POLLINATOR VISITATION AND REPRODUCTIVE SUCCESS IN TWO SPECIES OF MANGROVE PLANTS, IN BHITARKANIKA WILDLIFE SANCTUARY, ORISSA

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By
SHALINI PANDIT

UNDER THE SUPERVISION OF
B. C. CHOUDHURY

WILDLIFE INSTITUTE OF INDIA
DEHRADUN

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

CERTIFICATE

This is to certify that Shalini Pandit of the Wildlife Institute of India has carried out an original piece of research work entitled *"Pollinator visitation and reproductive success in two species of mangrove plants, in Bhitatkanika Wildlife Sanctuary, Orissa"* in partial fulfillment of the M.Sc. (Wildlife Science) degree of Saurashtra University. These investigations were carried out under my supervision at the Wildlife Institute of India from November 1996 to June 1997. I also certify that this work has not been submitted for any other degree of any university.

Date: 3rd July 1997
Place: Dehradun

Sh. B.C. Choudhury
Scientist - SE
Faculty of Wildlife Management

Post Box No. 18, Chandrabani, Dehradun - 248 001. India.
EPABX : 640112 to 640115; Fax : 0135-640117; Gram : WILDLIFE
E-Mail : wii@giasdl01.vsnl.net.in

CONTENTS

LIST OF TABLES

LIST OF FIGURES

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SUMMARY

Visitation patterns to the flowers of *Sonneratia caseolaris* and *Aegiceras corniculatum* were investigated between December 1996 and April 1997, in the mangrove forests of Bhitarkanika Wildlife Sanctuary, Orissa. The objectives of the study were to determine the pollination effectiveness of the different categories of visitors by quantifying their rate of visitation. The effect of environmental variables on visitation was examined, and the importance of the visitors to the reproductive success of the plant was investigated by conducting exclusion experiments (i.e., bagging flowers to prevent visitation). Nectar was analysed for volume and sucrose content in *S. caseolaris*, and the impact of predation on the reproductive success of the plant was examined.

The results of the study indicated that the flowers of both plant species attracted a wide array of visitors and did not show a specialised relationship with any one visitor species/category. Different categories of visitors were seen to vary in their pollination effectiveness for the two plant species. Environmental variables such as temperature, sun intensity and wind velocity were seen to influence the visitation of Lepidoptera to the greatest extent, and Hymenoptera to a lesser extent. Visitation by birds was found to be independent of the environmental variables. The territorial behaviour of purple-rumped sunbirds at the *S. caseolaris* site was seen to reduce visitation of other birds and of bees to the flowers of this species.

Results of the bagging set-ups indicated that there was no difference in the pollinator effectiveness of the nocturnal and diurnal visitors. Reproductive success was not pollinator-limited in either of the two plant species. In *S. caseolaris*, predation pressure was the single most important factor limiting fruit-set, while in *A. corniculatum*, fruit-set is probably resource-limited.

1. INTRODUCTION

1.1 General introduction

Sexual reproduction in angiosperms has three sequential stages: pollination, fertilisation and seed maturation (Lyons *et al.* 1989). Pollination is the transfer of pollen grains from the anther to the stigma of a flower (Dutta 1989). It may occur through two modes (Bertin 1989):

a. self- pollination and
b. cross-pollination.

The mode of pollination affects the gene flow in plant populations. In nature, cross pollination is often favoured over selfing, as it leads to increased variation in a population enabling it to adapt to a wider range of conditions (Proctor *et al.* 1996). Cross-pollination relies on an external agent (wind, water or an animal) to transfer pollen from one individual to another (Dutta 1989). The focus of this study is on the pollination system involving animals as the vectors of pollen.

All animals are not equally effective as pollinating agents. Pollination effectiveness has several components, one which is the rate of visitation of the pollinator to the flowers. This is influenced by a variety of environmental and ecological factors (Primack and Inouye 1993). Documentation of this pattern of visitation of the different pollinators to a flower is important in gaining an insight into the interaction between plants and their pollinators. As a result of this interaction, the plant gains reproductive success, as the transfer of pollen is a necessary prerequisite to sexual reproduction. The reproductive success of a plant is indicated by the extent of fruit and seed set (Stephenson 1981, Ganeshaiah and Uma Shaanker, *unpublished manuscript*). Measurements of visitation rates can thus identify the linkages among pollinators, plants, and subsequent fruit and seed set.

1.2 *Review of literature*

Pollination systems:

One view of pollination systems is that they tend towards specialisation (Stebbins 1970, Gilbert and Raven 1975, Howell 1979, Kress 1993). This view is implicit in the long-standing concept of "pollination syndromes" (Faegri and van der Pijl 1979), which are suites of floral traits proposed to reflect adaptations to one or another pollinator type. The established paradigm is that there are detectable associations between plant phenotypes and pollinators. This view, however, has been questioned by several authors (Thomson 1983, Howe 1984, Haber and Frankie 1989, Primack and Inouye 1993, Subramanya and Radhamani 1993, Waser *et al.* 1996, Bo`sch *et al.* 1997), who propose that there is a relatively unspecialised relationship between the plants and animals involved in pollination. Waser *et al.* (1996) suggest that there is no strong association of floral traits with pollinator types, as pollination syndromes would predict. Most plant species are visited by an array of visitor species, not all of which effect pollination (Subramanya and Radhamani, *in press*). Apart from pollinators, flowers are also frequented by visitors that use the pollen and nectar resources opportunistically (Gill *et al.* 1982, Santharam 1996). Inouye (1980) classified various types of visitors to plants on the basis of their behaviour related to methods of pollen/nectar harvest:

a. pollinators- obtain the reward and effect pollination in the process.

b. thieves- derive benefit (nectar or pollen), without harming the morphological integrity of the flower but at the same time preclude pollination due to mismatch of morphologies.

c. robbers- obtain the reward by damaging the flower and do not effect pollination.

Even amongst the pollinator species, there is considerable taxonomic variation in pollination effectiveness (Ashman and Stanton 1991, Fishbein and Venable 1996). Quantifying pollination effectiveness is central to many questions in pollination biology (Fishbein and Venable 1996). When the pollinator is an animal, its effectiveness would depend upon the rates of:

- visitation,
- pollen removal and
- pollen deposition (Herrera 1987).

Analysis of pollinator visitation rates can yield valuable information about the utility of the visitor species to the plant (Primack and Inouye 1993). The number of visits a flower receives in a certain period of time would depend upon several factors including environmental variables such as light levels, air temperature, relative humidity, and wind velocity (Vasudeva and Lokesha 1993). The study of variation in visitation rates of the different visitor species would help in obtaining patterns of visitation to the flowers.

A potential drawback in measurements of visitation alone, vis the fact that flower visitation may not necessarily translate into transfer of pollen onto the stigma of a flower (Primack and Inouye 1993). Microscopic examination is usually required to confirm that a flower visitor is in fact a pollinator, however it is usually obvious when species are foraging, as to which are nectar/pollen thieves and robbers.

The extent to which the visitors are effective as pollinators can be gauged by estimating the reproductive success of the plant in terms of fruit/seed-set. There are several proximate factors that limit fruit and seed production between anthesis and dispersal (Proctor *et al.* 1996), pollination being one of them (Murali 1993). The extent to which fruit-set is pollinator-limited would vary according to the species and would also depend on other factors such as resource availability, predation pressure (Stephenson 1981) and time of flowering (Casper and Niesenbaum 1993).

Pollination in mangroves:

Mangroves characteristically constitute tropical intertidal forest communities (Tomlinson 1986). They are adapted to conditions of periodic tidal inundation, salinity in the substratum and poor aeration of the soil, amongst other peculiarities of their environment.

An analysis of the sexual differentiation and floral mechanisms in mangroves shows that most taxa are hermaphroditic (i.e., retain the capacity for potential self-fertilisation), but show a trend towards outbreeding mechanisms (Primack and Tomlinson 1980). Theoretical arguments would support the idea that mangroves, if they are primarily colonising species, would retain the capacity for self-fertilisation if they are to establish populations in isolated localities, as argued by Primack and Tomlinson (1980). These authors contrast mangroves with trees in terrestrial lowland forest communities and relate observed differences to the pioneering propensities of mangrove taxa. However, more direct confirmation of this hypothesis is needed. Mangroves are almost exclusively pollinated by animals, the only exception being *Rhizophora*, which is wind pollinated (Chai, 1982). The diversity and generalised nature of mangroves allow two basic conclusions: **first**, the spectrum of pollinators is broad so that no plant is highly dependent on one specific pollinator; and **second**, plants are specialised only to the extent of being associated with a given category (which may be up to the taxonomic level of orders or above) of pollinator (Tomlinson 1986).

The mangrove plant community in Bhitarkanika Wildlife Sanctuary is characterised by an abundance of species flowering from February to April (*pers. obs.*), during which period there is a seasonal migration of bees into the area. During the study period from November 1996 to April 1997, two species were selected to be studied. Of them, *Sonneratia caseolaris* was aseasonal in its pattern of flowering, and a few individuals of the species were always in bloom. The other species, *Aegiceras corniculatum*, is strongly seasonal in its flowering pattern and bears flowers for only 4-5 weeks in a year, from mid-March to mid-April (Banerjee and Rao 1990, *pers. obs.*).

Sonneratia (Sonneratiaceae) is a genus restricted to mangrove communities. All six described species of *Sonneratia* belong to the Indo-Malayan group of mangroves, ranging from East Africa through Indo-Malaya to tropical Australia and into Micronesia and Malaysia (Tomlinson 1986). *Sonneratia caseolaris* is an evergreen tree growing upto 15 metres in height, with diffuse branching. It has essentially solitary flowers, numerous stamens, vestigial or no petals, a fruit that does not dehisce regularly, and seeds without extended tails. The stamens collectively render the open flower conspicuous with their reddish-purple colour. The flowers produce nectar and have been observed to be pollinated by bats and hawk moths (Tomlinson 1986).

Aegiceras (Myrsinaceae) is a genus also restricted to mangrove communities. The two species within this genus have a distribution from India and Sri Lanka to South China and Hong Kong, through Malaysia to the Philippines, New Guinea and tropical Australia but not known from the Pacific islands (Tomlinson 1986). *Aegiceras corniculatum* is a low evergreen shrub or tree growing to a height of 6 metres. Flowers are borne in umbels and are fragrant, perfect and pentamerous. Fruits are elongated, capsular and dehiscent, containing a single elongated seed without endosperm. The flowers contain nectar and are reported to be pollinated by insects (Tomlinson 1986).

1.3 *Objectives*

This study aimed to characterise pollination from the point of view of a plant species, by recording visitors to the flowers and assessing the importance of pollinators for the reproductive success of the plant.

The objectives specific to this study were:

- to document all visitors (diurnal and nocturnal) to the flowers of the two species being studied.
- to observe the temporal pattern of visitation across the day
- to examine the effect of environmental variables on the visitation of the different categories of visitors.
- to determine whether visitors were at all important to the reproductive success of the plant.
- to compare the relative importance of the diurnal *vs.* nocturnal visitors for successful fruit-set in the plant.
- to study the investment made by the plant in attracting visitors by estimating the rewards to visitors (nectar).
- to determine if any other factor controlled the reproductive success of the plant (e.g., predation), and to what degree it affected the success of fruit-set in the plant.

