MATING STRATEGIES OF TROPICAL INSECTS

R. Macías-Ordóñez
Departamento de Biología Evolutiva, Instituto de Ecología, A.C., México

L. Mendoza-Cuenca
Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo, México

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Summary

The set of mating strategies in a given population is known as the *mating system*. It has been suggested that environmental variables in general, more specifically key reproductive resources such as food, egg laying sites or females, define the most successful set of mating strategies and thus predict the type of mating system. Although a great deal of research has been carried out in tropical insects, they are still underrepresented in this field compared to those in more temperate regions given the enormous diversity of the tropics. In tropical regions, the great habitat diversity at all scales, as well as the diverse patterns of seasonal change, drive insect mating systems and probably cause great variation in mating strategies between species, and even between populations of the same species. The patterns of land use and pest control typical of tropical countries further influence mating systems in a unique way.

1. Introduction

1.1. Resource Distribution and Limitation Predict Mating Strategies

If you spend a night watching carefully the waters of a mangrove swamp in the Neotropics, you may be lucky enough to observe a magnificent giant water bug of the genus *Lethocerus* (see figure 1). These powerful predators may reach 12 cm, their front legs can catch fish twice their size, and even birds approaching water. Skillful swimmers, they can also fly several kilometers while dispersing. Males attract females creating water waves, just below the surface while standing on emergent vegetation, which they climb together once the female has arrived. At this point, they start a long session of repeated copulations that may last for hours. In between copulations the female lays two or three eggs, gradually forming an egg batch of about 100 eggs. As a result of this interaction, a thick foam layer, probably sperm and other ejaculate fluids from the male, completely covers the mating pair. After this, the female abandons the egg batch and never comes back, while the male stays throughout egg development, defending those eggs against predators. Furthermore, eggs must be kept humid so the male frequently climbs down to collect water on his proboscis, which he later carefully inserts in between egg. This greatly reduces the male foraging efficiency and exposes him to predation. In other genera of the same family, males brood those eggs throughout development not on emergent vegetation, but on their backs. Mating strategies include not only acquiring a mate, but maximizing survival and reproductive opportunities of the offspring. How can we explain this form of maternal desertion and exclusive male parental care?

Figure 1. A male belostomatid giant water bug of the genus *Lethocerus* broods a batch of eggs about 50 cm above water, on emergent vegetation at a natural pond in the Amazon rain forest in Brazil. Females in this genus lay a few eggs in between copulations until a batch of about 100 eggs is formed and then abandon the eggs. The male broods the eggs for up to two weeks, defending them against predators and moistening them with water carried on its proboscis that he must transport from the water surface to the egg batch several times a day (Photo by Rogelio Macías-Ordóñez).

As in other insect groups, females of some tropical butterfly species mate only once in their life, while in other species they mate with multiple males. Males however, typically mate with more than one female. Male mate locating strategies in butterflies can be divided in two main categories, "patrolling" and "perching". Patrollers actively look for mates in areas in which females look for resources, while perching males settle and wait at points favorable for female detection, such as "hilltops" or places containing resources for the females such as flowers on which females feed. These males typically take off to inspect all that resembles a co-specific female or an intruder. Additionally, in several species as *Heliconius* butterflies, some males are territorial and defend places associated to floral resources or egg laying hosts. This territorial defense commonly occurs in species in which females mate only once or very few times at big time intervals, and when mating takes place little after adult emergence of the females. By defending places where virgin females are distributed, males increase their probability to gain the whole offspring paternity of these females. In some cases, males guard and fight for access to female pupae, and they mate while the receptive female is still inside the cocoon (see figure 2).

Figure 2. Two males of *Heliconius charitonia* stand on a female pupa about to emerge in the tropical cloud forest of Veracruz, México. Up to eight or more males fight on a single pupa for two or three days continuously, for the right to copulate with the female by puncturing the pupal case. Females eclose while in copula and will never mate again. They lay their eggs on vines in the genus *Passiflora* where males follow larvae development and start visiting female pupae long before their eclosion (Photo by Luis Mendoza-Cuenca).

