Pollination ecology, nectar secretion dynamics, and honey production potentials of *Acacia ehrenbergiana* (Hayne) and *Acacia tortilis* (Forsk.)Hayne, Leguminosae (Mimosoideae), in an arid region of Saudi Arabia

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Running headline: Nuru *et al*. Pollination ecology of Acacia

Christopher Beatty Sep 25

to Editor, me

Dear Dr. Adgaba,
It is my pleasure to write and inform you that your manuscript No. MSE 3217 "Pollination ecology, nectar secretion dynamics,and honey production potentials of *Acacia ehrenbergiana* (Hayne) and *Acacia tortilis*(Forsk.)Hayne, Leguminosae (Mimosoideae), in an arid region of Saudi Arabia" has been accepted in Tropical Ecology, pending some minor editorial changes. I have attached a final version with comments for your correction. Mainly, multiple citations within the text need to be cited according to journal style (alphabetical by first author, separated by semicolon) and some corrections to the bibliography need to be made (journal names in italics, volume number in bold). Once these corrections are made please return a copy the manuscript to me so that I may forward it for typesetting.

Thank you very much for your submission to Tropical Ecology.
Regards,
Chris Beatty

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Abstract

This study was conducted to investigate the structuring of two sympatric and co-flowering acacia species—*Acacia ehrenbergiana* (Hayne) and *Acacia tortilis* (Forsk**.)**—in relation to their flowering period distribution, floral reward partitioning, nectar secretion dynamics, and visitor assemblages. This research was performed in an arid climatic zone of the Arabian Peninsula (Saudi Arabia). To determine if there ispartitioning of pollinators between the two species their peak flowering periods were monitored and the peak time of pollen release through the day was quantified as the ratio of polyads to anthers. The nectar sugar secretion dynamics were estimated following nectar sugar washing techniques. The types and frequency of visitors were recorded and correlated. The two species varied in their peak flowering time within a season and peak pollen release time within a day. Moreover, both species secreted significant amounts of nectar sugar. The sharing of pollinators and the partial monopoly of certain visitors were observed. The two sympatric acacia species are structured into a partial temporal separation of their peak flowering and pollen release times, which appears to be an adaptation to minimize pollinator competition.

Keywords: Acacia pollination; pollinators; floral rewards; temporal partitioning, nectar sugar dynamics; flower phenology.

Introduction

Many studies have investigated the pollination ecology and partitioning of pollinators of acacia species from Australia, Africa, and Latin America (Armbruster & Herzig 1984; Krüger & McGavin 1998; Stone *et al*. 1998, 2003; Tandon *et al*. 2001; Tybirk 1993). However, the lack of sufficient information on geographical variation in acacia pollination ecology and timing of pollen release has been identified as an important gap in our knowledge (Stone *et al.* 1998).Particularly, despite the presence of many acacia species in the Arabian Peninsula and their significant contribution to vegetative biomass, ecosystem functioning and the economy of communities in the region, the pollination ecology of most of the acacia species that are found in the region have not been studied. Furthermore, in this region, information on the type of pollinators and the partitioning of pollination niches is not available for most of the acacia species in general and for two widely distributed acacia species—*Acacia tortilis* and *A. ehrenbergiana*—in particular, which are the main focus of this study. In addition, the nectar secretion dynamics and honey production potentials of these species have not been documented.

Generally, acacias are important woody plants in many tropical and subtropical arid regions of the world (Ross 1981) accounting for their significant biomass (Wickens 1995). Acacias are well known as important sources of fuel, firewood, timber, forage, gum, tannins, fiber, folk medicine, and food and are also useful for environmental protection and soil and water conservation (Boulos1983; Midgely & Turnbull 2003; Wickens 1995). Moreover, acacias support large numbers of herbivorous vertebrates and invertebrates (Krüger & McGavin 1998) as well as many species of nectarivorous insects.

Among the many species of acacia, *Acacia tortilis* (*tortilis)* (Forsk.)(Hayne) and *A. ehrenbergiana* (Hayne) are major components of the vegetation of the coastal and inland plains of the vast Arabian Peninsula (UNESCO 1977; Walter & Breckle 1986). In particular, *A. tortilis* is naturally found in extensive areas of dry habitat in more than 20 countries in tropical and subtropical Africa and Asia and has been introduced to more than 15 countries (Midgley & Bond 2001; Wickens 1995). *A. ehrenbergiana* is also found in the Sahel climatic zones and deserts of Africa and the Middle East. These acacias are the most drought-tolerant species and survive in the rainfall belts of 50-400mm/annum (Le Houérou 2012; Wickens 1995).

Several studies have been devoted to acacia reproductive biology (Kenrick 2003; Sedgley *et al*. 1992; Tybirk 1993) their major floral rewards (Bernhardt & Walker 1984; Stone *et al*. 1998; Tandon *et al.* 2001), floral phenology (Raine 2001; Stone *et al*. 1998; Tandon *et al.* 2001; Tybirk 1993) and visitor assemblages (Kenrick 2003; Raine 2001; Sornsathapor & Owens 1998; Stone *et al*. 1998; Tybirk 1993). The intra- and interspecific competition among various acacia species for pollinators has also been studied (Friedel *et al.* 1994; Raine *et al.* 2002; Stone *et al*. 1998).

Competition for pollination is an important factor in the structure and timing of flowering of many plant communities (Pleasants 1983; Rathcke 1983, 1988). Sympatric species, which are unable to diverge in space, may use different pollinator guilds (Armbruster & Herzig 1984; Rathcke 1988) or may differ in flowering seasons (Pleasants 1983; Williams 1995) to avoid competition for pollinators. However, seasonal patterns, such as the availability of water and the thermo-period, may impose constraints on the flowering seasons of many sympatric species (Johnson 1992). In such cases, further divergence in time of pollen release through the day has been reported to minimize competition for pollinators (Levin & Anderson 1970; Ollerton & Lack 1992; Stone *et al*. 1996, 1998). In this regard, some information is available for many acacia communities in Africa, Australia, and Latin America. Many acacia species are widely distributed from Africa to Arabia (Ross 1981) and form part of a wide diversity of acacia assemblages (Tybirk 1993), however, information on the geographical variations in their pollination ecology and pollinator guilds are lacking (Stone *et al*. 1998).

In particular, related data on the two dominant acacia species, *A. tortilis* and *A. ehrenbergiana*, which grow sympatrically over a large altitudinal range, do not exist. These two species overlap in not only space but also flowering season; however, detailed studies on their pollination ecology (floral rewards, types of flower visitors, interspecific competition for pollinators, and potential pollinator competition avoidance in their respective climatic zones) had not been performed.

Moreover, detailed studies on the nectar secretion dynamics and honey production potentials of these two species are lacking. Such information is important from both pollination ecology perspectives and in estimating the socio-economic value of a species. The amount and concentration of nectar varies from plant to plant and over time (Chalcoff *et al*. 2006; Roubik 1991). Many studies have been conducted on different plant species to quantify the nectar secretion dynamics (e.g., Castellanos *et al.* 2002; Galetto & Bernardello 2004; Petanidou & Smets 1996). Moreover, quantitative studies on the nectar secretion of melliferous plants include: Horváth and Orosz-Kovács (2004); Nepi *et al.* (2001) and Zajácz *et al.* (2006).

In general, the flowers of species in the subgenus *Acacia*—to which *A. tortilis* and *A. ehrenbergiana* belong—have spherical inflorescences and have been reported to be nectarless or to secret only trace amounts of nectar (Stone *et al*. 1998, 2003). However, in the study areas where these acacias grow, beekeepers have been observed to bring hundreds of honeybee colonies during the flowering period of these two species to produce honey (Al-Jeffri 2009).

With this general background, we propose the following questions: 1) Do these two sympatric *Acacia* species have different pollinator guilds? 2) Are there any time variations in the peak flowering period of these two species within the same flowering season? 3) Is there any timing or partitioning of reward release through the day to avoid competition for pollinators? 4) Are all of the acacias with round inflorescences nectarless?

This study investigates the pollination biology (flower morphology, flowering phenology, floral rewards distribution, and temporal distribution of flower visitor assemblages) of *A. tortilis* and *A. ehrenbergiana* under the typical arid climatic conditions of the Arabian Peninsula. The quantities and dynamics of nectar secretion at different times of the day were recorded and compared between species, among trees, and between localities. Finally, the potentials of the species for honey production have been estimated.

Materials and methods

Study site and species

This study was conducted in the Al-Baha region of Saudi Arabia in March-May 2012 at two sites, one in Wadi Alkhatani (19°45”57.64N and 41°39”26.27E, 900m above sea level (masl)) with an altitude range of 400-1,000masl, representing a lowland habitat, and the other in Wadi Kahla (20°07”08.20N and 41°51”04.4E, 1,475masl) with an altitude range of 1,200-1,750masl, representing a midland habitat.

Flowering period distribution

Since these two species flower during the same season, their flowering patterns were monitored to determine whether any variations in their peak flowering periods within a season could have occurred. At the beginning of the flowering season, 40 individual trees in the lowland and another 40 in the midland (20 for *A. ehrenbergiana* and 20 for *A. tortilis)* were labeled for each locality, and the flowering patterns (commencing, peaking, and ending) were monitored and recorded. During selection and labeling, efforts were made to include mature trees of different sizes and ages in the sample. Moreover, trees growing in different land gradients like slope and topography were considered, and they were fairly scattered within approximately a hectare of land at each site. For each labeled tree, the peak flowering time was taken when more than 50% of the flower buds were in the blooming stages.

