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RESEARCH ARTICLE

Effects of nectar-robbing on plant reproduction and evolution

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Abstract The relationship between plant and pollinator is considered as the mutualism because plant benefits from the pollinator's transport of male gametes and pollinator benefits from plant's reward. Nectar robbers are frequently described as cheaters in the plant-pollinator mutualism, because it is assumed that they obtain a reward (nectar) without providing a service (pollination). Nectar robbers are birds, insects, or other flower visitors that remove nectar from flowers through a hole pierced or bitten in the corolla. Nectar robbing represents a complex relationship between animals and plants. Whether plants benefit from the relationship is always a controversial issue in earlier studies. This paper is a review of the recent literatures on nectar robbing and attempts to acquire an expanded understanding of the ecological and evolutionary roles that robbers play. Understanding the effects of nectar robbers on the plants that they visited and other flower visitors is especially important when one considers the high rates of robbing that a plant population may experience and the high percentage of all flower visitors that nectar robbers make to some species.

There are two standpoints in explaining why animals forage on flowers and steal nectar in an illegitimate behavior. One is that animals can only get food in illegitimate way because of the mismatch of the morphologies of animals' mouthparts and floral structure. The other point of view argues that nectar robbing is a relatively more efficient, thus more energy-saving way for animals to get nectar from flowers. This is probably associated with the difficulty of changing attitudes that have been held for a long time. In the case of positive effect, the bodies of nectar robbers frequently touch the sex organs of plants during their visiting to the flowers and causing pollination. The neutral effect, nectar robbers' behavior may destruct the corollas of flowers, but they neither touch the sex organs nor destroy the ovules. Their behavior does not affect the fruit sets or seed sets of the hosting plant. Besides the direct impacts on plants, nectar robbers may also have an indirect effect on the behavior of the legitimate pollinators. Under some circumstances, the change in pollinator behavior could result in improved reproductive fitness of plants through increased pollen flow and out-crossing.

Keywords plant reproductive ecology, nectar robbing, host, legitimate pollinator, reproductive fitness

1 Introduction

The relationship between animal pollinator and entomoplily plant represents a common interspecific interaction in nature. However, things become complex in another interspecific relationship between plants and animals. Nectar-robbing is specifically referred to phenomenon that animals, insects or birds, get the nectar rewards in an illegitimate way by drilling holes on the corolla tubes of flowers (Inouye, 1983; Maloof, 2000). This phenomenon commonly exists in the nature. It has been observed almost on every continent except for Antarctica land. The insects or birds that perform nectar-robbing behavior are called nectar robbers. Sometimes, animals such as squirrel can also be nectar robbers (Deng et al., 2003). According to the earlier researches, there are two types of nectar-robbers found in nature, primarily nectar robbers (get nectar by biting holes on the corolla) and secondary nectar robbers (do not bite holes, but get nectar through the holes created by primary nectar robbers). The most common nectar-robbers are bees, mostly bumble bees and carpenter bees. Some species of humming birds are also the frequently found nectar robbers in the North and South America. Beetles also bite holes on the corolla, but usually they forage on pollen grains instead of nectar, thus are not considered as nectar robbers (Utelli and Roy, 2001). The host plants, e.g. the plants which are robbed by nectar robbers, are mostly those with

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long flower tubes or flower spurs. Up to date, the phenomena of nectar-robbing are recorded in 59 families and 214 species of plants (Barrows, 1980; Irwin and Maloof, 2002). Because all of the plants which have long flower tubes or spurs can potentially be robbed, it is supposed that nectar-robbing is still uncovered in many species of plants. In the study of nectar-robbing, the influences of nectar-robbers on the reproductive fitness of host plants are always the focus of interests for a long time. Darwin thought that nectar robbing is harmful to plants. He wrote in his book that "all plant must suffer in some degree when bees obtain their nectar in a felonious manner by biting holes through the corolla" (Darwin, 1872). However, along with the more researches which had been conducted in past years, people started to realize that nectar-robbing is in no way so simple as usually thought. The effects of nectar-robbing on the reproductive success of plants are varied and the reasons undersurfaces are complex. The identity of nectar robbers, the breeding system of plant, and some other environmental factors all play their roles in the relationships of nectar-robbers and their host plants. There is not a common rule being found up to date (Newman and Thomson, 2005).

