

Floral humidity and other indicators of energy rewards in pollination biology

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Keywords: humidity gradient, nectar, floral profitability, floral display, vision, olfaction, hygroreception, honest signaling, transient rewardlessness

Floral traits that correlate with nectar availability or are linked functionally to nectar production carry the potential to enable remote assessment of energy rewards by pollinators. Such floral traits can be considered “honest” in the sense that they convey information about the quality or profitability of a flower to a pollinator. Recently a new sensory channel used in plant-pollinator interactions was identified. We demonstrated that evaporation of water from the nectar itself and the petals create local humidity gradients above *Oenothera cespitosa* (Onagraceae) flowers. Since these humidity gradients are directly linked to nectar volume, they convey reliable information about nectar rewards to hawkmoth pollinators (Sphingidae). Several studies document a variety of sensory cues that constitute honest signaling between plants and pollinators, and shed light on the central question of when the two parties should communicate honestly. In the following sections, I will comment on different honest signals mediating plant-pollinator interactions, with a special emphasis on our recent findings about floral humidity gradients.

Communication between flowering plants and animal pollinators has long attracted the attention of researchers seeking to decipher the role and influence of the various floral traits on pollinator behavior. As numerous studies show, a plant’s floral display is a multimodal signal that is often perceived by pollinators through different sensory channels.^{1,2} In return for providing efficient pollen transfer and outcrossing, pollinators usually gain an energetic reward. Floral nectar is considered the most common means by which plants enlist animals as pollen vectors.³ Animal-pollinated plants often invest considerable resources in the production of floral nectar, which can result in a trade-off between pollinator-mediated increases in numbers of fertilized seeds and decreases in seed number due to the cost of producing the nectar.⁴ However, signal and reward are not always coupled and some plants deceive their pollinators by signaling the presence of a reward without providing it.⁵ This phenomenon is most obvious with flowers that deceive insects by mimicking sexual partners, dung, urine, or carrion, but also occurs with flowers

(most notably many orchids) that resemble rewarding flowers of other species.^{5,6} In addition, pollinators foraging for floral nectar often encounter transiently rewardless flowers of plants that generally provide a reward. This can be due to (1) earlier visits of pollinators or nectar robbers that depleted the nectar, (2) availability/palatability of the reward only during certain periods in the life of a flower, or (3) abiotic factors affecting reward production. In addition intraspecific variation in nectar production and standing crops among flowers, plants and populations is common,^{7,8} and nectar secretion often ceases after anthesis.⁹ From the pollinator’s standpoint, visiting empty flowers is energetically costly and reduces the profitability of a patch, with attendant fitness-related consequences.^{10,11} Therefore, pollinators should be strongly selected to remotely obtain “honest” information from flowers concerning rewards. Indeed, in several plant-pollinator systems honest signals have been identified. However, honest signaling strategies differ in their accuracy of signaling profitability to pollinators, based on the type of signal and the strength of its quantitative association with the reward. Below, I propose a distinction of floral traits according to their link to the reward and their efficiency to indicate transient rewardlessness to pollinators (Table 1), similar to the classification of Maynard Smith and Harper of “conventional signals” and “assessment signals” established for animal-animal interactions.¹² Subsequently, I discuss the reliability to indicate floral profitability to pollinators of those two groups of floral traits.

Honest Signaling through Floral Traits that are Indirectly Linked to Energy Rewards

From early research on pollinator preference patterns, flower color was proposed as an example of honest signals in plant-pollinator interactions. In many plant species the corolla undergoes a distinct change in color at some point during the life of the flower and in some species the change occurs as the flower opens or at the onset of nectar production. Nectar secretion in *Streptosolen jamesonii* (Solanaceae) flowers commences around the time the flower opens and continues for about three days. Shuel¹³ described a gradual color change from yellow through orange to scarlet as flowers mature, allowing the pollinator to accurately estimate the age and possible nectar content of the flower. Barrows¹⁴ also proposed flower color as an

