

Foraging trip duration and density of megachilid bees, eumenid wasps and pompilid wasps in tropical agroforestry systems

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Summary

1. Most animals have to bridge some distances in space and time to provide all resources necessary for survival. Little is known about how the local and regional management of tropical agroforestry systems, differing in the availability of food resources and suitable nesting sites, determine foraging trip duration and density of bees and wasps (Hymenoptera Aculeata).

2. In this study, foraging trip duration and brood-cell density (in trap nests exposed for a 15-month period) were analysed for three species, which represent three guilds in 24 agroforestry systems in Central Sulawesi (Indonesia): the pollinator *Heriades* sp. aff. *fulvescens* (Apidae), the cacao caterpillar-hunting predator *Rhynchium haemorrhoidale umeroatrum* (Eumenidae) and the spider-hunting predator *Auplopus levicarinatus* (Pompilidae). The agroforestry systems were characterized by plant species richness, blossom cover of herbs, light intensity and distance from the nearest natural forest.

3. The correlation of foraging time to bee and wasp density showed the relative importance of food and nest-site availability for the pollinator and the spider-hunting predator, because both parameters are correlated with light intensity in the agroforestry systems. In contrast, foraging time and nest density of the eumenid predator were not correlated because of the distance between high quantities of food resources (in sites with dense cacao plants) and nesting sites (in adjacent natural forests).

4. The eumenid response to local and regional agroforestry management illustrates that species may survive only in landscapes that permit access to a multiple set of resources. Accordingly, habitat evaluations using only foraging time may lead to wrong conclusions, as key drivers of population dynamics may not be inside but outside the local systems, emphasizing the need for a landscape approach.

Key-words: bioindication, landscape ecology, pollination, predation, trap nests.

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Introduction

Most animals have to bridge some distances in space and time to provide all resources necessary for survival. Many birds forage in the open landscape but breed inside forests (Tworek 2002), butterfly adults search for nourishing flowers (Feber, Smith & Macdonald 1996), but also for food plants suitable for their offspring (Thomas *et al.* 2001) and the host searching behaviour

of adult parasitoids is influenced by their food resources such as nectar (Patt, Hamilton & Lashomb 1997; cf. Bunce & Howard 1990). Many species survive only in landscapes that provide access to multiple required resources (Dunning, Danielson & Pulliam 1992).

The global change in habitat destruction and patterns of habitat fragmentation (Tilman *et al.* 2001) should especially affect species using multiple and spatio-temporally separated resources such as flower-visiting bees and wasps (Cane 2001). In tropical landscapes, logging activities with high collateral damage or a conversion of rain forest to agroforestry and even non-shaded cropland is still increasing (Laurance 2000). In an area of such unprecedented land conversion, knowledge of the

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relative importance of land-use systems for conservation seems to be important, in particular for conservation of species that depend on a certain spatial arrangement of habitat types. Traditionally managed systems with several shade tree species may provide diversified resources, because of their near-natural complexity and plant diversity (Perfecto *et al.* 1996; Klein, Steffan-Dewenter & Tschardt 2003a,b). In Central Sulawesi (Indonesia), the focus area of this study, crops are managed mainly in a traditional, diversified way and, in addition, landscapes are made up of land-use types such as agroforestry and more or less distant remnants of natural forest.

Habitats of bees and wasps must provide suitable nesting sites and food resources within their foraging range to ensure successful reproduction (Sutherland 1996; Westrich 1996; Strohm & Marliani 2002; Goodell 2003). In many cases, the foraging range of bees and wasps is not restricted to the direct neighbourhood of their nesting habitat, as the surrounding landscape also offers important additional sources of food plants and nesting sites. For instance, foraging activity of stingless bees benefits strongly from increased foraging habitat diversity (Eltz & Brühl 2002), and Steffan-Dewenter & Kuhn 2003 found larger foraging distances of pollen-collecting honeybees in simple than in complex landscapes. Honeybees are known to cover much larger foraging distances than solitary bees, but the latter are still not confined to small habitat patches (Gathmann & Tschardt 2002; Steffan-Dewenter *et al.* 2002) and are often important plant pollinators (Corbet, Williams & Osborne 1991; Vinson, Frankie & Barthell 1993; Batra 1995). Above-ground nesting solitary species, which colonize trap nests, depend on holes of appropriate diameter left by wood-boring beetles and pithy or hollow plant stems of a suitable diameter (Westrich 1996; Cane 2001). In addition, these species require resources for nest building such as mud, resins, pebbles or plant hairs, which they use to line, partition and plug their nests (O'Toole & Raw 1991). The foraging trip distance can be measured indirectly with the foraging trip duration, to draw conclusions on the quality of the bees' and wasps' habitat (Gathmann & Tschardt 2002; Strohm *et al.* 2002). Prolonged searching for food or suitable nesting sites is an expensive activity in terms of time and energy, so that any behaviour that makes this process more efficient will be selected. Female bees often learn the position and habitat quality of their natal nest and return to it when founding their own nests (Jayasingh & Freeman 1980; A.M. Klein, personal observation). This type of limited dispersal behaviour is likely to evolve when there is a fitness advantage in selecting the most favourable nest sites in a habitat of high quality (Potts & Willmer 1997).

