Hawkmoth Pollination in Arizona’s Sonoran Desert: Behavioral Responses to Floral Traits

Robert A. Raguso and Mark A. Willis

Adult butterflies forage for a broad spectrum of resources, including floral nectar, pollen, fruit, sap, fungal fluids, mineral salts, and animal tissues, secretions and waste products (Owen 1971; Gilbert and Singer 1975; Ray and Andrews 1980; Boggs 1987b; DeVries 1988a; Boppré 1990). Flower-visiting butterflies have long been recognized as important pollinators (Delpino 1874; Knuth 1898; van der Pijl 1961), as their patterns of movement affect plant outcrossing distances and population structure (Levin 1978; Murawski and Gilbert 1986; Johnson and Bond 1994). Recent studies have explored the role of butterflies as pollen vectors (Cruden and Hermann-Parker 1979; Wiklund et al. 1979; Murphy 1984; Venables and Barrows 1985; Stanton et al. 1986), their effectiveness as pollinators of specific plants (Levin and Berube 1972; Opler et al. 1975; Spears 1983; Jennersten 1984; Schenske and Horvitz 1984; Erhardt 1990), their learning abilities in the context of floral feeding (Lewis 1986; Goulsom and Cory 1993; Weiss 1995, 1997), and their allocation of nectar resources to flight energetics and reproductive output (Watt et al. 1974; Boggs 1981a; Murphy et al. 1983; May 1992).

In parallel with butterflies, adult nectar feeding has evolved in a number of moth families and is especially prominent among hawkmoths (Sphingidae: Rothschild and Jordan 1903; Newman 1965; Hodges 1971; Schreiber 1978; Miller 1997). Nectar-feeding hawkmoths constitute an important class of pollinators in warm temperate and tropical habitats worldwide (Baker 1961; Gregory 1964; Silberbauer-Gottsberger and Gottsberger 1975; Grant 1983; Bawa et al. 1985; Nilsson et al. 1985; Haber and Frankie 1989; Singer and Cocucci 1997; Johnson et al. 1998). By virtue of their hovering flight, large body size, and high vagility, hawkmoths visit more flowers per foraging bout (Cruden et al. 1976; Heinrich 1983; Herrera 1989), carry
larger pollen loads (Kislev et al. 1972; Haber 1984; Nilsson et al. 1987), and move pollen greater distances (Stockhouse 1976; Linhart and Mendenhall 1977; Nilsson and Rabakonandrianina 1988) than do most other flower-visiting Lepidoptera. These characteristics, combined with hawkmoths' ability to travel long distances in search of mates, host plants, and appropriate habitat (Janzen 1971; Cross and Owen 1970; Powell and Brown 1990; Nilsson et al. 1992), underscore the importance of hawkmoth pollination to plant population dynamics. These insects effect pollen transfer and gene exchange between widely dispersed individual plants and plant populations (Schemske 1980; Haber 1984). Thus, fluctuations in hawkmoth abundance, whether natural or anthropogenic (Grant 1931; Kislev et al. 1972; Buchmann and Nabhan 1996), may have dire consequences for rare plants that depend exclusively on hawkmoths as pollinators, especially in fragmented habitats (Suzán et al. 1994; Buchmann and Nabhan 1996), dune remnants (Pavlic et al. 1993), and on islands (Lammers 1989; Boucher 1996).

During the past four years, we have studied the interactions between nectar-feeding, crepuscular hawkmoths and a guild of night-blooming, hawkmoth-pollinated plants in Arizona's Sonoran Desert. Specifically, we have characterized the chemical and physical properties of floral attractants produced by night-blooming plants, and we have performed behavioral assays testing the relative importance of visual and olfactory cues in attracting hawkmoths to flowers. Our investigations were motivated by the surprising paucity of studies on hawkmoth foraging behavior, despite decades of research on hawkmoth thermal biology, pollination ecology, and sensory neurophysiology. This chapter presents an overview of hawkmoth pollination and introduces our studies of the sensory ecology of hawkmoth-flower interactions. It is important to note that much of the previously published literature, at least for nocturnal hawkmoths, is anecdotal or based on observations from uncontrolled or unbalanced experiments. We begin with an overview of the ultimate and proximate reasons why hawkmoths visit flowers, then ask whether both visual and olfactory cues are necessary for hawkmoth attraction and feeding. We then summarize the behavioral experiments with which we addressed this question using naive and experienced hawkmoths, and conclude by discussing our results in the context of other studies of hawkmoth behavior.

Why include a chapter on hawkmoth nectar foraging in a book on butterfly ecology and evolution? From a phylogenetic perspective, butterflies are a monophyletic lineage of specialized, largely diurnal moths (Weller and Pashley 1995) whose neurosensory capabilities, physiological demands, and reproductive imperatives are comparable to those of most large moth families (Chapman 1998). Therefore, the questions that drive our experimental system—how hawkmoths integrate visual and olfactory cues during foraging and how larval diet, adult experience, and the physical environment
modify such behaviors—are broadly relevant to the evolutionary, ecological, and physiological concept structure by which butterflies and, indeed, all nectar-feeding insects are studied (Gilbert and Singer 1975; Heinrich 1983; Watt 1985b). In this way, the study of pyrrolizidine alkaloid use by arctiid moths (Pliske 1975; Boppré 1990; Conner et al. 1990), mud puddling (Smedley and Eisner 1995), and Müllerian mimicry (Miller 1996) in notodontid moths has provided important insights and context for considerations of butterfly chemical ecology and mating system evolution. Studies such as ours will contribute to an eventual comparative assessment of the effects of sensory physiology and life history parameters on the evolution of adult feeding strategies throughout the Lepidoptera (see Boggs and Ross 1993; Boggs 1997a; D. M. O'Brien 1998).