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Submitted: 11/01/12; Accepted: 11/01/12
<http://dx.doi.org/10.4161/cib.22750>

honest signal for nectar rewards as he showed a preference of butterfly pollinators for newly opened, yellow *Lantana camara* (Verbenaceae) flowers. Newly opened flowers are yellow and begin turning orange about nine hours after opening. Yellow flowers contain pollen and nectar, but by the time the flowers turn reddish-orange, they have negligible pollen and no nectar.¹⁵ A similar coupling of energy reward and flower color, and subsequent pollinator preference was reported for *Lupinus argenteus* (Fabaceae).¹⁶ The flowers are pale blue except for a yellow spot on the banner petal, which turns purple several days after anthesis. This color change presents an honest signal since it is correlated with significantly greater energy rewards (pollen) in yellow spotted flowers compared with purple spotted flowers. Indeed, Gori¹⁶ found that bumblebee pollinators visited almost exclusively flowers with a yellow spotted petal. These findings suggest that the bees learned the association between color and rewards and adjust their foraging behavior in response to the honest information provided by the floral display of *L. argenteus*. Besides flower color, flower shape has been shown to function as an honest signal as various relationships between morphological floral traits and nectar rewards were described for different plant species. In *Ipomopsis aggregata* (Polemoniaceae) corolla width is positively correlated with nectar production, and hummingbird flowers with wide corollas are more frequently visited by hummingbird pollinators.¹⁷ In another hummingbird pollinated plant (*Silene virginica*; Caryophyllaceae), flower size was associated with nectar rewards with larger flowers receiving more visits.¹⁸ The shape of the corolla can vary greatly even between co-occurring conspecific individuals and in various cases corolla shape was proposed as an honest signal conveying information about profitability. It was shown that pollinators are able to discriminate between flowers of the different corolla types and prefer the morphs that offer higher energy rewards.¹⁹⁻²²

Despite their general association with nectar rewards, the floral traits described above are limited in their accuracy to signal profitability to pollinators (Table 1). Corolla shape is static and changes in floral color happen slowly^{14,16} and do not precisely follow the dynamic pattern of nectar abundance. Barrows,¹⁴ who proposed petal color as an honest signal for profitability in *L. camara*, demonstrated in the same study the limitation of this signal. Butterfly pollinators were unable to distinguish between yellow rewarding flowers and yellow flowers that were robbed by stingless bees (32% in the case of *L. camara*). Even though robbed flowers offered no reward, their attractiveness to butterfly pollinators was not reduced. Therefore such floral traits fail to signal transient rewardlessness to pollinators. In spite of such lack of precision and occasional misinformation, relatively static signals can provide sufficient information for selection to favor a clear behavioral response by pollinators.

Honest Signaling through Floral Traits that are Directly Linked to Energy Rewards

As the previous section shows, floral traits that are correlated with energy rewards but change slowly over time are at best honest “on average” and advertise the potential to encounter floral

nectar or pollen rather than conveying more precise information about quantity and quality of the reward. On the other hand, floral traits that are directly linked with nectar rewards would more reliably indicate floral profitability to pollinators in that they have a higher temporal resolution and allow remote sensing of energy rewards (Table 1). It is up to debate what information is more valuable to a pollinator: (1) identifying flowers with a potentially high standing crop of nectar (mostly achieved through floral traits indirectly linked to rewards; e.g., 17) or (2) accurate detection of nectar presence/absence (mostly achieved through floral traits directly linked to rewards; e.g., 23). I suggest the latter since these floral traits allow pollinators to detect transient rewardlessness in flowers and therefore to avoid visiting empty flowers which would be costly in terms of time and energy. The following examples will illustrate this point.

