POLLINATION OF *PROSOPIS TAMARUGO* IN THE ATACAMA DESERT WITH REMARKS ON THE ROLES OF ASSOCIATED PLANTS

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ABSTRACT

A few species of *Prosopis*, growing in the desert of northern Chile have facilitated the settlement of a small human population keeping herds of goats, sheeps and llamas that graze on *Prosopis* seeds. The pollination of *Prosopis* occurs during the main spring- summer blooming season by *Centris mixta* (Anthophoridae), but during the autumn-winter period, the only available pollinators are some species of butterflies and moths. *Centris mixta* is polylectic over almost all of its geographic range, but it behaves as oligolectic in the area of *Prosopis*, the emergence and flight activities of the bee are synchronous with the sequential blooming period of the different species of *Prosopis*. The biology of *C.mixta*, with permanent nest sites, seems to promote intimate insect-plant relations. Survival of both, the plants and specially the pollinators are in jeopardy because of human activities in the area.

INTRODUCTION

A few species of *Prosopis*, established for a long time in the northern desert of Chile, can survive and show particular "adaptations" to the extreme water scarcity in the area. In the early 1900s, intensive mining activity in the desert resulted in an almost complete eradication of the arboreal *Prosopis,* but the implementation of conservation policies and the reforestation of large areas have now given rise to a new community with a few plant species associated with a small number of pollinators. This community has been found to be extremely fragile, with only a few plant and animal species (Bobadilla *et al.* 1987) distributed in isolated patches. After forestation, a small human population settled in the area and kept herds of domesticated sheep, goats and llamas that graze on *Prosopis* seeds.

Most of the trees, in the forest, are *Prosopis tamarugo* Phil. ("tamarugos" in this paper) and a few of intermixed plants of *Algarrobia sp.*, with *Prosopis alba* Gris, *P.atacamensis* Phil. and *P.flexuosa* DC# (Villaseñor *et al.* 1994). More taxonomic work is required to clarify the chilean *Algarrobia* (Palacios, personal communication).

The native vegetation in the area includes two other species of *Prosopis: P. strombulifera* (Lam.) Benth and *P. burkhartii* Muñoz. The first of these two species is a small bush, rather scarce, which grows in small patches frequently foraged by the native people who use their fruits as amulets. On the other hand, *P. burkhartii*, also bushy, is very rare, poorly known and probably very close to extinction. Besides *Prosopis*, one native bush *Caesalpinia sp.* is abundant in few, but large, patches widely isolated by barren desertic areas.

From the area's economic perspective, *P. tamarugo* is interesting and presents advantages over the *Algarrobia*. *P. tamarugo* blooms and produces fruit and seeds almost year round, which is very important for cattle when there is no other food available. The blooming period shows two main, very distinctive peaks in some years; one in spring, which is common for other species of *Prosopis*, although not exactly synchronous; and another, in the late fall. The *Algarrobia* bloom only during springtime, with flowers apparently more attractive to pollinators than those of "tamarugos" and with sweeter fruits. The fruits are also more attractive to cattle and to the human population that eats it directly or uses it to prepare alcoholic beverages.

Experiments made with fabric bags (used to block the access of insects) cover young inflorescences with no emerging pistils, have revealed a low percentage of self-pollination

(Villaseñor *et al.* 1996). Likewise, fine net bags, which allow pollen to be carried in by the wind, but not by insects, show absence of anemophilous pollination.

According to above, the amount of seeds available for the human population is mostly determined by the quality and quantity of pollinators and by the mass of herbivorous insects feeding on the flowers and seeds. Most of the pollination of *Prosopis*, during the spring blooming season, is mainly by the native bee *Centris mixta tamarugalis*, but during the colder seasons, there are no bees in the area and, therefore, pollination depends on various species of butterflies and moths.

Although the number of insect species associated with *Prosopis* (Ward *et al.*1997; Genise *et al.* 1990; Simpson *et al.* 1977) and recorded for the area is relatively high (Bobadilla *et al.*1987), only the following species have shown free pollen on the body hairs:

Hymenoptera
 Colletidae
  Colletes murinus Friese
  Chilimelissa luisa Toro y Moldenke
Halictidae
  Caenohalictus sp.
Anthophoridae
  Centris mixta Friese
  Centris moldenkei Toro y Chiappa
Apidae
  Apis mellifera Linné
Vespidae
  Pachodynerus peruensis Saussure.
Lepidoptera
Lycaenidae
  Leptotes trigemmatus Butler
Diptera
Bombyliidae
  Villa sp*.*

There are also few examples of Syrphidae, Tachinidae, Calliphoridae, Cecidomyidae and Sarcophagidae as flower visitors.

All the potential pollinators that were found are polylectic on a broad geographical scale; however, given the scarcity of species present in the desert, they are necessarily oligolectic there.