2. STUDY AREA

2.1 *Location*

Bhitarkanika Wildlife Sanctuary (20° 04' N to 20° 08' N and 86° 45'E to 87° 50' E), is located on the east coast of India in the state of Orissa, district Kendrapara. The sanctuary is bounded by the rivers Dhamara to the north, Maipura to the south, Brahmani to the west and the Bay of Bengal to the east (Kanvinde and Das 1994). The area was notified as a Wildlife Sanctuary on the 22nd of April, 1975 and extends over a total area of 170 sq. km., of which 115 sq. km. is under mangrove vegetation (Forest Department, Orissa; *pers. comm.*).

2.2 *Climate*

The climate is typically tropical monsoonal due to the latitude of the area coupled with the proximity of the sea (Roy 1989). Forest Department records indicate that the temperature varies from a minimum of 10°C in winter to a maximum of 45°C in summer. The average annual rainfall is 1200 mm and the main monsoonal months are August and September. Humidity is high throughout the year, varying between 75% and 95% (Kar 1981). The area is prone to severe cyclonic storms in April and May and again in October and November. During the study period, there was cyclonic weather throughout the months of March and April, 1997.

2.3 *Tidal cycle*

The deltaic mangrove swamps are subjected to regular tidal inundation and are extremely low lying. Elevation above mean tide level is between 1.5 and 2 metres (*pers. obs.*). The mosaic of rivers and creeks are influenced twice daily by high and low tides at approximately six hourly intervals. The maximum and minimum tide levels vary according to the lunar cycle and are also subject to seasonal variations.

2.4 Soil

The study area is influenced by heavy alluvial silt brought down by the rivers and deposited in the deltaic areas during tidal inundation. The soil is clayey loam with sand, overlaid by a rich humus layer. Areas lying on higher elevations lack mangrove cover and have a soil consisting predominantly of sandy loam (Dani and Kar, *unpublished manuscript*).

2.5 Vegetation

The mangrove vegetation of Bhitarkanika can be broadly classified into

a. the outer estuarine region, and
b. the inner estuarine region (Choudhury 1990)

Plants in the outer estuarine region are subjected to high salinity and wave action. *Avicennia marina* is common, forming a pioneer tree stand near the intertidal zone. *Sonneratia griffithii* is found in low gradient mud flats along the lower intertidal zone in mixed association with *Avicennia alba*, *Bruguiera parviflora*, *Bruguiera cylindrica*, and *Aegialitis rotundifolia*. These species are tolerant to the highly saline conditions and are found more commonly along the central parts of the funnel shaped estuarine bank.

The inner estuarine bank is strongly dissected by several creeks, channels and their distributaries. The force of the sea surf is broken due to the presence of several creeks, and vegetation is subjected to moderate salinity. These conditions make favourable habitat for many mangrove species and the flora is rich and diverse in this region. The dominant mangrove species in this region are *Avicennia officinalis, Sonneratia apetala, Sonneratia caseolaris, Excoecaria agallocha, Heritiera fomes, Phoenix paludosa, Kandelia candel, Xylocarpus granatum, Xylocarpus moluccensis, Rhizophora mucronata, Rhizophora apiculata, Aegiceras corniculatum, Merope angulata* and *Cerbera manghas*. A detailed account of the flora of Bhitarkanika is given in Banerjee and Rao (1990).

2.6 *Intensive study area*

Sampling was conducted in the inner estuarine zone where the vegetation consists largely of mangrove formations. This area falls in blocks VII, VIII, IX and Bhitarkanika block of the Sanctuary. There is a sharp distinction between the vegetation type along the banks of the creeks and that occurring further inland. As the species of interest occur almost exclusively along the waters edge, the sampling focused largely on the area bordering the creeks. *Sonneratia apetala* is the most dominant species here, occurring along with *Avicennia officinalis, Aegiceras corniculatum, Sonneratia caseolaris, Heritiera fomes, Excoecaria agallocha, Hibiscus tiliaceus, Brownlowia tersa, Phoenix paludosa, Xylocarpus granatum, Ceriops tagal* and *Cerbera manghas*.

3. METHODS

Data were collected from December 1996 through April 1997. The methods employed to conduct the study were:

Field methods:

- Selection of plant species to be studied.
- Documentation of visitors and patterns of visitation on flowers.
- Experiments on fruit-set in the presence and absence of visitors.
- Documentation of the duration of successive floral stages.
- Nectar extraction.
- Morphometric measurements of flowers.
- Quantification of losses incurred by the plant due to flower and fruit predation.

Analytical methods:

- Statistical analyses.

Field methods

3.1 *Selection of plant species to be studied*:

A fifteen day reconnaissance survey was undertaken at the study site. Patterns of distribution and flowering phenology of the mangrove plants were noted, following which *Sonneratia caseolaris* was selected as the species to be studied in the first half of the study period from December 1996 to February 1997. During March and April 1997, sampling was done on *Aegiceras corniculatum*. The following criteria decided selection of the study species:

- the flowers/inflorescences in both species are large and easily observable.
- the flowers attract a number of visitors.
- flowering in *Sonneratia caseolaris* is aseasonal and staggered throughout the year, while that in *Aegiceras corniculatum* is strongly seasonal and coincided with the study period. These traits enabled the study of the differences in visitation to plant species with different flowering strategies.
- *Aegiceras corniculatum* is a major source of nectar for mangrove honey, which is harvested by the local people (Banerjee and Rao 1990).

3.2 Documentation of visitors and patterns of visitation to flowers:

Initial observations revealed that visitors came to the flowers of *S. caseolaris* between 0530 hrs and 1730 hrs, and again from 1830 hrs to 0500 hrs. Units of observation were *apriori* classified as day and night units, to separately analyse visitation by diurnal and nocturnal visitors. Thus for the day units, observations were made between 0530 hrs and 1730 hrs and those for the night units were made between 1730 hrs and 0530 hrs. For *A. corniculatum*, the day units extended from 0530 hrs to 1800 hrs and the night units from 1800 hrs to 0530 hrs. In order to facilitate identification of the visitor species, specimens were collected with the help of insect-nets, and later taken to the Forest Research Institute (Dehradun) for identification.

Continuous observations to the nearest minute were made for units (day and night) of 12 hours each, undertaken in sampling sessions of two to four hours. Observations on *S. caseolaris* were made for a total of seven day units and one night unit, and those on *A. corniculatum* for five day units and one night unit. The day units were categorised into sunny and cloudy units depending on the weather conditions prevalent during that set of sampling sessions. This was done in order to separately examine visitation patterns under these environmental conditions. Observations during the night units were made using flashlights to scan a focal group of flowers at intervals of five minutes. During each sampling session, observations were made on a group of focal flowers (all being equally observable) from a boat, at a distance of five meters. The following details were noted:

- time.
- ambient temperature (upto 0.1°C accuracy), measured every 10 minutes using an open thermometer.
- intensity of sun graded on an ordinal scale of increasing intensity ranging from one to five. This was estimated visually and recorded every 10 minutes.
- velocity of wind was subjectively estimated at intervals of 10 minutes and graded on an ordinal scale of increasing velocity from one to four.

- species visiting the focal group. A visit was recorded from when the visitor first made contact with any flower of the group under observation until it left the group. Return visits to the group were recorded as fresh visits (Santharam 1996).
- number of flowers visited per visit by each individual visitor.
- foraging manoeuvre employed by different species of visitors. On the basis of this, the visitors were classified as pollinators, thieves and robbers (Inouye 1980).
- floral stage of each flower visited. The study classified the flowers of *S. caseolaris* into four categories depending on the stage of development, which were as follows:

a. closed buds (sepals fused)

b. young flowers (style exserted; corolla and stamens incurled)

c. mature flowers (anthers dehisced)

d. old flowers (stamens shed)

Each of these categories represents a different stage of reproductive maturity, and thus visitation to different stages would effect pollination differentially. It was assumed that visits to mature flowers would be most effective (as both stigma and anthers were exposed, pollen-deposition and pollen-removal would both be possible), followed by those to young flowers (only stigma exposed; thus pollen deposition was possible by the visitor, but it could not carry pollen from the flower). The flowers of *A. corniculatum* were visited only in the mature flower stage and were thus not classified further.

3.3 *Experiments on fruit-set in the presence and absence of visitors*:

These experiments were conducted in order to determine the importance of all pollinators for the reproductive success of the plant, and to examine the relative importance of diurnal *vs.* nocturnal visitors. In order to do this, individual flowers were marked using transparent plastic tags with numbered codes written in indelible ink. Visitors were excluded from flowers by bags made from synthetic mesh material (no. 40, with a mesh size of 0.5 mm) which were dyed green. This technique has been shown to least alter the environment of the flowers inside the bags (Kearns and Inouye 1993). There were four types of treatment:

- Buds that were covered with bags throughout their development till fruit-set (if any), excluding all visitors. This was done to determine the extent to which the flowers were able to self-fertilise in the absence of visitors.
- Buds that were covered with bags (throughout their development till fruit-set) from 0530 hrs to 1730 hrs excluding diurnal visitors but allowing the nocturnal ones. This would reveal the relative importance of diurnal visitors for successful fruit-set.
- A reciprocal set-up involving buds covered from 1730 hrs to 0530 hrs excluding only the nocturnal visitors (Goldingay *et al.* 1991), to determine the contribution of nocturnal visitors to fruit-set.
- Uncovered, tagged buds left open to all visitors, to estimate the level of reproductive success in the plant under natural, non-manipulated conditions.

Treatments were differentiated by tying coloured (brown and green) embroidery threads on the pedicels of the flowers (Pleasants 1980).

A. corniculatum was seen to occur in two different types of sites: pure stands of only *A. corniculatum*, and mixed stands where it occurred along with other species. At the mixed-stand site, the dominant species was *Heritiera fomes*, followed by *Phoenix paludosa* (flowering), *A. corniculatum* (flowering), *Hibiscus tiliaceus* (flowering) and *Acanthus ilicifolius* to a lesser extent. It was hypothesised that the higher concentration of flowers of *A. corniculatum* at the pure-stand sites would present a more attractive floral display to visitors, thus increasing rates of visitation at those sites, which may translate into more effective pollination of the flowers, and hence greater reproductive success, as compared to the mixed-stand sites. In order to examine if any such trend did exist, bagged/unbagged treatments were conducted separately in the two sites. Fruit-set was measured for all treatments by counting the number of fruits that had developed.

3.4 *Documentation of the duration of successive floral stages*:

Anthesis in the flowers of *S. caseolaris* occurs in several stages. Individual flowers were marked and their development followed through their life-span. The study classified floral stages as:

- Stage 1 (sepals fused)
- Stage 2 (sepals parted, style incurled)
- Stage 3 (style exserted, stamens incurled)

- Stage 4 (anthers dehisced)
- Stage 5 (stamens partly shed)
- Stage 6 (stamens fully shed)
- Stage 7 (fruit formed)

The duration of successive floral stages was recorded, in order to determine the difference in time between the maturation of style and stamens, and to estimate the average time period for which a flower stayed in bloom.