The community of trap-nesting bees and wasps is known to contain species with different habitat demands (Tschardt, Gathmann & Steffan-Dewenter 1998). Bees feed their larvae with pollen or nectar, whereas wasps feed their larvae with paralysed arthropods. Trap-nesting bees and wasps may increase seed set of

allogamous plants due to successful pollination by bees and biological control by predacious wasps (Tschardt *et al.* 1998). For example, *Ancistrocerus gazella* Panzer, a trap-nesting eumenid wasp species, was found to control pest caterpillars in New Zealand (Harris 1994). Other trap-nesting wasps, such as sphecids or pompilids, prey on spiders, so they are predators of higher trophic level that may interfere with the potential control exhibited by their prey (Okuyama 2002).

Foraging trip duration and successful reproduction in exposed trap nests were measured for (1) one bee species that provides its larvae with pollen, (2) one eumenid wasp species that provides its larvae with pest caterpillars feeding on cacao leaves and (3) one pompilid wasp species that provides its larvae with spiders, thereby acting as a predator of higher trophic levels. Agroforestry systems, differing in light intensity, plant diversity and distance from the nearest natural forest, were evaluated with these three trap-nesting hymenoptera. The following hypotheses were tested: (i) foraging trip duration depends on the food availability of the agroforestry systems and its regional neighbourhood, i.e. the availability of adjacent natural rain forest and (ii) brood cell density is related not only to food but also to the availability of nesting sites, both determining overall densities of bees and wasps.

Data on foraging trip duration and successful reproduction of these bees and wasps may help to understand distribution patterns in species depending on multiple resources, which is a prerequisite in the development of conservation strategies for local and regional agroforestry management.

Materials and methods

STUDY REGION AND SITES

The study was conducted from January 2001 to March 2002 in the vicinity of the Lore-Lindu National Park, in Central Sulawesi (Indonesia, see Klein *et al.* 2003). Twenty-four agroforestry systems, dominated by coffee but with different shade levels, vegetational and structural complexity, were studied. The light intensity (and therefore the shade ratio) per agroforestry system was measured with a luxmeter and the distance to the nearest natural forest with GPS (for more detailed information see Klein *et al.* 2003). The vegetation was mapped between November 2000 and January 2001 in two separated, randomized 25 m² plots per study field for herbs and within two separated, randomized 100 m² plots for shrubs and trees. All four plots were marked with a wooden stake and characterized at the same time per study field, resulting in estimates of the number of total plant species and the percentage of vegetation cover. Percentage cover of flowering plants was recorded for each system to estimate the resource availability for the pollen-collecting bee species between July and September, at the same time as the foraging trip durations were measured.

TRAP NESTS

Trap nests for Hymenoptera: Apidae, Sphecidae, Eumenidae, Pompilidae and their enemies were set up in January 2001 and removed in March 2002. Ten trap nests for each of the 24 agroforestry systems were hung with a solid wire in coffee, cocoa or shade trees (such as *Erythrina* sp. or *Gliricidia* sp.) at a height of 1.5 m to 2 m. Sticky glue was put onto each wire outside the trap nests to deter ants. The traps consisted of about 120 internodes of a mixture of common reed *Phragmites australis* (Cav.) Trin. and Japanese knotweed *Reynoutria japonica* Houtt, cut to a length of 20 cm and inserted into plastic tubes of 10.5 cm diameter and a length of 25 cm. The range of internal diameters of the reed or knotweed internodes varied between 2 mm and 20 mm. One month after the traps were set up, all occupied internodes were replaced monthly with unoccupied new internodes of a similar diameter. Nests were opened in the laboratory to make a preliminary identification of species and to establish the number of brood cells per species.

