

# The Diverse Mating Systems of Hilltopping Insects

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Entomologists have long known that some species of insects are much more likely to be encountered on hilltops, summits, and mountain peaks than elsewhere. Indeed, in his review of the subject, John Chapman credited two German entomologists (F. Boie and F. Brauer) with having noted the connection between topography and insect aggregations as early as the mid-1800s (Chapman 1954). In the 1950s, Chapman (1954) and Dodge and Seago (1954) demonstrated that certain hilltop aggregations in North America were composed primarily of *male* flies, butterflies, and ants. The hypothesis that the insects found on mountaintops have been carried passively on updrafts and deposited in high places predicts that females should be as likely as males to be found on hilltops, a prediction that is inconsistent with the male bias in hilltopping insects.

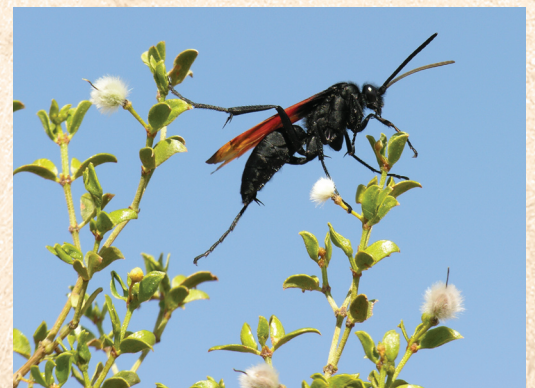
The currently accepted hypothesis for hilltop aggregations is that the males of some species actively seek out summits as mate-encounter sites, an argument first presented in English by E. B. Poulton (1904). The idea that hilltops provide sexual rendezvous points received strong confirmation from Oakley Shields (1967), who studied the butterfly species found on two hills in southern California. Shields reviewed a large number of possible explanations for hilltopping behavior and after evaluating the alternatives, he found the mate-rendezvous hypothesis to be best supported by the evidence. This hypothesis generates the following predictions:

Most individuals at hilltops will be males (which benefit by mating with several to many females) while females will be scarcer (because they mate only once or at considerable intervals). The females that appear on hilltops are more likely to be virgins than those found elsewhere; unmated females experimentally released some distance from a hilltop are more likely to go to

this location than a sample of simultaneously released but mated females.

By confirming all these predictions, as well as regularly finding mating pairs of certain insects on hilltops, Shields' work suggested that hilltopping behavior is a tactic used by some species in search of mates.

More recent work has strengthened this claim. Guy Pe'er and colleagues found that freshly liberated males and virgin females of the butterfly *Melitaea trivia* would fly toward a slope of maximal inclination within 50 m, but only if there were no other individuals within view. The butterflies continued uphill until reaching a summit. After mating there, females promptly abandoned the site and would no longer fly upslope, whereas mated males remained in place (Pe'er et al. 2004). Thus, in this species, scattered individuals in search of mates use a simple decision rule that controls their response to local topography and leads them uphill to places where they may encounter others of their species.



**Fig. 1.** A male tarantula hawk wasp, *Hemipepsis ustulata*, on his perch lookout—a prominent creosote bush growing on a high point on Usery Peak in central Arizona.





**Fig. 2.** A hilltop site, Usery Peak, used by tarantula hawk wasps and many other insects that are found in central Arizona. (a) A view along the undulating ridge that makes up Usery Peak. (b) A close up of the palo verde most often occupied by territorial male tarantula hawk wasps. This tree can also be seen growing on the high point visible in panel (a).

Likewise, males of a large tarantula hawk wasp, *Hemipepsis ustulata*, make an active choice to wait on hilltops. Marked individuals return for up to 40 d to perch on and defend particular plants (Fig. 1) growing on peaktops and ridgelines (Fig. 2) in central Arizona (Alcock 1979, 1981; Alcock and Carey 1988; Alcock and Bailey 1997). Individuals arrive at their favored hilltop perch site early in the morning and stay for a few to many hours each day, depending on the air temperature. Residents chase arriving intruders away or engage them in elaborate aerial contests in which the two rivals fly upward many meters at a steep angle before dropping back down to the tree or plant under dispute. They may repeat these ascending flights many times before one male, almost always the intruder, abandons the contest because prior residency confers a major advantage in the territorial conflicts of *H. ustulata* (Alcock and Bailey 1997). The perching plants defended by males apparently serve as visual landmarks for receptive females, which can occasionally be observed approaching a male territory. Copulations with residents can occur after the female has landed in the landmark plant territory (Fig. 3), although some also take place when males capture flying females as they travel toward a hilltop perching territory.