Recent findings from plant species endemic to Mauritius describe nectar color as a reliable signal allowing pollinators to assess the presence and size of a reward prior to flower visitation. The flowers of *Trochetia boutoniana* (Malvaceae) and *T. blackburnia* produce red and yellow nectar respectively.²⁴ Since signal and reward are coupled in colored nectar, Hansen et al.²⁵ hypothesized that color functions as an honest visual signal. Indeed, in a binary choice test *Phelsuma* geckos clearly preferred colored over clear nectar.²⁵ Further examples of nectar color acting as an honest signal were documented for bird pollinators. For instance, choice assays and anecdotal observations in the wild led to speculation that pollinating birds learn to associate the distinctive dark-colored nectar of *Aloe vryheidensis* (Xanthorrhoeaceae) with its presence in newly opened flowers, effectively acting as an honest signal and increasing pollination efficiency.²⁶ Recently, Zhang et al.²⁷ provided conclusive support for this hypothesis with a Himalayan shrub and its bird pollinators. *Leucosceptrum canum* (Labiatae) inflorescences are densely packed with small, cream-white flowers that open anthers, dehisce pollen and initiate stigma receptivity 48 h after the corolla opens. This coincides with reaching maximum nectar volume and sugar concentration.²⁷ At this point a pigment secreted into the nectar (1) changes the color from clear white to dark purple and (2) renders the nectar palatable to bird pollinators. Zhang et al.²⁷ showed in behavioral experiments that the dark purple nectar of *L. canum* acts as a foraging signal to the birds. This is an extraordinary example of simplicity rhyming with efficiency in that one molecule creates an honest foraging signal to increase pollination efficiency through nectar visibility and palatability.

Honest signaling using olfaction as a sensory channel was reported for *Datura wrightii* flowers (Solanaceae), where transient carbon dioxide (CO₂) emissions were shown to be associated with nectar production.²⁸ Guerenstein et al.²⁸ suggested that at least some of the CO₂ released by these flowers derives from the metabolic activity required to produce nectar, because nectar secretion and CO₂ emission decrease simultaneously. Subsequently it was demonstrated that naïve *Manduca sexta* (Sphingidae) moths prefer surrogate flowers emitting high levels of CO₂, a characteristic of newly opened, profitable *D. wrightii* flowers.²⁹ Goyret et al.³⁰ further investigated CO₂-mediated nectar foraging in *M. sexta* and showed that floral CO₂ is also a redundant stimulus with

floral odor and affects moth behavior already from a distance. A closer relationship of volatile organic compounds with nectar can be found when nectar is scented. Raguso³¹ outlined the potential of nectar scent as an honest signal, highlighting cases in which the scent of nectar is qualitatively or quantitatively distinct from overall floral scent. Marden³² provided some evidence that honeybees discriminate between artificial flowers with scented nectar and with water alone. Similar findings were reported for hawkmoths and hummingbirds. Nectaring duration was significantly increased when particular volatile organic compounds (e.g., cis- α -bergamotene, benzylacetone) were added to the nectar compared with scentless nectar.³³ Further evidence that pollinators are capable of directly detecting the presence of nectar rewards via volatile organic compounds was found in solitary bees in the genus *Osmia* (Megachilidae) visiting flowers of *Penstemon caesius* (Scrophulariaceae). Bees with uncovered antennae preferred rewarding flowers, whereas bees foraging with silicone-covered antennae and therefore impaired olfactory capabilities visited rewarding and empty flowers equally.³⁴ However, the volatile emissions of *P. caesius* flowers and nectar have not been characterized yet and the identity of the signal used by *Osmia* bees remains therefore speculative.

Floral Humidity: An Especially Efficient Floral Trait in Indicating Flower Profitability?