FORAGING TRIP DURATION

The three most common trap-nesting species, *Heriades* (*Michenerella*) sp. aff. *fulvescens* Cockerell (Megachilidae), *Rhynchium haemorrhoidale umeroatrum* Gusenleitner (Eumenidae) and *Auplopus levicarinatus* Wahis (Pompilidae), had already used the trap nests in the first month after exposure (February 2001). The foraging behaviour was observed from July to September 2001 between 9.00 a.m. and 3.00 p.m. of the three species in all 24 agroforestry systems. Observation was carried out while the weather was dry and sunny, because on cloudy and rainy days the foraging activity of trap-nesting bees and wasps was in general very low. Minor variations between the foraging time for every hour of the 6 h occurred. In a general linear model, the importance of day time and habitat characteristics (blossom cover, light intensity, forest distance and cacao cover for the pest-hunting species) were tested. The diurnal variation of the foraging activity was of minor importance in contrast to the tested habitat factors in all three species (Table 1). Therefore, in the Results section the focus is mainly on the mean value of the foraging time per agroforestry system and the agroforestry characteristics. The nest of each observed female was marked with acrylic colour. With a stopwatch, (1) the time an individual remained inside the nest between its arrival and departure for the next foraging trip and (2) the period between an individual has left the nest until its next return (= the foraging time) was measured. The type of material the individual collected was identified: (a) caterpillars, spiders or pollen as food and (b) nesting material such as soil, leaves or wood resin to construct the nest. Each of the three target species was observed for at least 10 arrival times per site. *R. haemorrhoidale* activity was observed in all 24, *A. levicarinatus* in 23 and *H. fulvescens* in 19 sites. Because of low density, *A.*

Table 1. Effects of blossom cover, light intensity, forest distance, day time and additionally cacao cover for the pest-hunting species, on the foraging time of (a) *H. fulvescens*, (b) *R. haemorrhoidale* and (c) *A. levicarinatus*. The results are of a general linear model analyses for all sources of variation and the complete model are given. We observed 534 species of *H. fulvescens* ($n = 534$), 288 species of *R. haemorrhoidale* ($n = 288$) and 287 species of *A. levicarinatus* ($n = 287$)

| Source of variation | d.f. | MS | F | P |
|-------------------------------------|------|--------|--------|---------|
| (a) <i>H. fulvescens</i> | | | | |
| Blossom cover (%) | 1 | 35.69 | 8.89 | 0.003 |
| Light intensity (W/m ²) | 1 | 8.91 | 2.22 | 0.137 |
| Forest distance (m) | 1 | 0.77 | 0.19 | 0.662 |
| Day time (h) | 1 | 2.12 | 0.53 | 0.467 |
| Model with all variables | 4 | 96.67 | 24.08 | < 0.001 |
| (b) <i>R. haemorrhoidale</i> | | | | |
| Blossom cover (%) | 1 | 143.96 | 9.86 | 0.002 |
| Light intensity (W/m ²) | 1 | 187.99 | 12.87 | < 0.001 |
| Forest distance (m) | 1 | 0.34 | 0.02 | 0.879 |
| Day time (h) | 1 | 1.59 | 0.11 | 0.742 |
| Cacao cover (%) | 1 | 653.16 | 44.71 | < 0.001 |
| Model with all variables | 5 | 169.81 | 11.62 | < 0.001 |
| (c) <i>A. levicarinatus</i> | | | | |
| Blossom cover (%) | 1 | 2.62 | 1.01 | 0.316 |
| Light intensity (W/m ²) | 1 | 790.18 | 303.97 | < 0.001 |
| Forest distance (m) | 1 | 20.57 | 7.91 | 0.005 |
| Day time (h) | 1 | 9.61 | 3.70 | 0.056 |
| Model with all variables | 4 | 384.85 | 148.04 | < 0.001 |

levicarinatus and *H. fulvescens* could not be observed during foraging in all 24 sites and *H. fulvescens* was even absent in some sites.