BRIGHT AND SWEET: FLORAL ADVERTISEMENTS AND REWARDS OF HAWKMOTH-POLLINATED PLANTS

Why do hawkmoths visit flowers? Floral nectar is an important energetic resource for hawkmoths, supporting their metabolically expensive poikilothermic flight physiology (Heinrich and Casey 1973; Casey 1976; O'Brien 1999) and long-distance dispersal (Cross and Owen 1970; Janzen 1986). Adult nectar feeding also may contribute directly to reproductive fitness via egg maturation in some hawkmoths (Ziegler 1991; D. M. O'Brien 1998). In Arizona's Sonoran Desert, at least seventeen species of hawkmoth-pollinated, night-blooming plants (representing twelve angiosperm families) produce large volumes of sucrose-dominated nectars (R. Raguso, unpub.). The nectar in hawkmoth-pollinated flowers is typically less concentrated (18–37% w/w) than the 40–50% syrups that characterize bumblebee-pollinated flowers (Pyke and Waser 1981; Baker and Baker 1983), but mean standing crop nectar volumes are often quite a bit larger, ranging in our sample from 3 to 80 μL per flower (R. Raguso, unpub.). Following the calculations of Bartholomew and Casey (1978) and Cruden et al. (1983), the caloric content of one of these flowers would support 25 seconds to 15 minutes of hovering flight by a hawkmoth weighing 2 g. Thus, Arizona's night-blooming flowers offer a nectar resource that is 10- to 360-fold richer in energy content per flower than that available from most day-blooming, bee-pollinated flowers (see Heinrich 1983).

The chemical composition and viscosity of nectars produced by hawkmoth-pollinated plants presumably represent a balance between the moths' high energetic demands and the biomechanical limitations of fluid extraction through a tubular proboscis (Watt et al. 1974; Kingsolver and Daniel 1979; Pyke and Waser 1981; Heyneman 1983). For example, in preference experiments, day-flying *Macroglossum stellatarum*, L. hawkmoths

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choose to visit artificial flowers offering 20–50% (w/w) sucrose solutions over those with 10% and 60% solutions (Josen and Farina 1997). The degree to which the moths’ choices were based on sugar concentration versus viscosity remains an open question.

Hawkmotth-pollinated flowers secrete nectar within deep corolla tubes or spurs, whose length frequently approaches or exceeds that of an extended hawkmoth proboscis (Gregory 1964; Miller 1981; Grant 1983; Nilsson et al. 1985). Nilsson’s (1988) elegant manipulative experiments suggest that this geometric relationship is a result of directional selection, in which longer tubes or spurs enhance plant reproductive fitness through pollen removal (male function) and receipt (female function) via contact with the moth’s body (Darwin 1865; plate 3.1). In some cases, hawkmoth-mediated runaway directional selection has resulted in nectar spurs exceeding 20 cm in length (Nilsson et al. 1987; Haber and Frankle 1989; Wasserthal 1997).

Hawkmotth-pollinated plants typically advertise the presence of nectar through both olfactory and visual displays. Their tubular or trumpet-shaped flowers often open at dusk and produce powerful, usually pleasant aromas, which are thought to attract hawkmoths from distances ranging from tens to hundreds of meters (Kerner von Marilaun 1895; Tinbergen 1958; Haber 1984). Although oxygenated terpenoids, aromatic esters, and nitrogenous volatiles are frequently present, chemical composition, blend complexity, and relative emission rates of floral scent have been found to vary greatly among hawkmoth-pollinated plants in Ecuador (Knudsen and Tollsten 1993), Japan (Miyake et al. 1998), and Arizona (R. Raguso, unpub.). This lack of tight chemical convergence reflects the diverse biosynthetic pathways available for volatile production in plants (Croteau and Karp 1991; Knudsen et al. 1993; Raguso 2001) and suggests that hawkmoths may respond to a broad spectrum of floral volatiles or learn to associate species specificity in fragrance chemistry with differences in nectar quality or quantity during foraging (see Roy and Raguso 1997).

In contrast to their fragrance, the coloration of hawkmoth-pollinated flowers worldwide and in Arizona is highly convergent: pale or white and strongly reflective at twilight, with deeply dissected or grooved petals, suggesting visual and mechanosenory guidance to the nectaries (Knoll 1925; Baker 1961; Kugler 1971; Brantjes and Bos 1980; White et al. 1994; plate 3.2A). Most flowers in our survey were bright white, reflecting light in all human-visible wavelengths but lacking UV reflectance, which is known to suppress feeding responses in Manduca sexta hawkmoths (White et al. 1994; Cutler et al. 1995). The combination of large, reflective individual flowers, densely clustered inflorescences, and patchy populations can produce extraordinary visual displays, probably visible to foraging moths over tens of meters (plate 3.2B), but also visible to florivores and nectar thieves. Similar visual displays, along with the tubular floral morphology, sucrose-rich

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nectar, and strong fragrances described above, typify hawkmoth-pollinated plants worldwide, have evolved repeatedly in most angiosperm families, and strike the observer as exaggerated or “supernormal” cues (sensu Baerends 1950).

Given the opportunistic foraging patterns of most hawkmoths (Kislev et al. 1972; Haber 1984; Wasserthal 1993) and the well-documented temporal fluctuations in their abundance (Miller 1978, 1981; Willmott and Búrquez 1996), many hawkmoth-pollinated plants employ alternative reproductive strategies, such as self-compatibility (Motten and Antonovics 1992), recruitment of secondary pollinators (Barthell and Knops 1997), or a long-lived perennial growth form (Suzán et al. 1994). Moreover, Haber and Frankie (1989) have suggested that obligately hawkmoth-pollinated plants may need to overproduce floral rewards and advertisements in order to compete with more predictable or abundant floral resources. Such elevated investment in pollinator attraction bears a heavy cost in photosynthetic currency (Vogel 1963, 1983) and in increased apparency to natural enemies (Baldwin et al. 1997), underscoring the importance of hawkmoth visitation to the plants’ reproductive fitness.

HAWKMOTH ATTRACTION AND FEEDING: HYPOTHESES AND PREDICTIONS

What are the relative contributions of olfactory and visual information to the foraging decisions made by nocturnal hawkmoths? Several lines of evidence suggest that hawkmoths can use olfaction or vision to find flowers. Hawkmoths have keen vision in dim light, many times more sensitive than that of humans (Schlecht 1979; Bennett and White 1989), and they often probe at bright nonfloral objects while foraging at flowers (Clements and Long 1923; Kugler 1971). In addition, both wild and laboratory-reared hawkmoths show acute olfactory sensitivity to individual floral volatiles and complex blends in electroantennogram (EAG) assays (Brantjes 1973; Raguso et al. 1996; Raguso and Light 1998), and they track floral odors to their sources in the absence of visual targets (Kerner von Marilaun 1895; Tinbergen 1958; Brantjes 1973, 1978). Many species of hawkmoths have been trapped with floral odor lures (Morgan and Lyon 1928; Hodges 1971) and fermenting fruit (Knoll 1925; Newman 1965; Brou and Brou 1997), implying olfactory attraction.