Recently, we provided a proof of principle that humidity gradients produced partly by nectar evaporation could indicate flower profitability to pollinators.²³ Our data remains inconclusive so far concerning whether this floral trait can be characterized as a signal or a cue. According to Bradbury and Vehrencamp,² the two major criteria that have to be fulfilled to characterize a sensory stimuli as a signal are (1) that the provision of the information is not accidental but only because it benefits the sender and (2) that the receiver must also benefit by having access to the provided information. We suggested that humidity gradients are likely to occur in other long-tubed or -throated flowers with an interstitial volume of air within the flower bud and copious nectar production,²³ all characteristics of the hawkmoth pollination syndrome. Hawkmoths can be highly effective pollinators of such flowers as it was found that one visit could be sufficient to achieve complete fertilization of a flower.³⁵ The elevated humidity levels we documented for freshly opened flowers with abundant nectar may benefit the plant by attracting pollinators to healthy, non-pollinated flowers. In this case, humidity gradients could ultimately function as a signal, providing benefits to both plant and pollinator.

Different aspects of the production and perception of humidity gradients suggest that this floral trait might be more reliable and efficient than the honest signals described above. This conclusion is based on two main points: (1) robustness to cheating and (2) targeting a well-suited sensory system for signal detection. Vulnerability to corruption by deceit arises whenever a signal is informative. There are, however, properties of signal design that can help to maintain honesty. According to Zahavi,^{36,37} mechanisms for the maintenance of honesty can be either that (1)

the signal is costly to produce and therefore the reliability of communication is increased in relation to the investment in the trait and/or (2) the production of the signal is physically constrained through a material link between the signal and the quality advertised by the signaler. With floral humidity gradients both conditions are fulfilled, suggesting a high robustness to cheating. It has been appreciated lately that water can be one limiting factor in the development of floral organs,^{38,39} and this is especially true in xeric environments because considerable water can be lost through transpiration. The transpiration rate of *Persea americana* (Lauraceae) flowers was shown to be approximately 60% that of leaves; around 13% of total transpirational water loss from tree canopies could be attributed to floral organs.⁴⁰ In the extreme case of the desert succulent *Agave deserti* (Asparagaceae), transpirational water loss from the inflorescence and the lateral floral branches exceeded leaf transpiration.⁴¹ Concerning the allocation of water to nectar production, it seems that because of water limitations nectar concentration is generally higher in xeric environments than in temperate environments (for a review see ref. 42). Nectar production can entail a cost to a plant in terms of growth and/or reproduction⁴ and in xeric environments the water component, the substrate for the generation of floral humidity gradients, might be as expensive as the sugar component of the floral nectar. Concerning Zahavi's argument of physical constraint, the production of floral humidity gradients is partly based on the evaporation of nectar^{23,43,44} a fundamental physical process occurring naturally during anthesis and therefore, mechanistically linked to the nectar reward.

Another reason why floral humidity gradients may be an effective indicator of flower profitability, at least for insect pollinator-plant interactions, is related to the sensory channel by which the signal is perceived. Regulations of temperature and water balance are primary components of homeostasis in all organisms, and insects are sensitive to ambient humidity levels they experience at any given time. Changes in humidity levels are detected by hygro-sensitive sensilla, which house receptor cells in an antagonistic pair of a dry and a moist cell together with a thermoreceptor.^{45,46} The general picture of hygro-sensitive sensilla follows the concept of protected exposure, being maximally exposed to the environment by their location mostly at the tip of the antennae, but protected from mechanical irritation or damage by their position in a groove.^{47,48} Recent studies documented exceptional sensitivity of insects to changes of ambient humidity levels.⁴⁹⁻⁵² Since insects possess dry and moist cells, their sensory system conveys qualitative and quantitative information to increasing as well as decreasing humidity levels, in contrast to olfaction for example. Floral humidity gradients are therefore well suited for detection by nectar foraging insect pollinators, since they are perceived by a highly sensitive sensory system, which in a different context is critical for microhabitat selection and survival.