3.5 *Morphometric measurements of flowers*:

Measurements were made by dissecting the floral parts and marking their dimensions on graph paper. The length of the style and that of the stamens was measured for both species. This was done to determine the extent to which the style and stamens were separated in space, thus estimating the possibility of self-pollination for the species. All measurements were made on mature, uninjured flowers.

3.6 *Nectar extraction*:

Total harvest of nectar was taken from randomly selected flowers of *S. caseolaris*. Flowers were categorised into the following floral stages:

a. Closed bud

b. Young flowers

c. Mature flowers

Measurements were made at two different times of day: between 0500 hrs and 0600 hrs, and between 1700 hrs and 1800 hrs, in order to estimate the resources available to the diurnal *vs.* the nocturnal visitors. Nectar was extracted using micro-capillaries (with a volume of one μl). Nectar volume was computed using the following equation (Cruden and Hermann 1983):

$$\text{volume of nectar} = \frac{\text{mm of nectar in capillary}}{\text{mm total length of capillary}} * \text{calibrated volume of capillary}$$

Sucrose concentration of nectar was estimated using a hand-held refractometer (Trombulak 1990). The model used was Erma (Tokyo) A-contrast 11-520-0, with a range from 0% to 32%.

Attempts at extracting nectar from the flowers of *A. corniculatum* using micro-capillaries or wicks cut from Whatman number one filter paper (Thomson *et al.* 1989), proved unsuccessful. The quantity of nectar per flower was too minute to be harvested by either technique.

3.7 *Quantification of losses incurred by the plant due to flower and fruit predation*:

A total count of the fallen buds/flowers/fruits of *S. caseolaris* was taken by clearing the ground beneath the tree. Flowers that had been preyed upon (largely by Rhesus macaques and three-striped palm squirrels) were distinguished from those that had fallen naturally by marks of injury/disfigurement on them. The count was taken twice a day, at 0530 hrs and again at 1730 hrs, for a period of three weeks, from the 28th of January to the 17th of February 1997. The floral stage (as classified in method **3.4**) and part of the flower injured were recorded. The floral stage was noted in order to determine which stages were more prone to predation. The more advanced the stage, the greater would be the loss to the plant, in the event of it being preyed upon. This is because the older stages would have greater investment of resources by the parent plant, than the less mature ones. Injuries were classified according to the floral parts damaged, which were:

a. Sepals

b. Style

c. Stamens

d. Ovary wall

e. Ovary

f. Pedicel

g. Fruit

Injuries to different floral parts would affect the reproductive success of the plant to different extents. Damage to the non-essential parts (sepals and pedicel) would affect the flower to a lesser extent, than injury to the essential parts (style, stamens and ovary). Injuries to fruits would be most detrimental to the plant.

This exercise was undertaken only for *S. caseolaris*, as the flowers of *A. corniculatum* were not subject to predation.

Analytical methods

3.8 *Statistical analyses*:

Data from the day units and the night units were analysed separately, as the method of observation in the two cases was different (given in method **3.2**). Observations during the night units revealed the category of nocturnal visitors to the flowers being studied. However, data on the pattern of visitation was not analysed for the night units as the method of observation (using flashlights to scan the flowers) introduced a bias that was likely to differentially affect the visitation by different species.

To minimise categories and permit the examination of larger patterns, all visitor species were assigned to one of five categories based on their taxonomic affinities. These categories were:

a. Lepidoptera

b. Hymenoptera

c. Diptera

d. Birds

e. Mammals.

Visitation patterns were analysed separately for the four cloudy and three sunny day units on *S. caseolaris*. All five day units on *A. corniculatum* were cloudy units. Data from the continuous observations through the 12 hours in each unit were blocked into subsets of 30 minutes each. Blocking was done to facilitate further analysis (Fishbein and Venable 1996), and 30 minutes was found to be the largest time block that did not distort the patterns of the original set of continuous observations. This was seen by plotting the frequency of visits of the different categories of visitors against time at one minute intervals, and then looking at the time interval at which visitation frequencies changed. The pattern of frequency of visits at intervals of 30 minutes was found to be representative of the original set of continuous observations.

Successive data points for frequency of visits of a given visitor cannot be assumed to be independent of each other (Burd 1994). The same would hold for conditions of temperature, sun intensity and wind velocity at intervals of 30 minutes. To overcome the condition of autocorrelation between data points, the bootstrap technique was used (Crowley 1992). Resampling was done by computing a single random draw with replacement per sample, and repeating the process 1000 times (Krebs 1989). The bootstrapped mean for each time unit (of 30 minutes) was assumed to be independent of that in the preceding/successive unit (Abrahamson *et al.* 1989). The bootstrap technique was chosen to resample the data as it is less dependent than other statistical methods on similarity in underlying statistical distributions among treatment levels (Manly 1990). The statistical program SIMSTAT 3.5e (Peladeau 1995) was used to execute this procedure.

Since the number of flowers observed in each sampling session varied, visitation rates were standardised to a unit flower to enable valid comparisons of visitation rates between day-units, and between visitor categories, using the Wilcoxon Matched-pairs Signed-ranks Test (Siegel 1956).

The proportion of flowers visited per time unit was calculated for each category of visitor by obtaining the product of the standardised visitation rate and the average number of flowers visited per visit, in a given time unit (Thomas *et al.* 1986). This figure was taken as an estimate of the utility of a given visitor category for the plant. It was compared between the different visitor categories and within each category across sunny and cloudy days, to determine the relative utility of the different categories of visitors, separately on sunny and cloudy days. Sunny and cloudy day units were kept separate as it was expected that environmental conditions would affect visitation rates (and hence utility) of the different visitor categories differentially.

Visits per flower per time unit by different categories of visitor species were correlated with each other, and with temperature, sun intensity and wind velocity (Mφller and Eriksson 1995), using the non-parametric Spearman Rank Correlation Coefficient (Siegel 1956). The environmental variables were correlated with each other using the same procedure.

Percentage fruit-set in *A. corniculatum* was compared between the bagged and unbagged treatments, separately for the pure and mixed stand sites, using the Wilcoxon Matched-pairs Signed-ranks Test. Percentage fruit set was compared between pure and mixed-stand sites, separately for the bagged and unbagged treatments using the Mann-Whitney U-Wilcoxon Rank Sum W Test (Zar 1984). Kruskal-Wallis One-Way Analysis of Variance was used to compare percentage fruit set between day-bagged *vs.* night-bagged *vs.* unbagged treatments (Morris 1996, Niesenbaum 1996). The Kruskal-Wallis test was used because the variances were heteroscedastic (Roy 1996). Fruit-set in *S. caseolaris* was poor, and thus not analysed statistically.

The mean, standard deviation and confidence interval was calculated for the difference in length between stamens and style of the flowers of the two plant species and for the duration of each floral stage in the flowers of *S. caseolaris.*

The Mann-Whitney U- Wilcoxon Rank Sum W Test was used to test for differences in nectar volume and sucrose concentration in young and mature flowers at 0530 hrs and 1730 hrs. To determine if nectar volume was correlated with sucrose content, the nonparametric Spearman Rank Correlation Coefficient was used.

The percentages of injured and uninjured flowers were calculated for each of the different floral stages. The percentages of the different types of injuries were also calculated for the same.

All statistical procedures were executed using SPSS for Windows, Release 6.0 (1993), unless otherwise stated.

4. RESULTS

4.1 *Sonneratia caseolaris*

Visitors to the flowers:

Observations during the seven day units on *S. caseolaris* recorded visits to the flowers by fourteen species belonging to the order Lepidoptera, seven species belonging to the order Hymenoptera, three species belonging to the order Diptera, five species belonging to the class Aves and three species belonging to the class Mammalia. All night visitors belonged to the order Lepidoptera and included at least three species of moths and one species of crepuscular butterfly. Of the visitor species, Lepidoptera, Hymenoptera and Aves were pollinators, Diptera were thieves and Mammalia were predators (robbers). A list of the species visiting the flowers of *S. caseolaris* is given in **Appendix I.**

Pollination effectiveness of the different visitor categories:

Considering frequency of visits to be a measure of pollination effectiveness, visitation rates were compared across the visitor categories. The frequency of visits per flower per 30 minutes was significantly higher for birds than for Hymenoptera, on both sunny and cloudy days. Lepidoptera showed a significantly higher visitation rate than Hymenoptera on sunny days, but this difference was not significant on cloudy days. Lepidoptera had significantly higher rates of visitation on sunny days than on cloudy days. Comparisons between different visitor categories, across sunny and cloudy day units are summarised in Table **4.1**.

The proportion of flowers visited per time unit was taken as an index of utility of the visitor category to the plant. With an increase in the proportion of flowers visited, the visitor is expected to effect the transfer of pollen more efficiently. This, however, holds true only for those visitors which are classified as pollinators (i.e., Lepidoptera, Hymenoptera and Birds). Visits by thieves (Diptera) would not contribute to the pollination of the flowers, and those by predators/ robbers (Mammals) are harmful to the flowers. The index of utility (Mean±95% C.I) was highest for birds (0.59±0.12), followed by Lepidoptera (0.25±0.16), and Hymenoptera (0.07±0.03).

Effect of environmental variables on visitation rate:

On correlating visitation with environmental variables (Tables **4.2** and **4.3**), Lepidoptera showed a significant positive correlation with temperature, sun-intensity and wind velocity on both sunny and cloudy days. The visitation of Hymenoptera was positively correlated with all three environmental variables on sunny days, but the correlation was seen to be significant only with temperature, on cloudy days. Birds did not show significant correlation with any of the environmental variables.

TABLE 4.1
Differences in the standardised visitation rates of different categories of species (i.e., Birds, Lepidoptera and Hymenoptera), visiting the flowers of *Sonneratia caseolaris* across sunny and cloudy day units (Wilcoxon Matched-pairs Signed-ranks Test), from Dec. 1996 to Feb. 1997, in Bhitarkanika Wildlife Sanctuary, Orissa.

PAIR	TEST STATISTIC	2-TAILED *P*	MEAN RANK
Birds (cloudy) *vs.* Birds (sunny)	Z = 0.00	*1.00*	11.6 10.5
Lepid. (cloudy) *vs.* Lepid. (sunny)	Z = -3.61	*0.00**	2.5 10
Hymn. (cloudy) *vs.* Hymn. (sunny)	Z = -1.25	*0.21*	6.3 9.1
Birds (cloudy) *vs.* Lepid.(cloudy)	Z = -1.46	*0.15*	14.4 6.6
Birds (sunny) *vs.* Lepid.(sunny)	Z = -1.10	*0.27*	8.4 12.2
Birds (cloudy) *vs.* Hymn.(cloudy)	Z = -2.09	*0.04**	11.5 8.2
Birds (sunny) *vs.* Hymn.(sunny)	Z = -2.41	*0.02**	13 5.8
Lepid. (cloudy) *vs.* Hymn. (cloudy)	Z = -1.10	*0.27*	6.6 6.3
Lepid. (sunny) *vs.* Hymn. (sunny)	Z = -3.34	*0.00**	9.2 6

N (number of time units in a day) = 25
* significant at $p \leq 0.05$

TABLE 4.2
Correlation (using Spearman Rank Correlation Coefficients), between standardised visitation rates of different categories of species (Birds, Lepidoptera and Hymenoptera) visiting the flowers of *Sonneratia caseolaris*, and environment variables (temperature, sun intensity and wind velocity) across sunny days, from Dec. 1996 to Feb. 1997, in Bhitarkanika Wildlife Sanctuary, Orissa.