The tarantula hawk wasp is only one of a large cohort of insects that fly to the top of Arizonan hilltops to find mates (Fig. 4). As was the case in Shields' study, butterflies, flies, and various bees, ants and wasps (Table 1) make up the bulk of the hilltopping species in Arizona, many of which have been observed copulating at or near the peak. The same holds true for hilltops in other parts of the world. In Queensland, Australia, the contingent of insects in search of mates at Mt. Marlay (Fig. 5) during the spring includes hesperiid, lycaenid, and nymphalid butterflies, bombyliid and tachinid flies, and the sand wasp *Bembix furcata* (Dodson and Yeates 1989), whose males spend the day patrolling back and forth along a consistent route in their territories high on the mountainside.

Just as with *H. ustulata* in Arizona, long-term studies of the bee fly *Comptosia tutela* (Dodson and Yeates 1990, Yeates and Dodson 1990) on Mt. Marlay have revealed annual use of traditional territories (Fig. 6). Several territories were re-occupied by males each year over a 4-yr period. When Mt.



**Fig. 3.** A mating pair of the tarantula hawk wasp *Hemipepsis ustulata* in a palo verde growing on the highest point in the Usery Mountains. A second male wasp, which presumably also pursued the incoming female, has landed on the pair and is trying (unsuccessfully) to copulate as well, illustrating the high sexual motivation of male hilltopping insects.





**Fig. 4.** Other species of insects that engage in hilltopping behavior in the Utery Mountains include males of (a) the great purple hairstreak (*Atlides halesus*), a territorial species whose males defend entire creosotebushes and palo verdes as perching territories; (b) the small wasp *Astata boharti* that perches on or very near the ground and rarely interacts with other males; and (c) the large bot fly *Cuterebra austeni*, which perches on the ground and regularly engages rivals in rapid pursuit flights over open ground near prominent landmarks like the palo verde shown in Fig. 2.

**Table 1. List of representative families of four hilltopping insect orders.**

Utery Mountains, AZ	Mt. Marlay, Queensland, Australia
<b>Diptera (No. of species)<sup>a</sup></b>	
Cuterebridae (1)	
Oestridae (2)	
Syrphidae (5)	
Tachinidae (3)	
Mydidae (1)	
Bombyliidae (3)	Bombyliidae (3)
<b>Lepidoptera</b>	
Noctuidae (1)	
Papilionidae (2)	
Hesperiidae (1)	Hesperiidae (3)
Nymphalidae (4)	Nymphalidae (2)
Lycaenidae (2)	Lycaenidae (1)
Pieridae (2)	
<b>Hymenoptera</b>	
Crabronidae (6)	Crabronidae (1)
Pompilidae (1)	
Apidae (1)	
Formicidae (3)	
Mutillidae (1)	
<b>Coleoptera</b>	
Cerambycidae (1)	

<sup>a</sup>The number of species listed is almost certainly an underestimate of the actual total.

Marley was revisited 20 yr later, these territories were still the focus of male competition. During the study seasons, males returned to the hilltop for up to 24 d, although most marked individuals held their territories for fewer than 3 d.

Resident and intruder males engage in spectacular aerial battles in which the opponents are damaged by each other's wing spines, one potential reason for the relatively short territorial tenure of males of this species relative to other hilltopping insects. Females approach male territories in a seemingly stealthy manner; they perch in or near these locations and are detected, pounced upon, and mated by territory holders when they move from their perches.