Although estimations vary widely, it is well accepted that most species of multicellular living creatures on earth are tropical insects. Thus, reviewing their mating strategies in depth would require several volumes. However, an ecological and evolutionary approach to their reproductive behavior allows a comprehensive understanding of their *mating systems* (that is, the set of mating strategies found in a given population). Although mating systems are usually referred to species, strictly speaking they are describe the mating strategies of populations. An ecological view of mating strategies implies that different populations may experience different environmental variables, especially in terms of resource availability and resource distribution. This implies that some mating strategies produce a better “pay-off” (in terms of reproductive success) in some populations than in others, thus selection is expected to drive evolution in the population towards the best set of mating strategies in any given circumstance. However, not only different populations may have different strategies. Different individuals in the same population frequently have different strategies as well. Even the same individual may change strategies at different times (in which case they are sometimes referred to as “tactics”).

All this has two corollaries. First, describing mating systems in tropical insects is way more ambitious if we address variations between populations, thus we will refer to species, or even generalize to higher groups (genera or families) when they share mating strategies. The reader, however, must keep in mind that mating systems must be viewed from a population perspective, and that they are dynamic both in evolutionary and ecological time.

Second, as suggested by Emlen and Oring in the 1970s in a now classical paper that set the ground for the study of mating strategies, the distribution and limitation of key resources for reproduction in time and space predict the optimal set of mating strategies in a population. In other words, these resources drive the evolution of mating strategies.

As most predators, giant water bugs have a hard time catching prey. The cost for giant waterbug females to stay and brood the eggs may be very high in terms of foraging efficiency, while in the case of males it may be less costly if they can still mate and forage (although at a lower rate) since producing ejaculates in their case is less costly than producing an egg batch. In the case of butterflies, host plants aggregate the distribution of females, especially when they pupate on their host plant and they are receptive still inside the pupal case or cocoon.

1.2. The Tropics

The tropics are diverse in more than one way. Their species richness is high, but also the variety of environments at different scales is noteworthy. The seasonal patterns also vary widely within the tropics and it is also common to find very different climates affecting small areas thus creating a climatic mosaic which in turn promotes diversity. Furthermore, the diversity of historical, political and economic circumstances in tropical countries has also left a mark on insect reproductive ecology. Several insect species have benefited from extensive agriculture. Attempts to control insect pests and vectors of several diseases have created resistant populations while greatly depleting natural populations of several harmless, and frequently beneficial, insect groups such as pollinators. Logging and cattle grasslands have further changed the landscape and thus the resource distribution, greatly modifying selection pressures acting on insect mating strategies.

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Biographical Sketches

Rogelio Macías-Ordóñez grew up in Morelia, on the Western state of Michoacán, in Mexico. He attended the Universidad Nacional Autónoma de México as a Biology major. He pursued a M.Sc. degree at the same institution studying exclusive male parental care in belostomatid water bugs and coral reef fish ecology. He obtained a Ph.D. in Behavioral and Evolutionary Biology from Lehigh University, in Pennsylvania, USA, studying mating strategies of harvestmen (arachnids in the order Opiliones) and fighting behavior in cichlid fishes. In 1998 he became a research scientist at the Instituto de Ecología, on the Eastern state of Veracruz, México. He has continued studies on giant water bugs, cichlid fish and harvestmen, as well as on butterflies, damselflies, flies, chrysomelid beetles and spiders.

Luis Mendoza-Cuenca grew up in Mexico City. He attended the Universidad Nacional Autónoma de México as a Biology major. For his M.Sc. degree at the same institution he worked on the parasitic relation between curculionid beetles and their parasitoids. He obtained a Sc.D. in Ecology and Natural Resource Management from the Instituto de Ecología, in Veracruz, México. In 2004 he became a professor at the School of Biology of the Universidad Michoacana de San Nicolás de Hidalgo, in Morelia, Michoacán, México.