Thus, hawkmoths respond physiologically and behaviorally to the visual and olfactory characteristics of the night-blooming flowers that specialize on them as pollinators. To what extent do inputs from these two sensory modalities interact? How does the scale at which visual or olfactory cues attract hawkmoths affect pollen movement within and between plant populations?
Are hawkmoths’ responses to floral cues modulated by their physiological state or prior experience?

Based on published studies of other flower-feeding Lepidoptera, we established six working hypotheses to consider the potential roles played by floral scent and visual display in hawkmoth attraction and feeding:

\textbf{H}_0: \textit{Null.} Floral scent has no attractive function; hawkmoth attraction and feeding are accomplished purely through visual stimuli. Rather, floral scent compounds might function as antimicrobial agents in nectar (Lawton et al. 1993), or could represent pleiotropic by-products of null mutations within pigment biosynthetic pathways (e.g., the aromatic precursors of anthocyanin pigments resulting in white flowers; see Dooner et al. 1991).

\textbf{H}_1: \textit{Scent releases visually guided feeding.} The presence of floral scent elicits visual searching or feeding behavior. This hypothesis implies synergistic interactions between visual and olfactory inputs within visual range (Ilse 1928; Baerends 1950; Tinbergen 1958; Brantjes 1973, 1978).

\textbf{H}_2: \textit{Visual attraction to flower, with scent-elicited landing or probing.} After visual guidance to a flower, scent triggers proboscis extension, landing, and feeding, as observed in some nymphalid butterflies (Pellmyr 1986) and noctuid moths (Brantjes 1978; Nilsson 1978).

\textbf{H}_3: \textit{Scent as the complete attractant/feeding cue.} Scent guides hawkmoths from a distance, orients them at close range, and modulates landing and feeding in the absence of visual cues, as observed for some geometrid and noctuid moths (Nilsson et al. 1990).

\textbf{H}_4: \textit{Olfactory distance attraction, with visually guided feeding (at least in part).} Hawkmoths enter an odor plume and fly upwind toward the odor source from a distance, but may transition to visual guidance at close range (Kerner von Marilaun 1895; Morgan and Lyon 1928; Haber 1984).

\textbf{H}_5: \textit{Scent as a positive or negative associative learning cue.} Scent may not be required for initial floral visits, but hawkmoths learn to associate nectar quality at different flowers with scent chemistry, perhaps in combination with visual cues. This possibility was suggested by the learned avoidance of deceptive nectarless flowers by hawkmoths (Haber 1984) and confirmed by recent experiments in which \textit{Manduca sexta} were trained to floral odors as Pavlovian conditioned stimuli (Daly and Smith 2000).

Not all of these hypotheses are mutually exclusive, and floral cues could have different functions depending on distance from the flower or on the physiological state or experience of an individual moth (see reviews by Williams 1983; Dobson 1994). Note that each of these hypotheses has some precedent among groups of flower-visiting Lepidoptera (table 3.1).

Our laboratory and field experiments directly test the hypotheses (\textbf{H}_0–\textbf{H}_5) that are relevant to close-range (0–10 m) hawkmoth attraction and
Table 3.1 Functions of floral scent for diverse nectar-feeding Lepidoptera

<table>
<thead>
<tr>
<th>Function</th>
<th>Taxa Studied</th>
<th>Family</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A. Butterflies</strong></td>
<td></td>
<td></td>
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<tr>
<td>Distance attraction and landing</td>
<td>Ithomelines (8 genera)</td>
<td>Nymphalidae</td>
<td>Pliske et al. 1976</td>
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<td></td>
<td><em>Lycoris cleobaea</em></td>
<td></td>
<td>DeVries and Stiles 1990</td>
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<td></td>
<td><em>Danais plexippus</em></td>
<td></td>
<td>Wagner 1973</td>
</tr>
<tr>
<td>Landing/probing</td>
<td><em>Danais glippus</em></td>
<td>Nymphalidae</td>
<td>Myers and Walter 1970</td>
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<tr>
<td></td>
<td><em>Argynnis paphia</em></td>
<td></td>
<td>Pellmyr 1986</td>
</tr>
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<td></td>
<td><em>Argynis rutilana</em></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td><em>Pieris napi</em></td>
<td>Pieridae</td>
<td>Goulson and Cory 1993</td>
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<tr>
<td></td>
<td><em>Pieris rapae</em></td>
<td></td>
<td>Honda et al. 1998</td>
</tr>
<tr>
<td>No function?</td>
<td><em>Battus philenor</em></td>
<td>Papilionidae</td>
<td>Weiss 1997</td>
</tr>
<tr>
<td></td>
<td><em>Papilio demoleus</em></td>
<td></td>
<td>Ilse and Vaidya 1956</td>
</tr>
<tr>
<td>Releasing cue</td>
<td><em>Aglais urticae</em></td>
<td>Nymphalidae</td>
<td>Ilse 1928</td>
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<tr>
<td></td>
<td><em>Nymphalis polychloros</em></td>
<td></td>
<td></td>
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<td></td>
<td><em>Hipparchia semele</em></td>
<td></td>
<td>Tinbergen et al. 1942</td>
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<tr>
<td></td>
<td><em>Pararge aegeria</em></td>
<td></td>
<td>Scherer and Kolb 1987b</td>
</tr>
<tr>
<td><strong>B. Moths</strong></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Distance attraction and landing</td>
<td><em>Cisseps fulvicollis</em></td>
<td>Ctenuchidae</td>
<td>Cantelo and Jacobsen 1978</td>
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<tr>
<td></td>
<td><em>Prochoreodes versatula</em></td>
<td>Geometridae</td>
<td></td>
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<tr>
<td></td>
<td><em>Evergestis pallidata</em></td>
<td>Pyralidae</td>
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<td></td>
<td><em>Plusines and Heliotrices</em></td>
<td>Noctuidae</td>
<td></td>
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<td></td>
<td><em>Trichoplois ni</em></td>
<td></td>
<td>Brantjes 1978</td>
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<td></td>
<td><em>Autographa gamma</em></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td><em>Cucullia umbratica</em></td>
<td></td>
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<tr>
<td></td>
<td><em>Hadena bicrurs</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Landing/probing</td>
<td><em>Hadenine, cuculline, and plusine noctuids</em></td>
<td>Noctuidae</td>
<td>Nilsson 1978</td>
</tr>
<tr>
<td></td>
<td><em>Zygaena trifoli</em></td>
<td>Zygaeidae</td>
<td></td>
</tr>
<tr>
<td>Complete attractant</td>
<td><em>Gigantoceras perperti</em></td>
<td>Noctuidae</td>
<td>Naumann et al. 1991</td>
</tr>
<tr>
<td></td>
<td><em>Melinoessa catenata</em></td>
<td>Geometridae</td>
<td>Nilsson et al. 1990</td>
</tr>
<tr>
<td>Associative learning</td>
<td><em>Spodoptera littoralis</em></td>
<td>Noctuidae</td>
<td>Fan et al. 1997</td>
</tr>
<tr>
<td>No function?</td>
<td><em>Macroglossa stellatarum</em></td>
<td>Sphingidae</td>
<td>Kelber and Pfaff 1997</td>
</tr>
</tbody>
</table>