Colletes murimus and *Caenohalictus* sp. are rather scarce in the area but show a broader distribution throughout the north of Chile, reaching heights of 2,500 m. They are associated with native vegetation and alfalfa. *Chilimelissa luisa* is a small bee found abundantly on *Cesalpinia aphylla*, with which it seems to be well associated. It also finds hollow stems on this plant in which to build its nests. This bee visits algarrobos and tamarugos and flies mainly around branches close to the ground. Because *Ch. luisa* has been detected only around some specific trees, it is concluded that its occurrence is spotty.

Apis mellifera shows variable population density. Previously it was a rare species, but it dramatically increased in number in a few years as a result of transhumanance beekeeping. In unprotected conditions, survival of *A. mellifera* is uncertain, not only because of environmental conditions but also because of the destruction of its hives for honey extraction. The search for colonies of honeybees in the *Prosopis* forest over a period of 4 years resulted in only three being found. Two were in hollow trunks and one in an abandoned well. Toro *et*

al. (1992) estimated the size of the colony by measuring the inflow of specimens into the hive (Toro *et al.*1992). For the three unprotected colonies under study, the inflow varied between 16-43 individuals in10 min. At the end of the study, the colony became extinct. At the same time, the flow of bees in protected, managed colonies was 143 specimens/10 min.

Most individuals of *A. mellifera* go to *Prosopis* for nectar. On average, only 25% of bees recorded had corbicular pollen loads, and very few among those showed full loads (11%). Transportation of pollen is greater in spring than in the rest of the year. The amount of highest nectar foraging seems to be related to water shortage. Nectar is widely used, besides for other metabolic functions, in thermo-regulation of individuals and colonies.

Nevertheless, data published by León (1985) reveal interesting results from the perspective of beekeeping. The average weight gain per colony was 36.95 kgs over the season. In addition to the bees obtaining honey, which is characteristic and virtually pure as far its plant origin is concerned, the weight gain means a significant volume of nectar has been harvested by the bees especially considering the 120 hives noted by León (1985). The nectar removal may influence resource availability for the native pollinators of the area.

The association of *Leptotes trigemmatus* (Lycaenidae) and possibly of *Prosopis* with some other moth species (marked "tamarugo-attacking insects", Bobadilla *et al.*1987, Vargas *et al.*1989) are interesting in the area, particularly in the fall-winter period, when Apoidea are not present. In the absence of Apoidea, these Lepidoptera are the only possible pollinators for *P.tamarugo*, in addition to being the most important pollinators for *Prosopis strombulifera* and *P. burkhartii*. Nevertheless, larvae of *L. trigemmatus* feed on *Prosopis* blossoms. For that reason, the density of this species has a direct effect on reducing the fruit yield and is considered a plague by the local people. With regard to self-regulation, the *Prosopis*-Lepidoptera association is interesting because the species that feed as larvae on flowers and green seeds are the same as those which act as pollinators. The long-term situation suggests a self-regulatory mechanism whereby the density of herbivorous species is quite dependent on the number of available flowers.

L. trigemmatus visits the inflorescence in a somewhat disorderly manner; it arrives at the inflorescence and stays at highly variable durations. It also moves over the flowers with no fixed trajectory, virtually independent of its nectar foraging time, which is sometimes tens of minutes, but approximately 5 min when the female is laying eggs. These two species appear to rely more on *L. trigemmatus* than the other *Prosopis sp.* do and show a blossoming peak when there are no other pollinators in the surroundings. Like other butterflies, *L. trigemmatus* easily goes from one tree to another, even distant trees, a behaviour particularly shown by the males in search mates.

Most pollination of *Prosopis* during the spring bloom is performed mainly by the native bee *Centris mixta tamarugalis* (Klein and Campos 1978; Toro *et al.*1993), an extremely abundant species in the area.

The *Prosopis*- *C. mixta* association is well synchronized. *Centris mixta* seems to recognize and respond to the same environmental stimuli as *Prosopis* does and shows a behavior more similar to a specialist than to a generalist pollinator. The adult bees appear in the area in late August or early September, at the time algarrobos bloom (*P. alba, P. flexuosa, P. atacamensis*).

Centris mixta spends the hibernation period as a post-defecating larva. In the absence of environmental stimuli, when it is kept away from its natural habitat, it continues hibernating so that when kept in the laboratory, it can live some years without transforming itself into pupa (Chiappa and Toro 1991). The emerging adults show a slight protandry.

In using the sequential *Algarrobia*-tamarugo blooming period, adults of *C. mixta* fly from September to December. In our observations we have registered a considerable reduction of males as the season progresses and by late December, they become rare. The single blooming period of algarrobos is from September to October, and the blooming peak of tamarugos occurs in the October-November. This blooming sequence allows *C. mixta* to have food for a long period, in a milieu that, in general, is characterized by very restrictive reproductive periods for most of the biota. From the plants' point of view, the sequence is mutualistic with evident benefits for *P. tamarugo*, which blooms when there is a high density of pollinators.

