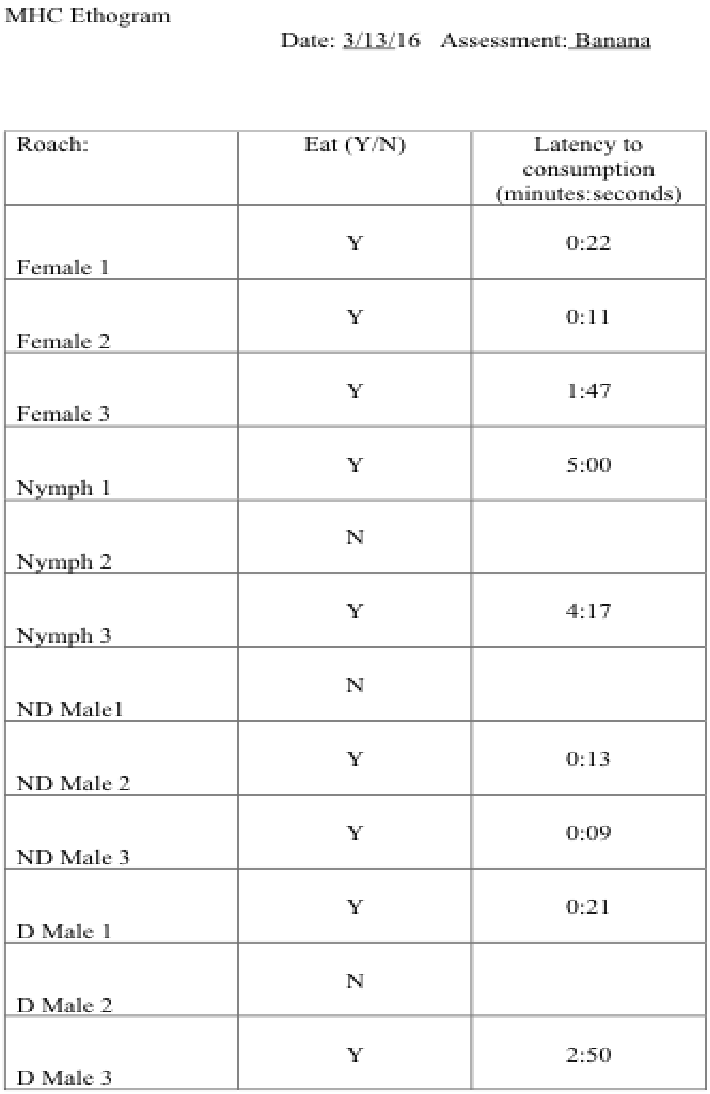
Figure 9. Conditional probability of antennal depression given drinking and water present. The values for the conditional probability of antennal depression given drinking and water present [p(T|Pn)] are shaded in the table. The conditional probability of drinking and water present given antennal depression [p(Pn|T)] are also shaded in the table. Both conditional probabilities [p(T|Pn) and p(Pn|T)] were greater for still shots where drinking occurred, and were not for when water was present.



	Dominant Male 1		Dominant Male 2		Female 1		Female 3		Non-Dominant Male 2		Non-Dominant Male 3		Nymph 3	
	Eating	Banana Present	Eating	Banana Present	Eating	Banana Present	Eating	Banana Present	Eating	Banana Present	Eating	Banana Present	Eating	Banana Present
$p(T \mid Pn)$	0.420	0.271	0.150	0.106	0.450	0.307	0.438	0.325	0.238	0.138	0.322	0.211	0.320	0.185
$p(T \mid \sim Pn)$	0.053	0.010	0.044	0.025	0.073	0.000	0.150	0.088	0.031	0.025	0.100	0.100	0.031	0.020
$p(T)$	0.181	0.181	0.079	0.079	0.062	0.062	0.246	0.246	0.100	0.100	0.174	0.174	0.129	0.129
$p(Pn \mid T)$	0.808	0.981	0.632	0.895	0.763	1.000	0.593	0.881	0.792	0.917	0.617	0.809	0.842	0.947
$p(Pn \mid \sim T)$	0.309	1.370	0.425	1.788	0.286	1.330	0.281	1.350	0.381	1.725	0.339	1.578	0.349	1.590
$p(Pn)$	0.347	0.653	0.333	0.667	0.342	0.658	0.333	0.667	0.333	0.667	0.333	0.667	0.339	0.661

Figure 10. Conditional probability of antennal depression given eating and banana present. The values for the conditional probability of antennal depression given eating and banana present [p(T|Pn)] are shaded in the table. The conditional probability of eating and banana present given antennal depression [p(Pn|T)] are also shaded in the table. Both conditional probabilities [p(T|Pn) and p(Pn|T)] were greater for still shots where eating occurred, and were not for when banana was present.