Flower phenology and time of pollen release

For the flower phenology study, three plants per species and eight flower head buds per plant a total of 24 mature flower head buds/species were labeled, and their phenology was monitored every 2 h from 0400 to 1800h. The time of opening of flowers, pollen release and nectar secretion were observed. To determine the peak time of pollen release and detect any partitioning of pollen release through the day between the two species, the time at which the pollen was released was determined by quantifying the relative abundance of polyads at different hours of the day (0600, 0800, 1000, 1200, and 1400h) following the protocol of Stone *et al.* (1998). The progress of anthesis over time was recorded by scoring the ratio of polyads to anthers.

Floral morphology

Additionally, the morphologies of the flower heads and florets were studied. The size of the flower head was determined by measuring 16 flower heads per plant for a total of 48 flower head per species and results were analyzed and the mean values compared between species. The number of florets per flower head was determined by counting all of the florets per flower head fora total of 50 flower heads per species. Moreover, to determine the number of stamens per floret and the proportion of florets with or without a stigma 60 flower heads per species were examined. To determine the relative pollen transfer efficiency of the species, their pollen-to-ovule ratios were determined by calculating pollen grains per polyad× 8 (polyads per anther) ×the average number of anthers per flower/proportion of flowers with stigmas and number of ovules per ovary following Baranelli *et al.* (1995) procedures. The number of pollen per polyad was determined through polyad reference slide preparation and microscopic examination.

Nectar sugar secretion

The dynamics of nectar sugar production were determined from a total of 13 trees, taking three to four plants/species at each site. The nectar sugar was estimated five times a day at 0600, 0900, 1200, 1500, and 1800h. The flower buds were bagged one day before their flowers opened using bridal-veil netting (Wyatt *et al.* 1992). The nectar sugar was measured from five flower heads from each plant and for each sampling time, yielding a total of 25 flower heads/day/plant/site. The measurements were repeated for three consecutive days for a total of 450 flower heads for two sites for each species. One flower head was used for only one time measurement.

The nectar was too viscous to extract and measure using capillary tubes due to the study area’s high average temperature (>35°C) and low relative humidity (RH) (<26%). A nectar concentration of 75% sucrose was reported for *A. zanzibarica* (Stone *et al.* 1998) which is difficult to remove using capillary tubes. Therefore, in this study the nectar sugar secretion amount was determined for flower heads by measuring the nectar sugar concentration following flower nectar sugar washing techniques of Mallick (2000). For this procedure, each flower head was removed and kept in a small, narrow plastic vial and washed with 1ml of distilled water for *A. ehrenbergiana* and 0.5ml for *A. tortilis* flowers. (The amounts of distilled water that were required to completely soak the flower heads were different because the average diameters of the flower heads were different). The flower heads were then left for 5 min in distilled water until the sugar was completely dissolved. From the pooled solution, a drop of clear solution was taken using micropipettes, and the concentration was measured using a pocket refractometer (*ATAGO, No. 3840,* Japan). The mass of the sugar in the secreted nectar for each flower head was calculated from the volume and concentration of the solution that was measured. The sucrose concentration readings (mass/total mass, g of sugar/100 g of solution) were converted to sucrose mass/volume using Weast's (1986) conversion table. The results were then compared between plants, species, and sites and among different times.

Honey production potential

The honey production potential was estimated by multiplying the average number of flower heads/plant by the average amount of sugar/flower head. The average number of flower heads/plant was determined from four trees/species by counting the numbers of flower heads/m^3 from four sampling units of 1m^3/tree. Then, the average number of flower heads/m^3 was multiplied by the average canopy volume of the trees. The average canopy volume of each species was determined by measuring the canopies of 83 and 54 individual plants for *A. ehrenbergiana* and *A. tortilis,* respectively. The canopy volume was calculated following Coder's (2010) plant crown shape formula (shape value 3/8(0.375) (crown diameter)^2× (crown height) × (0.2945) fat cone for *A. ehrenbergiana* and 2/3(0.667) (crown diameter)^2× (crown height) × (0.5236) spheroid for *A. tortilis,* depending on the crown shapes of the species). These data have been used to estimate the honey production potential per tree and per hectare of land that is covered with the species. The average number of trees that can be grown per hectare of land was estimated from the average canopy area of mature *A. ehrenbergiana* and *A. tortilis* trees.

Flower visitors

For the flower visitors, three flowering trees/species/site were selected, a 1 × 1m^2 area of branches with flowers were marked, and observations of flower visitors were made six times per day at 0600, 0800, 1000, 1200, 1400, and 1600h. During each observation period, the visitors were recorded for 10min for each tree. The observations were repeated for three consecutive days, and the types and frequency of visitors for each species were recorded. Voucher specimens and digital photographs of flower visitor species were taken and identified using experts and reference materials. The flower visitors were classified into order or family levels.

Weather data

Along with the other observations, the temperature and relative humidity (RH) of the study sites were taken at each sampling time using an Environment Meter *N09AQ, UK)and correlated with the other recorded data.

Statistical analysis

To compare the amount of sugar that was secreted per flower head per 3h period from the different trees, mixed-effects analysis of variance(ANOVA) was used with the amount of nectar sugar/flower head as the response variable; the location, species, and time of day as fixed factors; and the trees as random factors. Tukey’s multiple comparison test was used to determine the significant pairwise comparisons within the factors (Johnson & Wichern 2007). Independent *t*-tests were used to test for the mean differences between species in the flower head diameter, number of florets per flower head, and number of stamen per floret. A correlation analysis was performed between the environmental factors (temperature and RH of the area) and amount of nectar sugar secreted per flower head. Moreover, a correlation analysis was conducted to determine the presence of an association in the temporal distribution of flower visitors and any preference of insect visitors for different flower species. The analysis was performed using the STATISTICA© (StatSoft 2010) program.

Results

Flowering period distribution

The flowering periods varied between species and locations. According to the conditions of studied years, in the lowland habitat *A. ehrenbergiana* started to flower in early March 5-10,with a peak from March 18-25 and ending around April 15-18. For that of *A. tortilis*, the flowering began March 15-20, peaked on April 5-15 and ended on April 25-28 (Fig. 1, A & B).In the midland habitat, *A. ehrenbergiana* started to flower on April 5-7, peaked on April 15-20 and ended on May 15-20. At the same location, *A. tortilis* started to flower on April 18-20, peaked on May 10-20, and ended around May 26-29 (Fig. 1, A & B). Generally the flowering period of *A. ehrenbergiana* was earlier and relatively longer than that of *A. tortilis* in both habitats. Moreover, in both habitats despite the presence of overlapping of flowering periods of the two species, there were variations in their peak flowering time (Fig. 1, A & B).

Flower phenology and time of pollen release

Both species were observed to open their florets early (0400-0500h). From the average polyad-to-anther ratio, the peak pollen release time for *A. tortilis* was earlier (0600-0800 h)(Fig. 2, A) than that for *A. ehrenbergiana* (0800-1200h, peaking at around 11000h) (Fig. 2, B). In both species, the stigmas remained buried in dense stamens until 1200h but began to elongate from 1300 h. This observation indicates the protandrous nature of the two species, which is in agreement with Tybirk (1993) and Stone *et al.* (1996), who reported a similar phenology for other acacia species. According to the weather data records for the study period, the peak pollen release time of *A. tortilis* was associated with 30-40% RH and a temperature range of 25-30°C, whereas that of *A. ehrenbergiana* occurred at a relatively lower RH (25-30% RH) and higher ambient temperature (30-40°C).

Floral morphology

The mean flower head diameter of *A. tortilis* was significantly smaller (8.4±0.62mm) than that of *A. ehrenbergiana* (12.2±1.14mm) (*t*-test: $t = 20.6$, $df = 98$, $P<0.0001$). The average number of florets/flower head was significantly lower for *A. tortilis (*37.98±5.24) than for *A. ehrenbergiana* (51.94±6.77) (*t*-test: $t = 11.5$, $df = 98$, $P< 0.0001$). However, the average number of stamens per floret did not differ (46.52±6.18 and 46.67±6.83 for *A. ehrenbergiana* and *A. tortilis*, respectively). Moreover, the color of the flower head of *A. ehrenbergiana* is yellow, whereas that of *A. tortilis* is creamy white (Fig. 3).Three types of flower heads were observed for *A. ehrenbergiana* in the same tree. Each floret had a stigma in 75% of the flower heads, whereas all of the florets were without a stigma in 5% of the flower heads and 20% of flower heads had both types of florets. In such mixed flower heads, the florets without stigmas were mainly found at the bottom sides of the flower heads. Considering all three types of flower heads of the studied *A. ehrenbergiana* florets,85% of the florets had a stigma. However, all of the observed *A. tortilis* florets had one central stigma. The average numbers of pollen grains per polyad were 16 for both *A. tortilis* and *A. ehrenbergiana*. The average number of ovules per ovary was7.16 and 6.22 for *A. ehrenbergiana* and *A. tortilis*, respectively. Considering the proportion of florets with stigmas, ovules per ovary, the number of stamens per floretand number of monads per polyads; the pollen to ovule ratios of the two species were 978.40 and 960.41for *A. ehrenbergiana* and *A. tortilis* respectively.

Nectar sugar secretion

The nectar sugar analysis was based on measuring a total of $N = 900$ flower heads. The results of the mixed-effects ANOVA indicated that the average amount of nectar sugar that accumulated per flower head was significantly higher in *A. ehrenbergiana* (6.00±4.47 mg/flower head) than in *A. tortilis* (1.94±1.95mg/flower head) (Table 1 & Fig.4) (F =197.4, df = (1, 2.01), $P<0.0049$). Furthermore, the average amount of nectar sugar/flower head was significantly different between the two localities (F = 6,180.1, df= (1, 14.54), $P<0.0001$) (Table 1 & Fig. 5); however, the interaction between species and localities was not significant (F =6.97, df = (1, 2.0), P=0.1183). Moreover, a significant variation was observed in the average amounts of nectar sugar/flower head among different time periods (*F* = 6.59, *df* = (4, 8.03), *P*= 0.0119) (Fig.5). The interactions between the time periods and species (*F* = 6.39, *df* = (4, 8.08), *P* = 0.0128); and between the time periods and localities were significant (*F* = 4.09, *df* = (4, 8.08), *P* = 0.0424), but the interaction between the time periods, species, and localities was not significant (*P*=0.1492).