	Temp. (sunny)	Sun-inten. (sunny)	Wind vel. (sunny)
Birds (sunny)	-0.06 *p = 0.78*	0.06 *p = 0.78*	-0.04 *p = 0.87*
Lepid. (sunny)	0.81 *p = 0.00**	0.44 *p = 0.03**	0.61 *p = 0.00**
Hymn. (sunny)	0.78 *p = 0.00**	0.44 *p = 0.03**	0.70 *p = 0.00**

N (number of time units in a day) = 25
p = 2-tailed significance
* significant at $p \leq 0.05$

TABLE 4.3
Correlation (using Spearman Rank Correlation Coefficients), between standardised visitation rates of different categories of species (Birds, Lepidoptera and Hymenoptera) visiting the flowers of *Sonneratia caseolaris*, and environment variables (temperature, sun intensity and wind velocity) across cloudy days, from Dec. 1996 to Feb. 1997, in Bhitarkanika Wildlife Sanctuary, Orissa.

	Temp. (cloudy)	Sun-inten. (cloudy)	Wind vel. (cloudy)
Birds (cloudy)	-0.21 *p = 0.33*	0.16 *p = 0.44*	-0.21 *p = 0.32*
Lepid. (cloudy)	0.80 *p = 0.00**	0.57 *p = 0.00**	0.43 *p = 0 .03**
Hymn (cloudy)	0.56 *p = 0.04**	0.32 *p = 0.12*	0.29 *p = 0.15*

N (number of time units in a day) = 25
p = 2-tailed significance
* significant at $p \leq 0.05$

When the environmental variables were correlated with each other (Table **4.4**), there was a significant positive correlation between temperature, sun-intensity and wind velocity on sunny days. On cloudy days however, only temperature and wind velocity were seen to be significantly and positively correlated.

Effect of time of day on visitation rate:

The frequency of visits per flower per 30 minutes of the different categories of visitors reveals the temporal pattern of visitation of these visitor categories on sunny and cloudy days. Different categories are seen to have peak visitation rates at different times of day. Birds show maximum visitation in the early morning, while Lepidoptera and Hymenoptera visit more frequently during mid-day. The patterns are graphically represented for sunny (Figure **4.1 A**) and cloudy (Figure **4.1 B**) days.

Effect of interactions between the visitors on visitation rate:

It was observed that the purple-rumped sunbird (which was the most frequent avian visitor to the flowers) actively discouraged visits by other birds (conspecifics included) and Hymenoptera. This is reflected in a weak negative correlation between the frequencies of visitation of birds and Hymenoptera on cloudy days. Lepidoptera and Hymenoptera were seen to have a significant positive correlation with each other both on sunny and cloudy days. This is probably because both categories were similarly affected by the environmental variables, and thus reacted in the same manner. No direct interaction was observed between these two categories.

TABLE 4.4

Correlation (using Spearman Rank Correlation Coefficients), between environment variables (temperature, sun intensity and wind velocity), across sunny and cloudy days during the sampling period of *Sonneratia caseolaris*, from Dec. 1996 to Feb. 1997, in Bhitarkanika Wildlife Sanctuary, Orissa.

	Sun-inten. (sunny)	Wind vel. (sunny)	Sun-inten. (cloudy)	Wind vel. (cloudy)
Temp. (sunny)	0.71 *p = 0.00**	0.74 *p = 0.00**		
Sun-inten. (sunny)		0.54 *p = 0.01**		
Temp. (cloudy)			0.36 *p = 0.08*	0.68 *p = 0.00**
Sun-inten. (cloudy)				0.097 *p = 0.64*

N (number of time units in a day) = 25

p = 2-tailed significance

* significant at $p \leq 0.05$

FIGURE 4.1A

VISITATION PATTERN ON FLOWERS OF *Sonneratia caseolaris* ON SUNNY DAYS

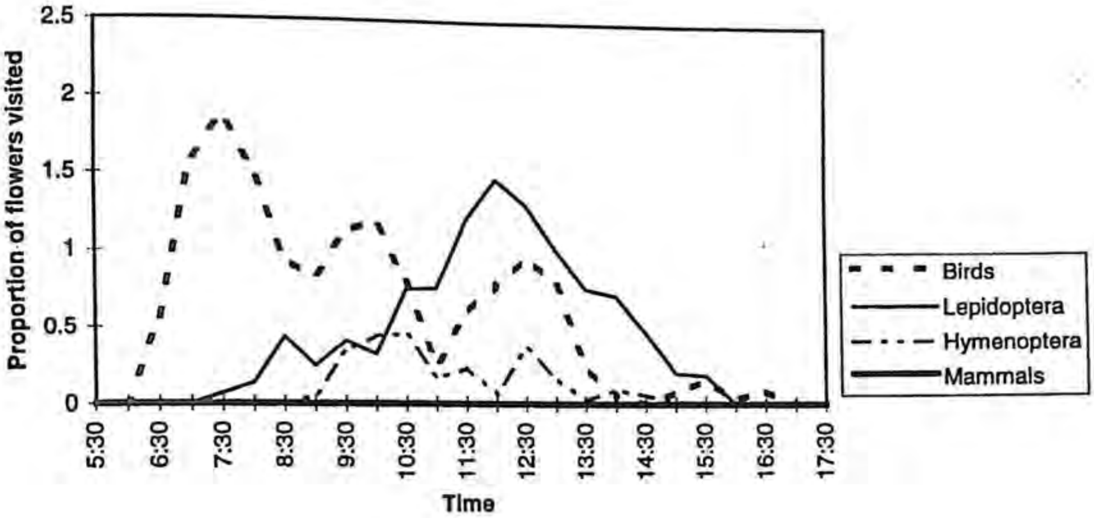
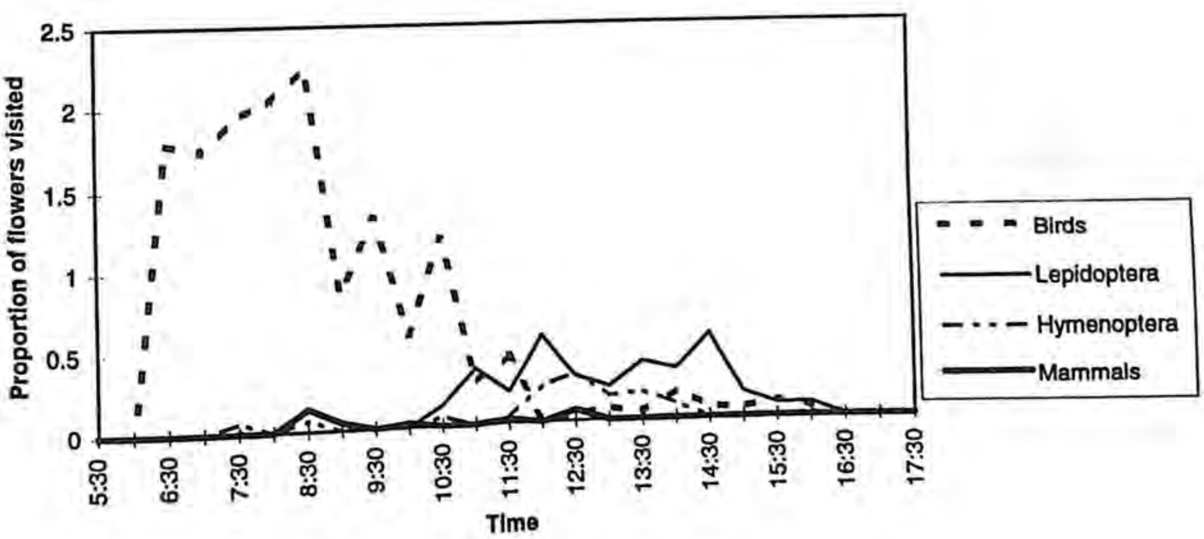


FIGURE 4.1B

VISITATION PATTERN ON FLOWERS OF *Sonneratia caseolaris* ON CLOUDY DAYS



Other categories were found to be uncorrelated with each other in their visitation patterns (Table **4.5**).

Importance of visitors to the reproductive success of the plant:

Due to heavy losses of buds, flowers and fruits, to predation, overall fruit-set in *S. caseolaris* was poor. Thus, under all four treatments (bagged, unbagged, day-bagged and night-bagged), the percentage fruit-set was too low to be compared using statistical tests. The figures are presented in Table **4.6**.

Floral stages two to five were the stages when the flower was in bloom and receptive to pollination. The duration of the different floral stages (Mean±95%C.I) was found to be 17.25±5.36 hours for stage 2; 25.13±12.00 hours for stage 3; 20.04±2.60 hours for stage 4; and 10.67±1.88 hours for stage 5. The total period for which a flower stayed in bloom was 73.09 hours. It was observed that the nocturnal visitors preferred visiting mature flowers (stages 4 and 5) while the diurnal ones visited both young (stages 2 and 3) and mature flowers.

Stage 3 (style exserted, stamens incurled) was the period when the style and stamens were separated in time within the flower. The styles of the were 3.52 ±0.71cm (confidence level 95%) longer than the stamens. This indicates that the style and stamens were also separated in space within the flower.

TABLE 4.5

Correlation (using Spearman Rank Correlation Coefficients), between standardised visitation rates of different categories of species (Birds, Lepidoptera and Hymenoptera) visiting the flowers of *Sonneratia caseolaris*, across sunny and cloudy days, from Dec. 1996 to Feb. 1997, in Bhitarkanika Wildlife Sanctuary, Orissa.

	Lepid. (sunny)	Hymn. (sunny)	Lepid. (cloudy)	Hymn. (cloudy)
Birds (sunny)	0.19 *p = 0.36*	0.18 *p = 0.387*		
Lepid. (sunny)		0.79 *p = 0.00**		
Hymn. (sunny)				
Birds (cloudy)			-0.23 *p = 0.26*	-0.04 *p = 0.84*
Lepid. (cloudy)				0.60 *p = 0.00**

N (number of time units in a day) = 25

p = 2-tailed significance

* significant at $p \leq 0.05$

TABLE 4.6

Percent fruit-set under different bagging treatments in *Sonneratia caseolaris* from Dec. 1996 to Apr. 1997, in Bhitarkanika Wildlife Sanctuary, Orissa.