Conclusions

During foraging bouts pollinators have a high probability of encountering rewardless flowers. Either the flowers cheat, a common strategy in animal-pollinated plants,⁵³ or flowers were

Table 1. Properties and information content of floral traits indicating flower profitability grouped according to their link to the energy reward

Floral traits indirectly linked to rewards	Floral traits directly linked to rewards
Properties	
Emitted by other floral parts, not the reward	Generally emitted by the reward itself
Production not linked to the reward or the physiological processes that produce it	Production can be mechanistically linked to the reward or the physiological processes that produce it.
Static or low temporal resolution (hrs, days)	Relatively high temporal resolution (mins)
Contain information about the potential profitability of a flower	Indicates the presence/absence of the reward. Occasionally, the floral trait contains more specific information about the quantity and/or quality of the reward
Consequences	
Indicate potentially rewarding flower to pollinators	Reliably indicates rewarding flower to pollinators
Transient rewardlessness in flowers cannot be detected by pollinators	Enable pollinators to detect transient rewardlessness
Encountering empty flowers is frequent but the floral trait provides sufficient information for selection to favor a clear behavioral response by pollinators	Empty flowers can be avoided by pollinators

emptied by earlier flower visitors. Nevertheless, under certain circumstances plant-pollinator systems adopt an honest signaling strategy, reflected by the multitude of examples described here. Interestingly, the honest signals described in plant-pollinator systems vary in their degree of reliability and information content. Honest signals that are directly linked to the energy reward seem to be more efficient and reliable to indicate floral profitability to pollinators (Table 1).

Further examples of honest signals would shed light on the mechanisms by which plants can couple signal and reward and the circumstances under which they can honestly reveal the presence and value of floral nectar. Post-pollination ethylene signaling in flowers⁵⁴ or the unexplained mechanism by which hummingbirds avoid nectar-robbed plants⁵⁵ could be promising avenues of future research. Furthermore, plant-pollinator interactions are

excellent systems to study honest signaling strategies, since signal modulation is relatively slow and experimental manipulations of the signal is often possible. Therefore, future research on plant-pollinator interactions could help to explain the maintenance of honest signaling between two partners with conflicting interests and contribute to ongoing discussions in the field of signal theory.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

Acknowledgments

I thank the Davidowitz Lab, Jessie Barker, Cécile Faucher, Robert Raguso and Nickolas Waser for comments on the manuscript. This work was funded by a Swiss NSF grant PBNE33-122757 and US NSF grants IOS-0923765 and IOS-0923180.

