

SEXUAL SELECTION IN TROPICAL INSECTS

R. Cueva del Castillo

Lab. de Ecología; UBIPRO; Universidad Nacional Autónoma de México, FES Iztacala, Mexico

Keywords: sexual selection, mate choice, male-male competition, runaway, good genes, sensorial bias, chase away, sperm competition, cryptic mate choice, species diversity, speciation.

Contents

1. Introduction
2. Intra and inter sexual selection
3. Sexual selection and speciation
4. Sensory bias and Sexual Conflict
5. Sperm competition and Cryptic female choice
6. Sexual selection in tropical Insects

Acknowledgements

Glossary

Bibliography

Biographical Sketch

Summary

Sexual selection arises from differences in reproductive success caused by competition over mates. The reproductive limits for each sex promote intrasexual selection, recognized as male–male competition by Darwin 1871, and intersexual selection, or female mate choice. This process originates from the differential cost that the gametes constitute for each sex and the imposition of different limits to their total reproductive success and overall fitness. Sexual selection can explain the evolution of sexual dimorphism, population differentiation and even speciation. In many animal species, including insects, males have evolved exaggerated ornaments and weapons. These traits can increase male reproductive expectations by male-male competition or female mate choice. Darwin focused on sexual selection events that occur before the mating. However, since the 1970s, different scientists have discovered that sexual selection occurs during and after the mating as well. Many behavioral and physiological female traits can permit females to choose sperm or zygotes after mating. Considering this new evidence, the relative importance of female mate choice has been re-evaluated. Female selective pressures on males can explain the evolution and diversification of complex male genitalia, antiaphrodisiacs and spermicidal compounds, which may evolve in males in order to manipulate or be favored by female preferences. Moreover, several alternative hypotheses to the original Darwinian theory have been proposed, suggesting that conflict and manipulation, rather than cooperation between sexes during reproduction can explain the evolution of behaviors and traits in females and males. Insects are excellent models to test evolution by sexual selection due to their diversity and abundance. Despite the high diversity in tropical regions, sexual selection in tropical insects has been poorly documented. This evidence is analyzed and discussed,

considering the possibility to support and to find a process other than that presently found.

1. Introduction

“Sexual selection depends on the successes of certain individuals over others of the same sex, in relation to the propagation of the species”... “Sexual selection is a struggle between individuals of the same sex. The result is not death to the unsuccessful competitor, but few or no offspring”... Charles Darwin, 1859

Sexual selection arises from differences in reproductive success caused by competition over mates. The reproductive limits for each sex promote intrasexual selection; recognized as male–male competition by Darwin in 1871, and intersexual selection, or female mate choice. Due to the differences in gamete size between the two sexes (known as anisogamy), there are different costs associated with the production of female and male gametes. Females produce fewer, larger and energetically more expensive gametes, whereas males produce a large number of small and energetically cheaper gametes. These energetic costs constitute for each sex the imposition of different limits to their total reproductive success and overall fitness. In general, because males produce a large number of gametes, their reproductive success is limited by the access to females to be fertilized, while the reproductive success of females is limited by their access to the resources to be invested in the egg production, zygote development, and the offspring care. As a consequence, males typically have a higher reproductive potential than females, leading to a male bias operational sex ratio, and more intense intrasexual competition among males. Since females invest more resources in reproduction, in order to produce the highest quality offspring (genetically), they are expected to be more selective in their choice of mates. Females may prefer to mate stronger males, males with more elaborate ornaments, more attractive displays, and/or with better territories.

In general, sexual selection is stronger in males than in females. However, females will be in conflict over the acquisition of resources, thus generating a sex role reversal. Males can be choosier than females, and females can compete for male-provided resources, including nuptial gifts, parental care and foraging and/or nesting sites. In some katydid species, male nuptial gift secretions can be more expensive than female reproductive investment (in some species the spermatophore may represent 25% or more of male body weight). Females displace rivals and have claspers that appear to be specialized in keeping their hold on males and in avoiding take-over attempts by other females. In species where males provide the parental care, the reproductive costs in males are higher than in females because they invest large quantities of resources and time after egg fertilization. Moreover, these factors decrease their subsequent male reproductive opportunities, and reduce the availability of males.