feeding. Three critical predictions allow us to distinguish among these hypotheses (see Alcock 1993a): (1) scent is required to initiate a feeding bout, (2) visual cues are required for feeding, and (3) scent is required for feeding at each flower (table 3.2). If hawkmoths do not feed at scentless flowers, then H₀ and H₁ would be rejected, and the two remaining alternative hypotheses could be evaluated after testing whether visual cues are necessary. In addition, we assessed the ability of naive hawkmoths to orient to floral fragrance in flight by challenging them to track floral scent plumes in a laboratory wind tunnel. While this experiment simulated potential hawkmoth responses to floral scent on a scale of meters to tens of meters, we did not directly test long-distance attraction (H₃) in the field. Potential roles for scent-based associative learning in the context of foraging behavior (H₃)
Table 3.2 Hypothesis tree for hawkmoth attraction to flowers

<table>
<thead>
<tr>
<th>Critical Predictions</th>
<th>$H_0$ No Role</th>
<th>$H_1$ Releasing Cue</th>
<th>$H_2$ Land or Probe</th>
<th>$H_3$ Complete Attractant</th>
<th>Experimental Results</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scent is required to initiate feeding</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>Greenhouse Bioassays</td>
</tr>
<tr>
<td>Visual cues are required for feeding</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>Field Tests</td>
</tr>
<tr>
<td>Scent is required to feed at each flower</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
</tbody>
</table>

have not yet been addressed directly with hawkmoths, although classical conditioning of Manduca sexta and noctuid moths to floral scent has been demonstrated recently in laboratory settings (Hartlieb 1996; Fan et al. 1997; Daly and Smith 2000).

INNATE RESPONSES OF NAIVE HAWKMOTHS TO FLORAL CUES

UPWIND ORIENTATION TO FLORAL SCENT PLUMES

Laminar flow flight tunnels are the arena of choice for demonstrating olfactory attraction and investigating odor-modulated insect behavior (Baker and Linn 1984). Odor-guided upwind flight orientation has been demonstrated previously for M. sexta males and females (Willis and Arbas 1991). In these experiments, the odor-modulated flight of male moths to female sex pheromone and of female moths to fresh leaves of Nicotiana tabacum L. (Solanaceae), a larval host plant, were found to be broadly similar. In both cases, the moths generated a temporally regular zigzagging flight pattern as they flew upwind to the appropriate odor source. Upon reaching the source, male moths initiated copulatory behavior and females attempted oviposition. Given that both sexes of M. sexta use similar strategies to locate distant unseen odor sources in flight, we predicted that they would use the same strategies to locate sources of floral volatiles when tested in our laboratory’s flight tunnel.

The results of our flight tunnel experiments are summarized in table 3.3. As predicted, naïve, unfed, and unmated male M. sexta hawkmoths were attracted to floral targets in the flight tunnel, executing zigzag upwind flight.
Table 3.3 Naive *Manduca sexta* responses to floral scent in wind tunnel assays

<table>
<thead>
<tr>
<th>Trial</th>
<th>Sex</th>
<th>Single Compound</th>
<th>Complete Floral Blend</th>
<th>Control Odors</th>
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<tr>
<td>1. Male</td>
<td></td>
<td>0/6&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2/10&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3/4&lt;sup&gt;c&lt;/sup&gt;</td>
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<td>2. Male</td>
<td></td>
<td></td>
<td>5/13&lt;sup&gt;d&lt;/sup&gt;</td>
<td></td>
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<td>3. Male</td>
<td></td>
<td>0/4&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2/11&lt;sup&gt;d&lt;/sup&gt;</td>
<td>7/7&lt;sup&gt;c&lt;/sup&gt;</td>
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<td>4. Male</td>
<td>Female</td>
<td>0/6&lt;sup&gt;e&lt;/sup&gt;</td>
<td>3/10&lt;sup&gt;d&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td></td>
<td>2/8&lt;sup&gt;d&lt;/sup&gt;</td>
<td></td>
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<tr>
<td>5. Male</td>
<td></td>
<td></td>
<td>2/14&lt;sup&gt;k&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Female</td>
<td></td>
<td></td>
<td>1/88&lt;sup&gt;e&lt;/sup&gt;</td>
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<tr>
<td>6. Male</td>
<td></td>
<td></td>
<td>2/8&lt;sup&gt;h,i&lt;/sup&gt;</td>
<td>0/8&lt;sup&gt;i&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