References

- Maynard Smith J, Harper DD. *Animal Signals*. Oxford: Oxford University Press, 2003.
- Bradbury JW, Vehrencamp SL. *Principles of Animal Communication*. Sunderland, MA: Sinauer Associates, 2011.
- Simpson BB, Neff JL. Floral rewards: alternatives to pollen and nectar. *Ann Mo Bot Gard* 1981; 68:301-22; <http://dx.doi.org/10.2307/2398800>.
- Pyke GH. What does it cost a plant to produce floral nectar? *Nature* 1991; 350:58-9; <http://dx.doi.org/10.1038/350058a0>.
- Renner SS. Rewardless flowers in the angiosperms and the role of insect cognition in their evolution. In: Waser NM, Ollerton J, eds. *Plant-pollinator interactions: from specialization to generalization*. Chicago, IL: University of Chicago Press, 2006:123-144.
- Vereecken NJ, McNeil JN. Cheaters and liars: chemical mimicry at its finest. *Can J Zool* 2010; 88:725-52; <http://dx.doi.org/10.1139/Z10-040>.
- Hodges SA. Consistent interplant variation in nectar characteristics of *Mirabilis multiflora*. *Ecology* 1993; 74:542-8; <http://dx.doi.org/10.2307/1939314>.
- Keasar T, Sadeh A, Shmida A. Variability in nectar production and standing crop, and their relation to pollinator visits in a Mediterranean shrub. *Arthropod-Plant Interact* 2008; 2:117-23; <http://dx.doi.org/10.1007/s11829-008-9040-9>.
- Percival MS. *Floral biology*. Oxford: Pergamon Press, 1965.
- Pyke GH. Optimal foraging in hummingbirds: testing the marginal value theorem. *Am Zool* 1978; 18:739-52.
- Smithson A, Gigord LDB. The evolution of empty flowers revisited. *Am Nat* 2003; 161:537-52; PMID:12776883; <http://dx.doi.org/10.1086/368347>.
- Maynard Smith J, Harper DGC, Brookfield JFY. The evolution of aggression: can selection generate variability? *Philos Trans R Soc Lond B Biol Sci* 1988; 319:557-70; PMID:2905492; <http://dx.doi.org/10.1098/rstb.1988.0065>.
- Shuel RW. Influence of reproductive organs on secretion of sugars in flowers of *Streptosolen jamesonii*, Miers. *Plant Physiol* 1961; 36:265-71; PMID:16655504; <http://dx.doi.org/10.1104/pp.36.2.265>.
- Barrows EM. Nectar robbing and pollination of *Lantana camara* (Verbenaceae). *Biotropica* 1976; 8:132-5; <http://dx.doi.org/10.2307/2989633>.
- Weiss MR. Floral colour changes as cues for pollinators. *Nature* 1991; 354:227-9; <http://dx.doi.org/10.1038/354227a0>.
- Gori DE. Floral color change in *Lupinus argenteus* (Fabaceae): why should plants advertise the location of unrewarding flowers to pollinators? *Evolution* 1989; 43:870-81; <http://dx.doi.org/10.2307/2409314>.
- Campbell DR, Waser NM, Price MV, Lynch EA, Mitchell RJ. Components of phenotypic selection: pollen export and flower corolla width in *Ipomopsis aggregata*. *Evolution* 1991; 45:1458-67; <http://dx.doi.org/10.2307/2409892>.
- Fenster CB, Cheely G, Dudash MR, Reynolds RJ. Nectar reward and advertisement in hummingbird-pollinated *Silene virginica* (Caryophyllaceae). *Am J Bot* 2006; 93:1800-7; PMID:21642126; <http://dx.doi.org/10.3732/ajb.93.12.1800>.
- Ashman T-L, Stanton M. Seasonal variation in pollination dynamics of sexually dimorphic *Sidalcea oregana* ssp. *spicata* (Malvaceae). *Ecology* 1991; 72:993-1003; <http://dx.doi.org/10.2307/1940599>.
- Møller AP. Bumblebee preference for symmetrical flowers. *Proc Natl Acad Sci USA* 1995; 92:2288-92; PMID:11607519; <http://dx.doi.org/10.1073/pnas.92.6.2288>.
- Armbruster WS, Antonsen L, Pélabon C. Phenotypic selection on *Dalechampia* blossoms: honest signaling affects pollination success. *Ecology* 2005; 86:3323-33; <http://dx.doi.org/10.1890/04-1873>.
- Gómez JM, Perfectti F. Evolution of complex traits: the case of *Erysimum* corolla shape. *Int J Plant Sci* 2010; 171:987-98; <http://dx.doi.org/10.1086/656475>.