### Convergence in Male Behavior among Hilltopping Species

Strong similarities exist in the behavior of males of certain hilltopping species, as documented in detailed studies of the butterfly *Papilio zelicaon* (Shields 1967), the wasp *Hemipepsis ustulata* (Alcock 1979, 1981), and the bee fly *Comptosia tutela* (Dodson and Yeates 1990, Yeates and Dodson 1990). All of these species (and many more hilltopping insects) are territorial; males compete to control the access of other males to perching sites where receptive females may appear. Territorial residents of this hilltopping contingent either pursue, assault, or engage in ritualistic combat with rivals, all of which remove a competitor from a hilltop site. As a single male in charge of his territory, the resident is presumably more likely to detect and copulate with an arriving female attracted to the visual landmark under his control (Fig. 7).

This territorial mating system is called "lek polygyny" because these insect species appear to be practicing tactics similar to those of lekking



vertebrates such as sage grouse and the Uganda kob, an African antelope (Alcock 1981). In lekking birds and mammals, males compete for territories that do not contain food or other resources that are valuable to females but instead are simply occupied by males that are potential mates for sexually receptive females (Höglund and Alatalo 1995). Males of lekking species are polygynous in that they may attract a series of females; their territories serve primarily as display arenas where males advertise their availability and suitability as mates. Once having selected a mate, females leave their partner's territory and go off to rear their young on their own. Likewise, female *P. zelicson*, *H. ustulata* and *C. tutela* do not feed or search for egg-laying or nesting sites in male territories, which are only beacons to attract receptive females. After mating, females go elsewhere for food or oviposition resources.

Convergence in mating tactics extends to such things as the shared evaluation of alternative landmark perching sites by males of many unrelated species (Alcock 1987). In the Userly Mountains of central Arizona, some palo verde trees (*Parkinsonia microphyllum*) grow on higher points along the ridgeline mountaintop than others. The highest and most conspicuous palo verde on the peak attracts male tarantula hawk wasp defenders on many more days during the spring flight season than do trees only a little lower in elevation (Alcock 2000). The preference for this site is consistent year after year for male tarantula hawks, and the same is true for a tachinid fly (*Leschenaultia adusta*) (Alcock and Kemp 2006) that also perches in many hilltop palo verdes but favors the palo verde shown in Fig. 2.

There are, however, some differences among the hilltopping-lek species. Males of certain species perch in a defended tree or shrub (e.g., the tarantula hawk wasps) or hover within the tree or shrub, as in the case of the bee *Xylocopa varipuncta* (Alcock 1993). Other species perch on and defend open ground near the landmark tree or shrub (e.g., the botfly *Cuterebra austeni* [Alcock and Schaefer 1983]; the butterfly *Chlosyne californica* [Alcock 1984], and the wasp *Astata boharti* [Alcock 2007]). The Australian bee fly defends several cubic meters of air space above perches on boulders, flat patches of grass, or segments of dirt roads. Irrespective of whether the focus of male–male competition is an entire tree or a patch of open gravel near a prominent tree or a volume of air, the territorial males appear to be guarding an observation post from which they may dart out to pursue an incoming female.