ANALYSES

Mean foraging times of all individuals observed in each site were used to present the data. The data were analysed using the software Statgraphics Plus for Windows 3.0 (Statgraphics 1997). All data were tested for normality and transformed if necessary. The independent variable 'forest distance' was always square root-transformed to achieve normal distribution; all other variables were distributed normally (Sokal & Rohlf 1995). Intercorrelations between the four independent habitat parameters forest distance, light intensity, blossom cover and plant species richness were tested using a Pearson correlation matrix (Table 2). In stepwise multiple regression analyses with backward selection, for each species the independent habitat factor that was most important for the foraging time was examined. Light intensity and blossom cover were not used simultaneously because of their high intercorrelation. For the caterpillar-hunting species the percentage of cacao cover was included in the analyses as a further habitat parameter, because the predated caterpillars were feeding on cacao leaves. Multiple regression analyses related the mean number of brood cells found in the 15 months for all of the three species to forest distance, light intensity and plant species richness.

Table 2. Pearson correlation matrix based on simple linear regression between habitat parameters. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$, $n = 15$

| | Forest distance (m) | Light intensity (W/m ²) | Blossom cover (%) |
|-------------------------------------|---------------------|-------------------------------------|-------------------|
| Forest distance (m) | | | |
| Light intensity (W/m ²) | -0.32 NS | | |
| Blossom cover (%) | -0.33 NS | 0.74*** | |
| Plant species richness | -0.46 NS | 0.44* | 0.42* |

Table 3. Mean foraging times of the pollen-collecting bee *H. fulvescens*, the caterpillar-hunting wasp *R. haemorrhoidale*, and the spider-hunting wasp *A. levicarinatus*. The mean trip duration for collecting different nesting material, and the number of parasitoids observed entering the nest are presented

| | <i>Heriades</i> | <i>Rhynchium</i> | <i>Auplopus</i> |
|---|-----------------|------------------|-----------------|
| Individuals observed with food | 107 | 109 | 105 |
| Number of observed foraging flights with food | 415 | 278 | 286 |
| Mean foraging time (min) | 2.68 ± 0.11 | 5.57 ± 0.20 | 3.82 ± 0.35 |
| Individuals observed with soil | 11 | 31 | 16 |
| Number of observed foraging flights with soil | 49 | 105 | 31 |
| Mean time collecting soil (min) | 1.30 ± 0.24 | 1.68 ± 0.21 | 1.86 ± 0.47 |
| Individuals observed with wood resin | 16 | – | 40 |
| Number of observed foraging flights with wood resin | 59 | – | 136 |
| Mean time collecting wood resin (min) | 1.80 ± 0.21 | – | 2.60 ± 0.27 |
| Individuals observed with other building materials | – | – | 6 |
| Number of observed foraging flights with other material | – | – | 25 |
| Mean time collecting other materials (min) | – | – | 0.88 ± 0.18 |
| Mean value turn up pollen (min) | 0.40 ± 0.13 | – | – |

The blossom cover for the explanation of brood-cell density was not used, because it was measured only during foraging observations and changed greatly between months because of the seasonal blooming periods of crop and noncrop plants. Simple linear regression models were shown when the multiple regression model is explained by only one factor. Arithmetic means ± standard errors are presented.

Results

A total of 240 trap nests (10 traps from each of the 24 agroforestry systems) resulted in 14 trap-nesting bee and wasp species with 13617 individuals (Klein *et al.* in preparation). Ninety-three per cent of all brood cells were occupied by the three species studied here: the bee *Heriades (Michenerella)* sp. aff. *fulvescens* (Megachilidae) was reared from 671 nests with 2754 individuals, the eumenid wasp *Rhynchium haemorrhoidale umeroatrum* (Eumenidae) was reared from 849 nests with 2326 individuals and the spider wasp *Auplopus levicarinatus* (Pompilidae) was reared from 2348 nests with 7567 individuals, respectively.

HERIADES (MICHENERELLA) SP. AFF. FULVESCENS

A total of 107 pollen-collecting female individuals and 415 foraging flights were observed. The bees needed more

time to collect pollen or nectar as food for their larvae and for their own activity than for the collection of soil or wood resin to construct their nests. In most cases an individual bee entered the nest moving forward, turned back to the entrance, and re-entered moving backward. Most probably the bee delivered the nectar first and then put the pollen off the ventral brush (Table 3).

