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Original article

Relation between size and foraging range in stingless bees (Apidae, Meliponinae)

MGL van Nieuwstadt [1]*, CE Ruano Iraheta [2]

[1] *Proyecto Regional de Apicultura y Meliponicultura, Universidad Nacional de Costa Rica,*
Apdo Postal 475-3000, Heredia, Costa Rica;
[2] *Facultad de Ciencias Agronomicas, Universidad de El Salvador, San Salvador, El Salvador*

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Summary — We estimated the maximum foraging distances of four species of neotropical stingless bees using two experimental methods. In the first experiment marked bees, which were released at different distances from the nest, were recaptured. The second method consisted of training bees on an artificial nectar source which was subsequently moved away from the nest till visitation ceased. In both experiments we found a positive linear relationship between the head width of the different species and their foraging range. However, the maximum foraging distances estimated by the capture–recapture experiment were about 300 m greater than those estimated by training the bees at an artificial source. It is concluded that the distance delimiting the area in which 95% of the foraging activity occurs lies in between the distances indicated by these two methods.

Apidae / Meliponinae / stingless bee / flight distance / body size

INTRODUCTION

The stingless bees (Hymenoptera, Apidae, Meliponinae) are a pantropical group of eusocial insects which live in perennial colonies. In their nests they build up reserves of pollen and honey, which help them to survive dearth periods. Like all animals which forage from a central place (Schoener, 1979), the foraging area is limited. As a result food competition is restricted to a certain number of neighbouring colonies (Hubbell and Johnson, 1977).

Because of the sessile character of a colony the pollination capacity of stingless bees is limited too (Free, 1993). Pollen is not dispersed further than the foraging area of the colony. Notwithstanding the high densities of stingless bees in the tropics this may limit their importance as pollinators,

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* Present address: Department of Comparative Physiology, Utrecht University, PO Box 80 086, 3508 TB Utrecht, the Netherlands

especially as far as small species are concerned.

Although the maximum foraging range and the distribution of the foragers of a nest of stingless bees are of fundamental importance for our understanding of a bee community and the importance of stingless bees as pollinators, detailed data on this subject are scarce. Some scattered information is available from studies that have been performed in the neotropics, usually by training bees on an artificial nectar source (Kerr, 1959; Lindauer and Kerr, 1960). More detailed information has been gathered on *Melipona fasciata* and *Trigona (Cephalotrigona) capitata* by releasing marked foragers at different distances from the nest (Roubik and Aluja, 1983). But no comparison has been made between the results obtained by the releasing of marked bees and by training bees on an artificial source, nor has any attempt been made to uncover the relation between the size of the various stingless bee species and their respective foraging ranges. In this study, we investigate the foraging ranges of several species of stingless bees and estimate the relation between the size of a species and its foraging range.

MATERIALS AND METHODS

The research was done in Pozo Azul, a village in the neotropical dry forest zone in Guanacaste, Costa Rica (10°10'24"N; 85°00'24"W; altitude 170 m). The village is situated in the tropical dry forest zone and is surrounded by a hilly landscape with a savannah woodland vegetation. Along the rivers are small strips of secondary gallery forest. We studied four species of stingless bees: *Trigona (Trigona) corvina* Cockerell, *Partamona* aff *cupira* Smith, *Trigona (Tetragonisca) angustula* Illiger, and *Nannotrigona testaceicornis perilampoides* Cresson. Species names are abbreviated as *Tc*, *Pc*, *Ta* and *Nt*, respectively. Nomenclature follows Roubik (1992). The colonies studied had been present at the research site for at least 3 months before the experiments were conducted.

The investigations were carried out in April and May 1995, at the end of the dry season, and consisted of two experiments. The first experiment was a modified version of the experiments done by Gary (1971) and Roubik and Aluja (1983). We determined the fraction of bees that returned after being released at various distances from the nest. Bees feeding on an artificial nectar source in front of the nest were captured and given a distance-specific colour mark. The captured bees were fed a 50% honey water solution. Subsequently 30 bees for each distance were released at different distances from the nest. The ones that actually flew away were counted. We recaptured the returning workers of *Ta* by replacing the original colony by an empty nest box, which was provided with the entrance tube of the original colony and which contained some honey. The released workers of the other three species were recaptured on the nectar source in front of the nest for 2.5–3 h after the release. The experiment was repeated twice with *Pc* and four times with *Ta*, *Nt* and *Tc*.