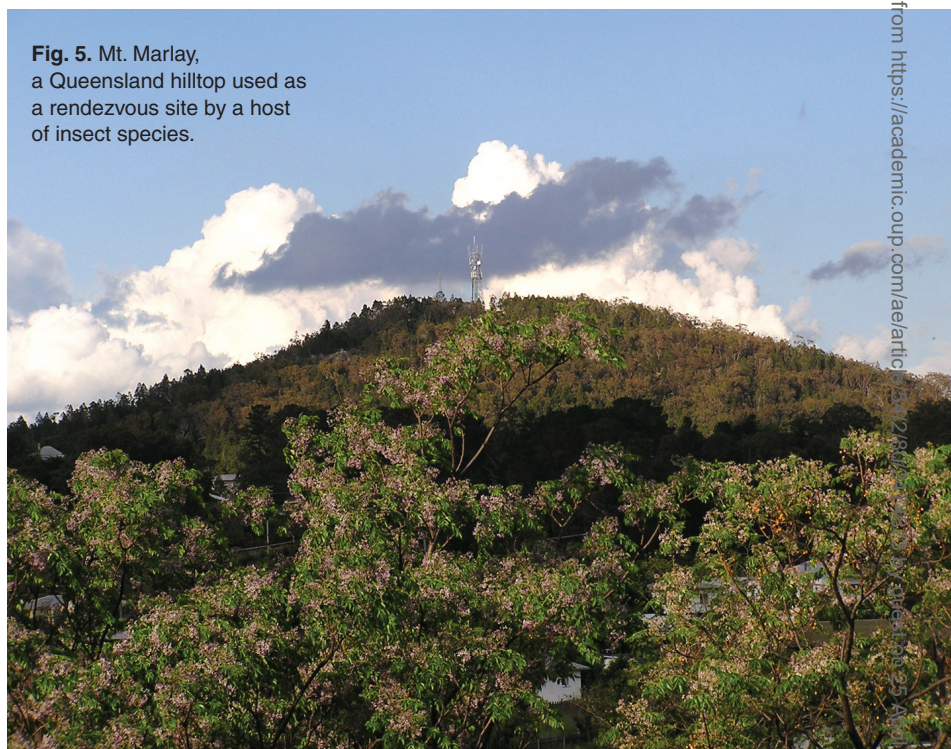
The hilltopping-lek mating system may have evolved in many unrelated insects because these species share a key ecological factor—scarce and widely distributed receptive females (Rutowski 1991). Students of hilltopping have often remarked that the species found on mountaintops or other elevated species tend to be ones that are rare and seldom seen elsewhere (Shields 1967, Scott 1970). For males of such species, we assume that few opportunities exist to encounter receptive females

elsewhere in their environment. Receptive virgin females of the tarantula hawk wasp and the bee fly are surely widely scattered in nature. Fresh adult female wasps emerge here and there from highly dispersed nest burrows, and adult bee flies emerge from difficult to find subterranean hosts. Under these circumstances, males that wait at landmarks for females to come to them may have more success than males that search over a much wider area for females that have just made the transition to adulthood.

### Divergence in the Mating Systems of Hilltopping Insects

The hypothesis that hilltopping-lek behavior is a mating system of last resort for insect species whose females are rare and widely distributed generates the prediction that male mating tactics will be different in those species whose females are

**Fig. 5.** Mt. Marlay, a Queensland hilltop used as a rendezvous site by a host of insect species.



**Fig. 6.** The bee fly *Comptosia tutela*, one of the Mt. Marlay hilltoppers. Resident males leave their perches to intercept male intruders or to pursue females entering the vicinity of their territories.





(a)

concentrated spatially by some feature of their environment. The cerambycid *Trachyderes mandibularis* tests this prediction (Goldsmith and Alcock 1993). Although males are found primarily around the top of Usery Peak rather than lower on the slopes, the hilltopping males alight on and defend ripe saguaro fruits on cacti growing near the peak (Fig. 8). Territorial males use their formidable jaws to grasp rivals and remove them from desirable fruits. When females visit the fruits to feed upon their contents, the territorial resident is able to copulate with them. This species therefore exhibits a blend of hilltopping and resource defense polygyny,



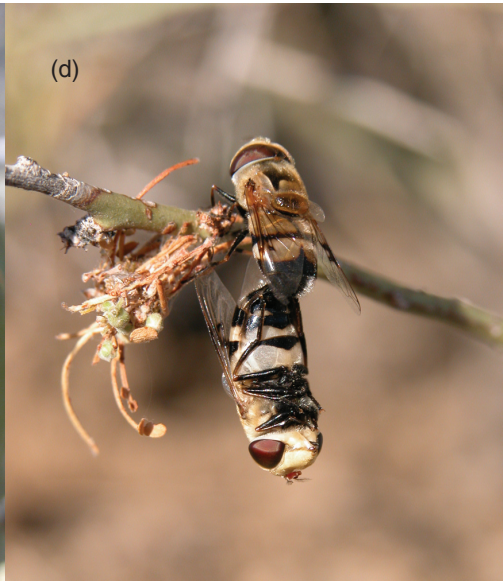
(b)

a mating system that is thought to evolve when a resource valuable to receptive females (e.g., a single saguaro fruit) is concentrated in a small enough area to be economically defended by one male (Emlen and Oring 1977).