The effect of the habitat factors forest distance, plant species richness and blossom cover on foraging time was tested using multiple regression analysis. Blossom cover was the only explanatory factor and foraging time decreased with increasing blossom cover (89.0%; see the simple regression, Fig. 1a). In a multiple model with light intensity instead of blossom cover, the foraging time decreased with increasing light intensity (79%; see the simple regression, Fig. 1b). The bee species foraged primarily on a common species of Asteraceae within the study sites, but also foraged on coffee plants when they were flowering. Neither the plant species richness ($r^2 = 0.03$, $n = 19$, $P = 0.948$) nor the forest distance ($r^2 = 9.02$, $n = 19$, $P = 0.212$) were correlated with the foraging time. The mean number of all brood cells reared in a total of 15 months per system was also correlated positively with light intensity (Fig. 1c), but neither with forest distance ($r^2 = 3.41$, $n = 19$, $P = 0.449$) nor plant diversity ($r^2 = 0.21$, $n = 19$, $P = 0.390$). The number of brood cells was related negatively to the foraging time, but with only marginal significance ($r^2 = 0.17$, $n = 19$, $P = 0.08$).

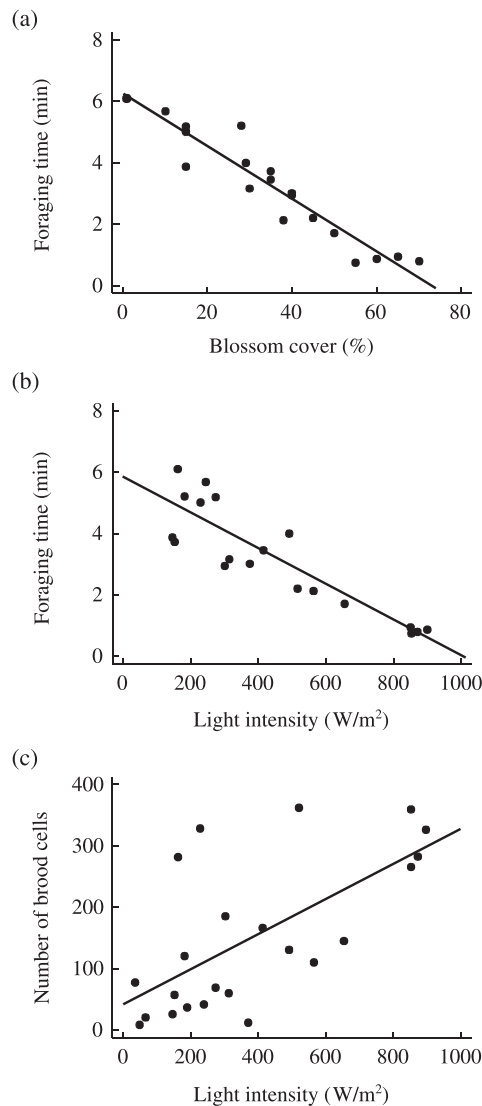


Fig. 1. (a) Relationship between the foraging time of *H. fulvescens* and the blossom cover: $y = 6.24 - 0.09x$, $r^2 = 0.89$, $n = 19$, $P < 0.001$. (b) Relationship between the foraging time of *H. fulvescens* and the light intensity: $y = 5.71 - 0.01x$, $r^2 = 0.79$, $n = 19$, $P < 0.001$. (c) Relationship between the number of brood cells of *H. fulvescens* and the light intensity: $y = 41.03 + 0.29x$, $r^2 = 0.42$, $n = 23$, $P < 0.001$.

RHYNCHIUM HAEMORRHOIDALE
UMEROATRUM

A total of 109 caterpillar-hunting female individuals and a total of 278 foraging flights were observed. The wasps needed around 4 min more for collecting caterpillars than for the collection of soil for nest building (Table 3).

The effect of the habitat factors forest distance, plant species richness, blossom cover and, separately, light intensity on foraging time was also tested using multiple regression analyses. The percentage of cacao cover was also included in the analyses, because the predated caterpillars were feeding on cacao leaves. Foraging time decreased significantly with increasing cacao cover of the agroforestry systems and was the only significant factor