* Linalool (most abundant component of floral scent in c, d, e below)
* *Penioceras greggi* (Cactaceae)
* One female-equivalent *M. sexta* sex pheromone extract
* *Teloschnia rucksapulensia* (Apocynaceae)
* Nerolidol (second most abundant component of floral scent in d below)
* Leaves of tomato, *Lycopersicon esculentum* (Solanaceae), oviposition host plant for *M. sexta*
* *Denothera caesiptosa* (Onagraceae)
* *Calypheus tournoi* (Onagraceae); scent introduced into wind tunnel via Teflon tube
* 2/8 moths flew upwind to odor source, but did not extend proboscis
* Filtered air, introduced into wind tunnel via Teflon tube

tracks similar to those observed in males tracking pheromone plumes and females tracking plumes of host plant odors (fig. 3.1B, D). Our observations revealed several important features of the moths’ innate responses to floral odors. First, no naive *M. sexta* were attracted to odor plumes of single compounds. None of the test moths showed any responses to linalool or nerolidol, two of the most abundant and widespread fragrance compounds found in hawkmoth-pollinated flowers (Kaiser 1993; Knudsen and Tollsten 1993; Miyake et al. 1998; Levin et al. 2001). Second, when offered living, open flowers, approximately 30% of naive test moths tracked the odor plume along the 3 m length of the flight tunnel, showing the slow, zigzag path characteristic of odor-guided flight, then actively fed at the flowers (fig. 3.1C, E). Moths that did not respond to the odor stimulus flew around the flight tunnel showing no preferred orientation (fig. 3.1A). Finally, when fragrance from living flowers was trapped and introduced as a plume into the flight tunnel, again approximately 30% of the naive moths tracked the plume to its source. In this case, however, the moths never extended their proboscides or attempted to feed. Thus, naive *M. sexta* can track plumes of floral scent to their source, but once there, feeding behavior is not elicited in the absence of a visual cue. These results are supported by the behavior of moths in the trials with living flowers, which displayed a typical odor-modulated flight track until they approached the flower, then extended their proboscides and flew a more direct line to the flower to feed (fig. 3.1C, E). This adjustment during approach to the flower suggests a switch from odor-guided to visually guided flight.
Figure 3.1 Flight tracks of Manduca sexta recorded in flight tunnel experiments. Direction of wind flow is R to L, velocity = 60 cm/s. (A) Nondirected flight of male moth that did not respond to odor stimulus. (B) Male moth flying upwind to female sex pheromone. (C) Same individual flying upwind to Peniocereus greggii (night-blooming cactus) flower. (D) Female moth flying upwind to tomato leaves. (E) Same individual flying upwind to Telosiphonocarpus nucipersis (rock trumpet) flower. Note linear approach flights to the target in C, D, E. Scale bars = 20 cm.

Although investigations of the chemical ecology of moth attraction to flowers have been ongoing for some time (e.g., Grant 1971), only recently has the technology to fully characterize floral scent chemistry become generally available (Dobson 1994; Raguso and Pellmyr 1998). In experiments investigating the interaction between the noctuid moth Trichoplusia ni (Hübner) and flowers of Abelia grandiflora (André) (Caprifoliaceae), no significant differences were found between the number of naïve moths that flew upwind to a synthetic blend matching the floral scent and the number that flew...
to phenylacetaldehyde, the single most abundant compound in the blend (Haynes et al. 1991). Heath et al. (1992) observed the same pattern in T. ni moths' responses to the nearly identical floral scent of Cestrum nocturnum L. (Solanaceae). Our results suggest that M. sexta's behavior does not fit this model, as naive moths of this species appear to require a complex blend of compounds to elicit upwind orientation to a flower. An earlier report of M. sexta being attracted to single compounds was based on field trapping of wild hawkmoths with amyl salicylate, a compound found in many night-blooming flowers (Morgan and Lyon 1928). In this case it must be assumed that the trapped moths were not naive and had already experienced this compound in the context of a blend emitted by flowers they had visited. It is possible that once a moth has formed an association between a nectar reward and a complex floral scent blend, it is able to "generalize" that association and respond to a simpler scent (i.e., to one or a few of the compounds in the blend). Generalization in olfactory learning has been clearly demonstrated in honeybees (Smith 1993; Smith and Getz 1994; Menzel and Müller 1996), and also appears to occur in M. sexta (Daly et al. 2001). Alternatively, the odor lure may have been perceived as a complex blend, as the traps were located along the borders of large tobacco fields, which produced formidable vegetative and floral emissions detectable by the moths.

Our flight tunnel work clearly demonstrates that naive M. sexta moths can track floral scent plumes to their source from at least 3 meters away, supporting the idea that wild moths may use strong fragrances to locate floral resources at greater distances in nature (Haber 1984). The responses of naive M. sexta to diverse floral scent blends from three different plant families are comparable, suggesting a flexible, chemically unspecialized response to floral volatiles. Additionally, these data suggest that once moths reach the odor source, proboscis extension does not occur in the absence of a visual target.

CLOSE-RANGE ORIENTATION AND FEEDING WITHIN PATCHES OF FLOWERS

We observed the behavioral responses of naive M. sexta moths to arrays of artificial flowers with and without floral scent in small greenhouse arenas (Raguso and Willis 2002). In these experiments, the artificial flowers were modeled after those of Oenothera sp., using paper that matched the reflectance spectrum of the real flowers and artificial nectaries filled with 25% sucrose. Floral scent was provided by living Oenothera neomexicana (Small) Munn plants concealed within a cheesecloth cage below the artificial flower array. A similar array with an empty cheesecloth cage served as a control.

Three important aspects of naive hawkmoths' foraging behavior were revealed in this study. First, artificial flowers that were arranged in a clump or bouquet were far less attractive than 3 x 3 arrays of evenly spaced individual
flowers. Second, naive moths were attracted to artificial flowers without floral scent present, but did not approach or feed from them. Third, the introduction of floral scent to an array of artificial flowers elicited feeding behavior from naive moths (see fig. 3.2 and plate 3.3), as well as approaches to the hidden odor source (without probing). All measured parameters of the moths’ behavioral responses (i.e., duration of visit, number of hovering events, etc.) increased significantly when floral odors were presented with the artificial flowers (Raguso and Willis 2002).

When we repeated the experiments using a modified floral array of five paper flowers and four natural Oenothera flowers, the total number of feeding events increased from 10 to 61, and the proportion of experimental animals that fed increased from 16 to 52%. Other behavioral states were less dramatically affected. Interestingly, no consistent preference (positive or negative assortative visitation) for natural or paper flowers was observed: hawkmot flower visits simply reflected the relative abundance of each flower type in the array. Similarly, the moths showed no visitation constancy, as the number of transitions within and between natural and paper flowers was essentially
random (Raguso and Willis 2002). Thus, despite measurable differences in odor, nectar volume, relative brightness, and texture between the natural and paper flowers, the hawkmoths did not distinguish between them. In light of this result, it is more likely that increased feeding from the mixed arrays was a response not to the presence of scented individual flowers, but to the enhanced odor plume emanating from the entire array. In sum, either visual cues or floral scent alone were sufficient to attract the attention of naive M. sexta moths, but both cues were necessary to elicit feeding.