TREATMENT	NO. OF BUDS	NO. OF FRUIT DEVELOPED	PERCENT FRUIT-SET
Unbagged	223	13	5.83%
Day-bagged	46	1	2.17%
Night-bagged	29	0	0%
All-bagged	76	0	0%

Nectar analysis:

The volume of nectar (Mean±95%C.I) in young flowers was 30.60±2.86μl at 0530 hrs, and 20.40±14.20μl at 1730 hrs. For mature flowers it was 204.12±74.29μl at 0530 hrs and 58.73±6.14μl at 1730 hrs. Sucrose concentration (Mean±95%C.I) in the nectar of young flowers was 12.00±0.99% at 0530 hrs and 21.13±5.75% at 1730 hrs. For mature flowers it was 16.24±2.55% at 0530 hrs and 22.92±2.29% at 1730 hrs. A comparison of nectar volume at two different times of day (Table **4.7**), showed that both young flowers and mature flowers had significantly higher volumes of nectar at 0530 hrs than at 1730 hrs and that mature flowers had significantly higher volumes of nectar than young flowers. Sucrose concentration of nectar was significantly higher at 1730 hrs than at 0530 hrs, and it was higher in mature flowers than in young flowers, at 0530 hrs (Table **4.8**). Nectar volume and sucrose concentration were uncorrelated (Spearman Correlation Coefficient = -0.1414, p = 0.601).

Impact of predation on reproductive success:

To estimate the effect of predation on the different floral stages, percentages of injured and uninjured flowers in the various floral stage categories are compared in Figure **4.2.** The floral stage most frequently injured is stage 1 (sepals fused), followed by stage 6 (stamens fully shed) and stage 7 (fruit). Other floral stages are injured to a much lesser extent. The percentage of injured flowers was higher than the percentage of uninjured ones for all floral stages except stage 2 (open bud, with

TABLE 4.7

Differences in nectar volume between young (Y.fl.) and mature (M.fl.) flowers *of Sonneratia caseolaris*, at 0530 hrs and 1730 hrs (Mann-Whitney U-Wilcoxon Rank-Sum W Test), from Dec. 1996 to Feb. 1997, in Bhitarkanika Wildlife Sanctuary, Orissa.

PAIR	TEST STATISTIC	2-TAILED *P*	MEAN RANK	N
Y. fl. (0530 hrs) *vs.* Y. fl. (1730 hrs)	Z = -1.99	*0.05**	5 2	6
M. fl. (0530 hrs) *vs.* M. fl. (1730 hrs)	Z = -2.61	*0.01**	8 3	10
Y. fl. (0530 hrs) *vs.* M. fl. (0530 hrs)	Z = -2.25	*0.02**	2 6	8
Y. fl. (1730 hrs) *vs.* M. fl. (1730 hrs)	Z = - 2.24	*0.03**	2 6	8

* significant at $p \leq 0.05$
N = number of flowers

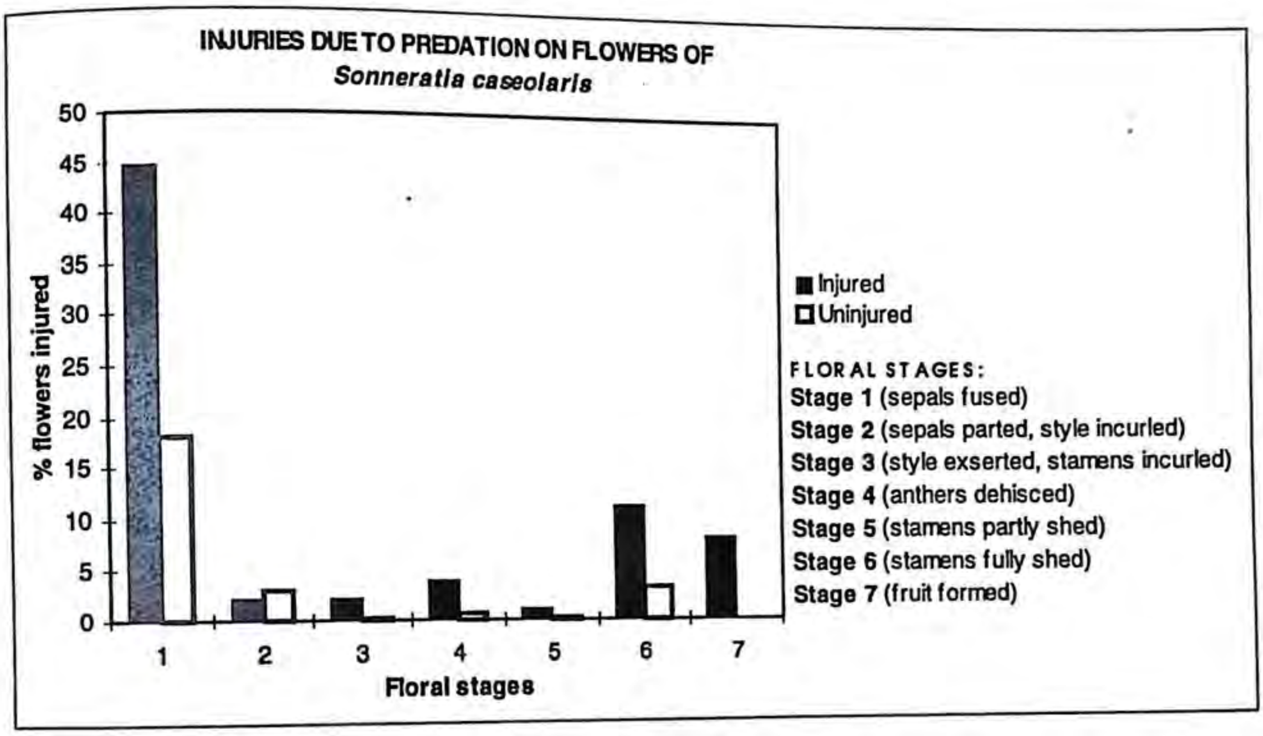
TABLE 4.8

Differences in the sucrose concentration of nectar, between young (Y.fl.) and mature (M.fl.) flowers of *Sonneratia caseolaris*, at 0530 hrs and 1730 hrs (Mann-Whitney U-Wilcoxon Rank-Sum W Test), from Dec. 1996 to Feb. 1997, in Bhitarkanika Wildlife Sanctuary, Orissa.

PAIR	TEST STATISTIC	2-TAILED *P*	MEAN RANK	N
Y. fl. (0530 hrs) *vs.* Y. fl. (1730 hrs)	Z = -1.96	*0.05**	2 5	6
M. fl. (0530 hrs) *vs.* M. fl. (1730 hrs)	Z = -2.62	*0.01**	3 8	10
Y. fl. (0530 hrs) *vs.* M. fl. (0530 hrs)	Z = -2.25	*0.02**	2 6	8
Y. fl. (1730 hrs) *vs.* M. fl. (1730 hrs)	Z = -1.04	*0.30*	3.33 5.20	8

* significant at $p \leq 0.05$
N = number of flowers

FIGURE 4.2


INJURIES DUE TO PREDATION ON FLOWERS OF
Sonneratia caseolaris
50
45
40
35
30
25
20
15
10
5
0
% flowers injured
1
2
3
4
5
6
7
Floral stages
Injured
Uninjured
FLORAL STAGES:
Stage 1 (sepals fused)
Stage 2 (sepals parted, style incurled)
Stage 3 (style exserted, stamens incurled)
Stage 4 (anthers dehisced)
Stage 5 (stamens partly shed)
Stage 6 (stamens fully shed)
Stage 7 (fruit formed)

style and stamens incurled). A comparison of the percentages of the different floral parts injured (Figure **4.3**), showed that the most frequent injury was to the sepals, followed by the pedicel, ovary wall, stamens, style, fruit and ovary, in order of decreasing percentages of the floral part injured. However, most flowers were seen to have sustained multiple injuries (i.e., more than one floral part injured).

4.2 *Aegiceras corniculatum*

Visitors to the flowers:

Observations for the five day units on *A. corniculatum* revealed a total of nine species of the order Lepidoptera, nine species of Hymenoptera, two species of Diptera, one species of Coleoptera and three species belonging to the class Aves, visiting the flowers during the day. All nocturnal visitors belonged to the order Lepidoptera. Lepidoptera, Hymenoptera, Diptera and Aves were pollinators, while Coleoptera were classified as thieves. The species of visitors to the flowers of *A. corniculatum* have been listed in **Appendix II.**

Pollination effectiveness of the different visitor categories:

The frequency of visits per flower per 30 minutes was significantly higher for Lepidoptera and Hymenoptera than for the birds. Lepidoptera had a significantly higher rate of visitation than Hymenoptera or Diptera, and Hymenoptera visited more frequently than Diptera. Results are given in Table **4.9**.

FIGURE 4.3

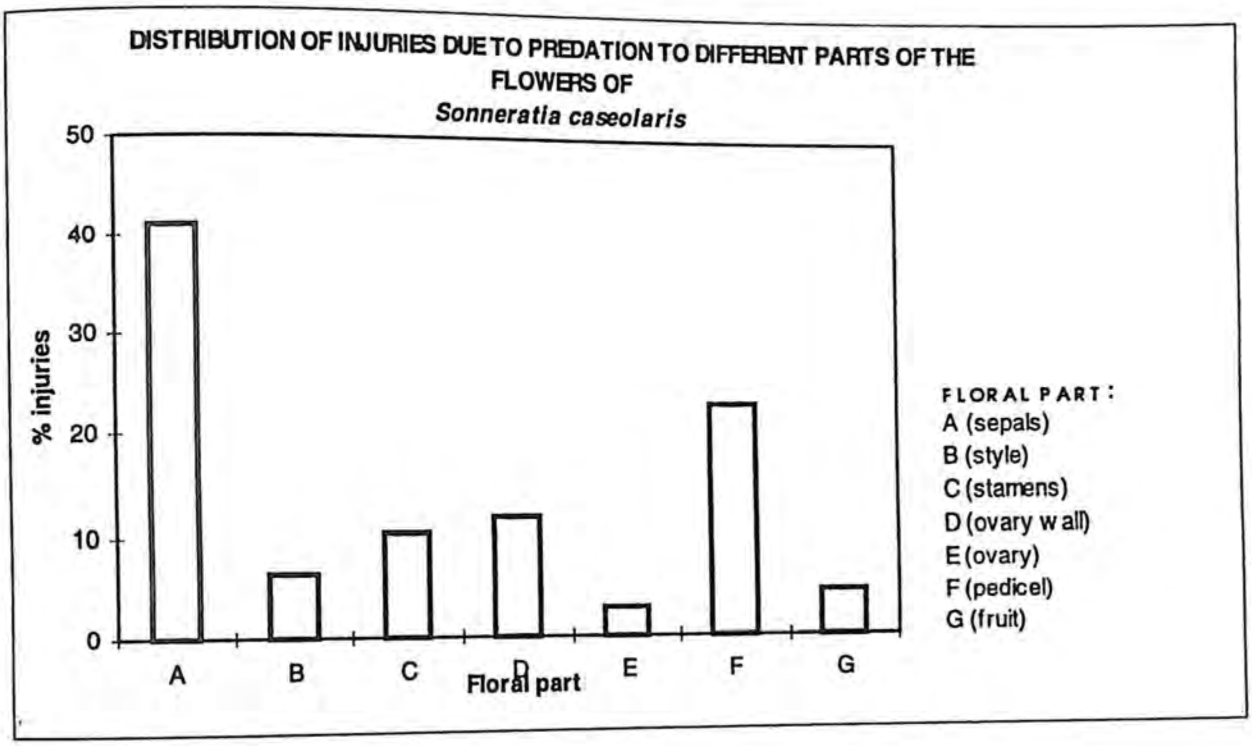

DISTRIBUTION OF INJURIES DUE TO PREDATION TO DIFFERENT PARTS OF THE FLOWERS OF
Sonneratia caseolaris
% injuries
0
10
20
30
40
50
A
B
C
D
E
F
G
Floral part
FLORAL PART:
A (sepals)
B (style)
C (stamens)
D (ovary wall)
E (ovary)
F (pedicel)
G (fruit)

TABLE 4.9

Differences in the standardised visitation rates of the different categories of species (i.e., Birds, Lepidoptera, Hymenoptera, and Diptera) visiting the flowers of *Aegiceras corniculatum* (Wilcoxon Matched-pairs Signed-ranks Test), from Feb. to Apr. 1997, in Bhitarkanika Wildlife Sanctuary, Orissa.