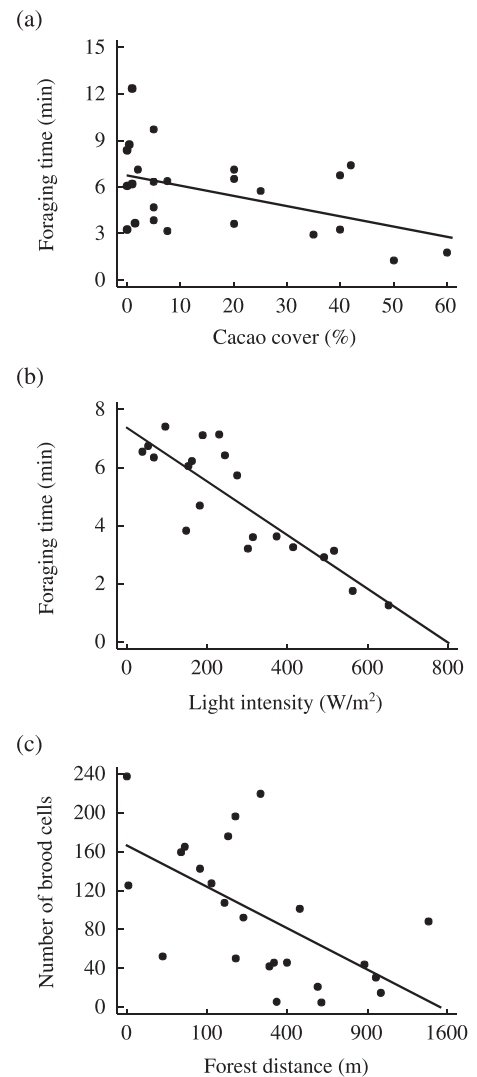


Fig. 2. (a) Relationship between the foraging time of *R. haemorrhoidale* and the cacao cover: $y = 6.67 - 0.06x$, $r^2 = 0.21$, $n = 24$, $P = 0.022$. (b) Relationship between the foraging time of *R. haemorrhoidale* and the light intensity (excluding agroforestry systems without intercropped cacao plants): $y = 7.37 - 0.01x$, $r^2 = 0.74$, $n = 20$, $P < 0.001$. (c) Relationship between the number of brood cells of *R. haemorrhoidale* and the forest distance: $y = 165.77 - 4.24x$, $r^2 = 0.36$, $n = 23$, $P = 0.002$.

in the multiple model (21%; see the simple regression, Fig. 2a). Forest distance ($r^2 = 0.12$, $n = 24$, $P = 0.873$), plant species richness ($r^2 = 3.66$, $n = 24$, $P = 0.370$), blossom cover ($r^2 = 2.84$, $n = 24$, $P = 0.432$) and light intensity ($r^2 = 5.82$, $n = 24$, $P = 0.256$) were not correlated significantly with foraging time. Excluding four agroforestry systems that had no cacao plants, the foraging time – also tested in a multiple model with light intensity, forest distance and plant diversity – decreased with increasing light intensity (74%; see the simple regression, Fig. 2b) and with blossom cover of the agroforestry systems (21%) when tested with blossom cover instead of light intensity. The mean number of all brood cells reared in 15 months decreased with increasing forest distance (36%; see the simple regression, Fig. 2c), and was not related to light intensity ($r^2 = 9.70$, $n = 24$, $P = 0.139$)

and plant diversity ($r^2 = 1.16$, $n = 24$, $P = 0.616$). The number of brood cells was not correlated with the foraging time ($r^2 = 0.03$, $n = 19$, $P = 0.401$).

AUPLONUS LEVICARINATUS

A total of 105 female pompilids and a total of 286 foraging flights were observed. On average, this wasp species needed 2 min longer for spider collection than for the collection of soil. The collection of wood resin was only around 1 min faster than the spider collection. The collection of other materials was very fast; most of them were remains of empty internodes that were occupied already by other individuals and species. This included dry soil, leaves, reed or knotweed remainders, dead spiders, caterpillars or larvae (Table 3).

In multiple regression analyses, the foraging time increased significantly only with increasing light intensity (88%; see the simple regression, Fig. 3) and increasing forest distance, but only when tested in a simple regression analysis ($r^2 = 0.18$, $n = 23$, $P = 0.045$). In simple regression analyses the foraging time even increased with increasing plant species richness ($r^2 = 16.18$, $n = 23$, $P = 0.053$) and blossom cover ($r^2 = 43.69$, $n = 23$, $P < 0.001$). The number of brood cells per system decreased with increasing light intensity only in the multiple model (28%; see simple regression, Fig. 3b), and was related to plant diversity in a simple model ($r^2 = 17.41$, $n = 23$, $P = 0.043$), but not to forest distance ($r^2 = 3.18$, $n = 23$, $P = 0.404$). The

number of brood cells was correlated negatively with the foraging time in a simple regression analysis ($r^2 = 0.18$, $n = 23$, $P = 0.037$).