FORAGING DECISIONS OF EXPERIENCED WILD HAWKMOTHS

How do wild, presumably experienced moths respond to visual and olfactory floral stimuli? We performed three experiments on the grounds of the Arizona-Sonora Desert Museum, in thornscrub habitat within the Tucson Mountains, Pima County, AZ. We observed a guild of nocturnal hawkmoths (Agris cingulatus [Fabricius], Manduca quinquemaculata [Haworth], M. rustica [Fabricius], and M. sexta) feeding at the flowers of a native night-blooming plant, Datura wrightii Regel (Solanaceae). We physically decoupled floral scent and visual display by covering Datura flowers with clear acetate bags (visual display, no odor, no nectar) or cheesecloth bags dyed green-brown (odor, no visual display, no nectar) and creating paper model flowers (visual display, nectar, no odor). We designed a series of experiments, in each case observing hawkmoth approaches and visits to evenly spaced flowers modified with respect to olfactory or visual traits (fig. 3.3A).

In the first experiment (fig. 3.3A), hawkmoths approached all floral treatments in two mixed plots, but significantly more visits occurred at open control and paper flowers, where nectar was available, than at either class of bagged flowers. Interestingly, a few hawkmoths poked at the plastic-bagged flowers with extended proboscides, but essentially ignored the cloth-bagged flowers. However, due to the large plume of floral and vegetative volatiles emanating from the plants, no treatment in this experiment was truly scentless.

In the second experiment (fig. 3.3B), hawkmoths were attracted to each of three treatments in homogeneous plots, but attempted to feed only when visible flowers were present. Although the moths approached the cloth-bagged flowers, none extended their proboscides to probe or feed. The combination of paper flowers and floral scent attracted more visits than did paper flowers alone, but surprisingly, the differences were not statistically significant (R. Raguso and M. Willis, unpub.). One interpretation of these results is that the strong vegetative odor of Datura foliage, when present with visual stimuli, was sufficient to elicit hawkmoth attraction and feeding in the

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absence of *floral* scent. An alternative explanation is that wild hawkmoths learn landmarks, return to the same location, and orient to visual cues alone. Another alternative is that the moths may have made an association between floral shape and display and *Datura wrightii*’s impressive nectar rewards. A truly hungry, experienced hawkmoth might relax its normal requirements for the presence of both visual and odor cues in order to feed.

To distinguish between these possibilities, we performed a third experiment controlling for the presence of vegetative odors and proximity to landmarks, using two large *Datura* plants growing 15 m apart in soil and three potted plant treatments rotated between different positions nearby (fig. 3.3C). Since hawkmoths fed from open control *Datura* flowers during all observational periods, the small number of approaches and the absence of feeding at the scentless treatment throughout the experiment indicated that visual cues alone were insufficient to promote hawkmoth attraction.
and feeding. Thus, the functional distance of a Datura odor plume as a cue eliciting visually guided approach and feeding behavior must have been less than 15 m in this experiment. The remaining treatments did not differ significantly in their attractiveness to hawkmoths, suggesting that (1) relative position did not affect attraction, and (2) the presence of vegetation neither enhanced nor diminished the attractiveness of floral scent in combination with visual cues.

The results of our field experiments clearly suggest that either bright visual displays or plant odors, whether vegetative or floral, can attract foraging nocturnal hawkmoths, but a combination thereof is required to elicit naturally observed levels of feeding. These results do not differ substantially from those observed for naïve M. sexta moths in the greenhouse experiments. In the presence of plant odors, hawkmoths attempted to feed from any bright object, while in the absence of floral scent, strong vegetative volatiles appeared to function as a reasonable surrogate cue. Given our results, it appears unlikely that the wild nocturnal hawkmoths in our study are able to find flowers and feed without some plant odor.

SYNTHESIS AND DISCUSSION OF FUTURE DIRECTIONS

A Combination of Floral Cues Is Necessary to Elicit Hawkmoth Feeding

Visual and olfactory stimuli clearly interact at close range (0–10 m) to mediate the nectar-feeding behavior of both naïve and wild hawkmoths in Arizona’s Sonoran Desert. In flight tunnel assays, greenhouse experiments, and field tests, a combination of visual cues and plant odors was necessary for M. sexta and related hawkmoths to extend the proboscis and feed from flowers. These findings allow us to reject the null hypothesis (H₀) that scent has no behavioral function in hawkmoth attraction and feeding and an alternative hypothesis (H₃) that scent functions as the complete floral attractant/feeding stimulant (see table 3.2). Furthermore, while scent cues were required for feeding, scent was not required on an individual flower level, as both naïve and experienced hawkmoths foraged avidly from both natural (scented) and paper (unscented) flowers in the presence of a larger cloud of plant volatiles. Thus, scent does not function strictly as a landing or feeding cue (H₂). The model (H₁) propounded by Baerends (1950) and Brantjes (1978), in which scent releases visually guided foraging, is the most likely explanation for how nocturnal hawkmoths respond to floral scent and visual cues within 10 m of their source. For M. sexta and other nocturnal hawkmoths, the presence of a “scent cloud” above a patch of flowering plants, as described by Baker (1961), Cruden (1970), Nilsson (1978),
and Eisikowitch and Rotem (1987), provides the contextual cue that elicits visually guided close-range orientation, proboscis extension, and feeding.

However, scent may play additional roles in hawkmoth-flower interactions. First, there appears to be an incremental effect of scent concentration, as the inclusion of natural scented flowers within our greenhouse arrays increased the frequency of M. sexta feeding above that observed when scent was emanating from beneath paper model flowers. Additional work will be needed in order to identify the minimum threshold of odor concentration required to initiate upwind orientation flight as well as the functional subset of scent components and their potential synergism with other plant cues (e.g., plumes of carbon dioxide or water vapor). Second, our flight tunnel data indicate that scent can induce upwind flight in the absence of visual cues and suggest that strong fragrances could attract moths from distances greater than 3 m (H4). Field trapping and release-recapture studies will be needed to quantify the distances from which hawkmoths can be attracted by fragrance alone.