Appendix B: Data Sheets

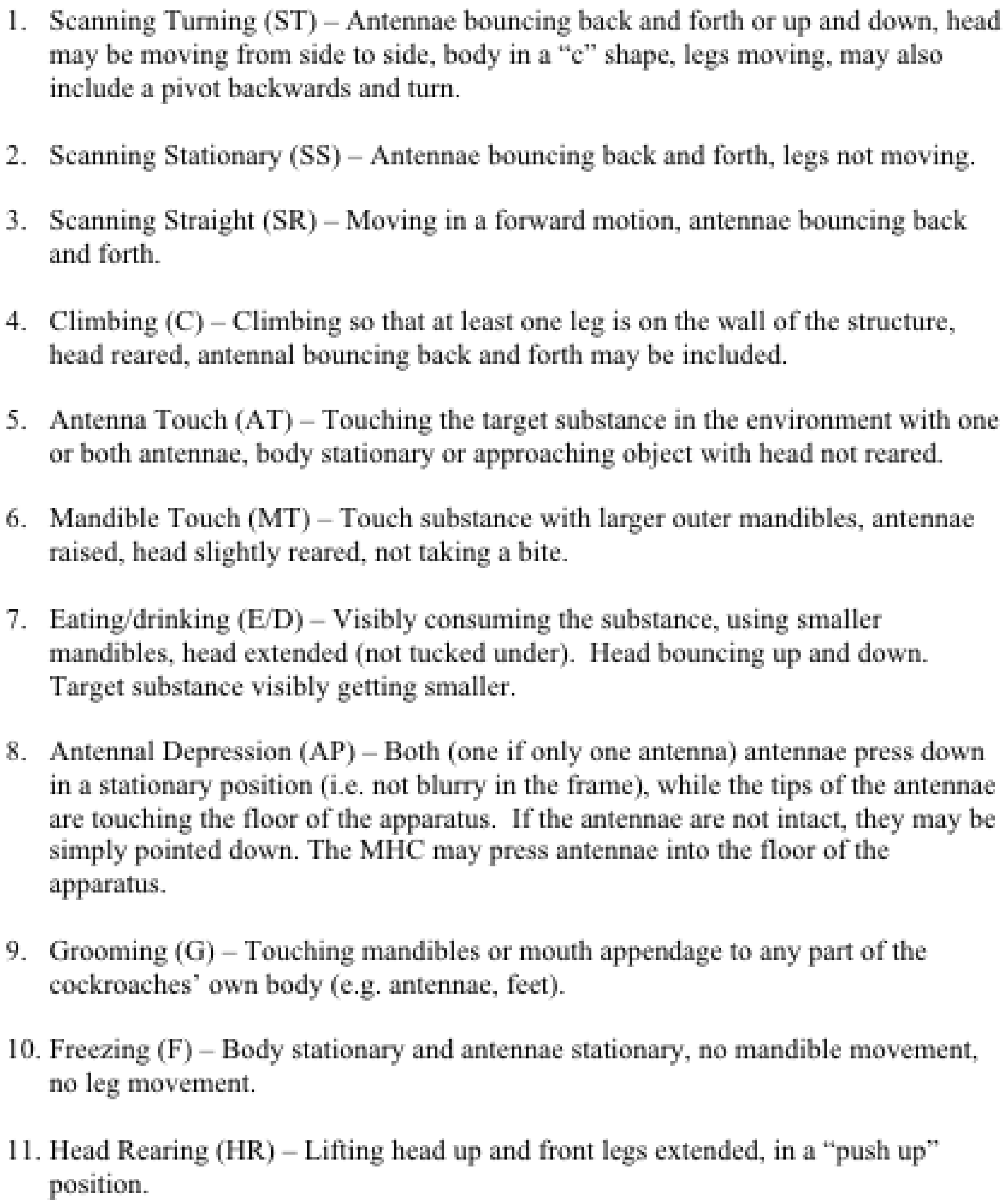


MHC Ethogram

Date: 3/13/16 Assessment: Banana

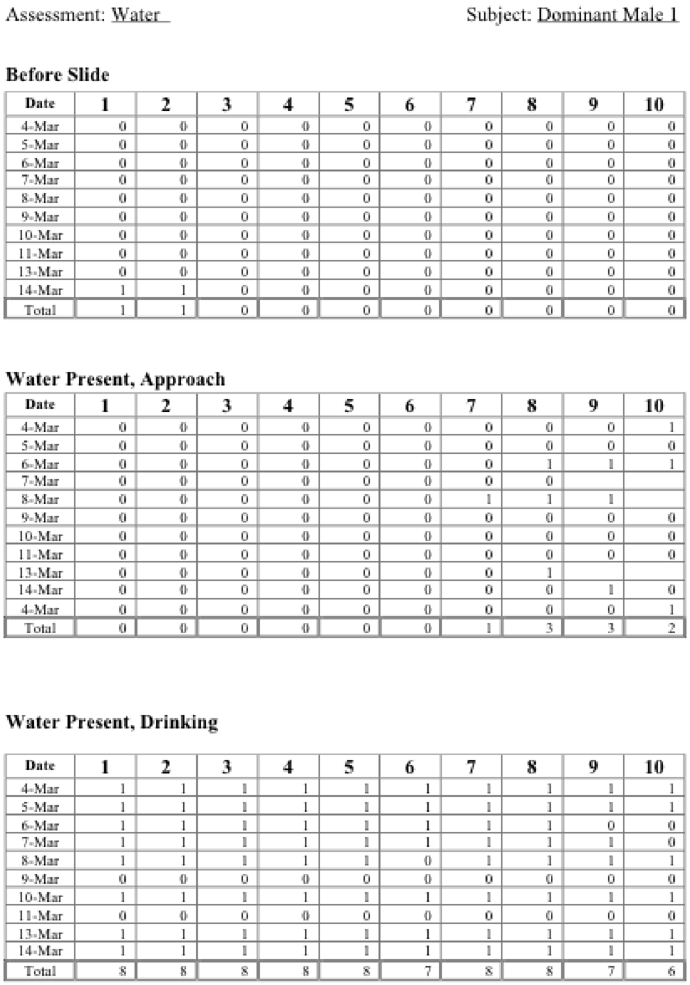
Roach:	Eat (Y/N)	Latency to consumption (minutes:seconds)
Female 1	Y	0:22
Female 2	Y	0:11
Female 3	Y	1:47
Nymph 1	Y	5:00
Nymph 2	N	
Nymph 3	Y	4:17
ND Male1	N	
ND Male 2	Y	0:13
ND Male 3	Y	0:09
D Male 1	Y	0:21
D Male 2	N	
D Male 3	Y	2:50

Appendix B.1. Example latency to consumption data sheet. This data sheet was used to determine the latency to consumption once a food item was placed in the apparatus. This data sheet was used to track whether each roach consumed water or banana on at least 8 out of 10 consecutive opportunities.



1. Scanning Turning (ST) – Antennae bouncing back and forth or up and down, head may be moving from side to side, body in a "c" shape, legs moving, may also include a pivot backwards and turn.
2. Scanning Stationary (SS) – Antennae bouncing back and forth, legs not moving.
3. Scanning Straight (SR) – Moving in a forward motion, antennae bouncing back and forth.
4. Climbing (C) – Climbing so that at least one leg is on the wall of the structure, head reared, antennal bouncing back and forth may be included.
5. Antenna Touch (AT) – Touching the target substance in the environment with one or both antennae, body stationary or approaching object with head not reared.
6. Mandible Touch (MT) – Touch substance with larger outer mandibles, antennae raised, head slightly reared, not taking a bite.
7. Eating/drinking (E/D) – Visibly consuming the substance, using smaller mandibles, head extended (not tucked under). Head bouncing up and down. Target substance visibly getting smaller.
8. Antennal Depression (AP) – Both (one if only one antenna) antennae press down in a stationary position (i.e. not blurry in the frame), while the tips of the antennae are touching the floor of the apparatus. If the antennae are not intact, they may be simply pointed down. The MHC may press antennae into the floor of the apparatus.
9. Grooming (G) – Touching mandibles or mouth appendage to any part of the cockroaches' own body (e.g. antennae, feet).
10. Freezing (F) – Body stationary and antennae stationary, no mandible movement, no leg movement.
11. Head Rearing (HR) – Lifting head up and front legs extended, in a "push up" position.