The onset of the "tamarugo" bloom overlaps with that of the "algarrobos". In the Atacama, *C. mixta* shows a strong preference for flowers of *Algarrobia* with exceptional individuals visiting "tamarugos". The end of the blossoming of algarrobos makes for a new situation for *C. mixta*, which must then learn to collect on tamarugo in order to meet its food requirements. This behavior points to *C. mixta* as a selective force for the beginning of the blooming period of the algarrobos, although we have found scattered flowers before the emergence of *Centris*. In the same way, *C. mixta* is also selective in the sequential blooming of algarrobos and tamarugos because of the visiting preference to algarrobos.

The bushy species of *Prosopis (strombulifera* and *burkhartii*) are not considered as an attractive resource for pollinators because of the small number of plants present in the area.

However, the synchronic blooming of *Cesalpinia aphylla*, the only native species abundant in the area besides *Prosopis*, is clearly an important nectar and pollen resource in the area. In the absence of *Algarrobia*, *C. mixta* prefers *P. tamarugo* rather than the flowers of *C. aphylla*. The latter is pollinated by the tiny species *C. luisa* (Xeromelissinae) and another species of *Centris*, (*C. moldenkei*), also showing oligolectic behavior, and rarely found on *Prosopis. L. trigemmatus (Lycaenidae) and some Diptera also visit Cesalpinia*.

Centris mixta used permanent nest sites close to *Prosopis* trees. The sedentary nature of the chief pollinator quite unlike the vagility of other species of *Centris* (Rozen and Buchmann 1990), is probably determined by restrictive environmental conditions. The bees require soil with great amounts of salt. The absolute absence of resources beyond the forest, may also result in a stability in the pollinator-plant interaction over time (e.g. synchronicity, phenology, etc.). This situation must also affect the population density of both the pollinator and the plant. Besides, the permanent use of the nest site gives rise to a population of parasites and predators, dependent and synchronized on their host. This community clearly shows Mutillidae and Bombyliidae as parasites, other than predator birds and lizards, all dependent on *C. mixta*.

Pollination behaviour of *C. mixta*. As a result of a particular reproductive behaviour, differences in the frequency of visits of males and females to flowers were observed in the course of the day. In the morning, the great mass of males patrols the nesting territory and waits for emerging virgin females. The mated females mostly collect nectar and pollen to supply the nest cells. Their visits to flowers decrease between 13 to 15 hrs. as ambient temperatures rise. Many individuals rest in the shade, with their glossae protruding and evaporating nectar. In the afternoon, the number of males at flowers increases, while large numbers of females were found on the ground and working in their tunnels.

Both males and females pay short and quick visits to the flowers (X=11.26sec +/- 8.74 (S.D.), n=36). On most individuals (80%) arrive at the distal or central part of the inflorescence, then following a spiral path from the distal to proximal end. At the end of its visit, the bee flies to another inflorescence, in the same tree or in another distant tree. The bee's trajectory on each inflorescence favours efficient pollen flow among protogynous inflorescences (the

stamens are first exposed in the proximal end, when the pistils are already exposed along the whole inflorescence).

The following practices are considered potential problems for the proper conservation of the pollinators and in the whole system of the Atacama desert:

1. *Prosopis* is used as fuel because the isolation and difficult access to the area make gasoline and other petroleum derivatives expensive and difficult to get. This generates a strong pressure for the people to use *Prosopis* (there is no other wood resource) for fuel and the pressure is strong to produce charcoal. There are few other economic opportunities to supply the demand of the local mining companies.

2. The blooming spring-summer peak also generates pressures from honeybee keepers. The beekeepers are non-local people and bring in a number of hives and house them in the *Prosopis* forest. As pointed out before, *A. mellifera* collects a large amount of nectar and the pollen is probably significant too but difficult to assess. The low diversity in vegetation suggests a limited pollen-nectar resource would produce competition with native pollinators and that this competition should be stronger towards the end of the blooming period. When there is no *A. mellifera* in the area, the availability of nectar-pollen for *C. mixta* is guaranteed because only females are present and males have previously been eliminated by predation or other causes.

3. The nesting sites located in open flat grounds are used occasionally, or sometimes frequently, as roads for cars or other kinds of vehicle. The traffic produces high mortality of *C. mixta* during the reproductive period, spoiling the nesting tunnels and smashing the males while they are waiting for females to emerge.

4. The defoliation and seed damage caused by lepidopteran larvae have induced people to try pesticides derived from *Bacillus thuringiensis*. This practice has shown positive results as many more seeds are obtained than without pesticide use. Nevertheless, in a relatively short term, intensive applications could result in great damage because the eradication of Lepidoptera also means the eradication of the pollinators for the fall-winter blooming period. The recovery of pollinators by their immigration from adjacent areas is considered very difficult because of the strong isolation created by the desert between areas with vegetation.

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