Our experimental findings, if broadly applicable to other nocturnal hawkmoths, suggest the following predictions for hawkmoth-pollinated plants:

1. Floral scent attracts hawkmoths at a patch or population level and should not affect fine-scale movement of hawkmoths between individual flowers or neighboring plants. In fact, odor need not emanate from floral tissues, as we found to be the case in Calylophus hartweggi (Onagraceae), Ipomopsis longifolia ( Polemoniaceae) (R. Raguso, unpub.), and our experiments with Datura wrightii foliage.
2. If fragrance production has fitness-related costs, there should be balancing selection for optimum emission levels, frequency-dependent selection for scentless mutants within a population, or scentless “parasitic” species that co-bloom with and exploit fragrant plants.
3. The attraction of hawkmoths to bright, reflective flowers with fragrance can be exploited by Batesian mimics whose flowers lack nectar, such as Plumeria tubra (Apocynaceae: Haber 1984), or by fraudulent female flowers in dioecious, automimetic plants, such as Carica papaya (Caricaceae: Knudsen and Tollsten 1993).

THE EFFECT OF LARVAL DIET AND ADULT PHYSIOLOGICAL STATE ON NECTAR FEEDING

The hawkmoths used in our laboratory and field experiments differed in at least two important details: adult feeding experience and larval diet. Disparity in larval diet may explain what appeared to be gross differences in the

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feeding rates of wild versus laboratory-reared hawkmoths. The hawkmoths used in our flight tunnel and greenhouse assays were reared as larvae on an artificial diet, did not wander extensively before pupation, and eclosed as adults with substantial abdominal fat bodies (R. Raguso and M. Willis, unpub.). This large “onboard” energy store may affect the propensity of the moths to feed (fig. 3.4), which could explain the low numbers of moths responding to whole-flower emissions (see table 3.3), even after being starved for 3 days (see Simpson and Raubenheimer 1996). However, similar results have been observed in feeding behavioral assays of other laboratory-reared moths (Fan et al. 1997), and M. sexta needed to be starved for a week before being conditioned to odor cues by Daly and Smith (2000). In contrast, the lean, wild hawkmoths studied in our field experiments carried negligible fat bodies (R. Raguso and R. Chapman, unpub.) and often were so eager to feed that they would pry apart unopened Datura and Calylothus buds with their
proboscides and legs (plate 3.4, see Gregory 1964). We are currently studying ways to rear adult hawkmoths with reduced fat bodies in an effort to increase the efficacy of our laboratory assays.

There are other ways that larval diet or adult physiological state could potentially influence a hawkmoth’s propensity to feed, including (1) the effects of ambient temperature and thermoregulatory requirements (Cruden et al. 1976; Heinrich 1983; Martínez del Río and Búrquez 1986), (2) the effect of exposure to plant compounds in the larval diet on neurosensory development (Bernays and Chapman 1998), (3) the effect of a larval diet deficient in carotene precursors of visual pigments (Bennett and White 1989), (4) adult physiological water balance and its relation to nectar use (Calder 1979; Pyke and Waser 1981), (5) starvation or frequency of adult feeding and exercise (Brantjes 1978), and (6) the effect of mating status and a potential refractory period toward feeding (see Haynes et al. 1991). Few of these avenues have been explored in the context of any nectar-feeding insect’s response to floral attractants. It will be important to address the contributions of these factors directly in our continuing investigations of hawkmoth flower-feeding behavior.

**Observations of Diverse Hawkmoths and Habitats**

Our experiments are the first to examine hawkmoth responses to both visual and olfactory floral attractants using balanced experimental designs and controlling for previous foraging experience. However, our results are consistent with anecdotal observations and circumstantial evidence from other studies using naive *M. sexta* moths in laboratory feeding experiments (table 3.4). Earlier experiments on the feeding response of *M. sexta* to artificial flowers or other visual stimuli (Bell and Joaquim 1976; White et al. 1994; Cutler et al. 1995) were confounded by the presence of a live tobacco plant in the same room, included to encourage female oviposition for unrelated purposes. Again, tobacco vegetative volatiles probably were sufficient to provide the necessary contextual odor cues eliciting feeding behavior in these moths. Brantjes (1973, 1978) performed flight cage bioassays in which naive *M. sexta* responded to the introduction of floral odor into a small flight chamber by wing shivering, initiating flight, and active searching behaviors. Interestingly, Brantjes (1973) observed proboscis extension and probing by *Deilephila elpenor* L. hawkmoths at flowers hidden within a perforated box in the flight cage, a behavior not observed by himself or us in similar experiments with *M. sexta*. However, the unexplored potential for visual contrast in Brantjes’ experiments, combined with the unknown physiological status of his experimental animals (e.g., starved vs. fed, wild-collected vs. laboratory-reared) precludes further interpretation.
<table>
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<th>Critical Predictions</th>
<th>Releasing Cue Model</th>
<th>Naive Hawkmoths (Lab)</th>
<th>Experienced Hawkmoths (Field)</th>
<th>Haber 1984</th>
<th>Many Spp.</th>
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<tr>
<td>Scent is required to initiate feeding</td>
<td>+</td>
<td>+/?^a</td>
<td>+</td>
<td>?^b</td>
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<td>Visual cues are required for feeding</td>
<td>+</td>
<td>+</td>
<td>+/-^c</td>
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<tr>
<td>Scent is required to feed at each flower</td>
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^a +/? = circumstantial evidence
^b ? = not directly tested
^c + for M. sexta, - for D. elpenor
Although comparable data are limited, our observations of hawkmoth feeding behavior in the field appear to be applicable to other nocturnal nectar-feeding hawkmoth species in temperate and tropical habitats worldwide (see table 3.4). Many species of wild hawkmoths collected at light traps will feed from artificial paper or plastic flowers in outdoor flight cages when natural fragrant flowers are present (Haber 1984, in Costa Rica) or when scented corollas are attached to plastic model flowers (Wasserthal 1993, 1997, in Madagascar). Our observation that visual cues govern approaches to individual flowers at close range is in agreement with published reports of various hawkmoth species flying directly between flowers once they arrive at a patch (Hyles lineata [Fabricius] in California: Baker 1961; Eumorpha achemon [Drury] and Sphinx chersis [Hübner] in Utah: Cruden 1970) or probing at white or highly reflective objects while feeding from flowers in natural settings (Manduca quinquemaculata in Colorado: Clements and Long 1923; Agrius convolvuli [L.] in Yugoslavia: Kugler 1971). It also is consistent with Knoll’s (1925) laboratory experiments with naive Hyles lineata livornica (Esp.), in which the moths repeatedly probed at scentless natural and paper flowers pressed between sheets of glass while in the presence of the scented flowers and foliage of Lonicera impexa Aiton (Caprifoliaceae), Nicotiana affinis (= alata) Moore (Solanaceae), and Salvia officinalis L. (Labiatae). Knoll correctly concluded that H. l. livornica was guided to flowers by visual signals at close range, but did not consider that the plant odors permeating the air of his experimental chamber were eliciting visually guided feeding in his assays, as was suggested later by Ilse (1928), Tinbergen et al. (1942), and Baerends (1950).