This paper discussed the ecological and evolutionary significance of nectar robbing on the basis of the researches conducted by earlier researchers and the observation by the authors. Four questions are mainly addressed in this paper: (1) the economical relationship between nectar-robbers and host plant; (2) the influences of nectar-robbers on the normal pollinators; (3) the impacts of nectar-robbing on the evolution of flower morphologies; (4) the relationships of identity of nectar-robbers, foraging behavior of nectar-robbers, hosting plants and some environmental factors. For most nectar-robbers are insects, the relationship of insect nectar-robbers and plants is mainly discussed.

2 Relationship of nectar-robber and plant

The interaction of animal and plant commonly exists in nature. Examples of animals in this relationship are mainly herbivorous animals, pollinators, seed predators and seed dispersers (Maloof and Inouye, 2000). The relationship between plants and pollinators is considered to be reciprocally beneficial (i.e. mutualism). The plants provide food rewards to pollinators while the animals provide pollination service to plants. Nectar-robbers were considered as abnormal or illegitimate flower visitors. Their relationships with plants are possibly much more complex than that of pollinators and plants. General interests had been ignited among researchers in recent years. Emerging evidences showed that in most cases, nectar-robbers are mutualists rather than antagonists of plants (Waser and Real, 1979; Guitian et al.; Morris, 1996; Irwin and Brody, 1999; Maloof, 2001; Richardson, 2004). The reciprocal beneficial interaction relationship is sometimes obvious (increasing female fitness) and other times hidden (increasing male fitness). A few examples showed that, nectar-robbers had negative effects on their host plants. However, certain resisting mechanisms had evolved in these plants during long time evolution.

2.1 Causes of nectar-robbing

How is the "abnormal" behavior of nectar-robbing evolved? For a long time, there were two distinguished opinions held by different researchers. One is that nectar-robbers can get the nectar rewards only through the illegitimate way because of the mismatch of the trophi and the floral morphologies, especially of the floral tubes or spurs. The most powerful evidence supporting this opinion is that, usually, those short-tougued bee species are more likely to be nectar-robbers, and those plants with long floral tubes or spurs are more likely to be robbed. It is easy to understand that nectar-robbing behavior is evolved in short-tougued bees to meet the need of food, but it is difficult to explain why not all short-tougued bees behave like nectar-robbers. In fact, those short-tougued nectar-robbing bumble bees have dense teeth, while those who never perform nectar-robbing behaviors do not have. It seems bewildering that, for those short tougued bumble bees, some species perform nectar-robbing behavior while others do not. The other opinion on the origin of nectar-robbing behavior is that by drilling holes at the base of corolla tubes, nectar-robbers can save much time. That means, in terms of hunting for food, nectar-robbing is more efficient than the normal way. Inouye (1980) observed that short tougued bumble bee spent less time on getting nectar than long-tougued bumble bee did on the flowers of the same population of plant. The former species of bumble bee spent averagely 4.6 s on each flower while the later species spent 6.6 s. The secondary nectar-robbers are even more efficient at getting nectar than the primary nectar-robbers are. A question arise here that whether the behavior of nectar-robbing is congenital or learned by experience. Some experiments showed that the behavior of cutting holes was congenital, while positioning of the holes were learned by experience (Olesen, 1996; Arizmendi, 2001).

2.2 Effects on hosting plants

Although nectar-robbing behavior of illegitimate pollinator commonly exits in nature, people know little about its ecological and evolutionary significance. As a habit of thinking, many people still think that nectar-robbing is harmful to plant because the nectar-robbers "steal" nectar reward from flower and provide no pollinating service. The opinion was popular for a long time in the past. According to the results in the recent 20 years, the effects of nectar-robbing on host plants can be classified as three categories: 1) negative effects; 2) positive effects; and 3) neutral effects (Maloof, 2000; Newman and Thomson, 2005).