Foraging distances were also estimated by training foragers on an artificial nectar source. The source consisted of a styrofoam platform with about 40 small holes which floated on a clove-scented 35% sugar solution. To facilitate orientation, the source was marked with coloured paper. As soon as the source was frequented by at least 25 bees, it was moved away from the nest in steps of 5–10 m till visitation ceased. The number of visiting bees was counted every 10 m. Foragers of other bee species were removed from the source. The experiment was repeated three times with *Nt*, *Ta*, and *Tc* and four times with *Pc*.

Before fitting linear regression lines to the results of the capture–recapture experiment we excluded the distances from which no bees returned, since these might have distorted the analysis of the relationship between head width and foraging distance (Roubik and Aluja, 1983). In the source experiment, we estimated the area in which 75, 95 and 100% of the bees foraged cumulatively. We compared the results of the two experiments by using two-tailed *t*-tests with repeated measurements in order to assess the degree of similarity of the distribution of bees in the two experiments.

We estimated the relation between the size of the bee species and their foraging range. As an estimate of body size we used the head width, because this is a well-defined characteristic which can be measured unequivocally and, within the tribe of stingless bees, relates well to the body size.

RESULTS

The percentages of returning bees released at different distances from the nests are shown in figure 1. In all cases we obtained significant results from linear regression lines that were fitted through the data (table I). Maximum foraging distances of the four species varied from 623 to 853 m. In three cases the regression line indicates that the percentage of returning bees would be between 60 and 70% if the bees were released at 0 m from the nest. In the case of *Ta*, where the returning bees were captured by changing the maternal nest box, the percentage of recaptured bees was lower.

The distribution patterns of foragers trained at the artificial nectar source differ for the different species. The number of foragers of *Tc* and *Nt* decreases gradually with increasing distance (fig 2). The num-

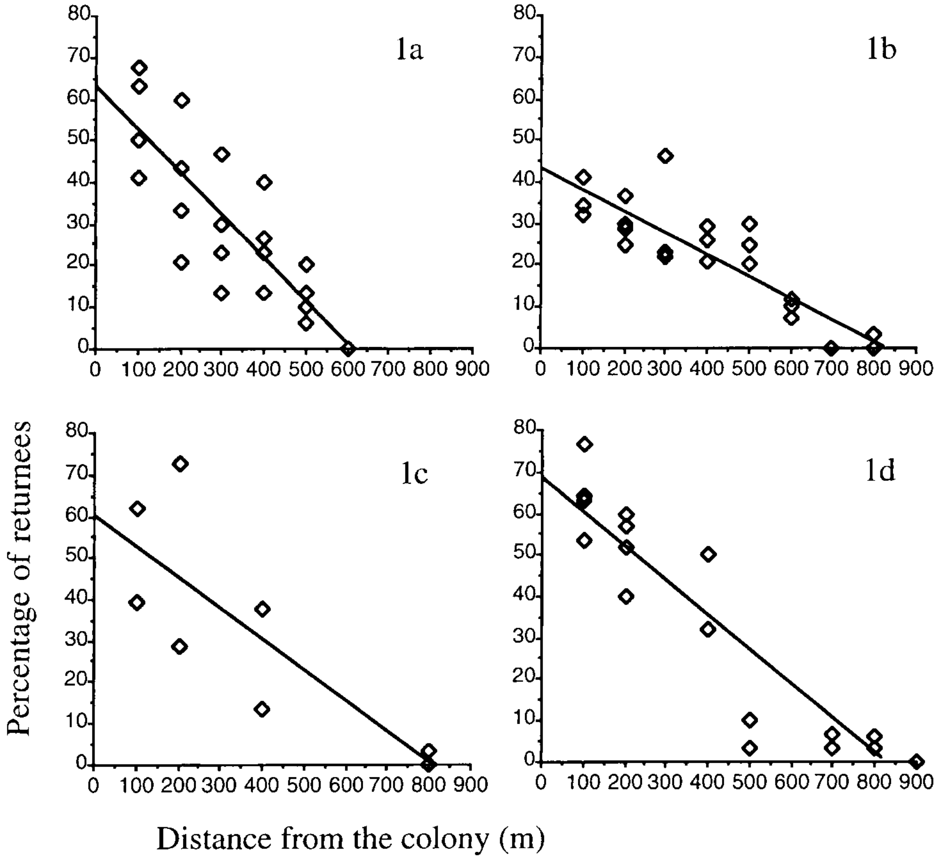

Fig 1. Percentage of returning bees versus the distance between the nest and the point of liberation (in metres). Given are the results for: (**a**) *Nt*, (**b**) *Ta*, (**c**) *Pc* and (**d**) *Tc*. Mathematical and statistical descriptions of the fitted linear regressions are given in table I.