Territoriality centered on a food resource appears to be rare among hilltopping species. A far more common alternative to lek polygyny is an entirely nonterritorial mating system. When Shields (1967) catalogued 45 species of hilltopping butterflies, he found that only 21 were characterized by site-faithful males that repelled intruder males from their territories. Males of the other species exhibited different behavioral tactics, typically involving the nonaggressive patrolling of hilltops. Males of this sort made no attempt to monopolize particular sites on the tops of mountains and hills, indeed they often traveled about in the company of their fellow males while barely interacting with them. In the Userys, the



(c)



(d)

butterfly *Anthocaris pima* is an exponent of this kind of hilltopping, with males flying along the ridgeline either singly or in small groups without establishing a defended area around a perch of any sort (Alcock 1987).

The males of these nonterritorial species appear to engage in what has been called scramble competition polygyny. In these animals, mating success is dependent upon endurance and skill at locating potential mates as males compete by trying to outrace their opponents to receptive females as they appear—with great rarity—along their patrol route.

The hypothesis for why many hilltopping species might engage in scramble competition as compared with lek territoriality is still largely untested. Perhaps when male density is very low, males that patrol routes past a series of rendezvous points do better than males that wait at a single spot (Courtney and Anderson 1986).

Another consideration is that when male density becomes very high, the cost of attempted territoriality (the time and energy invested in repelling intruders) could exceed its benefits (sole access to incoming females), leading males to forego territorial expenses and invest instead in trying to find receptive females before their fellow males do (Thornhill and Alcock 1983). This hypothesis generates the prediction that species engaged in scramble competition at hilltops will be those with very low and very high densities relative to lekking territorial species. We know of no systematic effort to collect the relevant data needed to test this prediction. It is true, however, that in seasons when the number of male *Chlosyne californica* changes over the course of a day (with few males present in the early morning but many more by midday), males practice hilltop territoriality at first, but then switch to scramble competition, patrolling away from the hilltops (Alcock 1994). The change in behavior is correlated with an apparent increase in the density of males competing for mates, but it also could be linked to increases in the availability of eclosing females in areas away from hilltops.

The bee fly *C. tutela* also exhibits alternative mating tactics. In addition to the hilltop territoriality described earlier, Yeates and Dodson (1990) observed males and females in higher densities at a nectar resource away from any hilltop. The three matings they observed there in a single visit

**Fig. 7.** Hilltopping insects are occasionally found mating on hilltops: (a) the papilionid butterfly *Battus philenor* shown here in a large palo verde regularly visited by patrolling males; (b) the nymphalid butterfly *Chlosyne lacinia*, a species whose males defend territories on the ground near plant landmarks; (c) the forester moth *Alypia ridingsi*, a sporadic visitor to prominent palo verdes on Usery Peak around which the patrolling males fly; (d) the syrphid fly *Copestylum apiciferum*, the males of which hover near prominent plants growing along the ridgeline that forms Usery Peak.



were apparently the result of scramble competition among males.

Further anecdotal evidence on the relationship between an abundance of competitors and the use of scramble competition as a mating tactic comes from two species of harvester ants (*Pogonomyrmex rugosus* and *P. pima*) that mate only on a few days after summer rains (Hölldobler 1976). During these days, thousands of males fly to or near the most prominent landmark plants on mountaintops in central Arizona, where they search frantically for females (Fig. 9). The analogous mating systems in vertebrates is the explosive mating assemblage, a label applied to those species, (such as certain amphibians) in which the period of mating is restricted to one or a few days annually (Emlen and Oring 1977). Given the large number of competitors and the limited number of days on which females are available, it is not surprising that males of these species make no effort to defend perches from which to scan for incoming females.

Note that the hilltopping harvester ants (and some scramble competitors) constitute an exception to the general rule that hilltopping evolves in insects that are so scarce and widely distributed that males have no viable way to find mates by searching for them at emergence, feeding, or nesting sites. In the hilltopping harvester ants, perhaps females gain by going to hilltops as a means of securing one or more partners almost certain to be from a nest other than their own. The costs of inbreeding in the Hymenoptera may select for the mass assembly of female and male ants at landmarks where outbreeding is likely.