In the bagged flower heads of the two species, nectar secretion began early (0600 h) with an average of 3.6 ± 2.27 mg/flower head for *A. ehrenbergiana* and 1.09 ± 0.79 mg/flower head for *A. tortilis,* and the nectar secretion peaked between 1200 and 1500 h in both species (Fig. 5). However, after 1500 h, the accumulated amount of nectar was observed to slightly decrease in *A. tortilis* for Kahla and remain more or less the same in Alkhatani localities, whereas there was still a slight increase in the Kahla but a decrease in the Alkhatani localities for *A. ehrenbergiana* (Fig. 5).

The average amount of nectar sugar that accumulated per flower head in all of the trees in the two localities at the end of the flowering stage (1800 h) was 8.47±5.14mg/flower head and 2.32±2.31 mg/flower head for *A. ehrenbergiana* and *A. tortilis*, respectively, and was significantly different (Tukey's test: *P* < 0.0001). Considering the average number of florets/flower head and the average amount of accumulated nectar sugar/flower head, the average amount of accumulated nectar sugar/floret was calculated to be 0.16 and 0.06 mg/floret for *A. ehrenbergiana* and *A. tortilis*, respectively.

The daily average amount of nectar sugar secreted per flower head differed significantly between localities for *A. ehrenbergiana* (from 6.82 ± 5.06 mg/flower head at Kahla to 4.35 ± 2.17 mg/flower head at Alkhatani; Tukey's test: *P* < 0.0001) but not for *A. tortilis* (from 2.07 ± 2.02 mg/flower head at Kahla to 1.80 ± 1.86 mg/flower head at Alkhatani; Tukey's test: *P* = 0.7526).

The lowest average amount of nectar sugar/flower head was recorded for *A. tortilis* tree with 1.86±1.83 mg/flower head, whereas the maximum average was recorded for an *A. ehrenbergiana* tree with 7.59±4.92 mg/flower head (Fig.6). There was no significant variation among the trees in the average amount of nectar sugar per flower head when using the mixed-effects model ($F = 3.55$, $df = (2, 0.04)$, $P = 0.9106$). However, when considering all 13 trees individually using Tukey's post-hoc comparisons, there was a significant variation in the average amount of nectar sugar/flower head among the trees between species (Tukey'stest: $P< 0.0001$) as well as among the *A. ehrenbergiana* trees at Kahla (Tukey's test: $P=0.0043$) and between localities (Tukey's test: $P< 0.0342$) but not among the trees at Alkhatani (Tukey's test: $P > 0.9999$) (Fig. 6). There was no significant difference among the *A. tortilis* trees (Tukey's test: Kahla: $P > 0.9999$; Alkhatani: $P> 0.8514$) (Fig. 6).

In addition to nectar and pollen, the flowers of *A. ehrenbergiana* also produce a strong scent in the afternoon; this scent may be associated with the peak period of nectar secretion. Generally, the amount of nectar sugar that was secreted by the two species in both localities was slightly positively correlated with the temperatures of the area ($r = 0.15$, $P < 0.0001$) and negatively correlated with the RH ($r = -0.20$, $P < 0.0001$).

Honey production potentials of the plants

The honey production potential of the species was estimated from the average amount of accumulated nectar sugar that was extracted at the end of the flowering stage (1800h), which was 8.47±5.14mg/flower head for *A. ehrenbergiana* and 2.32±2.31mg/flower head for *A. tortilis*. These values were multiplied by the average of 2,901.5 flower heads/m^{3}for *A. ehrenbergiana* and 6,370 flower heads/m^3 for *A. tortilis*. These results were then multiplied by the average tree canopy area of 32.2m^{3}for *A. ehrenbergiana* and 22.77m^3 for *A. tortilis*. Accordingly, the average amount of nectar sugar that was obtained per tree was estimated to be 791.34g for *A. ehrenbergiana* and 336.50g for *A. tortilis*. Considering the number of plants per hectare (285.7 for *A. ehrenbergiana* and 400 for *A. tortilis*), it is possible to obtain approximately 226.08 and 134.6kg nectar sugar/hectare for *A. ehrenbergiana* and *A. tortilis*, respectively. With an average moisture content of honey (18%), the estimated amount of honey that can be obtained from a hectare of *A. ehrenbergiana* and *A. tortilis* forests is 275.70 and 163.41kg, respectively.

Insect visitors

In the total observation period of three consecutive study days, a total of 994 individual insect visitors representing four orders were recorded. The dominant insects were hymenopterans (Apidae, Megachilidae, Halictidae, and Formicidae), accounting for 88.24% and 82.41% of the total visits to *A. ehrenbergiana* and *A. tortilis* plants, respectively. The remaining insects were Lepidoptera (6.25% and 4.99%), Coleoptera (4.78% and 9.42%), and Diptera (0.74% and 3.19%) on *A. ehrenbergiana* and *A. tortilis* respectively.

Temporal distribution of flower visitors

The pattern of insect visitation differed significantly with the time of day (F =6.08, df = (5,114), P<0.001) (Fig. 7). A relatively higher number of visitors were observed at 0800-1000h for *A. tortilis*, where as the relative frequency of visitors in *A. ehrenbergiana* was high at 1000-1400h (Fig. 7), which more or less aligned with the species' pollen release times and nectar secretion dynamics.

Although the peak pollen release times occurred in the morning, the insect visitations continued into the after noon because the nectar secretions in both species continued. Since most of the insects collected both pollen and nectar their frequencies were not restricted to the pattern of pollen release.

The insect taxa that exhibited significant variation in their visitation times of the two species included honeybees (F = 10.94, df = (5,114), P < 0.001), wild bees (F = 9.74, df = (5,114), P<0.001), and Coleoptera (F = 4.18, df = (5,114), P<0.01). Their frequencies were higher in the morning than in the afternoon, which was associated with the timing of pollen availability. The other insects did not exhibit significant visiting time variations across the day, including Formicidae (F =2.09, df = (5,114), P = 0.072) and Diptera (F =1.95, df = (5,114), P=0.092).

Insect visitor preference for flower species

Many flower visitors, including honeybees, ants, and small-sized wild bees, visited both species. However, there was a significant difference in the total insect visitation between the flowers of the two acacia species (*F* =28.14, *df* = (1,118), *P*< 0.001) in that a higher number of visits were observed for *A. tortilis* than *A. ehrenbergiana* (Fig. 7). There was also a difference in the categories of visitors between the two species in that insects with a larger body size, such as nectar-feeding wasps and wild bees (*Xylocopa sp*.), as well as nectar-feeding birds, were observed to visit only *A. ehrenbergiana* flowers (Fig. 8).

Moreover, there was a significant difference between the two flowering species, with a higher number of visitations to *A. tortilis* by honeybees (*F* = 10.85, *df* = (1,118), *P*< 0.01), Formicidae (*F* = 25.41, *df* = (1,118), *P* < 0.01), Diptera (*F* =15.42, *df* = (1,118), *P* < 0.001), Coleoptera (*F* =9.5, *df* = (1,118), *P* < 0.01), and Lepidoptera (*F* = 4.30, *df* = (1,118), *P* < 0.05) but not wild bees (*F* = 0.03, *df* = (1,118), *P* = 0.867).

Weather data

The range of temperature that was recorded during the study period was 20-44°C. The RH of the area was also very low, with a range of 13-61.60%.

Discussion

Although the two species were grown in and share the same habitats (altitude, rainfall, temperature, soil type, and slopes) with some degree of overlap during the flowering season, there was a distinct difference in their peak flowering times in both the lowland and midland locations in that *A. ehrenbergiana* flowered earlier than did *A. tortilis (*Figs. 1 A & B). Therefore, in these two sympatric acacia species, which overlap in both space and flowering season, the avoidance of pollinator competition appears to be partially achieved through differences in their peak flowering times within the same season. The distribution of flowering peaks of species due to competitive displacement has been predicted in other acacia species

(Pleasants 1983; Williams 1995). Moreover, the flowering period separation among related species has been considered as a selective response to competition for pollination (Pleasants 1994; Stone *et al*. 2003; Williams 1995).

In addition to the differences in their peak flowering periods, variations in the peak pollen release times of the two species through the day were also observed. The peak pollen release time was 0600-0800h for *A. tortilis* and around 1000h for *A. ehrenbergiana.* Hence, relatively more pollen collector insects (honeybees, wild bees, and ants) were observed on *A. tortilis* flowers than on *A. ehrenbergiana* flowers at 0600-0800 h (Fig.7). Because the two species have some degree of overlap in their flowering times, the variations in their peak pollen release time (Fig. 2) could be a further adaptation of the two species in the partitioning of pollinators within the day to minimize competition. Similarly, in some co-flowering sympatric African acacia species, the partitioning of pollinators was achieved by significantly spacing their peak pollen release into a specific time period within a day from dawn to dusk (Stone *et al.* 1998). The daily structuring of flower visitor activities was tracked following the sequence of pollen dehiscence from different acacia species in which flower visitors arrive soon after the dehiscence of one species and depart to another when the pollen standing crop becomes low (Stone *et al.* 1998).One of the mechanisms through which the shared pollinators track the daily sequence of pollen release in acacia assemblages is associated with the release of strong species-specific scents, which may provide synchronizing cues announcing the presence of fresh standing crop (Willmer & Stone 1997).