PAIR	TEST STATISTIC	2-TAILED *P*	MEAN RANK
Birds *vs.*	Z = -4.29	*0. 00**	0
Lepidoptera			12.5
Birds *vs.*	Z = -3.25	*0.00**	6.2
Hymenoptera			13.6
Birds *vs.*	Z = -1.44	*0.15*	10.8
Diptera			7.5
Lepidoptera *vs.*	Z = -3.70	*0.00**	14
Hymenoptera			5.1
Lepidoptera *vs.*	Z = 4.29	*0.00**	12.5
Diptera			0
Hymenoptera *vs.*	Z = -3.08	*0.00**	12
Diptera			2

N (number of time units in a day) = 26

* significant at $p \leq 0.05$

The proportion of flowers visited per time unit was highest for Lepidoptera (1.05 ±0.14, confidence level 95%), followed by Hymenoptera (0.59 ±0.32, confidence interval 95%), Aves (0.07 ±0.06, confidence level 95%), and Diptera (0.02 ±0.03, confidence level 95%).

__Effect of environmental variables on visitation rate__:

Correlation coefficients were significant and positive between the visitation frequencies of Hymenoptera and the environmental variables of temperature, sun-intensity and wind velocity. Visitation of Lepidoptera was significantly positively correlated only with sun-intensity, while visitation of Diptera and birds did not show any correlation with environmental variables (Table **4.10**). All three environmental variables were significantly positively correlated with each other (Table **4.11**).

__Effect of time of day on visitation rate__:

The standardised visitation rates of the different categories of visitors have been plotted against time (Figure **4.4**) to examine the temporal pattern of visitation across a day. Different visitor categories have peak visitation rates at different times of day. Lepidoptera show maximum visitation in the early and mid-morning hours, while Hymenoptera visited more frequently during mid- and late-afternoon.

TABLE 4.10
Correlation (using Spearman Rank Correlation Coefficients), between the standardised visitation rates of the different categories of species (Birds, Lepidoptera, Hymenoptera and Diptera) visiting the flowers of *Aegiceras corniculatum*, and environment variables (temperature, sun intensity and wind velocity), from Feb. to Apr. 1997, in Bhitarkanika Wildlife Sanctuary, Orissa

	Temperature	Sun-intensity	Wind velocity
Birds	-0.20 *p* = 0.32	0.12 *p* = 0.54	-0.17 *p* = 0.40
Lepidoptera	0.31 *p* = 0.12	0.62 *p* = 0.00*	0.17 *p* = 0.41
Hymenoptera	0.72 *p* = 0.00*	0.40 *p* = 0.04*	0.66 *p* = 0.00*
Diptera	0.26 *p* = 0.19	0.10 *p* = 0.64	0.16 *p* = 0.44

N (number of time units in a day) = 26
p = 2-tailed significance

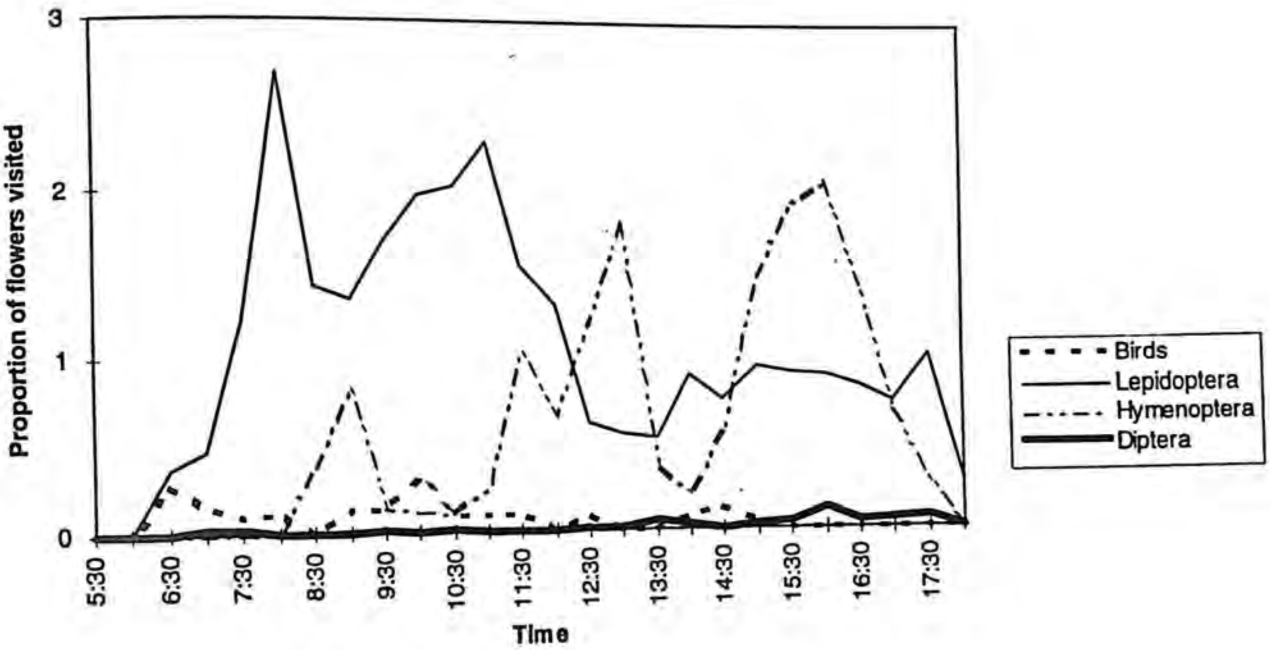
TABLE 4. 11
Correlation (using Spearman Rank Correlation Coefficients), between environment variables (temperature, sun intensity and wind velocity), during the sampling period of *Aegiceras corniculatum*, from Feb. to Apr. 1997, in Bhitarkanika Wildlife Sanctuary, Orissa.

	Sun-intensity	Wind velocity
Temperature	0.81 *p* = 0.00*	0.76 *p* = 0.00*
Sun-intensity		0.60 *p* = 0.00*

N (number of time units in a day) = 26
p = 2-tailed significance
* significant at $p \leq 0.05$

FIGURE 4.4

VISITATION PATTERN ON FLOWERS OF *Aegiceras corniculatum*



Effect of interactions between the visitors on visitation rate:

On correlating the frequency of visits of the different visitor categories with each other, birds were found to have a significant positive correlation with Lepidoptera, and a significant negative correlation with Hymenoptera. The latter relationship may be ascribed to the same reasons discussed earlier for *S. caseolaris*. Correlations between the other visitor categories were seen to be insignificant (Table **4.12**).

Importance of visitors to the reproductive success of the plant:

No significant difference was found between the percentage fruit-set in mixed and pure-stands of *A. corniculatum*, or across the different treatments (Table **4.13**). The percent fruit-set (Mean±95%C.I) in *A. corniculatum* was 63.46±9.09%.

Anthesis involved simultaneous bloom of all four whorls. Thus maturation of the style and stamens was not separated in time, within a flower. The style of the flowers of *A. corniculatum* was 0.12 ±0.06 cm (confidence level 95%) longer than the stamens, indicating that the stigma and anthers were not separated in space so as to preclude the possibility of self-pollination.

TABLE 4.12
Correlation (using Spearman Rank Correlation Coefficients), between the standardised visitation rates of the different categories of species (Birds, Lepidoptera, Hymenoptera and Diptera), visiting the flowers of *Aegiceras corniculatum*, from Feb. to Apr. 1997, in Bhitarkanika Wildlife Sanctuary, Orissa.

	Lepidoptera	Hymenoptera	Diptera
Birds	0.40 p = *0.04**	-0.40 *p = 0.04**	-0.27 *p = 0.18*
Lepidoptera		0.05 *p = 0.80*	-0.113 *p = 0.58*
Hymenoptera			0.34 *p = 0.09*

N (number of time units in a day) = 26
p = 2-tailed significance
* significant at $p \leq 0.05$

TABLE 4.13
Differences in percent fruit-set under different bagging treatments and in different sites in *Aegiceras corniculatum*, from Feb. to Apr. 1997, in Bhitarkanika Wildlife Sanctuary, Orissa.

TREATMENT	TEST	TEST STATISTIC	2- TAILED PROBABILITY (*P*)	SAMPLE SIZE (N)
Bagged in Mixed-stands *vs.* Bagged in Pure-stands	Mann-Whitney U-Wilcoxon Rank Sum W Test	Z = -1.89	*0.06*	1493
Unbagged in Mixed-stands *vs.* Unbagged in Pure-stands	Mann-Whitney U-Wilcoxon Rank Sum W Test	Z = -1.70	*0.09*	1512
Bagged *vs.* Unbagged in Mixed-stand sites	Wilcoxon Matched-Pairs Signed-Ranks Test	Z = -0.51	*0.61*	2048
Bagged *vs.* Unbagged in Pure-stand sites	Wilcoxon Matched-Pairs Signed-Ranks Test	Z = -0.37	*0.72*	957
Day-bagged *vs.* Night-bagged *vs.* Unbagged	Kruslal-Wallis 1-Way Anova	$\chi^2 = 1.97$ df = 2	*0.37*	244

N = number of flowers for which percent fruit-set was calculated

5. DISCUSSION

5.1 Visitors to flowers of the two study species:

S. caseolaris and *A. corniculatum* were visited by a wide taxonomic spectrum of species (Appendices I and II), both nocturnal and diurnal. Several of the visitor species were common to both (a proportion of 0.27 of the total visitor species were in common). Some of the visitors were pollinators while others were thieves or robbers (flower predators). This pattern would support the view of the generalised nature of the plant-pollinator interaction: the use of several plant species by a pollinator and of several pollinator species by a plant (Thomson 1983, Howe 1984, Haber and Frankie 1989, Primack and Inouye 1993, Subramanya and Radhamani 1993, Waser *et al.* 1996, Bosch *et al.* 1997). The non-specialised morphology of the flowers of *S. caseolaris* and *A.corniculatum*, along with easily accessible resources (pollen and nectar) would enable a wide array of visitors to exploit the floral resources, further confirming this view. This also supports the hypothesis put forth by Tomlinson (1986), that pollination mutualisms in mangroves are diversified and opportunistic. The generalist strategy of the plant would reduce its dependence on any one species of pollinator, and allow it to exploit a greater amplitude of pollinator resource (Vieira and de Carvalho-Okano 1996). This would also decrease the risk of its extinction linked to that of its specialised pollinator (Rathcke and Jules 1993).

