Feeding & Flight: Physiology & Behaviors of the Hawkmoth, *Manduca sexta*

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**Abstract**

The relation between flight, olfactory, color constancy and other visual stimuli allow the hawkmoth, or hummingbird moth, *Manduca sexta* to forage for nectar-producing plants with the highest energy values to assist in their hovering flight behaviors. Through relational studies on the diurnal moth *Macroglossum stellatarum* and another nocturnal moth *Deilephila elpenor*, it is important to understand that the hovering behavior of hummingbird moths expends a great deal of energy and requires sources of high nectar which these moths have evolved to find through multi-sensory inputs that increase when they are in hovering flight. The capacity for the *Manduca sexta* moth to adapt to its surrounding is also important, showing how this animal has evolved to allow for a more generalized feeding between different nectar sources while still preferring certain colors and nectar compounds if they are available. Also, the ability of wild moths versus moths raised in captivity raises the question as to whether or not wild moths have a greater chance of survival due to their exposure to the reality of the world outside the laboratory. Wild moths performed much more efficiently than naïve moths raised in captivity (Raguso and Willis, 2002) and suggest more research need to be done to find
out the cue and preference differences between moths raised in captivity and those captured from the wild.

**Introduction**

By looking at the fundamentals of insect flight, mainly hovering, as well as looking at studies done on the olfactory and visual cues of other hawkmoths, this paper will explore the relations between stimuli for the nocturnal hawkmoth *Manduca sexta* and show what leaders in the field have found about this insect’s ability to learn and differentiate to adapt and find the food sources with the greatest energy nectar source. I will also be examining the studies of wild versus naïve hawkmoths and studies relating to other diurnal and nocturnal hawkmoths as they may relate to the choices and behavior preferences of *Manduca sexta*.

**Fundamentals of Insect Flight and Hovering**

Insects and birds have a strong induced flow structure, partially self-created, that envelops their bodies during flight. The flow structure influences many physiological processes included, but not limited to, the delivery of odor and mechanical stimuli to the animal. Over the last fifteen years, attention to detailed aerodynamics measurements and flow visualization has been an area of scientific interest in insects. Moreover, the change from the belief that flight and hovering were associated with wakes created behind the insects, more studies are focusing on the proximate mechanism of aerodynamic force generation that allows the insects to fly. It is possible that a detailed understanding of these flows may allow us to determine the odor plume dynamics and their relation to antennal receptors during flight to explain how moths and other insects track odors during flight (13).
This induced flow is necessary because it is the byproduct of high Reynolds numbers wing-based locomotion. Due to the phasic and tonic components of the induced airflow in experiments involving *Manduca sexta*, the induced flow is thought to affect the mechanosensory structures, suggesting that it may affect insect behaviors including aggregation, swarming, olfactory processes and pheromone detection, and the timetables for those behavioral reactions (12).

For a long time, it was believed that insect flight depended on unsteady mechanisms and effects that needed to be studied as well as a three action control of movements that allows for insect maneuverability (15). The idea has been overturned due to the complex processes and behaviors insects have developed for flight. There is still a general inadequacy accounting for the observed lift production of insects through their flight control mechanism, however; the ‘quasi-steady assumption’ had been challenged on the account of field work where the flight speeds change directly with wing beat kinematics (18). An unresolved problem is how wing and body movements change with flight speed because they are essential for aerodynamic modeling of insects which may be useful in human technology (17).

Hovering is problematic for scientists because the range of wing movements appropriate for sustained flight at a fixed position and orientation seem to have inverse problems that would make hovering difficult or nearly impossible. One way to look at hovering and its challenges is to assess the importance of flight control in correlation to the ability to hover. However, hawkmoths like *Manduca sexta* have the means to maintain position and orientation with considerable freedom, suggesting that there may
be factors beyond the aerodynamic or physical that affect the ability for hovering flight (6).

**Hovering and Forward Flight in *Manduca sexta***

The genera *Manduca* and *Drosophila* are two of the best studied for insect flight, especially for examples intended to determine odor plume dynamics and their relation to antennal receptors during flight. Sane and Jacobson (12) have found that the approximate induced flow speeds of *Manduca sexta* wings can be approximated because in an experiment, they found that the flow is directly proportional to the wing stroke frequency and amplitude which provided a greater understanding of how wing flows over the bodies of the hawkmoths during flight (13).