2.2.1 Negative effects

The negative effects of nectar-robbing on host plants have been noticed for a long time. In this case, the nectar-robbers are not pollinators. Instead of providing pollination service, they "steal" nectar and destroy floral structures, thus reducing the attractiveness of flower and shortening the flower anthesis. They may also destroy the nectary and the ovules, causing extra loss for the plant. Sometimes, the nectar-robbers changed the behavior of normal flower visitors and disturb the normal pollinating process by leaving scent marks on the corolla, thus decreasing the pollen output (reduce male fitness) and stigmatic pollen load (reduce female fitness) (Traveset et al., 1998; Irwin and Brody, 1999; Irwin, 2003). Irwin and Brody (1999) used pollen mimic powder to study the effects of nectar-robbing on the pollen flow of *Ipomopsis aggregate*, and found that the activity of nectar-robbers significantly reduced the female fitness by disturbing the foraging behavior of the normal pollinators, humming birds. The activity of bumble bees reduced the visiting frequency and visiting time span of humming birds, thus reduced the pollination rate and the fruit set of the flowers. Sometimes, serious nectar-robbing can significantly reduce the fruit set of host plant because the pollinators avoid visiting the robbed flowers (Irwin, 2003; Dedej and Delaplane, 2004). Traveset et al. (1998) found that nectar-robbers reduced the seed set of *Fuchsia magellanica* by 20% because they destroyed the corollas and parts of the ovules. In *Linaria vulgaris*, nectar-robbers reduced the visiting rate of normal flower visitors and pollen output of flowers, but did not affect the seed production, viz. the female fitness (Newman and Thomson, 2005). The above examples showed that nectar-robbing can reduce the reproductive fitness of hot plants. What is more, the host plant has to allocate more resources by secreting extra nectar to compensate the loss. It is understandable that the extra allocation may affect the quality and quantity of seeds (Irwin and Brody, 1999; 2000).

The nectar-robbers are often described as "cheaters" because they get nectar rewards or even destroy the flower structures and provide no pollination service (Darwin, 1872; Inouye, 1983; Maloof and Inouye, 2000; Richardson, 2004). Obviously, the relationship has a negative effect on the host plants, and for no reason can be called mutualism. In spite of this, the kind of interaction is not rare and always exited in nature. A potential reason is that, although the nectar-robbers decrease the fruit set of the host plant, they could possibly increase the out-crossing rate by changing the behavior of legitimate pollinators (Fenster, 1991).

2.2.2 Positive effects

Some earlier researches showed that some nectar-robbers can contact with the sexual organs (e.g. anther and stigma) of the plants when visiting flowers, thus pollinating the plants (Waser and Real, 1979; Guitian et al., 1994; Navarro, 2000). In such cases, nectar-robbers are part of the pollinating system. Higashi et al. (1988) named them as "robber-like pollinator". Navarro found that the densely robbed flowers of *Anthyllis vulneria subsp*. *vulgaris* (Fabaceae) had a higher seed set than unrobed ones did. He argued that the positive effect of nectar-robbing in *A*. *vulneria* may attribute to the behavior of nectar-robbers and the structure of inflorescences. In the study of *Impatiens capensis* (Zimmerman and Cook, 1985) and *Corydalis caseana* (Maloof, 2001), it was found that nectar-robbing can lead to further distance of pollen transportation which leads to higher out-crossing rate. This could be beneficial to the plants.

In the example of positive effects, the nectar-robbers provide pollination service when performing nectar-behavior. There are some species of plant that mainly rely on nectar-robbers as their pollinators to maintain their high seed set level (Scott, 1989). Although some researches showed that the pollinating efficiency of nectar-robbers is lower than normal legitimate pollinators (Kendall and Smith, 1976), they are considered as mutualists of plants.