In this study, the variation in the peak pollen release time could be associated with the different RH ranges that were recorded for the two species. An association between the RH and anther dehiscence has been reported for different African acacia species (Stone *et al.* 1998). The observed peak pollen release time of *A. tortilis* was interestingly similar to that of the same species reported for an African population (Stone *et* *al.*1998). However, the RH at which the peak pollen release took place in this study was significantly lower than that in reported for African *A. tortilis* populations.

Moreover, in this study, floral morphology (size) variations were observed to contribute to the partitioning of flower visitors, i.e., large flower visitors were observed on relatively larger flowers. Such conditions were also noted for African acacia species (Stone *et al.* 1998, 2003).

In African acacia species, in addition to variations in their peak pollen release times, the partitioning of pollinators is further achieved either by growing in different locations or flowering in different seasons (Stone *et al*. 1998). Similarly, in the Arabian Peninsula, besides the variation in peak pollen release time, many acacia species have spatial and temporal variations to minimize pollinator competition (Nuru *et al.* 2012).

In this study, the dominant flower visitors of the two acacias were Hymenopterans (Apidae, Megachilidae, Halictidae, and Formicidae), and the less dominant visitors were Coleoptera, Diptera, and Lepidoptera. Moreover, nectar-feeding wasps and birds were also observed. Similarly, honeybees, megachilids, halictid bees, pollen-feeding flies (Caliphoridae), Lepidoptera, and nectar-feeding wasps were reported as the major visitors in pollen- and nectar-bearing African acacias species (Stone *et al.* 1996, 1998). This observation indicates that acacia flower visitors of the two regions are more or less similar.

Insects with a large body size—wild bees (*Xylocopa sp*.) and nectar-feeding wasps—as well as some nectar-feeding bird species were only observed on relatively large *A. ehrenbergiana* flowers (Fig. 8),whereasthe small size *A. tortilis* flowers were only visited by small-sized insects, such as honeybees (*Apis mellifera*), wild bees (Megachilidae), small pollen-feeding coleoptera, flies, and ants. This observation could be due to the morphology of the *A. ehrenbergiana* flower heads, which are significantly larger in diameter and have thick florets which are relatively strong to support the landing of large insects.

This flower size difference may also influence certain variations in the pollinator guilds between the two sympatric species. Similarly, the major flower visitors of African *A. tortilis* were small species, such as honeybee (*Apis mellifera)*, megachilids, halictid bees, and pollen-feeding flies (Caliphoridae) (Stone *et al*. 1998). Moreover, monopolizing of larger nectar-feeding insects and birds was mainly found on African acacia species, such as *A. Senegal* (Stone *et al.* 1998). In this regard, Stone *et al.* (2003) reported that inflorescences (flower heads) with a small number of flowers are unable to support large insects, indicating that in addition to the types of floral rewards and their temporal availabilities, the morphology of flowers may also determine the types of flower visitors. The presence of variations in pollinators that were recruited as a result of floral dimension variations (Kenrick*et al.* 1987) and the use of different pollinator guilds among sympatric species have been reported (Armbruster & Herzig 1984; Rathcke 1988).

Moreover, the observation of large flower visitors on *A. ehrenbergiana* flowers only, could be because the species secretes a significantly greater amount of nectar than *A. tortilis*, possibly indicating that the amount of nectar secreted may serve as a pollinator-partitioning mechanism. In this regard the interactions between nectar secretion time periods and acacia species were significant (F = 6.39, df = (4, 8.08), P = 0.0128). Similarly, in Africa, *A. senegal* produces a large amount of nectar, which leads to the monopolizing visitation by large nectar-feeding butterflies, wasps, and sunbirds (Waser 1982).

Generally, the types of flower visitors that were observed in this study, particularly in *A. tortilis*, were similar to the visitors of the same species in African populations (Stone *et al.* 1998). However, Stone *et al.* (1996, 1998) reported that at some of their study sites, honeybees were observed to visit *A. tortilis* flowers for pollen only and *A. senegal* for nectar, and the authors suggested that variations in the availability of floral rewards may substantially contribute to differences in visitor guilds across African acacia species. However, in our study, honeybees collected both pollen and nectar from the same species. Such variations between the two regions could be associated with the foraging behaviors of the honeybees, which may be related to their preferences and depend on both the colony nest demand and the quality and quantity of floral resources available at a particular time and place.

Generally, some small- to medium-sized insects, such as honeybees, Megachilidae and Diptera are important pollen vectors and are shared between the two sympatric species, which may result in interspecies pollen transfer. This inter species pollen transfer might serve as a selective force in the variations in the peak flowering and pollen release times of the two species. The selective pressure of shared pollinator guilds among sympatric species and its role as a driving force in the evolution of temporal partitioning has been reported (Stone *et al*. 1996, 1998, 2003; Typirk 1993). In addition, the release of a strong scent by the *A. ehrenbergiana* flowers may serve as an important means of attracting pollinators, and this release has been considered an olfactory advertisement with advantages in co-flowering acacias (Bernhardt & Walker 1984; Willmer & Stone 1997).

Generally, the two sympatric acacia species have been observed to share some pollinator guilds, and this sharing may have led to the structuring of the two species into a partial temporal separation of their peak flowering and pollen release times and a partial division of flower visitor assemblages due to the selective response to competition for pollination. Such phenomena are known as common factors for the structuring of other sympatric acacia species (Pleasants 1983; Rathcke 1983).

The pollen-to-ovule ratios of the two species were very close to each other which was 978.40 *A. ehrenbergiana* and 960.41 for *A. tortilis*. The values were higher than *A. caven's* ratio (821.49) in Latin America, (Baranelli *et al.* 1995) and much lower than the two African acacia species, *A. nilotica* and *A. Senegal* which were estimated to be 4229.69 and 1212.44 respectively based on available secondary data of FAO (1983); Kordofani & Ingrouille (1992); Stone *et al.* (2003); Tantawy *et al*. (2005). Since low pollen-ovule ratio is highly associated with high pollination efficiency of a species (Harder & Johans

(2008), the two Arabian Peninsula acacia species might be considered as more efficient in their pollen transferring abilities than the African acacia species.

The flowers of the two acacia species secrete significant amounts of nectar sugar, which can attract many pollinators. However, the amount of nectar that was recorded for *A. ehrenbergiana* was greater than that recorded for *A. tortilis*. Similarly, substantial variation in the quality and quantity of nectar among different acacia species has been well documented (Stone *et al.* 2003).From the amount of nectar that was extracted from different flower heads at different times, we can see that nectar secretion begins early (0600h) and continues to increase until after 1200 h. The distribution of nectar secretion over most of the daytime would be an important adaptation of the species to attract visitors for a longer time throughout the day to ensure pollination.

In this study, the positive correlation between the temperature and amount of nectar sugar may indicate the adaptation of the species to hot climatic zones. The presence of a positive correlation between the temperature and nectar secretion was observed for *Thymus capitatus* under Mediterranean conditions (Petanidou & Smets 1996) and for *Ziziphus spina-christi* (Nuru *et al*. 2012).

Unlike the previous general reports on the absence or trace amount of nectar in many acacia species with spherical flower heads (subgenus *Acacia)* (Stone *et al.* 1998, 2003), in this study, the two species secreted large amounts of nectar sugar (6.00±4.47mg/flower head and 1.94±1.95mg/flower head or 0.12 and 0.05mg/floret for *A. ehrenbergiana* and *A. tortilis,* respectively), which may indicate these species' potential for flower visitors and honey production.

The previous reports on the absence or trace amounts of nectar for the genus acacia (Stone *et al.*, 1998, 2003), could be due to either ecological variations or the use of estimation techniques (micropipettes) that could not properly extract very viscous nectar of high concentrations. Stone *et al.* (2003) reported a sucrose concentration of 75% for *A. zanzibarica* and *A. senegal*. Similarly, Ettershank & Ettershank (1993) reported that *Eucryphia lucida* (Eucryphiaceae) flowers produce nectar starting from the night until 1000 h and they concluded the absence of nectar secretion afterward, typically due to the difficulties in removing and measuring dehydrated nectar (>70% concentration) using capillary tubes. However, later Mallick (2000) commented on the unsuitability of such a technique for flowers where the nectar is produced in very small quantities and/or where the nectar is highly viscous. Using washing techniques, Mallick demonstrated that the same *E. lucida* flowers produced nectar continuously throughout the day and that two thirds of the nectar was produced after 1000h.

Moreover, the potential of the two species for honey production is reflected in the estimated amount of honey (275.70and 163.41kg/hectare of *A. ehrenbergiana* and *A. tortilis*, forests respectively) and thousands of honeybee colonies that are annually moved during the flowering periods of these acacias (Al-Jeffri 2009 and personal observation). Similarly, large amounts of honey production have been reported per hectare for other plant species, such as *Asclepias syriaca* L. (500-600kg/ha; Zsidei 1993), *Trifolium pratense* L. (with an estimated sugar yield of 883kg/ha/flowering period (Szabo & Najda 1985), and various *Tilia* species (90–1,200kg/ha, Crane *et al.* 1984 and 900kg/ha, Nuru *et al*. 2012).

Despite the greater amount of nectar in *A. ehrenbergiana* than in *A. tortilis*, honeybees prefer to collect nectar in the latter. Beekeepers also confirmed that bees collect more honey from *A. tortilis* than from *A. ehrenbergiana* (personal communication), possibly because the longer, stronger, and thicker florets of *A. ehrenbergiana* might preclude the full accessibility of the honey bees to freely collect nectar in such flowers. This and other biochemical factors may require further investigation to pinpoint the possible reasons for the variations.