The hawkmoths, also called hummingbirds moths commonly, are convenient to work with because they readily flap their wings when they are tethered and are not as constrained by temporal elements as other Lepidopterons. Unlike many other species that bask in the sun to gain strength from heat, the hawkmoths attain heat by means of muscle thermogenesis through rapid wing vibration (shivering). They are also ideal subjects because they practice active flight. From Sane and Jacobson’s (12) anemometry experiments with these moths, they have extrapolated that the inherent pulsatile odor delivery, or delivery that corresponds to the rise of each wing flap, may extend and describe the amplification affect of the plume structure in not only the *Manduca sexta* moth, but other species as well. Because the active flight typically demands higher wing amplitudes and frequencies for the beating of wings, the wing kinematics need to be fine tuned and synchronized in order for the *Manduca sexta* moths to carry out their olfactory-based behaviors (12).
The flight mechanisms in *Manduca sexta* are not unsteady as once believed. As the flight speed of the insect changes, the relative velocities and forward motion have also changed (18). Unlike some vertebrate fliers, there is no distinct gait change that occurs in the moths between hovering and forward flight; it is much more gradual. One of the keys to understanding the differences between forward flight and hovering has to do with the wing-tip path and rotation velocity. The flight at low speeds is characterized by long periods with a steady body position and steady flight maneuverability. The rotation in a hovering wing beat is much greater, however, unlike previously thought, the hawkmoths retain their symmetry as they beat their wings faster to hover synchronously and remarkably consistent. The change between forward flight and hovering is marked by a gradual change in wing beat instead of a gait change (17).

Hawkmoths generate locomotor forces by torquing their wings with induced air flow to support them. When these forces are all applied to the animal, moths like *Manduca sexta* have the ability to hover and retain mobility at the same time. In fact, Hedrick and Daniel found that the hawkmoths could retain their position within a sphere of 0.65 centimeters. Their study reinforced the ability of *Manduca sexta* to retain its position despite air flow and wing beat versus weight considerations, allowing for the discovery of twenty different kinematic parameter sets that allow for hovering flight. The main three documented with high frequency are the mean angle elevation, sweep angle phase, and rotation angle amplitude. These factors make it unlikely that *Manduca sexta* hawkmoths ever have under-actuated flight when hovering. The next step for research would be to look at the relation between the body trajectory of the moths and the abdominal flexion angle and its relation to hovering in *Manduca sexta*. 

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Flower Tracking Behavior of *Manduca sexta*

The nocturnal feeding behaviors of the *Manduca sexta* hawkmoth relate easily to those of the diurnal feeding behaviors of *Macroglossum stellatarum* because both animals must track their flowers as they hover while feeding, making their ingestion dynamics and choice of flowers similar as hovering expends a lot of energy that the animal must replace through feeding. They flap their wings 70-80 Hz during hovering flight, and the nectar intake of *Macroglossum stellatarum* depends on the morphological characteristics of a combination of the feeding apparatus, the fluid properties, and the negative pressure produced by the hawkmoth to ingest the nectar (7).

Hawkmoths cope with flower motion by tracking those motions to maintain contact with the nectar source. *Manduca sexta* are equally capable of tracking flowers moving in the horizontal and vertical motion axes; however, they have trouble tracking flowers moving in the looming axis (14). The hawkmoths were almost unable to maintain contact with a nectar source moving at 3 Hz. Because flower tracking is vital to hawkmoth survival, the tight coevolution between plants and pollinators needs to be examined to explain the ability of the hawkmoths to track along the axes. The movement of the animal’s torso in conjunction with the vibrational properties of the plants could be responsible for the ability of the moth to track on all but the looming axes of the flowers they feed from. This theory suggests that hawkmoths actively prefer to feed from flowers with the highest fitness benefit and can detect these flowers from the vibrations and movement of the flowers (14).

**Optics and Color Recognition**
*Manduca sexta*, like *Deilephila elpenor*, is a nocturnal moth. Unlike *Macroglossum stellatarum*, a diurnal hummingbird moth, little research has been done on the physiological optics of the animal. However, comparing the day-active hawkmoth’s compound eye without ommatidia to the related behaviors of the two moths may provide insight into how *Manduca sexta* perceives its environment.

*Macroglossum stellatarum* has outstanding spatial resolution and like *Manduca sexta* is an excellent hoverer and sucks nectar in the manner likened to the way hummingbirds do. A matrix of photoreceptors and an overlying imaging system made out of a completely independent matrix of lens elements made up the compound eye (16). This hawkmoth or hummingbird moth also uses color cues to discriminate between flower but can learn to use non-color cues instead (8). This is important because it was believed nocturnal moths cannot use color alone to discriminate between flowers due to the absence of color that diurnal hawkmoths had adapted to detect and discriminate using.