Table I. Linear relationships between the distance at which bees were released and the percentage of returns.

Species	*Linear relation between distance and % return* [a]	R^2	*Interpolated distance (m) delimiting the area of* x *% cumulative return*		
			75%	*95%*	*100%*
Nt	$y = -0.10\,x + 62.3$	0.614	312	484	623
Ta	$y = -0.051\,x + 43.5$	0.69	427	662	853
Pc	$y = -0.075\,x + 60.1$	0.668	403	622	801
Tc	$y = -0.094\,x + 71.4$	0.848	380	590	760

[a] For the calculation of the linear regression, 0-values (see fig 2) have been omitted.

ber of foragers of *Pc* and *Ta* decreases more rapidly at the shorter distances, while at the longer distances a low number of bees persistently visits the source. Especially some foragers of *Ta* were very persistent in visiting the source. In all cases, the number of bees increased over the first 10–50 m of the experiment, because at the beginning of the experiment, we started moving the nectar source before the maximum number of visitors had been reached.

We compared the distances at which each species had attained 95% cumulative foraging activity as predicted by the two experiments, using a two-group *t*-test. For all species, the distances predicted by the capture–recapture experiment were significantly larger than the distances reached with the artificial nectar source (*Nt*: $df = 5$, *t*-value = 19.5, $P < 0.0001$; *Ta* : $df = 5$, *t*-value = 13.4, $P < 0.0001$; *Pc*: $df = 4$, *t*-value = 8.68, $P = 0.001$; *Tc*: $df = 5$, *t*-value = 4.08, $P = 0.0095$).

We analysed the relationship between the head width and the range within which 95% of the bees returned cumulatively (including the results of Roubik and Aluja (1983), table II, fig 3), based on the predicted values of the linear regressions. Although the distances reached by species in our study are not strictly related to the

Table II. Linear relationships between the distance at which bees were released and the percentage of returns.

Species	*Linear relation between distance and % return*	R^2	*Interpolated distance (m) delimiting the area of* x *% cumulative return*		
			75%	*95%*	*100%*
Cephalotrigona capitata	$y = -0.0315\,x + 52$	0.52	825	1 282	1 651
Melipona fasciata	$y = -0.025\,x + 61$	0.59	1 201	1 865	2 402

Data from Roubik and Aluja (1983), linear relations estimated from a figure in that article.

head width of the species, the overall relationship is highly significant ($P = 0.0026$).

We also compared the distance that delimited the area in which cumulative foraging at the artificial source was 95% and the head width of the species (fig 3). The results of the experiment with the artificial nectar source could not be compared with other studies. The distances delimiting the area in which 95% of the cumulative foraging occurred and head width are significantly related in this experiment ($P = 0.0013$).

The results of the two experimental methods are remarkably similar. The slopes of