In both species, the onset of flowering occurs before the onset of vegetative growth (during the leafless stage) using previously stored reserves. This pattern is a typical adaptation of plants to dry climatic conditions and has been considered a strategy for partitioning resource use between vegetative and reproductive functions (Singh & Kushwaha 2006). In this regard, beekeepers also report that acacias that have leaves at flowering time are not a good source of nectar (personal communication), possibly due to resource trade-offs between reproductive and vegetative functions. Therefore, the flowering of the species before the vegetative period may indicate its potential for better nectar secretion. Moreover, the presence of a sweet scent has been mentioned as a characteristic of nectar-secreting acacias (Stone *et al*. 2003) and has also been observed in this study for *A. ehrenbergiana*.

This study has revealed temporal structuring of these two acacia species in this particular ecology, potentially in response to adaptation to minimize competition for pollinators. Moreover, this study demonstrated the potential of these species for nectar secretion, honey production, and supporting a diverse insect fauna, adding to our knowledge of the value of these plants in the production of high-value non-timber products (honey) and their contribution to maintaining the rich biodiversity of the ecosystem. This information may serve as a basis for planting recommendations and species conservation for both environmental and economic reasons in such harsh environments.

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References

Al-Jeffri, J.H. 2009.Economic viability of *Acacia ehrenbergiana* (Selam) plantations in the Tihama Region, the Republic of Yemen. Hodiedah, Yemen, 1-23Pp.

Armbruster, W.S. & A.L. Herzig. 1984. Partitioning and sharing of pollinators by four sympatric species of *Dalechampia* (Euphorbiaceae) in Panama. *Annals of the Missouri Botanical Garden* **71**: 1-16.

Baranelli, J.L., A.A. Cocucci & A.M. Anton. 1995. Reproductive biology in *Acacia caven* (Mol.) Mol. (Leguminosae) in the central region of Argentina. *Botanical Journal of the Linnean Society*, **119**: 65–76.

Bernhardt, P. & K. Walker. 1984. Bee foraging in three sympatric species of Australian *Acacia*. *International Journal of Entomology* **26**: 322 -330.

Boulos, L. 1983.*Medicinal Plants of North Africa*. Algonac, Michigen, pp, 115 -117.

Castellanos, M.C., P. Wilson & J.D. Thomson. 2002. Dynamic nectar replenishment in flowers of *Penstemon* (Scrophulariaceae). *American Journal of Botany* **89**: 111-118.

Chalcoff, V.R., M.A., Aizen & L. Galetto. 2006. Nectar concentration and composition of 26 species from the temperate forest of South America. *Annals of Botany* **97**(3): 413–421.

Coder, K.D. 2010. Assessing Soil Water Resource Space. *Tree Water Availability Series, WSFNR10-11* February 2010.School of Forestry and Natural Resources, University of Georgia, pp 16.

Crane, E., P. Walker & R. Day.1984. *Directory of Important World Honey Sources*. International Bee Research Association, London, 384pp.

Ettershank, G. & J.A. Ettershank. 1993. Tasmanian leatherwoods (*Eucryphia*spp.): floral phenology and the insects associated with flowers. Tasmanian National Rainforest Conservation Program Technical Report no. 11. Forestry Commission, Tasmania and DASETT, Canberra.

FAO. 1983. Hand book on *Seeds of Dry-zone Acacias*, 101pp, www.fao.org/docrep/006/q2190e/Q2190E03. htm accessed on 12 June, 2012

Friedel, M.H., D.J. Nelson, A.D. Sparrow, J.E. Kinloch & J.R. Maconochie. 1994. Flowering and fruiting of arid zone species of acacia, in central Australia. *Australian Journal of Arid Environments* **27(3)**: 221-239. DOI: 10.1006/jare.1994.1060

Galetto, L. &G. Bernardello. 2004. Floral nectaries, nectar production dynamics and chemical composition in six *Ipomoea* species (Convolvulaceae) in relation to pollinators. *Annals of Botany* **94**: 269–280.

Harder, L.D. & S.D. Johanson. 2008. Function and evolution of aggregated pollen in angiosperms. *International Journal of Plant Science* **169**(1):59–78. DOI: 10.1086/523364

Horváth, A. & Z.S. Orosz-Kovács. 2004. Individual variability of nectar secretion in the flowers of plum cv. 'Reine-Claude d'Althan'. *Acta Horticulturae* **636**: 357-363.

Johnsons, S. D. 1992. Climatic and phylogenetic determinants of flowering seasonality in the Cape flora. *Journal of Ecology* **81**:567–572.

Johnsons, R.A. &D.W. Wichern. 2007. *Applied Multivariate Statistical Analysis*, 6th ed., Pearson Prentice Hall, Upper Saddle River, New Jersey, 773pp.

Kenrick, J., P. Bernhardt, R. Marginson, G. Beresford, R.B. Knox, I. Baker & H.G. Baker. 1987. Pollination related characteristic in the mimosoid Legume in *Acacia terminalis*. (leguminosae). *Plant Systematics and Evolution* **157:**49 – 62.

Kenrick, J. 2003. Review of pollen-pistil interactions and their relevance to reproductive biology of *Acacia. Austeralian Systematic Botany* **16**: 119 -130.

Kordofani, M. & M. Ingrouille. 1992. Geographical variation in the pollen of Acacia (Mimosaceae) in Sudan. *GRANA***31**(2):113-118.DOI: 10.1080/00173139209430730

Krüger, O. & G.C. McGavin. 1998. The insect fauna of *Acacia* species in Mkomazi Game Reserve, North east Tanzania. *Ecological Entomology* **22**: 440 -444

Le Houérou, H. 2012. *Acacia ehrenbergiana* Hayne, FAO, http://www.fao.org/ag/AGP/AGPC/doc/

Levin, D.A. & W.W. Anderson. 1970. Competition for pollinators between simultaneously flowering species. *American Naturalist* **104**: 455–467.

Mallick, S.A. 2000. Technique for washing nectar from the flowers of Tasmanian leatherwood (*Eucryphia lucida* Eucryphiaceae). *Australian Ecology* **25**: 210–212. doi:10.1046/j.1442-9993.2000.01010.x

Midgely, S.J. & J.W. Turnbul. 2003. Domestication and uses of Australian acacias: case studies of five important species. *Australian Systematic Botany* **16**: 89 -102.

Midgley, J.J. & W.J. Bond. 2001. A synthesis of the demography of African acacias. *Journal of Tropical Ecology* **17**: 871-886.

Nepi, M., M. Guarnieri & E. Pacini. 2001. Nectar secretion, reabsorption, and sugar composition in male and female flowers of *Cucurbita pepo*. *International Journal of Plant Science* **162**: 353-358.

Nuru, A., M.A. Awad, A.A. Al-Ghamdi, A.A. Abdulaziz & S.E. Radloff. 2012. Nectar of *Ziziphus spina-christi* (L.)Willd (Rhamnaceae): dynamics of secretion and potential for honey production. *Journal of Apicultural Science*, **56** (2): 49-59, doi: 10.2478/v10289-012-0023-9

Ollerton, J. & A. J. Lack. 1992. Flowering phenology: an example of relaxation of natural selection? *Trends in Ecology and Evolution* **7 (8)**:274–276. DOI: http://dx.doi.org/10.1016/0169-5347(92)90175-B

Petanidou, T. &E. Smets. 1996. Does temperature stress induce nectar secretion in Mediterranean plants. *New Phytologist* **133**: 513 – 518.

Pleasants, J.M. 1983. Structure of plant and pollinator communities. PP 375–393 *In* C. E. Jones and R. J. Little, (eds.) *Hand Book of Experimental Pollination Biology*. Van Nostrand Reinhold, New York.

Pleasants, J.M.1994. A comparison of test statistics use to detect competitive displacement in body size. *Ecology* **75**: 847-850.

Raine, N.E. 2001. The pollination ecology of a Mexican Acacia community, PhD Thesis, University of Oxford, UK.

Raine, N.E., P.G. Willmer & G.N. Stone. 2002. Spatial structuring and floral avoidance behavior prevent ant–pollinator conflict in a Mexican ant-acacia. *Ecology* **83**: 3086 – 3096.

Ross, J.H. 1981. Analysis of the African acacia species: their distribution, possible origin and relationships. *Bothalia* **13**: 389 -413.

Rathcke, B. 1983. Competition and facilitation among plants for pollination. Pages 305–329 *in* L. Real, (ed.). *Pollination Biology*. Academic Press, New York.

Rathcke, B. 1988. Flowering phenologies in a shrub community: competition and constraints. *Journal of Ecology* **76**:975– 994.

Roubik, D.W. 1991. Aspects of Africanized honey bee ecology in tropical America. P. 259-281 inM. Spivak, D.J.C. Fletcher, and M.D. Breed, editors. *The African Honey Bee*. Westview Press, Boulder.

Sedgley, M., J. Harbard, R.M.M. Smith, R. Wickneswari & A.R. Griffin. 1992. Reproductive biology and interspecific hybridization of *Acacia mangium* and *Acacia auriculiformis* A.cunn. ex Benth. (Leguminosae: Mimosaceae). *Australian Journal of Botany* **40**: 37 - 48.

Singh, K.P. & C.P. Kushwaha. 2006. Diversity of flowering and fruiting phenology of trees in a tropical deciduous forest in India. *Annals of Botany* **97**(2):265–276.

Sornsathapor, P. & J.N. Owens. 1998. Pollination biology in tropical acacia hybrid (*Acacia mangium* and *Acacia auriculiformis* A. cunn. ex Benth). *Annals of Botany* **81**: 631- 645.

StatSoft, Inc., 2010.STATISTICA, version 10.0, www.statsoft.com

Stone, G.N., W. Pat & N. Sean. 1996. Daily partitioning of pollinators in an African acacia community. *Proceedings of the Royal Society: Biological Science* **263**(1375): 1389-1393.