5.2 Pollination effectiveness of different categories of visitors:

Different categories of visitors are expected to differ in their effectiveness as pollinators (Ashman and Stanton 1991, Fishbein and Venable 1996). Pollination effectiveness can be partitioned into components, including rates of visitation, pollen removal and pollen deposition (Herrera 1987). The distinction between overall effectiveness and components is important because some visitors may be effective at one component (e.g., visitation rate), but ineffective or detrimental at another (e.g., pollen removal) (Fishbein and Venable 1996). The extent to which visitation rate is an accurate estimate of pollination effectiveness would vary for different species of visitor, depending on their morphology and foraging strategy (Proctor *et al.* 1996). Observations on the effective pollinators of *Asclepias tuberosa* by Fishbein and Venable (1996), indicate that differences among pollinating taxa were due largely to variation in visitation rate. However, contradictory trends were found by Pellmyr and Thompson (1996), who reported that visitation rate is the least informative measure of pollinator effectiveness. They have indicated evenness of visits across plants, pollen-transfer abilities, diurnal visitation patterns (i.e., time of visitation relative to dehiscence schedules), and the quality of pollen transferred, as closer estimates of pollinator effectiveness.

The results of this study found that visitors differed in frequency of visits as well as the number of flowers visited per visit (Tables 4.1 and 4.9). Considering both variables, if the proportion of flowers visited per time unit was taken as an index of utility of the visitor category, it was seen that the same category of visitor differed in its effectiveness as pollinator for the two plant species (pages **24** and **38**). Schemske and Horvitz (1984) reported Hymenoptera to be more effective as pollinators than Lepidoptera. In this study, however, Lepidoptera were seen to have a higher rate of visitation (Tables **4.1** and **4.9**), and to visit a higher proportion of flowers per time unit (pages **24** and **38**) than Hymenoptera, for both *S. caseolaris* and *A. corniculatum*. It is possible though, that flower visitation need not necessarily translate into transfer of pollen (Primack and Inouye 1993). Wilson and Thomson (1991), have suggested that *Apis* (Hymenoptera) are less effective as pollinators because they remove large amounts of pollen, preventing its transport by good pollinators, but fail to deposit it perhaps due to their active pollen collection and effective grooming. Frequent visitors may increase levels of pollinator-mediated self-pollination (geitonogamy), and thus lead to the production of less fit offspring through inbreeding depression in the case of self-compatible species, or to pollen wastage (Hessing 1988, de Jong *et al.* 1993), and stigma clogging with self-pollen (Waser and Price 1991), in the case of self-incompatible species.

Besides differing in frequency of visits to flowers of the two species, the visitor categories also differed in their foraging strategy across the plant species. Dipterans were seen to be nectar thieves on *S. caseolaris*, but served as pollinators for the flowers of *A. corniculatum*. This is probably because the larger flowers of *S. caseolaris* were mismatched in morphology to the small-sized Dipterans, who failed to make contact with the anthers or stigma of the flowers while taking nectar. Santharam (1996) reported that butterfly visitors to flowers of *Helicteres isora* in south India are nectar-thieves for the same reason. However, the extent to which nectar thieves are detrimental to the plants reproductive success is uncertain.

Frequent visitors that consume pollen, nectar, or other floral tissues, may reduce the reproductive success that would be achieved in their absence (McDade and Kinsman 1980, Wilson and Thomson 1991). Contradictory to this, Morris (1996) reported that nectar thieving by bumble bees does not reduce female or male success of the flowers of bluebells.

5.3 *Factors affecting visitation rate*:

Visitation rate may be determined by several interacting factors. One or more of the environmental variables of temperature, relative humidity, wind velocity and light intensity have been found to be important in determining the rate of visitation to flowers (Vasudeva and Lokesha 1993). Results of this study (Tables **4.2**, **4.3** and **4.10**) indicate that visitation rates of Lepidoptera and Hymenoptera increased with increase in temperature, sun intensity and wind velocity. Abrol (1987) recorded increased visitation by bees with increase in temperature and light intensity. Primack and Inouye (1993) reported visitation rates to increase with temperature and sun intensity, but decrease with wind velocity. Increase of visitation with wind velocity in this study may be explained by the fact that wind velocity was found to be positively correlated with temperature and sun intensity (Tables **4.4** and **4.11**), and thus increase in visitation may not be a direct consequence of increase in the velocity of wind, but of the increase in the other variables of temperature and sun intensity. This would be further supported by the fact the visitors to *A. corniculatum* showed a marked preference to visit flowers on the leeward side of the tree on windy days (*pers. obs.*).

Environmental variables were seen to affect the visitation rates of different categories to different extents. Lepidoptera were the most sensitive to changes in temperature and sun intensity, followed by Hymenoptera. Visitation by birds was independent of changes in environmental variables (Tables **4.2**, **4.3** and **4.10**). This pattern could be explained by the fact that, unlike birds, Lepidoptera and Hymenoptera are dependent on solar radiation to maintain their body temperature (Mani 1982). It is also possible that environmental variables influence visitation rates through effects on nectar production, pollen presentation, or the physiology of the visitor (Primack and Inouye 1993).

Visitor activity was also seen to change along a temporal gradient, with time of day (Figures **4.1 A**, **B** and **4.4**). Different visitor categories showed peak visitation at different times of day. Similar trends have been reported by Primack and Inouye (1993) from woodland-meadows in Belmont, and shrublands in Cape Province; and by Santharam (1996) from southern India. Visitation is, however, unlikely to be affected independently by time of day, and probably reflects the change in temperature and sun intensity at different times of day.

Interactions between the visitors were also seen to affect visitation rates. It was observed that the purple-rumped sunbird (refer to Appendices for scientific names), which was the most frequent bird visitor to the flowers of both plant species, exhibited territorial behaviour, by temporarily defending a clump of flowers at the *S. caseolaris* site. It actively kept away conspecifics, and other species of birds (white-eyes, ioras, tailor birds and purple sunbirds) by chasing them aggressively. It did not display aggression towards the visiting Lepidoptera, but attacked and consumed bees visiting the flowers, thus keeping the latter away from the site. This may explain the negative correlation between frequency of visits by birds and Hymenoptera (Tables **4.5** and **4.12**). Such territorial behaviour has been extensively reported for hummingbirds (Trombulak 1990, Kodric-Brown and Brown 1978, Hixon *et al.* 1983) and honeyeaters (Beehler 1994). Although sunbirds do not exhibit clear territoriality (Subramanya and Radhamani 1993), instances of territorial behaviour in sunbirds have been reported by Ali and Ripley (1983) and Davidar (1983a, b).

Besides the factors discussed above, visitation rates may be affected by the absolute or relative abundance of flower species, or of flower visitors (Primack and Inouye 1993). Toledo (1977) reported that Passerines show most interest in nectar-feeding during periods of low fruit abundance and minimum insect availability. A similar situation has been reported by Vieira and de Carvalho-Okano (1996) for the visitors of *Mabea fistulifera* in southeastern Brazil. Visitation would also be influenced by the size of the floral display (Heinrich 1975, Schemske 1980, Klinkhamer *et al.* 1989, Dudash 1991, Robertson and Macnair 1995); and would vary with seasons (Bosch *et al.* 1997), sites (Primack and Inouye 1993) and between years (Fishbein and Venable 1996).

5.4 *Relative importance of diurnal vs. nocturnal visitors*:

Fruit-set in *S. caseolaris* was poor (Table **4.6**) because of heavy losses incurred due to flower and fruit predation. Thus the relative importance of the diurnal *vs.* nocturnal visitors could not be estimated from the day/night reciprocal bagging set-up. Tomlinson (1986) has reported *S. caseolaris* to be exclusively night-pollinated, either by bats or alternatively by hawk moths (Primack *et al.* 1981). The wide range of diurnal visitors (32 species) recorded by this study, and the high frequency of visitation during the day (Figures **4.1 A, B**), would, however, indicate otherwise. The nocturnal visitors (moths) were far fewer than the diurnal ones (3 species of nocturnal visitors and 32 species of diurnal ones), and the frequency of their visits was much lower (*pers. obs.*). Literature describes the flowers of *S. caseolaris* to bloom in the evening, last for one night, and shed by morning. Stamens and petals have been recorded to be ephemeral, falling within 12 hours of opening (Tomlinson 1986). These observations are not supported by the findings of this study. Flowers lasted for an average of 48 hours after anthesis, and were seen to be in bloom both at night and during the day. The flowers had more concentrated nectar during the evening, than in the morning. In plants that have abundant floral resources mainly at night, diurnal visitors are often not considered as pollinators, even though they are commonly seen as visitors to the flowers (Hopkins 1984). A few authors have compared the efficiency of nocturnal *vs.* diurnal pollination of these plants (Alcorn *et al.* 1961, McGregor *et al.* 1962) and the results showed that diurnal and nocturnal visitors were equally effective. Though the results of this study are not conclusive about this aspect of *S. caseolaris*, the pollinator effectiveness of diurnal visitors to this species cannot be ruled out.

There was no difference in the pollinator effectiveness of nocturnal and diurnal visitors to the flowers of *A. corniculatum* (Table **4.13**). Thus visitation by pollinators both at night and during the day was equally important for the plant.

5.5 *Importance of visitors to the reproductive success of the plant*:

The reproductive success of *S. caseolaris* was determined more by predation than by any other factor (Figure **4.2**). However, the morphology of the flower suggests that it would require an external agent to bring about the transfer of pollen from anther to stigma. This is because the maturation of the style occurs before that of the stamens (protogyny), and the style is far exserted above the stamens (herkogamy). The results of this study, however, remain inconclusive regarding this aspect of pollinator-dependence in *S. caseolaris.*

In *A. corniculatum*, fruit-set was equally successful in the presence or absence of visitors, suggesting that the flowers were able to self-fertilise, and that reproductive success was not pollinator-limited. This is supported by the fact that the anthers and stamens in a flower matured simultaneously, and that the stigma was almost at level with the anthers. It has been suggested that flowers adapted for pollination by animals would retain the ability to self-fertilise and set fruit in the absence of pollinators, as animals are not very reliable as a pollinator-resource (Proctor *et al.* 1996). Similar results were found by Vieira and de Carvalho-Okano (1996), for the flowers of *Mabea fistulifera*, which were also visited by a wide range of nocturnal and diurnal visitors, but in which fruit-set was equally successful in the absence of either diurnal, nocturnal, or all visitors.