Appendix B.2. Operational definitions of approach and consummatory behaviors. This figure is a list of the discrete behaviors identified by pilot studies; an arrangement similar to the ethological studies. Two experimenters observed a video of each subject eating a small piece of banana in the ethological study apparatus. Discrete behaviors were identified and operationally defined based upon mutual agreement of the two experimenters after viewing each video.



Assessment: Water Subject: Dominant Male 1

Before Slide

Date	1	2	3	4	5	6	7	8	9	10
4-Mar	0	0	0	0	0	0	0	0	0	0
5-Mar	0	0	0	0	0	0	0	0	0	0
6-Mar	0	0	0	0	0	0	0	0	0	0
7-Mar	0	0	0	0	0	0	0	0	0	0
8-Mar	0	0	0	0	0	0	0	0	0	0
9-Mar	0	0	0	0	0	0	0	0	0	0
10-Mar	0	0	0	0	0	0	0	0	0	0
11-Mar	0	0	0	0	0	0	0	0	0	0
13-Mar	0	0	0	0	0	0	0	0	0	0
14-Mar	1	1	0	0	0	0	0	0	0	0
Total	1	1	0	0	0	0	0	0	0	0

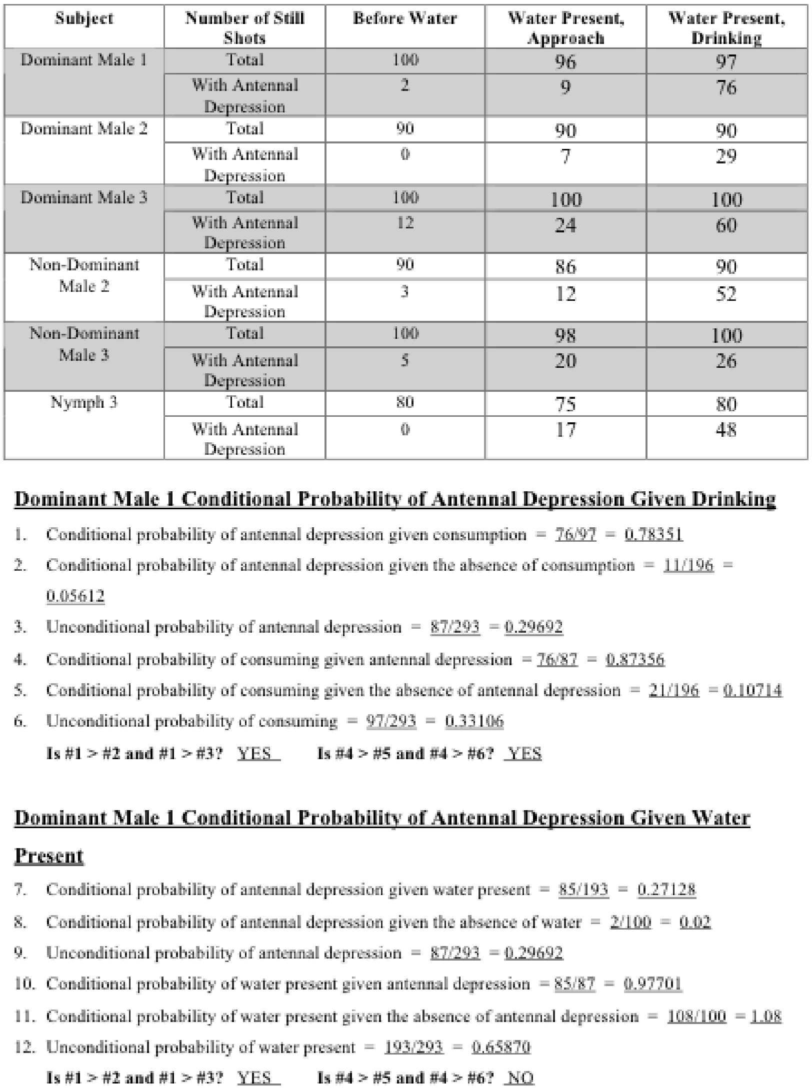
Water Present, Approach

Date	1	2	3	4	5	6	7	8	9	10
4-Mar	0	0	0	0	0	0	0	0	0	1
5-Mar	0	0	0	0	0	0	0	0	0	0
6-Mar	0	0	0	0	0	0	0	1	1	1
7-Mar	0	0	0	0	0	0	0	0		
8-Mar	0	0	0	0	0	0	1	1	1	
9-Mar	0	0	0	0	0	0	0	0	0	0
10-Mar	0	0	0	0	0	0	0	0	0	0
11-Mar	0	0	0	0	0	0	0	0	0	0
13-Mar	0	0	0	0	0	0	0	1		
14-Mar	0	0	0	0	0	0	0	0	1	0
4-Mar	0	0	0	0	0	0	0	0	0	1
Total	0	0	0	0	0	0	1	3	3	2

Water Present, Drinking

Date	1	2	3	4	5	6	7	8	9	10
4-Mar	1	1	1	1	1	1	1	1	1	1
5-Mar	1	1	1	1	1	1	1	1	1	1
6-Mar	1	1	1	1	1	1	1	1	0	0
7-Mar	1	1	1	1	1	1	1	1	1	0
8-Mar	1	1	1	1	1	0	1	1	1	1
9-Mar	0	0	0	0	0	0	0	0	0	0
10-Mar	1	1	1	1	1	1	1	1	1	1
11-Mar	0	0	0	0	0	0	0	0	0	0
13-Mar	1	1	1	1	1	1	1	1	1	1
14-Mar	1	1	1	1	1	1	1	1	1	1
Total	8	8	8	8	8	7	8	8	7	6

Appendix B.3. Antennal depression still shot scoring data sheet. This data sheet was used to score the still shots taken from the ethological assessment. A separate score was recorded for each still shot, and one still shot was taken for; each of 10 seconds before the water or banana was placed in the apparatus, the 10 seconds before drinking or eating, and the 10 seconds after drinking or eating began. For the light assessment, still shots were created for each of the 10 seconds before the light was turned on, the 10 seconds before the MHC's head came within 1 cm of the light, and the 10 seconds after the MHC's head came within 1 cm of the light.