Discussion

In a comparison of the foraging time and density of three trap-nesting species from three ecological guilds (pollinator, predator of pests and predator of higher trophic levels) light intensity, blossom cover and distance from the nearest natural forest emerged as important characteristics of the studied agroforestry systems. As expected, foraging time of all species appeared to be influenced strongly by the availability of food for their offspring.

The foraging time of the pollen-collecting bee species *H. fulvescens* was correlated negatively with the blossom cover of flowering plants and light intensity of agroforestry systems. This is in support of the expectation that two major factors determine foraging behaviour and activity patterns in nectar and pollen foraging insects: first, microclimatic conditions influence the foraging behaviour and activity of bees (Corbet *et al.* 1993; Stone 1994; Stone, Loder & Blackburn, 1995; Stone *et al.* 1999; Bosch & Kemp 2002). In the morning and on cloudy days, individuals of *H. fulvescens* rested in the entrance of their nest. As soon as the sunlight reached their nest, the bees began to forage pollen and nectar for their larvae and themselves (A.M. Klein, personal observation). Similarly, the nesting activity of *Osmia rufa* L. is also determined by temperature (Strohm *et al.* 2002), but Stone *et al.* (1995) observed *Anthophora plumipes* Pallas also at low temperatures with frequent breaks for basking. The second factor determining foraging behaviour of nectar- and pollen-collecting insects is the quality and quantity of floral rewards available, including sugars, amino acids and water (Corbet *et al.* 1993; Stone 1994). In the first 9 months after traps were set up the bee *H. fulvescens* nested in only 19 of 24 sites and five sites, which were colonized with a few brood cells later, were probably too shaded for nesting. This means less suitable nesting conditions because of high humidity inside the nests and few flowering plants. Coverage of flowering plants can be used as a surrogate for pollen and nectar resource availability (Tscharnkte *et al.* 1998). Klein *et al.* (2003a,b) found a similar pattern with respect to coffee flower-visiting solitary bees in that a reduction of shade and a high weed density provided more nectar and pollen resources, thereby increasing the density of pollinating bees and increasing coffee fruit set.

The duration of foraging trips by the caterpillar-hunting eumenid wasp *R. haemorrhoidale* decreased only with increasing cacao cover of the agroforestry systems, because the arctiid caterpillars found in trap nests were cacao leaf-feeding pests. However, when the four agroforestry systems without cacao plants were excluded, the foraging time of this wasp was correlated positively with light intensity and blossom cover. For this cacao caterpillar-hunting species, food abundance for their offspring appeared to be the most important factor

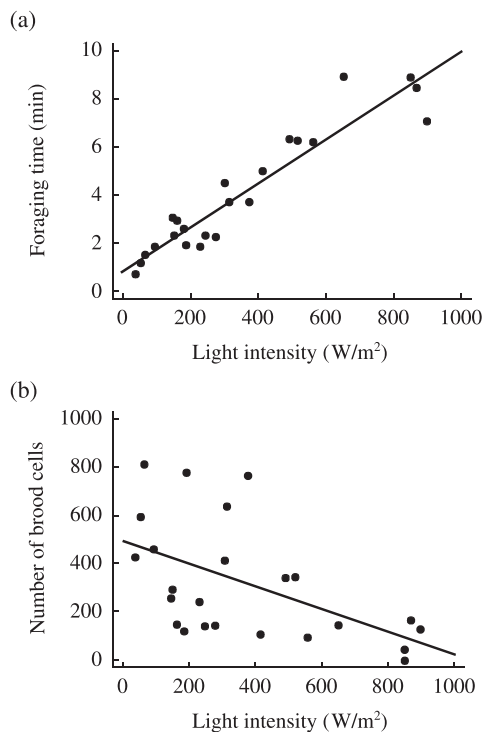


Fig. 3. (a) Relationship between the foraging time of *A. levicarinatus* and the light intensity: $y = 0.86 + 0.01x$, $r^2 = 0.88$, $n = 23$, $P < 0.001$. (b) Relationship between the number of brood cells of *A. levicarinatus* and the light intensity: $y = 489.96 - 0.47x$, $r^2 = 0.28$, $n = 24$, $P = 0.007$.

affecting foraging time and light intensity, and blossom cover seems to be important only when cacao-caterpillars are not in the direct vicinity of the trap nests.