Stone, G.N., P.G. Willmer & J.A. Rowe. 1998. Partitioning of pollinators during flowering in an African Acacia community. *Ecology* **79**: 2808 -2827.

Stone, G.N., E.R. Nigel, P. Matthew & P.W. Pat. 2003. Pollination ecology of acacias (Fabaceae, Mimosoideae). *Australian Systematic Botany* **16:**113 -118.

Szabo, T.I. & H.G. Najda. 1985. Flowering, nectar secretion and pollen production of some legumes in the Peace River Region of Alberta, Canada. *Journal of Apicultural Research* **24** (2): 102-106.

Tandon, R. & K.R. Shivanna. 2001. Pollination biology and breeding system of Acacia in Senegal. *Botanical Journal of the Linnean Society* **135**: 251-262. doi:10.1006/bo.i1.2000.0401.

Tantawy, M.E., S.F. Khalifa, K.A. Ahmed & H.M. Elazab. 2005. Palynological Study on Some Taxa of Mimosoideae (Leguminosae). *International Journal of Agriculture and Biology*. 1560–8530/2005/07–6–857–868.http://www.ijab.org accessed on July 2012

Tybirk, K. 1993. Pollination, breeding system and seed abortion in some African acacias. *Botanical Journal of the Linnean Society* **112**: 107-137.

UNESCO.1977. Map of the *World Distribution of Arid Regions*. MAB Technical Note 7. UNESCO, Paris.

Walter, H. & S.W. Breckle. 1986. Ecological systems of the geobiosphere.Vol. 2, Tropical and Subtropical Zonobiomes. Springer-Verglag, Berlin, Heidelburg.

Waser, N. M. 1982. A comparison of distances flown by different visitors to flowers of the same species. *Oecologia* (Berlin) **55**:251–257.

Weast, R. (ed.) 1986. *CRC Handbook of Chemistry and Physics,* 67th ed., CRC Press, Inc., Boca Raton, Florida.

Wickens, G. E. 1995. Role of Acacia species in the rural economy of dry Africa and the Near East. FAO Conservation Guide **27**, pp137 http://www.fao.org/docrep/V5360E/V5360E00.htmaccessed on May 25 2012.

Williams, M.R. 1995. Critical values of a statistic to detect competitive displacement. *Ecology* **76**: 646-647.

Willmer, P.G. & G.N, Stone. 1997. Ant deterrence in Acacia flowers: Aggressive ant-guards assist seed-set. *Nature* **388**: 165-167.

Wyatt, R., S.B. Broyles & G.S. Derda. 1992. Environmental influences on nectar production in milkweeds (*Ascelapiassyriaca*and *A. exaltata*). *American Journal of Botany* **79**: 636–642.

Zajácz, E., Á.Zaják, E. Szalai-Mátray&T. Szalai.2006. Nectar production of some sunflower hybrids. *Journal of Apicultural Science* **50**(2): 7-11.

Zsidei, B. 1993. *Méhészetiismeretek*.Fazekasésfiainyomdája, Szarvas.Pp. 125-151 inFarkas, A. &Zajácz, E. (reviewed). 2007. *Nectar Production for the Hungarian Honey Industry*.*The European Journal of Plant Science and Biotechnology*. Global Science Book.

Table 1. Mixed-effects analysis of variance (ANOVA) results for the amount of nectar sugar/flower head as the response variable; location, species and time of day (hours) as fixed factors; and trees as a random factor.

Source	**Type**	**SS**	***df***	**MS**	**Den. Syn. Error *df***	**Den. Syn. Error MS**	***F*-value**	***P*-value**
Intercept	Fixed	11278.54	1	11278.54	2.007	19.424	580.635	0.0017
1 Locality	Fixed	356.35	1	356.35	14.539	0.058	6180.064	<0.0001
2 Species	Fixed	2672.25	1	2672.25	2.011	13.540	197.359	0.0049
3 Tree	Random	38.95	2	19.47	0.035	5.483	3.551	0.9106
4 Hours	Fixed	967.05	4	241.76	8.027	36.704	6.587	0.0119
Locality*Species	Fixed	226.93	1	226.93	2.005	32.574	6.967	0.1183
Locality*Tree	Random	0.04	2	0.02	1.867	32.748	0.001	0.9993
Species*Tree	Random	27.13	2	13.56	1.787	31.969	0.424	0.7067
Locality*Hours	Fixed	209.80	4	52.45	8.078	12.825	4.090	0.0424
Species*Hours	Fixed	308.02	4	77.01	8.083	12.045	6.393	0.0128
Tree*Hours	Random	295.32	8	36.91	2.485	12.142	3.040	0.2291
Locality*Species*Tree	Random	65.36	2	32.68	8.083	12.755	2.562	0.1375
Locality*Species*Hours	Fixed	116.04	4	29.01	8.078	12.756	2.274	0.1492
Locality*Tree*Hours	Random	102.87	8	12.86	8.000	12.789	1.005	0.4971
Species*Tree*Hours	Random	96.58	8	12.07	8.000	12.789	0.944	0.5315
1*2*3*4	Random	102.31	8	12.79	840.000	8.361	1.530	0.1429
Error		7023.50	840	8.36				

Figure legends

Fig. 1. The peak flowering period distribution of the *A. ehrenbergiana* and *A. tortilis* in the lowland and midland habitats (1st, 2nd, etc. are the weeks of the months).

Fig. 2. Peak pollen release times of the two species based on the polyad-to-anther ratio at different times; A = *A. tortilis* trees, B = *A. ehrenbergiana* trees.

Fig. 3.*A. ehrenbergiana* (A) and *A. tortilis* (B) showing inflorescences with different flowering stages (from flower buds to full opened stages) and individual floret with and without female part and forager honeybees sucking nectar.

Fig. 4.Average amount of nectar sugar secreted for (a) *A. ehrenbergiana* and (b) *A. tortilis*.

Fig.5 Average amounts of accumulated nectar sugar (mg/flower head) at different localities and time periods for *A. ehrenbergiana* and *A. tortilis*.

Fig. 6.Variations in the average amount of nectar sugar secreted per day (mean ±s.d.) in individual trees (1,2,3,…,13), (A.e = *A. ehrenbergiana,* A.t = *A. tortilis,* Kah= WadiKahla, and Alkah = Wadi Alkhatani).

Fig. 7.Types and frequency of flower visitors at different times of a day for the two acacia species.

The observations were performed on a 1 × 1m portion of a branch.

Fig. 8. Flower visitors that were associated with only *A. ehrenbergiana* flowers. (a) *Xylocopa sp*., (b)Halictidae (c)*Vespa orientalis,* and (d) nectar-feeding bird.

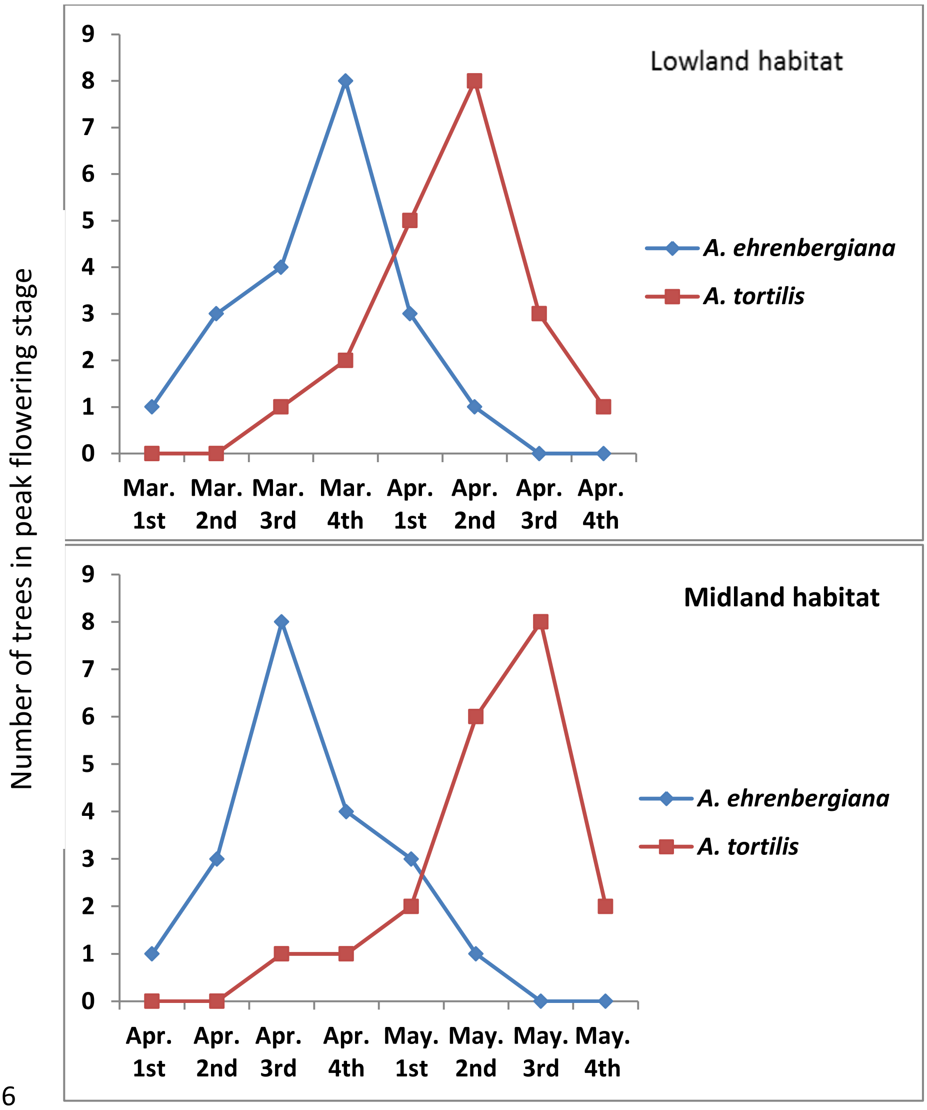
Number of trees in peak flowering stage
Lowland habitat
9
8
7
6
5
4
3
2
1
0
Mar. 1st
Mar. 2nd
Mar. 3rd
Mar. 4th
Apr. 1st
Apr. 2nd
Apr. 3rd
Apr. 4th
A. ehrenbergiana
A. tortilis
Midland habitat
9
8
7
6
5
4
3
2
1
0
Apr. 1st
Apr. 2nd
Apr. 3rd
Apr. 4th
May. 1st
May. 2nd
May. 3rd
May. 4th
A. ehrenbergiana
A. tortilis

Fig.1.