2.2.3 Neutral effects

There are some examples showed that nectar-robbers did not have a significant effect on the reproductive fitness of plants. In these cases, the nectar-robbers neither pollinate the plants nor disturb with the normal pollinators. Their effect on the plant is neutral (Guitian et al., 1993; Morris, 1996; Malloof, 2001). Although their behavior causes slight destruction on the corolla or spur, they never destruct the nectary or ovule. Natural abortion of seeds and predation by herbivorous insects may affect the reproductive success than nectar-robbers do (Stout et al., 2000). In the study on *Corydalis* by Olesen and Knudsen (1994), the bumble bees robbed the flowers only after the fertilization was happened and the seed started to develop. These flowers did not wither quickly after fertilization, they prolonged their anthesis and served to enhance the floral display in attracting more flower visitors for the population.

2.3 Effects of identity of nectar-robbers and different foraging behaviors on plant reproductive fitness

The nectar-robbing behavior is varied between different species of nectar-robbers and different genders of the same species. Studies indicated that different species of bumble bees and different series of same species of bumble bee, show different nectar-robbing behaviors in terms of operating positioning and time schedule (Ranta, 1983; Villalobos and Shelly, 1996). In *Pedicularis sp*., the queens of certain species of bumble bee were the main nectar-robbers. The workers can perform both like normal pollinators and nectar-robbers.

Waser and Real (1979) mentioned that the males and females of carpenter bees show different foraging behaviors when robbing the flowers of *Fouquieria splendens*. The differences in the behaviors of males and females may attribute to their division of social works and differentiation of ecological niche (Fussell, 1992). Some other species of nectar-robbers may change their roles during the process of foraging. They may swing back and forth between nectar-robbers and legitimate pollinators. The diversity of the behaviors could be evolved as an adaptation to the diversified reproductive strategy of plants. The structure and the opening schedule of flowers can influent the behavior of nectar-robber. For example, the flowers with short anthesis provide both pollen grains and nectar at the same time, while those with relatively longer anthesis provide their rewards only in certain period of time. Some provide rewards on the first day of their anthesis, and then provide nothing on the second day. Some others provide neatar and pollen grains sequentially on different days. They may provide pollen grains on the first day and then nectar on the second day, or reversely in some other species of plants (Ranta, 1983; Rathcke, 1988). They provide different rewards in different periods of time, thus attracting different flower visitors, or causing certain species of insects to perform different visiting behaviors in synchronization with the flowering behavior of plants. For example, bumble bees often switch their roles between nectar-robbers and legitimate pollinators when visiting flowers (Macior, 1966; Morris, 1996; Olesen, 1996). The flowers of *Corydalis ambigua* and *C. cava* produce pollen in the early stage of flowering anthesis, and secret nectar in the later stage of flowering anthesis. Bumble bees collect pollen grains through the front opening of the flowers as normal pollinators when visiting the flowers of early stage, but rob nectar by biting holes on the flower spurs when visiting the flowers of later stage (Olesen, 1996; Arizmendi, 2001). On the flowers of *Mertensia paniculata*, bumble bees were also observed to switch their roles frequently as nectar-robbers and normal visitors (Morris, 1996).

3 Effects of nectar-robbers on the normal flower visitors

Nectar-robbers can directly affect the reproduction of plants, either decrease the reproductive fitness by causing damage to flowers or pollinate the flowers. They may also affect the plants indirectly by changing the behavior of normal flower visitors. The hidden ecological impact has been studied in the past few years. One study (Miller and Travis, 1996) showed that bumble bees tended to fly a larger distance to visit the next flower after visiting a flower with little nectar, and tended to fly a shorter distance to visit the next flower after visiting a flower with much nectar. Nectar-robbing decreases the nectar volume of flowers, thus increasing the flight distance of normal flower visitors. This was confirmed by observations on several species of plants (Zimmerman and Cook, 1985). Maloof (2000) observed that in some species of plants, high nectar-robbing rate increased the flight distance of normal visitors. Other researches showed that when the nectar volume in the flowers was lower than a certain value, the pollinators seldom visited these flowers or the inflorescences. In these plant populations, nectar-robbers acted as regulators of nectar volume (Pyke, 1982; Hodges, 1985).