Females may compete to monopolize parental care. Although in insects there are few examples of male parental care, it can be found in belostomatid waterbugs. The male allows the female to glue her eggs onto his back: However, the male may not accept the eggs unless he has fertilized them. He broods the eggs until the nymphs hatch, 2 to 4 weeks later. The eggs are large, and reduce the ability of the male to fertilize many

females. They probably make the male less efficient in catching prey, and increase its predation risk. In this species both sexes court. However, the courtship is usually initiated by females, and sometimes females are rejected by the males.

2. Intra- and Inter- Sexual Selection

In general, because the access to females limits the reproductive success of males, the males compete among themselves for access to females, or for resources that the females require for themselves and their offspring. Thus, intrasexual selection or male-male competition can explain the evolution of morphological traits and behaviors that increase the possibilities of the males to gain access to the females. Large body size, weapons, territoriality and early sexual maturation (protandry) are some of the attributes that have evolved by intrasexual selection. In many animal species, including insects, larger males are more competitive and tend to monopolize females or the resources that they need, excluding smaller males that have few or no matings. Sequestering of females and forced copulation may also favor large male size. Males with more developed weapons are also more competitive. Males with longer horns and mandibles can use them to fight, or for take-over attempts when rivals are copulating. In Lamellicornid and other beetle species, the male horns can be as long as the male's body. Nevertheless, a large body size or large weapons are not always better. Early sexually mature males can start their reproductive life before the rest of the male population. Under scramble competition to inseminate females, the early matured males in many protandrous insect species are smaller than the rest of the population, and can attain the highest mating success. In addition, small males can be favored in some cases where courtship occurs on the ground. Thus, in the fly *Drosophila subobscura*, smaller males are better than large males at tracking females during the courtship dance.

Sometimes females reject stronger males or males with better territories, and mate with subordinate males. Thus, no matter how strong intrasexual selection may be, intersexual selection or female mate choice can determine male mating success. This kind of selection can explain the evolution of exaggerated ornaments and complex courtship displays of males. In insects, these courtship mechanisms include the emission of signals such as pheromones, which are produced by species from the Diptera, Hymenoptera, Lepidoptera, Homoptera, Coleoptera and Orthoptera Orders. Courtship pheromones, used after the sexes have met, are issued in many cases by males. In the queen butterfly *Danaus glippus* and the arctic moth *Utetheisa ornatrix*, the chemical stimulation of the female is necessary for male mating success. Species of the Coleopteran family Lampyridae (fireflies) emit light. Males flying in darkness emit a species-specific pattern of light flashes, which are answered by perching receptive females. The color and temporal variation of the flash system contribute to the success in attracting females. Acoustic signals are produced by many groups, including several orthopteran species (grasshoppers, crickets, bush crickets and allies), neuropterids, cicadas, flies, cave planthoppers, leafhoppers and treehoppers. In crickets and other Orthopterans, loudness and/or uninterrupted songs often attract more females. In other insects, females choose a mate in relation to aspects of his songs. In any case, it is possible that females compare the songs of several males before making a choice.

The effect of mating on female fitness may vary depending upon the kind of benefit that

the females receive from males as result of their choice. The benefits can be direct and indirect (genetic). Direct benefits include nutritional resources to be used by females. Donation of food to mates is common in insects. Males can offer prey to the female, as occurs in scorpion flies and dance flies; seeds collected by the male, as in a lygaeid bug; regurgitated nectar donated to their mates by thynnine male wasps; or even dung, as in dung beetles. Males can donate secretions or nutritional substances to the females, which are transferred in the ejaculate or produced by male glands that can contribute to increase female fecundity or to increase her lifespan. These types of compounds are produced by several orthopteran species, butterflies, flies and beetles. In the polyandrous butterfly *Pieris napi*, a virgin male can transfer an ejaculate containing 14% nitrogen by dry mass. The amount of transferred nitrogen is equivalent to that found in 70 eggs. Females use the male-transferred nutrients to increase their pool of nutrients used for egg production, and show a positive relationship between amount of ejaculate material received and lifetime reproductive output, as male-transferred material also increases female longevity.

In some insect species, males can donate some body parts to females, such as the leg spurs or the fleshy hindwings of jumped-winged crickets, or they may be completely cannibalized, as occurs in mantis, some dipterous, scorpions and some spider species. Interestingly, Maydianne Andrade from the University of Toronto, found that males of the red-back spider that are eaten by their partners fertilized more eggs than uneaten males.