23. von Arx M, Goyret J, Davidowitz G, Raguso RA. Floral humidity as a reliable sensory cue for profitability assessment by nectar-foraging hawkmoths. *Proc Natl Acad Sci USA* 2012; 109:9471-6; PMID:22645365; <http://dx.doi.org/10.1073/pnas.1121624109>.
24. Olesen JM, Rønsted N, Tønderlund E, Cornett C, Møgaard P, Madsen J, et al. Mauritian red nectar remains a mystery. *Nature* 1998; 393:529; <http://dx.doi.org/10.1038/31128>.
25. Hansson DM, Beer K, Müller CB. Mauritian coloured nectar no longer a mystery: a visual signal for lizard pollinators. *Biol Lett* 2006; 2:165-8; PMID:17148354; <http://dx.doi.org/10.1098/rsbl.2006.0458>.
26. Johnson SD, Hargreaves AL, Brown M. Dark, bitter-tasting nectar functions as a filter of flower visitors in a bird-pollinated plant. *Ecology* 2006; 87:2709-16; PMID:17168015; [http://dx.doi.org/10.1890/0012-9658\(2006\)87\[2709:DBNFAA\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2006)87[2709:DBNFAA]2.0.CO;2).
27. Zhang FR, Cai XH, Wang H, Ren ZX, Larson-Rabin Z, Li DZ. Dark purple nectar as a foraging signal in a bird-pollinated Himalayan plant. *New Phytol* 2012; 193:188-95; PMID:21919913; <http://dx.doi.org/10.1111/j.1469-8137.2011.03894.x>.
28. Guerenstein PG, A Yopez E, Van Haren J, Williams DG, Hildebrand JG. Floral CO₂ emission may indicate food abundance to nectar-feeding moths. *Naturwissenschaften* 2004; 91:329-33; PMID:15257387; <http://dx.doi.org/10.1007/s00114-004-0532-x>.
29. Thom C, Guerenstein PG, Mechaber WL, Hildebrand JG. Floral CO₂ reveals flower profitability to moths. *J Chem Ecol* 2004; 30:1285-8; PMID:15303329; <http://dx.doi.org/10.1023/B:JOEC.0000030298.77377.7d>.
30. Goyret J, Markwell PM, Raguso RA. Context- and scale-dependent effects of floral CO₂ on nectar foraging by *Manduca sexta*. *Proc Natl Acad Sci USA* 2008; 105:4565-70; PMID:18212123; <http://dx.doi.org/10.1073/pnas.0708629105>.
31. Raguso RA. Why are some floral nectars scented? *Ecology* 2004; 85:1486-94; <http://dx.doi.org/10.1890/03-0410>.
32. Marden JH. Remote perception of floral nectar by bumblebees. *Oecologia* 1984; 64:232-40; <http://dx.doi.org/10.1007/BF00376876>.
33. Kessler D, Baldwin IT. Making sense of nectar scents: the effects of nectar secondary metabolites on floral visitors of *Nicotiana attenuata*. *Plant J* 2007; 49:840-54; PMID:17316174; <http://dx.doi.org/10.1111/j.1365-3113.2006.02995.x>.
34. Howell AD, Alarcón R. *Osmia* bees (Hymenoptera: Megachilidae) can detect nectar-rewarding flowers using olfactory cues. *Anim Behav* 2007; 74:199-205; <http://dx.doi.org/10.1016/j.anbehav.2006.11.012>.
35. Willmot AP, Búrquez A. The pollination of *Merremia palmeri* (Convolvulaceae): can hawk moths be trusted? *Am J Bot* 1996; 83:1050-6; <http://dx.doi.org/10.2307/2445994>.
36. Zahavi A. Mate selection—a selection for a handicap. *J Theor Biol* 1975; 53:205-14; PMID:1195756; [http://dx.doi.org/10.1016/0022-5193\(75\)90111-3](http://dx.doi.org/10.1016/0022-5193(75)90111-3).
37. Zahavi A. The cost of honesty (further remarks on the handicap principle). *J Theor Biol* 1977; 67:603-5; PMID:904334; [http://dx.doi.org/10.1016/0022-5193\(77\)90061-3](http://dx.doi.org/10.1016/0022-5193(77)90061-3).
38. Ram HYM, Rao IVR. Physiology of flower bud growth and opening. *Proceedings of the Indian Academy of Sciences-Plant Sciences* 1984; 93:253-74.
39. Galen C, Sherry RA, Carroll AB. Are flowers physiological sinks or faucets? Costs and correlates of water use by flowers of *Polemonium viscosum*. *Oecologia* 1999; 118:461-70; <http://dx.doi.org/10.1007/s004420050749>.