As nectar-robbers increase the flight distance of pollinators, they may indirectly increase the out-crossing rate of plant by expanding the distance of pollen flow. This could be beneficial to plants because higher out-crossing rate can lead to higher seed set and stronger viability of the offspring (Gliddon and Saleem, 1984; Charlesworth and Charlesworth, 1987; Fenster, 1991; Husband and Schemske, 1996). What is more, the reduction of nectar volume may cause pollinators leave the inflorescences quickly, thus reducing the geitonogamy and promoting the pollen output (Klinkhammer and de Jong, 1993). This is important to increase male fitness in those self-compatible plants with many flowers in one inflorescence. Excepting for the influence on the flight distance and visiting frequency, nectar-robbing can also cause the normal pollinators to shorten their visiting span on each flower (Zimmerman and Cook, 1985; Thomson, 1986; Maloof, 2000). If the pollinators spent more time on each flower, the stigmatic pollen load may be increased (Thomson and Plowright, 1980; Feisinger, 1983; Lanza et al., 1995). Because nectar-robbing leads to the pollinators to spent less time on each flower, it may have a negative effect on female fitness by indirectly decreasing the stigmatic pollen load. At the same time, the pollinators may visit more flowers to compensate for the lessening of nectar in each flower. This could be possibly beneficial to the plant (Maloof and Inouye, 2000).

4 Effects on the evolution of floral morphologies

Contradicting to the traditional conception that nectar-robbing is harmful to plants, emerging evidences showed that the relationships between nectar-robbers and host plants are reciprocally beneficial in most cases. The negative effects of nectar-robbing are in no case as common as people thought before. However, the effects of nectar-robbing on the reproductive success are very varied, at least superficially. This is confusing sometimes. The differentiation of foraging behavior and the plant breeding system may contribute to the great variability of the effects of nectar-robbing (Morris, 1996; Olesen, 1996; Arizmendi, 2001).

A commonly accepted point of view is that pollinator can affect the evolution of flowers by selecting on their structure, color or other morphological characters (Pyke, 1982). Although nectar-robbers can affect the reproductive fitness of plant, their selective functions in the evolution of floral morphologies are generally neglected. Usually flowers with long floral tubes or spurs are more likely to be robbed. Long flower tubes and spurs are selected for as a regulation mechanism on the posture of flower visitors. Correct posture of pollinators is important to efficient pollination (Nilsson, 1988). However, if the tube or spur is longer than the length for which the normal pollination required, the selective function of nectar-robbing becomes significant. This selective function is fascinated either directly (in robber-like pollinators) or indirectly (by changing the behavior of normal pollinators) by the behavior of nectar-robbers. For example, if the nectar volume in the flower tubes is always lower than the volume that normal pollinators can get because of heavy nectar-robbing in the population, the pollinator may turn to other nectar resources. If the nectar-robbers can pollinate the flowers when visiting flowers, the long flower tubes or spurs could be selected for. Flowers with long tubes or spurs are possibly favored by nectar-robbers because competition for nectar could be less (Maloof and Inouye, 2000). Roubik et al. (1985) observed that in *Quassia amara*, the population which was heavily robbed had longer flower tubes than that from which nectar robbers were excluded. The flower morphologies of *Fouquiera splendens* are very varied. Waser and Real (1979) believed that the variability maybe attributed to the selection by the nectar-robbing behavior of carpenter bees. Other researchers have noticed that if plants produced nectar for both nectar-robbers and normal pollinators, they got maximum amount of seeds (Barrows, 1980; Pyke, 1982). In the heavily robbed populations of *Quassia amara*, the plants produced averagely 45.3 μL of nectar per flower, while in the unrobed populations, each flower produced 30.8 μL on average. Morris (1996) considered the correlation of high nectar-robbing rate and high nectar production is the result of co-evolution between plant and nectar-robber. When nectar-robbing consistently imposes a negative impact on plant, defensive structures or mechanisms might evolve in the plant. For example, some plants have extro-flower nectaries to attract ants expelling nectar-robbers (Elias and Gelband, 1975). Developing specialized structures could be low-cost choices to defense nectar-robbers. *Thunbergia grandiflora* discourages nectar-robbers by thickened floral tissue. *Lonicera involucrate* has thickened calyx and bracts to avoid nectar-robbing (Proctor et al., 1996). Densely arranged inflorescence is another stratagem to avoid nectar-robbing. Special chemicals could also be exploited in defending nectar-robbers, but they are too expensive sometimes (Inouye, 1983).