5.6 *Impact of predation on the reproductive success of the plant*:

The upper limit to the number of fruits that can be produced by an individual plant during a reproductive episode is set by the number of female flowers. The fraction of this reproductive potential that is realised depends upon the number of pollinated flowers, the number of fertilised ovules, flower/fruit/seed predation, weather conditions and the ability of the maternal plant to provide the necessary resources for development (Stephenson 1981, Ganeshaiah and Uma Shaanker, *unpublished manuscript*). In *S. caseolaris*, predation was the single most important factor governing successful fruit-set. Predators were both nocturnal and diurnal, and were observed to prey upon buds, flowers and fruits. Thus, reproductive success in this species is not pollinator-limited, but determined by the intensity of predation. Although predation limits fruit-set in *S. caseolaris*, seed-set in this species has been reported to be high (Tomlinson 1986). As each fruit has numerous seeds, it is possible that the plant is able to withstand the effect of predation because of the high rate of successful seed-set in the surviving fruits.

There was no predation on *A. corniculatum*, and fruit-set was not pollinator-limited (as discussed earlier). Thus, it is likely that fruit-set would be limited by other factors such as nutritional resources provided by the parent plant. This would support the argument put forth by Stephenson (1981), that fruit-set in most cases is likely to be resource-limited.

5.7 *Flowering phenology of S. caseolaris and A. corniculatum*:

The phenological pattern of flowering in *S. caseolaris* may be described as the "steady state" pattern where the species exhibits the production of a few flowers each day, the flowers being short-lived (Primack 1985). Flowering in *S. caseolaris* is aseasonal and occurs throughout the year, as contrasted with the strongly seasonal flowering in *A. corniculatum*. It is difficult to ascribe reasons for the different flowering strategies adopted by the two species, but several possibilities exist. One view is that in evolutionary time, plants might avoid competition through specialisation, independence from pollinators, or displacements in flowering times (Rathcke 1984). Therefore the typical staggered flowering pattern in *S. caseolaris* may be interpreted as reflecting the outcome of past competition for pollination.

It has been suggested that seasonality in flowering is a trait designed to attract certain classes of pollinators (Herrera 1988). This view is supported by the study of Herrera (1988), in the Spanish Mediterranean scrublands, where species flowering at about the same time tended to be visited by similar insects, irrespective of their floral features. However, contradictory patterns have been documented by Bosch *et al.* (1997), who examined the relationship between flowering plants and their insect visitors in a Mediterranean plant community, and found that flowering period had the least effect on the types of pollinators attracted, despite the seasonality shown by insect groups. In the case of *A. corniculatum*, it is unlikely that its seasonal flowering is directed towards attracting a certain class of pollinators, judging by the generalised nature of its visitors. However, it flowers at a time when most species in the area are flowering, and this abundance of seasonal (floral) resources draws bees into the area in great numbers. The bees are frequent visitors to a number of flowering plants in the area, (including *A. corniculatum*), and leave shortly after the flowering intensity declines.

5.8 *Conclusion*

This study found that the nature of interaction between the flowers of both *Sonneratia caseolaris* and *Aegiceras corniculatum* is generalised, involving a diverse spectrum of nocturnal and diurnal pollinators. Results regarding the pollination effectiveness of the different categories of visitors, however, remain inconclusive. Determining the rates of pollen removal and pollen deposition by different pollinators would present closer estimates of the relative importance of different visitor categories. Environmental variables and time of day affected visitation to the flowers of both species. Fruit-set in both plants was equally successful in the presence, and in the absence of pollinators. Diurnal and nocturnal visitors did not affect fruit-set differentially. Pollinator availability was not a limiting factor for the reproductive success of either plant species. Reproductive success in *S. caseolaris* was limited by predation, while that in *A. corniculatum* is likely to be resource-limited.

It is important to consider that this study focuses on just two plant species at a single time and place, and so provides only a fraction of the total perspective required to understand the system in its entirety. There is a need to study the variance in interactions at different temporal (e.g., diurnal, seasonal, annual) and spatial (e.g., neighbourhood, landscape, geographic) scales (Waser *et al.* 1996), in order to understand patterns of plant reproductive success across sites, seasons and ecological contexts.

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* Not seen in the original.

APPENDIX I

List of species visiting the flowers of *Sonneratia caseolaris* between Dec. 1996 and February 1997, in Bhitarkanika Wildlife Sanctuary, Orissa.

S. No.	CLASS	ORDER	FAMILY	GENUS/ SPECIES	D/ N*
1.	Insecta	Lepidoptera	Danaidae	*Euploea core* Cram.	D
2.	Insecta	Lepidoptera	Danaidae	*Danais aglea* Cram.	D
3.	Insecta	Lepidoptera	Danaidae	*Danais limniace* Cram.	D
4.	Insecta	Lepidoptera	Danaidae	*Danais plexippus* Linn.	D
5.	Insecta	Lepidoptera	Nymphalidae	*Hypolimnas bolina* Linn.	D
6.	Insecta	Lepidoptera	Lycaenidae	*Zizeeria* sp.	D
7.	Insecta	Lepidoptera	Pieridae	Unidentified	D
8.	Insecta	Lepidoptera	Pieridae	*Terias* sp.	D
9.	Insecta	Lepidoptera	Pieridae	*Catopsilia pomona* Fabr.	D
10.	Insecta	Lepidoptera	Hesperiidae	*Baoris mathias-mathias* Fabr.	D
11.	Insecta	Lepidoptera	Hesperiidae	*Baoris* sp.	D
12.	Insecta	Lepidoptera	Hesperiidae	*Argina cribraria* Clk.	D
13.	Insecta	Lepidoptera	Hesperiidae	*Chromus* sp.	D
14.	Insecta	Lepidoptera		Unidentified	D
15.	Insecta	Lepidoptera	Noctuidae	*Othreis salaminia* Fabr.	N
16.	Insecta	Lepidoptera	Noctuidae	Unidentified	N
17.	Insecta	Lepidoptera	Satyridae	*Melanitis leda* Drury	N
	Insecta	Lepidoptera		Unidentified	
18.	Insecta	Hymenoptera	Apidae	*Apis dorsata* Fabr.	D
19.	Insecta	Hymenoptera	Eumenidae	*Rhynchium brunneum* Fabr.	D
20.	Insecta	Hymenoptera	Scoliidae	*Campsomeris phalerata* Sauss.	D
21.	Insecta	Hymenoptera	Apidae	*Xyloeopa lepis* Drury.	D
22.	Insecta	Hymenoptera	Apidae	*Xyloeopa verticalis* Lepel.	D
23.	Insecta	Hymenoptera	Vespidae	*Icaris* sp.	D
24.	Insecta	Hymenoptera		Unidentified	D
25.	Insecta	Diptera		Unidentified	D
26.	Insecta	Diptera		Unidentified	D
27.	Insecta	Diptera		Unidentified	D
28.	Aves	Passeriformes	Nectariniidae	*Nectarinia zeylanica*	D
29.	Aves	Passeriformes	Nectariniidae	*Nectarinia asiatica*	D
30.	Aves	Passeriformes	Zosteropidae	*Zosterops palpebrosus*	D
31.	Aves	Passeriformes	Irenidae	*Aegithina tiphia*	D
32.	Aves	Passeriformes	Muscicapidae	*Orthotomus sutorius*	D
33.	Mammalia	Rodentia	Sciuridae	*Funambulus palmarum* Linn.	D
34.	Mammalia	Rodentia	Muridae	*Rattus rattus frugivorus* Rafn.	D
35.	Mammalia	Primates	Cercopithecidae	*Macaca mulatta* Zimm.	D

* D = diurnal visitors; N = nocturnal visitors

APPENDIX II

Partial** list of species visiting the flowers of *Aegiceras corniculatum* between February and April 1997, in Bhitarkanika Wildlife Sanctuary, Orissa.

S.No.	CLASS	ORDER	FAMILY	GENUS/SPECIES	D/ N*
1.	Insecta	Lepidoptera	Danaidae	*Danais aglea* Cram.	D
2.	Insecta	Lepidoptera	Danaidae	*Danais limniace* Cram.	D
3.	Insecta	Lepidoptera	Danaidae	*Danais plexippus* Linn.	D
4.	Insecta	Lepidoptera	Danaidae	*Danais chrysippus* Linn.	D
5.	Insecta	Lepidoptera	Danaidae	*Euploea core* Cram.	D
6.	Insecta	Lepidoptera	Nymphalidae	*Hypolimnas bolina* Linn.	D
7.	Insecta	Lepidoptera	Lycaenidae	*Zizeeria* sp.	D
8.	Insecta	Lepidoptera	Papilionidae	*Tros hector* Linn.	D
9.	Insecta	Lepidoptera	Pieridae	*Catopsila pomona* Fabr.	D
10.	Insecta	Lepidoptera	Noctuidae	*Thalatta fasciosa* Moore.	N
11.	Insecta	Lepidoptera	Noctuidae	*Heliothis armigura* Hubner.	N
12.	Insecta	Lepidoptera	Noctuidae	*Hypocala rostrata* Fabr.	N
13.	Insecta	Lepidoptera	Arctiidae	*Argina cribraria* Clk.	N
14.	Insecta	Lepidoptera	Pyralidae	*Maruca ambionalis* Feld.	N
15.	Insecta	Lepidoptera	Pyralidae	*Syngamia* sp.	N
16.	Insecta	Lepidoptera	Geometridae	Unidentified	N
17.	Insecta	Hymenoptera	Apidae	*Apis dorsata* Fabr.	D
18.	Insecta	Hymenoptera	Apidae	*Xyloeopa verticalis* Lepel.	D
19.	Insecta	Hymenoptera	Apidae	Unidentified sp.	D
20.	Insecta	Hymenoptera	Eumenidae	*Eumenis petiolata* Fabr.	D
21.	Insecta	Hymenoptera	Sphegidae	*Bembex orientalis* Handl.	D
22.	Insecta	Hymenoptera	Vespidae	*Vespa cineta* Fabr.	D
23.	Insecta	Hymenoptera	Vespidae	*Polistes marginatus* Fabr. var. *stigma* Fabr.	D
24.	Insecta	Hymenoptera	Scoliidae	*Campsomeris phalerata* Sauss.	D
25.	Insecta	Hymenoptera	Scoliidae	Unidentified	D
26.	Insecta	Coleoptera	Scarabaeidae	*Popillia* sp.	D
27.	Insecta	Diptera		Unidentified	D
28.	Insecta	Diptera		Unidentified -	D
29.	Aves	Passeriformes	Nectariniidae	*Nectarinia zeylanica*	D
30.	Aves	Passeriformes	Nectariniidae	*Nectarinia asiatica*	D
31.	Aves	Passeriformes	Zosteropidae	*Zosterops palpebrosus*	D

* * Several nocturnal visitor specimens awaiting identification

* D = diurnal visitors; N = nocturnal visitors