

## Scientific note

### A scientific note on stratified foraging by Sabahan bees on the yellow flame tree (*Peltophorum pterocarpum*)

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#### *Apis* / *Trigona* / interspecific competition / resource partitioning

Observations were made at the Agricultural Research Station near Tenom (6°N, 117°E). We surveyed bee species foraging at different elevations on a tree in full bloom. The top, middle and bottom strata of the tree were divided into four, eight and seven 'zones' each having 1.0 to 1.7 m<sup>3</sup> of flower clusters. Zones were inspected at regular intervals on 3 days; numbers of foragers of several species of bees were counted. *A. dorsata* and *A. andreniformis* were recorded as individual species; *A. cerana* and *A. koschevnikovi* were recorded as a group as were two small similarly sized *Trigona* spp.

The frequencies of the species groups at three foraging heights were analyzed with a Poisson response Generalized Linear Model (McCullagh and Nelder, 1989). These models, unlike standard multiple regression models, use the discrete structure of ordinal data. Our model assumed that counts were a function of species, foraging stratum, time of day, and volume of flower zone. The model was:  $\ln(\text{mean count}) = \beta_0 + \text{species} + \text{stratum} + (\text{species} \times \text{stratum}) \text{ interaction} + \text{date} + \text{time}(\text{nested in date}) + \beta_1 \text{ volume}$ .

This model considers species and stratum as main factors and species by stratum effects as

interactions. Date and time (nested in date) are expected to have varied species responses (Oldroyd et al, 1992) and hence are used as blocking factors, accounting for possible systematic variation associated with data collection periods. Cluster volume is used as a covariate accounting for additional non-systematic variability; a linear trend is assumed between cluster volume and  $\ln$ .  $\beta_0$  is the overall mean. All effects were estimated by maximum likelihood.

The highly significant species by stratum interaction was examined using contrasts on the interaction effects, taking advantage of the logarithm link function for the Poisson model. Within species, contrasts of stratum effects are equivalent to comparing differences in log counts. Such differences can be viewed as logarithms of count ratios. Confidence intervals were constructed using the covariance matrix of interaction effects. The probabilities of count ratios for species across strata were determined.

Data were overdispersed (scale estimated as 3.34). Summary Wald statistics indicate that each model factor was significant (table I). Species had different forager frequencies with *Trigona* spp and *A. cerana* / *A. koschevnikovi* for-

agers being more common, foragers at the tree top being more frequent and foragers at the tree bottom being less frequent (fig 1). Forager frequency varied with date and time. Forager frequency was positively correlated with the volume of the observational zone.

A highly significant species by stratum interaction (table I) indicated that different species had different proportions of foragers in the top, middle and bottom of the tree. Analysis of the ratio of foragers within species at different strata indicated each of the forager groups was unique in its stratified arrangement of foragers (table II, fig 1). The significantly largest number of *Trigona* foraged in the top. The middle and bottom of the tree had similar numbers of *Trigona* foragers. *A. cerana/A. koschevnikovi* also foraged more frequently at the top but foraged at the middle and bottom in highly significantly fewer and fewer numbers. *A. dorsata* foraged equally at the top and middle and significantly less frequently at the bottom. *A. andreniformis* foraged in all strata equally.

These data suggest that a 'stratum fidelity syndrome' may result in resource partitioning facilitating sympatry. It is unclear whether stratified foraging results from preference differences or other factors. An alternative explanation for the stratified foraging is that nectar and pollen production was non-uniform. However, the uniform distribution of *A. andreniformis* and *A. dorsata* within the top and middle strata in contrast to reduced numbers of both the *Trigona* spp and *A. cerana/A. koschevnikovi* in the middle strata argues against this explanation. This is especially so, since the *A. dorsata* data were sufficient to detect reasonably small ratio differences, had they occurred.

The associations of different bee sizes having high foraging frequencies on similar tree strata indicate that better resources do not necessarily go to the largest bees. Much more complex relationships evidently determine the spacial separation of foragers of sympatric species.

These data indicate that along with other important factors in resource partitioning by sympatric species (eg, flower specialization, Frankie and Haber, 1983; and temporal separation, Oldroyd et al, 1992), differential foraging height also has a role. Such stratum specificity probably varies by time and species of forage. Our observations of one tree, are not statistically extendable in detail to other trees. However, our observations of strat-

ified foraging suggest that stratified foraging in some form may often occur.

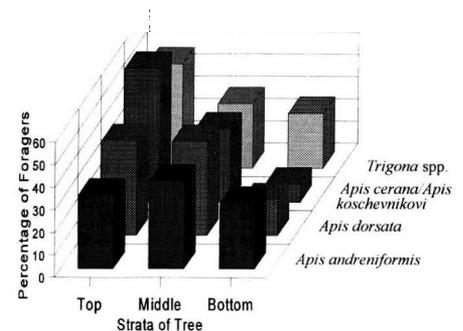
**Note scientifique sur le butinage en strates des abeilles de Sabah (Bornéo) sur l'arbre *Peltophorum pterocarpum***

**Wissenschaftliche Notiz über Unterschiede in der Höhenverteilung von Sammelbienen in Sabah auf dem Baum *Peltophorum pterocarpum***

**Table I.** Analysis of deviance from the Poisson model.

Source	df	$\chi^2$	P value
Species	3	276	0.0001
Stratum	2	43.5	0.0001
Species x Stratum	6	44.7	0.0001
Date	2	n i	n i
Time nested in date	4	n i	n i
Volume	1	3.9	0.0474

n i: no interest.



**Fig 1.** Percentage of foragers of four groups of bee species (adjusted for unequal numbers of foraging zones) at the top, middle or bottom of a yellow flame tree.

**Table II.** Count ratio comparisons within species groups between foraging strata showing estimated ratios, upper and lower 95% confidence intervals and P values for the hypothesis that the ratio is 1.

Comparisons	Estimated ratio	Lower 95% interval	Upper 95% interval	P-value for ratio = 1
<i>Trigona</i> spp				
Top to bottom	1.77	1.36	2.31	4.0 x 10 <sup>-5</sup>
Middle to bottom	1.20	0.91	1.60	0.199 ns
Top to middle	1.47	1.12	1.92	0.005 **
<i>A. cerana</i> and <i>A. koschevnikovi</i>				
Top to bottom	9.99	6.23	15.91	1.0 x 10 <sup>-15</sup> **
Middle to bottom	4.35	2.68	7.09	3.1 x 10 <sup>-9</sup> **
Top to middle	2.29	1.74	3.06	4.7 x 10 <sup>-9</sup> **
<i>A. dorsata</i>				
Top to bottom	2.39	1.26	4.53	0.008 **
Middle to bottom	1.86	1.02	3.42	0.043 *
Top to middle	1.28	0.75	2.19	0.370 ns
<i>A. andreniformis</i>				
Top to bottom	1.99	0.72	5.53	0.186 ns
Middle to bottom	2.27	0.93	5.52	0.072 ns
Top to middle	0.88	0.38	2.03	0.763 ns

## References

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