5 Effects of plant and environment on nectar-robbing behavior

The most frequently robbed plants are those with morphological restriction on the normal foraging behavior of flower visitors. The polymorphism in flower design and opening habit can profoundly affect the behavior of nectar-robbers (Olesen and Knudsen, 1994; Navarro, 2001). For example, large inflorescence can attract more flower visitors including nectar-robbers (Ohara and Higashi, 1994), plain color of flower and low concentration of sugar in nectar are less attractive to visitors. The variation of flower color and sugar concentration in nectar among individuals affects the behavior of nectar-robbers (Goulson et al., 1998). The structure of spur is the crucial factor in determining the success nectar-robbing behavior of bumble bees (Kato et al., 1991). Environmental factors also affect the nectar-robbing behavior of insects. Observations on the plant *Aconitum napellus* showed that the populations of a high altitude (2,000 m) are more likely to be robbed by bumble bees than the populations of a lower altitude (500 m) are (Utelli and Roy, 2001). The common nectar-robbers, short-tougued bumble bees prefer opening environments and large patches, and the middle-and-long-tougued bumble bees are forced to small patches. This phenomenon is obviously observed in the populations of *Symphytum officinalis* and *Aconitum napellus* (Sowig, 1989). The behaviors of nectar-robbers are affected by plants and their environment, and can affect the reproduction of plants in turn. The complex interactions influence the dynamic population of plants.

6 Prospects

In the ecosystem, plants and animals are correlated with each other closely in many aspects. The correlations between plants and insects are extremely complex. It is one of the outstanding masterpieces of nature (Qin, 1987). There are still a lot to be done in exploring the evolutionary significance of nectar-robbing in the reproductive success, and the subtle interaction of nectar-robbers, pollinators and plants in the microevolution of plant.

For nectar-robbers, nectar-robbing behavior is a very efficient way to get nectar. Bumble bees can detect the volume of nectar in flower tubes or spurs by the ultraviolet (UV) reflection pattern of flowers (Throp et al., 1975). Getting nectar by cutting holes on flower tubes or spurs is obviously more efficient than getting nectar through the opening of flowers in a normal way. The energy-saving behavior is beneficial to foragers. Long-tougued bumble bees are adapted to visiting flowers as normal visitors while short-tougued bumble bees are adapted to nectar-robbing. The similar cases are found between humming birds with relatively longer beaks and those with relatively shorter beaks (Irwin and Brody, 2000). In bumble bees, the visiting behaviors of short-tougued nectar-robbers and long-tougued normal visitors are differentiated both spatially and temporally in natural populations. In the interactions of nectar-robbers, pollinators and plants, different species occupy different ecological niches in the ecosystem. This exemplifies the allocation of energy and the employment of resources in nature.

For the host plants, nectar-robbers are mutualists rather than antagonists in most cases. Nectar-robbers are pollinators sometimes. Sixty percent of the flowers of *Corydalis ambigua* are pollinated by nectar-robbers (Olesen, 1996). Some other studies showed that the behaviors of nectar-robbers and their effects on other pollinators often lead to a larger distance of pollen flow, and thus causing a higher out-crossing rate and lower inbreeding depression (Irwin, 2003). In some cases, the negative effects of nectar-robbing are obvious. They disturb with the normal pollination and decrease the reproductive success of plants. The interactions between pollinators, nectar-robbers and plants are the very complex ones in nature, it is not surprise to find different, or opposite effects of nectar-robbing on different species of plants or even on the same species of plant in different environments.

It is noteworthy that the present studies on nectar-robbing are generally neglected in China. Systematic and extensive researches on the subject are scanty (Zhang and Guo, 2006; Zhang et al., 2006). It was prospected that more and more researchers would be interested in the subject in the near future.

Generally, nectar-robbing is a complex ecological phenomenon, the significance of which on the co-evolution of flower morphologies and the animal behaviors is not clear. The interaction among nectar-robbers, pollinators and plants and the subtle relationships among these organisms deserve more extensive researches.

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