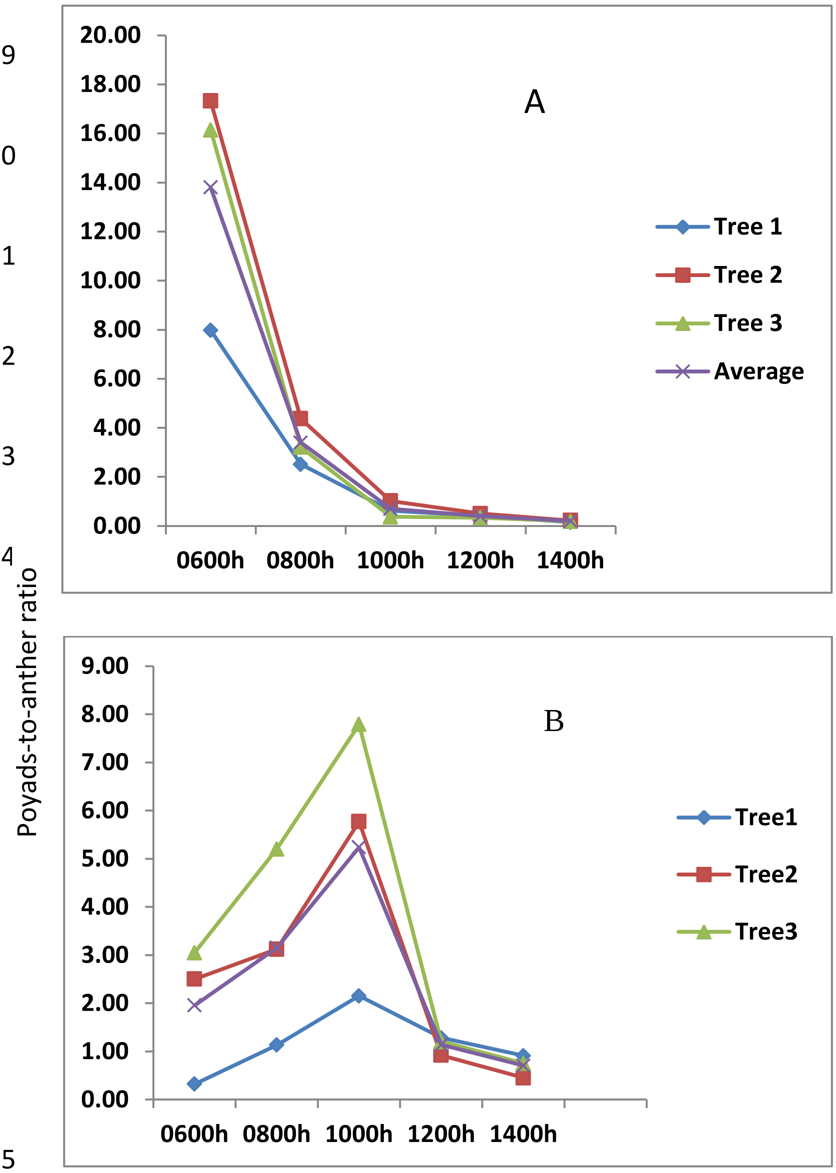
A
Poyads-to-anther ratio
20.00
18.00
16.00
14.00
12.00
10.00
8.00
6.00
4.00
2.00
0.00
0600h
0800h
1000h
1200h
1400h
Tree 1
Tree 2
Tree 3
Average
B
9.00
8.00
7.00
6.00
5.00
4.00
3.00
2.00
1.00
0.00
0600h
0800h
1000h
1200h
1400h
Tree1
Tree2
Tree3

Fig. 2.

Fig. 3.

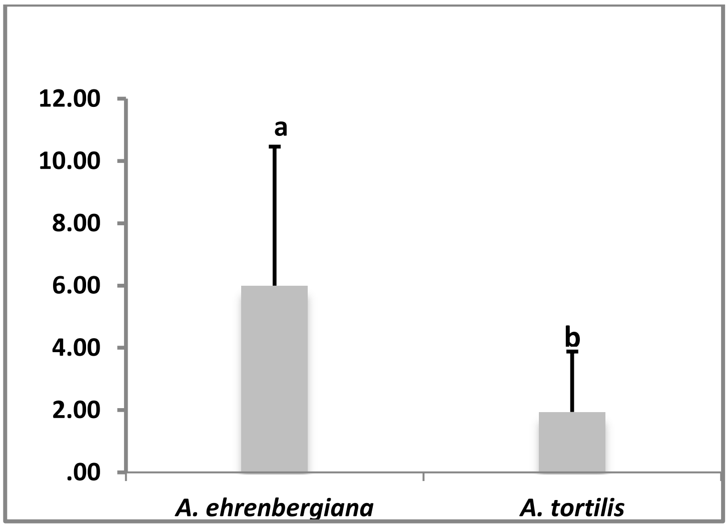

Fig. 4.

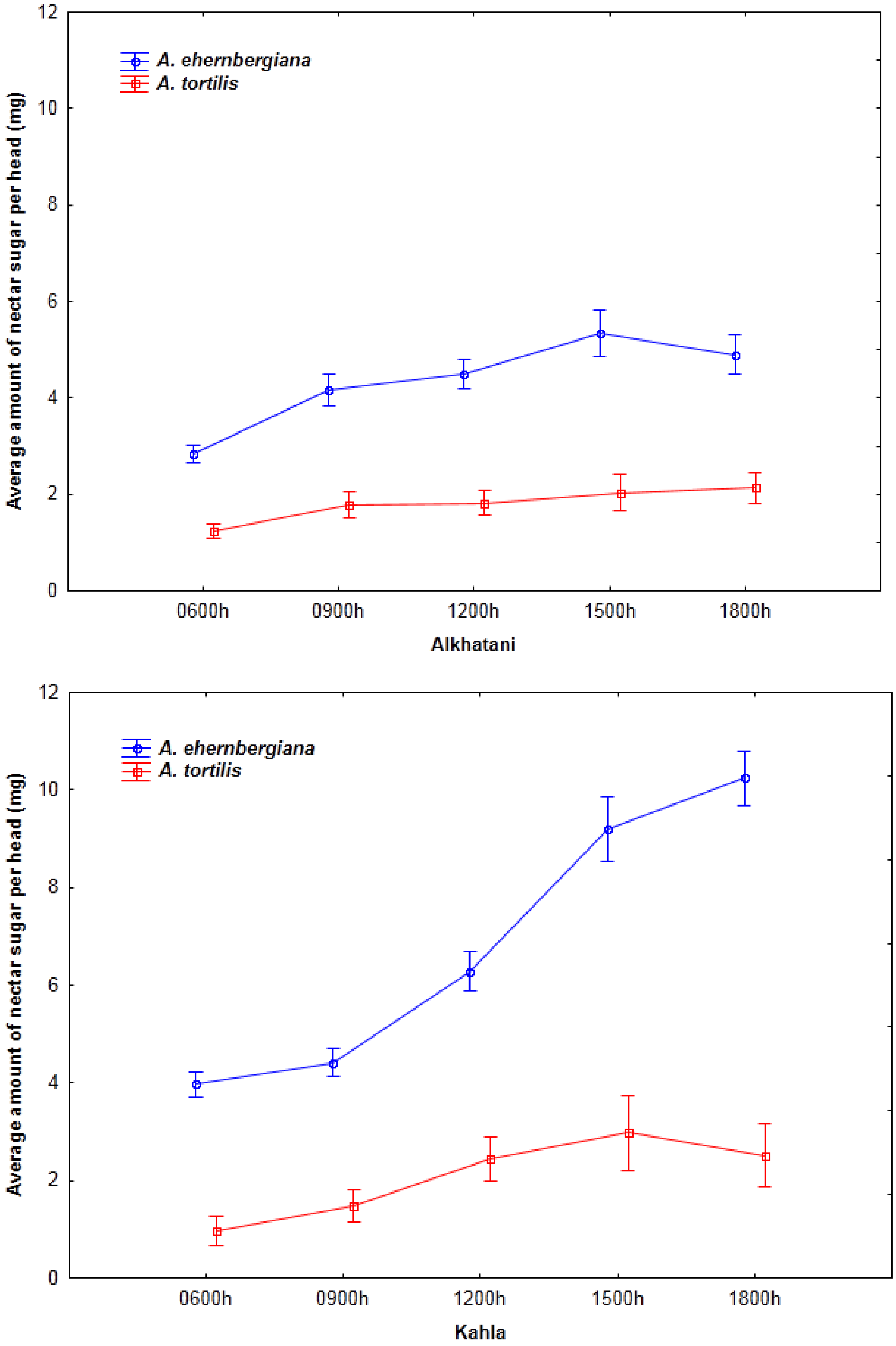
A. ehernbergiana
A. tortilis
Average amount of nectar sugar per head (mg)
0
2
4
6
8
10
12
0600h
0900h
1200h
1500h
1800h
Alkhatani
A. ehernbergiana
A. tortilis
Average amount of nectar sugar per head (mg)
0
2
4
6
8
10
12
0600h
0900h
1200h
1500h
1800h
Kahla

Fig. 5.