Diverse adult feeding strategies abound within the Sphingidae, which range from large guilds of nocturnal nectar-feeding hawkmoths (Nilsson et al. 1985; Haber and Frankie 1989) to diurnal species that ignore odor during foraging (e.g., Macroglossum stellatarum: Kelber 1996; Kelber and Pfaff 1997; Josens and Farina 1997), specialists that feed on unusual foods (Acherontia atropos L. on beehive honey: Knoll 1925; Newman 1965), and species whose adults do not feed at all (e.g., Pachysphinx modesta Harris: Hodges 1971). Given the diverse functions of scent documented for flower-feeding nymphalid butterflies and noctuid moths (see table 3.1), it is reasonable to expect some sphingid species to respond differently to olfactory and visual stimuli in the context of feeding. Electroantennogram studies suggest that butterflies and moths can detect most floral volatiles, such that sensory discrimination is more likely to result from central nervous system processing than peripheral olfactory screening (Topazzini et al. 1990; Naumann et al. 1991; Gabel et al. 1992; van Loon et al. 1992; Raguso et al. 1996; Raguso and Light 1998; Omura et al. 1999a, 1999b). Field studies in Central America (Haber 1984; Haber and Frankie 1989), Israel (Eisikowitz and Galil 1971; Kislev et al. 1972), Africa and Madagascar (Harris and Baker 1958; Nilsson et al. 1985, 1987; Baum 1995; Wasserthal 1997), and Japan (Miyake
et al. 1998) suggest that there is little evidence for extreme specialization in flower choice among nectar-feeding hawkmoths worldwide. The combination of multivoltinism and high vagility in many hawkmoth species underscores the adaptive nature of generalized floral foraging. Acherontia atropos, the death’s head hawk, has a short, stiff proboscis that is ideal for piercing honeycombs, a major source of adult nutriment, and may limit its extrafloral foraging to flowers with short nectar tubes (e.g., citrus and privet: Newman 1965) or, perhaps, to nectar robbing. The potential to use fragrance alone as the complete attractant/feeding cue is greatest for this species and those that include fermenting fruit and sap in their adult diets, such as Amphinom floridensis B. P. Clark (D: M. O’Brien 1998) and Darapsa pholus Cramer (Hodges 1971).

Finally, the effects of daily foraging periodicity on the feeding strategies of different hawkmoth species have been largely ignored. For example, the diurnally active Macroglossum stellatarum uses exclusively visual cues to feed from flowers in well-lit laboratory and field settings, but is also known to forage from fragrant plants in the evening along the Mediterranean coast of Europe (Newman 1965; Herrera 1992). Similarly, Hyles lineata, the most abundant and widespread hawkmoth in North America, forages under daylight, crepuscular, or purely nocturnal conditions, depending on altitude, temperature, and perhaps other factors (Holland 1903; Grant 1937; Chase and Raven 1975; Miller 1978, 1981; Willmott and Bürquez 1996). The possibility that these species’ behavioral responses to floral stimuli vary with relative light intensity deserves closer scrutiny, and could explain such paradoxical observations as Hyles’s apparent preference for white over red Ipomopsis flowers in northern Arizona (Paige and Whitham 1985) but for red and pink over white Ipomopsis flowers in montane Colorado (Elam and Linhart 1988; Campbell et al. 1997). Assays testing the behavioral responses of Hyles lineata to visual and olfactory floral cues, performed under light regimes appropriate to diurnal, crepuscular, and nocturnal foraging, would provide insights into the complex contributions of these moths to floral evolution in western North America.

SUMMARY AND CONCLUSIONS

We have discussed the available evidence from our own and others’ investigations of the use of floral fragrance and visual cues by nectar-feeding nocturnal hawkmoths. Naive Manduca sexta track floral scent plumes to their sources in laboratory assays, indicating their innate ability to orient to plant odors from a distance. The small proportion of naive individuals performing this behavior under our experimental conditions strongly suggests modulation of feeding responses by nutritional state, available energy reserves, and other...
adult physiological conditions that beg further study. At close range, both naive and experienced *M. sexta* are attracted to bright visual arrays or hidden odor sources, but require the combination of visual and olfactory signals in order to approach a flower, extend the tubular mouthparts, and feed. We were surprised to observe that wild, experienced *M. sexta* do not visit scentless artificial flowers, given that a wide array of bats (Voigt and Winter 1999), butterflies (Weiss 1997), bees (Real 1981), and diurnal hawkmoths (Farina and Josens 1994) can learn to feed from odorless plastic feeders. However, there is ample variation among flower-feeding insects in their ability to generalize among sensory modalities and signals (see Roy and Raguso 1997). The associative learning capabilities of hawkmoths have only recently begun to be studied (Kelber 1996; Kelber and Henrique 1999; Daly and Smith 2000). Relatively little is known about the factors that constrain lepidopteran learning and memory with respect to floral characteristics (Lewis 1986; Murawski and Gilbert 1986; reviewed by Weiss 2001).

Our observations suggest at least two discrete roles for floral scent in this system: long-distance attractant and close-range contextual cue, synergizing with visual stimuli to elicit nectar feeding. Depending on the density of the visual display, large floral aggregations may also attract moths visually from a distance, and visual cues *within* flowers clearly play important roles in proboscis placement and feeding, as they do for bees, long-tongued flies, and many butterflies (reviewed by Dafni and Kevan 1996). These findings are consistent with what little is known of other nocturnal hawkmoth species worldwide. Rather than considering these patterns static rules for foraging behavior, we see them as a framework of hypotheses from which to explore the limits of plasticity and adaptability in nectar foraging within and among hawkmoths and other flower-feeding lepidopterans.

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