Indirect benefits can be categorized under two different evolutionary theories: runaway and good genes models. Runaway and good genes models can explain the evolution of exaggerated attributes such as the peacock's tail, deer's antlers, or the eye stalks of the stalked flies. The key difference between both models is related to the offspring survival expectations. Under the runaway model the sons are just sexy, whereas under the good genes model, in addition to sexiness, both sons and daughters inherit genes that increase their survivorship capacities.

Sexually selected traits can evolve in a runaway process as a result of female preferences. Female mate choice genes, and genes for the preferred male traits, can be inherited together. Female preferences and male traits spread together as new mutations affecting the traits occur. In each generation, females may produce more attractive sons, which, by definition, will achieve greater mating success. This mechanism can explain the evolution of the exaggerated eye stalks of the stalked flies. In this species, females prefer to mate males with long eye stalks, and both eye stalks and female preferences show genetic variation. On the other hand, the good genes model predicts that highly selective females may produce more viable offspring by mating with males who bear viability and "attractiveness" alleles, which are inherited by sons and daughters. Male traits and courtship displays provide information to a female that enables her to choose males with genes that improve the offspring fitness, increasing anti-predatory or foraging skills and/or resistance to diseases. Individuals that can signal that they are free of parasitic infections should be desirable mates. Females of many cricket species choose their mates according to their song patterns. It has been found in some cricket species that the calling songs of unparasitized males are different from those of parasitized males, and females tend to mate with them.

The runaway process would end when natural selection against costly or risky male traits operates against them, or if the genetic variation in these traits is depleted. However, both runaway and good genes models require genetic variation in male traits and female preferences in order to evolve. Selection imposed by female choice would deplete genetic variation in male traits, and the potential benefits derived from female choosiness.

-
-
-

TO ACCESS ALL THE 16 PAGES OF THIS CHAPTER,
Visit: <http://www.eolss.net/Eolss-sampleAllChapter.aspx>

Bibliography

Andersson M. (1994). *Sexual Selection*. 599 pp. Princeton, N.J, USA. Princeton University Press. [This book presents a comprehensive general discussion of the fate of sexual selection].

Arnqvist G. & Rowe L. (2004). *Sexual Conflict*. 330 pp. Princeton, N.J, USA. Princeton University Press. [This text recognizes the conflict between sexes as a new factor that has modeled the evolution of mating systems and sexual selection].

Choe JC & Crespi BJ. (1997). *Mating Systems in insects and arachnids*. 387 pp. Cambridge University Press. Cambridge. [This work provides analysis concerning several sexual selection subjects in insects].

Eberhard W.G. (1996). *Female control. Sexual selection by cryptic female choice*. 501 pp. Princeton, N.J, USA. Princeton University Press. [This work presents a comprehensive and detailed discussion of the fate of cryptic female choice].

Greenfield M. D. (2002). *Signalers and Receivers. Mechanisms and evolution of Arthropods communication*. 414 pp. Oxford UK. Oxford Univ. Press. [This interesting book provides extensive and carefully discussed information concerning communication mechanisms and its evolution in insects].

Simmons L.W. (2001). *Sperm competition and its evolutionary consequences in the insects*. 434 pp. Princeton, N.J, USA. Princeton University Press. [This work provides extensive and carefully discussed information concerning sperm competition in insects and its evolutionary consequences].

Sivinski J. Aluja M. Dodson G. Freidberg A. Headrick D. Kaneshiro K & Landolt P. (2000). Fruit Flies (Tephritidae): Phylogeny and Evolution of Behavior. *Topics in the evolution of sexual behavior in the Tephritidae*. (eds. M. Aluja & A.L. Norrbom), 751-792. CRC Press LLC, Boca Raton, Florida. [This work provides extensive information concerning Fruit Flies evolution].

Thornhill R. & Alcock J. (1983). *The Evolution of Insect Mating Systems*, 546 pp. Cambridge, MA. USA. Harvard University. Press. [This work provides extensive analysis concerning sexual selection in insects].

Biographical Sketch

Raúl Cueva del Castillo is Professor of Ecology at the Research Division of the campus Iztacala of the National Autonomous University of Mexico (UNAM). He carried out his Postdoctoral work at the University of Toronto at Mississauga, and his main research interests are the evolution of insect mating systems, the evolution of sexual size dimorphism, and speciation by sexual selection.