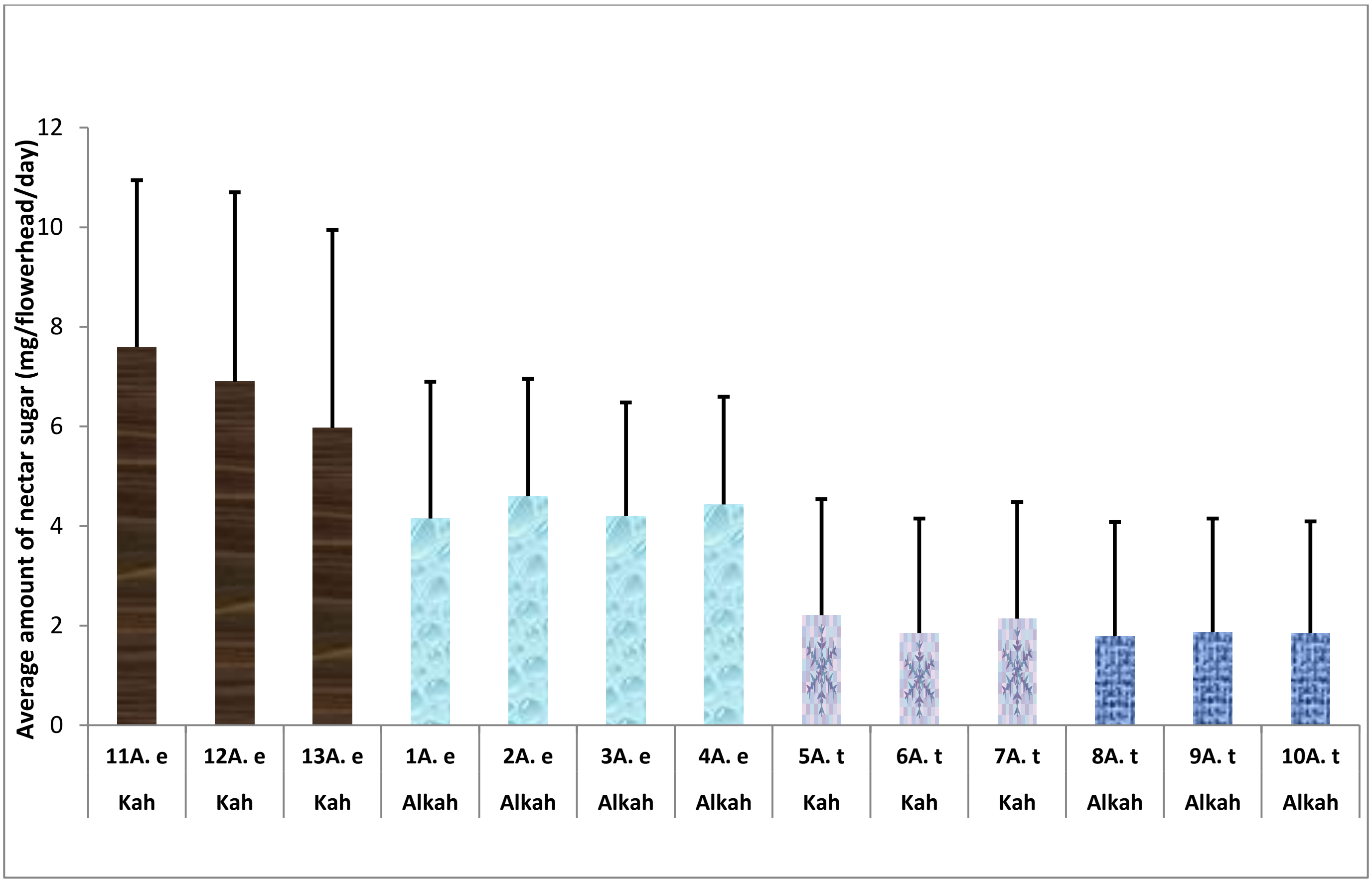
Average amount of nectar sugar (mg/flowerhead/day)
12
10
8
6
4
2
0
11A. e Kah
12A. e Kah
13A. e Kah
1A. e Alkah
2A. e Alkah
3A. e Alkah
4A. e Alkah
5A. t Kah
6A. t Kah
7A. t Kah
8A. t Alkah
9A. t Alkah
10A. t Alkah

Fig. 6

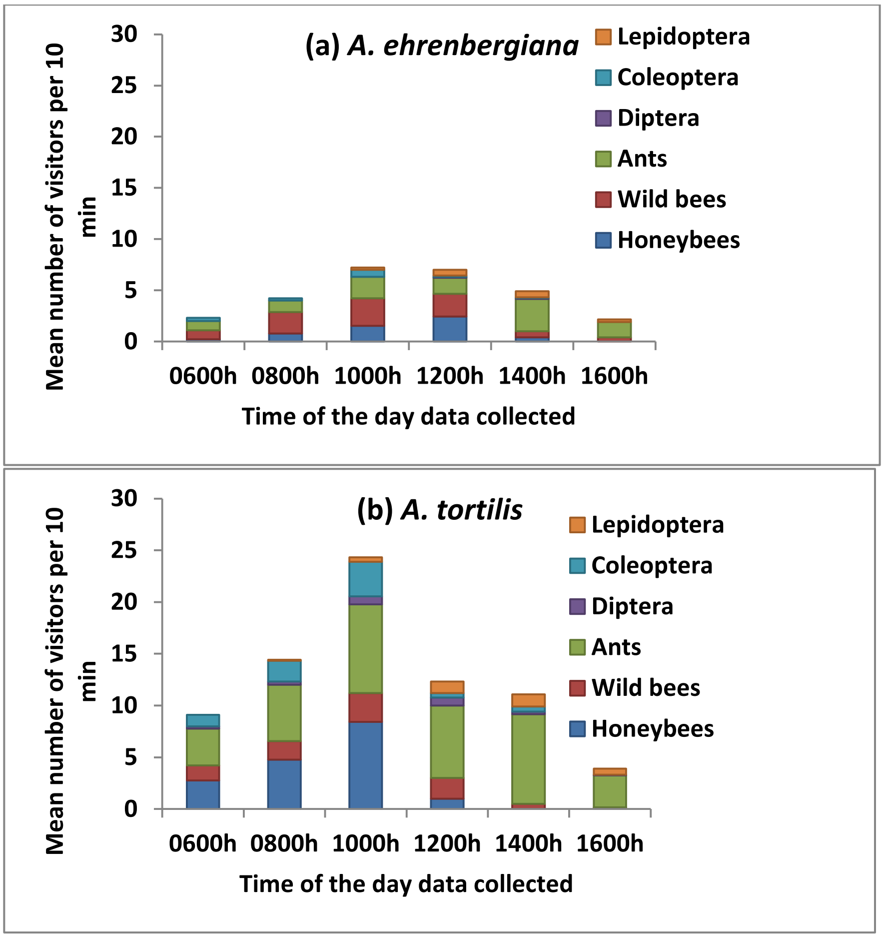
(a) A. ehrenbergiana
Mean number of visitors per 10 min
30
25
20
15
10
5
0
0600h
0800h
1000h
1200h
1400h
1600h
Time of the day data collected
Lepidoptera
Coleoptera
Diptera
Ants
Wild bees
Honeybees
(b) A. tortilis
Mean number of visitors per 10 min
30
25
20
15
10
5
0
0600h
0800h
1000h
1200h
1400h
1600h
Time of the day data collected
Lepidoptera
Coleoptera
Diptera
Ants
Wild bees
Honeybees

Fig. 7.

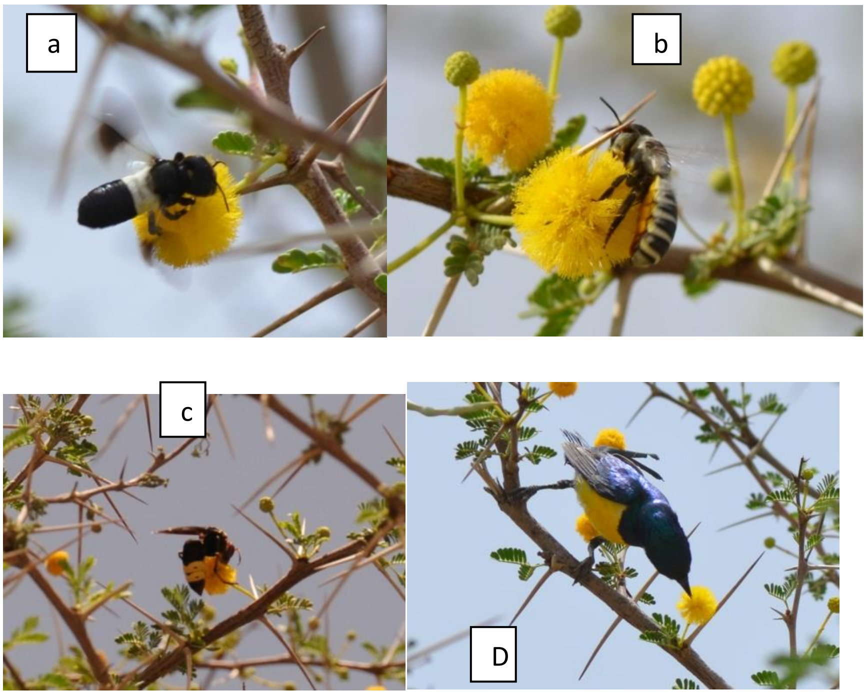
a
b
c
D

Fig. 8.