### Remaining Research Questions

Despite the widespread and conspicuous nature of hilltopping among insects, we have barely begun to do much more than document the diversity of mating systems that have evolved within the hilltopping guild. As just indicated, we do not know why some ants exhibit the hilltopping tactic even though receptive females of these species are not scarce or especially difficult to locate (with hundreds of alate females leaving conspicuous nests on a few days each year).

Other aspects of hilltopping behavior also remain unresolved at the moment. Hilltopping species differ not only in their mating systems, but also in the timing of mate competition. Thus, males of the wasp *H. ustulata* (Alcock 1981) and the fly *C. tutela* (Dodson and Yeates 1990) are active primarily in the morning (during the warmer part of spring), whereas other hilltoppers arrive at their sites in the late afternoon to evening, like the carpenter bee *Xylocopa varipuncta* (Marshall and Alcock 1981). Seasonal variation in timing also occurs; some species are only present in spring (e.g., the tarantula hawks). Others, such as the nymphalid butterfly *C. californica*, have a spring and a fall flight period (Alcock 1994). Still others are found only during the height of the summer, as is true for example three species of crabronid wasps belonging to the genus *Tachytes* (Alcock 2007).

**Fig. 8.** Males of the cerambycid beetle *Trachyderes mandibularis* fly to hilltop saguaros where they defend ripe saguaro cacti fruit, a food source that receptive females find attractive.



**Fig. 9.** Male ants of *Pogonomyrmex pima* engage in scramble competition for mates centered around the crown of the palo verde (see Fig. 2b) growing on the highest point on Usery Peak.



Does this temporal variation reflect a partitioning of the site in ways that reduce costly interspecific interactions among waiting males, as suggested by Callaghan (1982)? Or do these differences in timing arise strictly because of other ecological pressures that have selected for particular periods of availability of receptive females, with the males merely responding to this key variable?

Finally, what about the differences among territorial species in the methods that males use to defend their observation posts? In some species, outright combat seems to be the rule, with males apparently capable of damaging their opponents; in these insects, perhaps winners can force losers to concede or else be physically harmed (Dodson and Yeates 1990). In other species, little or no contact takes place among rival males, although the residents usually win after elaborate aerial contests. In these cases, the resident's advantage (which applies to many different hilltopping insects) is puzzling because the winners often are not larger or more flight-capable than the males they defeat nor are the winners apparently younger (and stronger) or older (and more experienced) (Kemp and Wiklund 2001, Takeuchi 2006). So, for example, the resident's advantage persists in tarantula hawk wasps even after the outer 15% of the male's wings have been removed, a handicap that should reduce flight acceleration; but even so, wing-reduced resident males usually still win aerial contests with their territorial rivals (Kemp et al. 2006). Just why residents should have such an advantage, even though they do not even touch their opponents, remains a real puzzle.

The opportunity to resolve the many continuing mysteries associated with hilltopping behavior should motivate entomologists and students of animal behavior to make the climb to their local hills and mountains. Let us hope that when they do so, they do not encounter a massive array of electronic relay towers (see Fig. 5) or a housing development or a plantation of an exotic tree species. Change a mountaintop and one risks eliminating or damaging the special habitat properties that attract certain insects in search of sexual partners (Lawrence and Samways 2002). Although insects are a low priority for most environmental organizations, the fact that so many scarce insect species find mates on hilltops means that entomologists and others interested in biodiversity should promote the conservation of these places. Perhaps we need a new bumper sticker – Hilltops Are For Mating (Insects) – to make the point that insects, and their habitats, deserve our protection as much as the panda and the polar bear.


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- John Alcock**, although recently retired from Arizona State University, plans to continue climbing to the top of the Utery Mountains for as long as possible in order to study the delightful insects found there. He can be reached at [j.alcock@asu.edu](mailto:j.alcock@asu.edu). Having grown up in the Appalachians, **Gary Dodson** understands the urge to fly off in search of hilltops. For now he can be found vainly scanning the horizon from his Ball State University base in central Indiana ([gdodson@bsu.edu](mailto:gdodson@bsu.edu)). 

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