Subject	Number of Still Shots	Before Water	Water Present, Approach	Water Present, Drinking
Dominant Male 1	Total	100	96	97
	With Antennal Depression	2	9	76
Dominant Male 2	Total	90	90	90
	With Antennal Depression	0	7	29
Dominant Male 3	Total	100	100	100
	With Antennal Depression	12	24	60
Non-Dominant Male 2	Total	90	86	90
	With Antennal Depression	3	12	52
Non-Dominant Male 3	Total	100	98	100
	With Antennal Depression	5	20	26
Nymph 3	Total	80	75	80
	With Antennal Depression	0	17	48

Dominant Male 1 Conditional Probability of Antennal Depression Given Drinking

1. Conditional probability of antennal depression given consumption = 76/97 = 0.78351
2. Conditional probability of antennal depression given the absence of consumption = 11/196 = 0.05612
3. Unconditional probability of antennal depression = 87/293 = 0.29692
4. Conditional probability of consuming given antennal depression = 76/87 = 0.87356
5. Conditional probability of consuming given the absence of antennal depression = 21/196 = 0.10714
6. Unconditional probability of consuming = 97/293 = 0.33106

Is #1 > #2 and #1 > #3? YES Is #4 > #5 and #4 > #6? YES

Dominant Male 1 Conditional Probability of Antennal Depression Given Water Present

7. Conditional probability of antennal depression given water present = 85/193 = 0.27128
8. Conditional probability of antennal depression given the absence of water = 2/100 = 0.02
9. Unconditional probability of antennal depression = 87/293 = 0.29692
10. Conditional probability of water present given antennal depression = 85/87 = 0.97701
11. Conditional probability of water present given the absence of antennal depression = 108/100 = 1.08
12. Unconditional probability of water present = 193/293 = 0.65870

Is #1 > #2 and #1 > #3? YES Is #4 > #5 and #4 > #6? NO

Appendix B.4. Conditional probability calculation data sheet. This data sheet was used to calculate the conditional probability of antennal depression given consuming and consumables present. If the conditional probabilities calculated in item 1 and item 4 were higher than the other conditional probabilities it was determined that antennal depression was either a likely or unlikely approach or consummatory response. The results in the data sheet above suggest that antennal depression is a likely consummatory response, and an unlikely approach response.