Due to the photoreceptors and diurnal behaviors of *Macroglossum stellatarum*, there was believed to be little relation to *Manduca sexta* until research was done on the perceptual functions using chromatic and achromatic cues in the nocturnal hawkmoth *Deilephila elpenor*. When Kelber at al. (9) found that color vision was also useful for discriminating objects at night for the hawkmoth, they realized that the preferred flowers of the species, white nocturnal flowers, absorbed ultraviolet light. Like *Macroglossum stellatarum*, nocturnal hawkmoths have large and sensitive superposition compound eyes that allow the nocturnal moths to rely on color discrimination for choosing flowers just as diurnal species do (9).
Although the constancy of colored flowers chosen by diurnal and nocturnal hawkmoths seems consistent, A. Balkenius and A. Kelber determined that there must be another process involved that allows the animals to further discriminate between nectar sources because the color choices of the moths are independent of the spectrum of illumination. Where *Macroglossum stellatarum* has an innate preference for blue and yellow flowers, but can learn to prefer abnormal colored flowers as food sources. Only color would matter to the insects if color constancy was the only element affecting their recognition of food sources (1).

**Odor Perception & its Relation to Color Cues**

Moths have shown an increased preference for the single volatile chemicals present in the odors of flowers on which they forage for food (4). The communications between flowering plants and their pollinators, in this case the hawkmoth, involve innate, deceptive, learned sensory signals. The strongly scented nocturnal flowers feed on and pollinated by *Manduca sexta* are among some of the more strongly scented flowers known. However, the scent alone cannot attract the moths to the flowers. Raguso and Willis (10, 11) found that both floral fragrance and visual display are innately attractive to the male *Manduca sexta*, but neither alone will elicit proboscis extension and feeding. Both the visual cues and the odor perception are necessary.

Because both visual and olfactory stimuli in synchrony are required for the extension of the proboscis, the idea that single-modality signals eliciting feeding under extreme cases of sensory impairment has not been observed. Like many Lepidopterons, visual-olfactory feeding behavior is common, and research confirms that *Manduca sexta* is equipped with a foraging strategy that can adapt readily to changes in nectar
availability in an unpredictable landscape as it can both smell and see to find its food sources (10).

Unlike *Macroglossum stellatarum* and *Deilephila elpenor*, however, *Manduca sexta* does not favor one stimulus more strongly than another. Balkenius and Kelber (1, 2) found that in the diurnal hawkmoth, visual stimuli were favored and in the nocturnal hawkmoth, olfactory stimuli were favored. *Manduca sexta* does not seem to require or favor one over the other (3). However, when Raguso and Willis (10, 11) used wild instead of naïve hawkmoths in their experiments, they found that they could get a moth to feed from paper flowers with vegetative scents when floral stimuli were not present, suggesting that both stimuli are usually required but may be able to be surpassed in times when the animal needs to find food for its survival.

Because hawkmoths need to meet the demands for the energy they expend in hovering flight, dispersal and migration occurs as well as the ability to feed from a broad spectrum of nectar-rich flowers. They do have an innate preference for certain floral, color, and odor patterns, but these can be reversed through operant conditions suggests that the learning capabilities of captive and wild moths may differ. Although usually both olfactory stimuli and visual cues and color constancy are needed for proboscis extension most of the time, survival instincts suggest that moths could be trained if they are not raised in captivity (11).

Goyret and Raguso (5) found that *Manduca sexta* could learn to associate particular odors with nectar rewards. The foraging behavior of *Manduca sexta* seems to follow a sequential pattern of the senses, with different modalities at each stage. Mechanoreception as well as visual and olfactory cues detected by the moth is involved
in their nectar feeding. It is also important to note that due to their need for high energy nectar, the adults in the experiments could adapt and learn to improve their handling abilities of a nectar resource in the course of a single foraging bout (5).

**How Recognition Behaviors Affect Flight**

The *Manduca sexta* track floral odor plumes upwind to their sources (10). Because they are adept flyers that hover instead of perching while they feed, hawkmoths require a greater amount of energy that must be ingrained in their ecology and evolution. Hawkmoths contend with flower motion by utilizing both natural airflows and the induced flow of air created by their beating wings. (14)

**Conclusion**

Through understanding the high energy expenditure of hawkmoths requiring a greater viscosity of nectar energy intake, the behaviors of the *Manduca sexta* hawkmoth can be attributed to the evolutionary sensory changes that allow the animal to be most efficient at foraging for food in flight. More research needs to be conducted as to the differences between naïve and wild moths and their ability to survive and detect the most nutrient-rich nectars, but it is fairly conclusive that hawkmoths require a combination of both olfactory and visual color constancy cues in combination with a certain plant vibration component that allows them to survive and continue finding the energy for their hovering flight.

**References Cited**