Foraging time of the spider-hunting pompilid wasp *A. levicarinatus* increased with increasing light intensity. This is in contrast to the general expectation that insect activity profits from sunlight. The preference of shade was not due to a generally higher activity early in the morning or while it was raining or shortly after rain (A.M. Klein, personal observation). However, the decreasing foraging time and decreasing brood-cell density of these pompilids with increasing light intensity could be explained by food availability in the agroforestry systems. Almost all spiders found in their nests belong to the spider family Salticidae. In a former study, Klein, Steffan-Dewenter & Tschardtke (2002) found an increase of spider densities with decreasing light intensity.

Many insect communities are known to be influenced not only by the local habitat conditions, but also by the surrounding landscape matrix (Huston 1999; Ricketts 2001; Perfecto & Vandermeer 2002; Steffan-Dewenter 2002; Tschardtke *et al.* 2002). Such a regional effect has also been shown for trap-nesting species (Tschardtke *et al.* 1998; Steffan-Dewenter 2002; Steffan-Dewenter 2003; Klein, unpublished data). This study shows that foraging time as well as brood-cell density of the bee species was influenced positively by light intensity, so foraging time was a (marginally significant) predictor of the number of brood cells per site. In contrast, the foraging time and the number of brood cells of the spider-hunting pompilid wasp were related negatively to light intensity, presumably because the spider prey of this predator was most abundant in shaded sites and both foraging and nesting success were related. The distribution pattern of the cacao caterpillar-hunting eumenid wasp showed that foraging time and brood-cell density may be related weakly, because foraging time was related to cacao cover, while the number of brood cells declined with distance from the nearest forest. This eumenid species appeared to depend mainly on the wealth of nesting sites in undisturbed forests, so only the successful colonizers of cacao-rich sites profited from the large food supply, resulting in an overall independence of foraging time and number of brood cells. This indicates a possible trade-off between suitable nesting sites and food availability for the larvae.

Furthermore, the body size of the eumenid wasp was greater than that of the two other species. Foraging distance of bees is known to increase with increasing body length (vanNieuwstadt & Iraheta 1996; Gathmann & Tschardtke 2002), and body size appeared to be a good predictor of colonization ability in trap-nesting species (Gathmann, Greiler & Tschardtke 1994). Because of these size differences, the eumenid wasp could bridge longer distances between forest with suitable nesting sites and land-use systems with suitable food resources. This is indicated by (a) the dependence of the number of brood cells on forest distance and (b) the longer foraging time of this species compared to the other two species.

The duration of foraging trips of all three species was, on average, short. Gathmann & Tschardtke (2002) examined the foraging time of eight trap-nesting bee species in Germany. The fastest bee species need 6 min on average and the slowest species 33 min for one foraging trip. Strohm *et al.* (2002) found about 13 min for one foraging trip of the megachilid bee *Osmia rufa* L. in Germany. This temperate-tropical difference may be due to the higher temperature and the higher food availability in the tropical agroforestry systems. Strohm *et al.* (2002) found that females needed about three-quarters of the total time for a brood cell to forage for pollen and nectar, whereas construction of cell partitions was comparatively rapid. For the bee species in this study, the mean time spent collecting material for cell construction was about 1.55 min, whereas an average of 2.68 min was spent foraging for pollen. The relatively small difference between these values and the fast foraging time in general indicate that the agroforestry systems in which the bee nests provide a great amount of available pollen, in particular of one all-year flowering Asteraceae species.

In conclusion, the foraging time and brood-cell density of trap-nesting species shows the relative importance of food and nest-site availability for the performance of a bee pollinator, an eumenid predator of pest caterpillars and a spider-hunting predator belonging to the Pompilidae. Brood-cell density and foraging time were correlated only in the pollinator and in the spider-hunting predator, but not in the eumenid predator, because of a trade-off between high quantities of food resources (in sites with dense cacao plants) and nesting sites (in adjacent natural forests). The eumenid predator response to local and regional agroforestry management illustrates that species may survive only in landscapes that permit access to multiple required resources. Accordingly, habitat evaluation using only foraging time may lead to wrong conclusions, as key drivers of population dynamics may be not inside but outside the local agroforestry systems, emphasizing the need for a landscape approach.

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