40. Whitley A, Chapman K, Saranah J. Water loss by floral structures of avocado (*Persea americana* cv. Fuerte) during flowering. *Aust J Agric Res* 1988; 39:457-67; <http://dx.doi.org/10.1071/AR9880457>.
41. Nobel PS. Water relations of flowering of *Agave deserti*. *Bot Gaz* 1977; 138:1-6; <http://dx.doi.org/10.1086/336888>.
42. Petanidou T. Ecological and evolutionary aspects of floral nectars in Mediterranean habitats. In: Nicolson SW, Nepi M, Pacini E eds. *Nectaries and Nectar*. Dordrecht: Springer, 2007:343–375.
43. Corbet SA, Unwin DM, Prys-Jones OE. Humidity, nectar and insect visits to flowers, with special reference to *Crataegus*, *Tilia* and *Echium*. *Ecol Entomol* 1979; 4:9-22; <http://dx.doi.org/10.1111/j.1365-2311.1979.tb00557.x>.
44. Corbet SA. Nectar sugar content: estimating standing crop and secretion rate in the field. *Apidologie* 2003; 34:1-10; <http://dx.doi.org/10.1051/apido:2002049>.
45. Yokohari F, Tateda H. Moist and dry hygroreceptors for relative humidity of the cockroach, *Periplaneta americana* L. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 1976; 106:137-52; <http://dx.doi.org/10.1007/BF00620495>.
46. Yokohari F, Tominaga Y, Tateda H. Antennal hygroreceptors of the honey bee, *Apis mellifera* L. *Cell Tissue Res* 1982; 226:63-73; PMID:7127426; <http://dx.doi.org/10.1007/BF00217082>.
47. Altner H, Loftus R. Ultrastructure and function of insect thermo- and hygroreceptors. *Annu Rev Entomol* 1985; 30:273-95; <http://dx.doi.org/10.1146/annurev.en.30.010185.001421>.
48. Steinbrecht R. The fine structure of thermo-hygro-sensitive sensilla in the silkworm *Bombyx mori*: receptor membrane substructure and sensory cell contacts. *Cell Tissue Res* 1989; 255:49-57; <http://dx.doi.org/10.1007/BF00229065>.
49. Nishino H, Yamashita S, Yamazaki Y, Nishikawa M, Yokohari F, Mizunami M. Projection neurons originating from thermo- and hygroreceptor glomeruli in the antennal lobe of the cockroach. *J Comp Neurol* 2003; 455:40-55; PMID:12454995; <http://dx.doi.org/10.1002/cne.10450>.
50. Tichy H. Low rates of change enhance effect of humidity on the activity of insect hygroreceptors. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 2003; 189:175-9; PMID:12664093.
51. Merivee E, Must A, Luik A, Williams I. Electrophysiological identification of hygroreceptor neurons from the antennal dome-shaped sensilla in the ground beetle *Pterostichus oblongopunctatus*. *J Insect Physiol* 2010; 56:1671-8; PMID:20615410; <http://dx.doi.org/10.1016/j.jinsphys.2010.06.017>.
52. Chown SL, Sørensen JG, Terblanche JS. Water loss in insects: an environmental change perspective. *J Insect Physiol* 2011; 57:1070-84; PMID:21640726; <http://dx.doi.org/10.1016/j.jinsphys.2011.05.004>.
53. Thakar JD, Kunte K, Chauhan AK, Warve AV, Warve MG. Nectarless flowers: ecological correlates and evolutionary stability. *Oecologia* 2003; 136:565-70; PMID:12838401; <http://dx.doi.org/10.1007/s00442-003-1304-6>.
54. Hoekstra FA, Weges R. Lack of control by early pistillate ethylene of the accelerated wilting of *Petunia hybrida* flowers. *Plant Physiol* 1986; 80:403-8; PMID:16664633; <http://dx.doi.org/10.1104/pp.80.2.403>.
55. Irwin RE. Hummingbird avoidance of nectar-robbed plants: spatial location or visual cues. *Oikos* 2000; 91:499-506; <http://dx.doi.org/10.1034/j.1600-0706.2000.910311.x>.