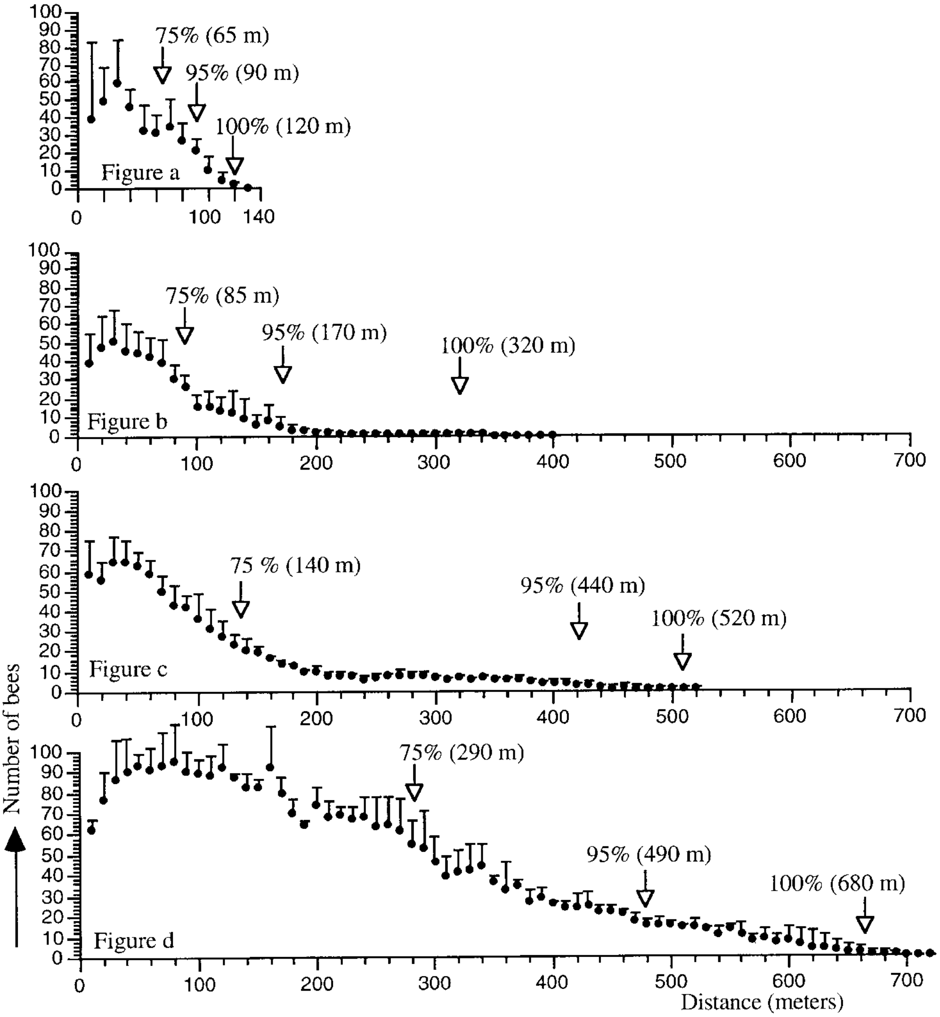

Fig 2. Foraging activity at an artificial nectar source versus distance from the nest. Given are the average plus the standard deviation. The figures represent: (**a**) *Nt*, (**b**) *Tc*, (**c**) *Pc*, (**d**) *Ta*. Arrows indicate the distances that delimite the areas of 75%, 95% and 100% cumulative foraging activity. Low initial values were due to the fact that we started moving the source before the maximum number of visitors was reached.

both regression lines are almost identical. On the other hand, the maximum foraging distances found in the capture–recapture experiment are about 300 m longer than in the experiment with the artificial source.

DISCUSSION

Our study, combined with the data presented by Roubik and Aluja (1983), show that there is a positive linear relation between the maximum flight range of stingless bees and their head width. However, the linear relations obtained with the two experimental methods differ by some 300 m. Probably, the distance delimiting the area in which 95% foraging activity occurs in the natural situation lies in between the two calculated regression lines, because both methods have their shortcomings.

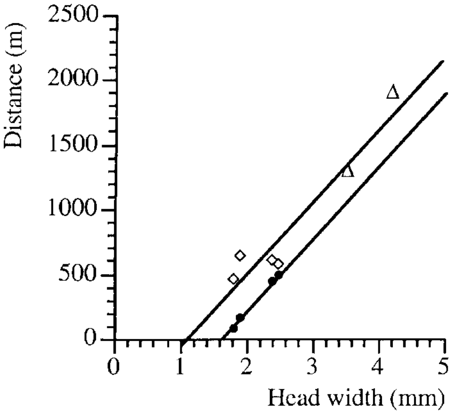

Fig 3. The relationship between the head width of stingless bee species and flight range. Distance delimiting the area of 95% cumulative return in capture–recapture experiments versus the head width of six species of stingless bees is given for the data presented in this article (four species, open squares) and data of Roubik and Aluja (1983) (open triangles). Black squares represent the distance delimiting the area in which 95% of the foraging activity at an artificial source occurred versus the head width of four species of Trigonini. The functions of the linear regressions through the data are: $y = 550.9x - 579.1$, $R^2 = 0.917$ (Anova: $F_s = 44.3$; $P = 0.0026$) and $y = 560.8x - 908.2$; $R^2 = 0.997$ (Anova: $F_s = 758.7$; $P = 0.0013$), respectively.

Releasing bees at a certain distance from the nest probably results in an overestimation of the actual foraging distance because the bees have to fly only one way. On the other hand, the percentage of returnees from long distances might be underestimated if the bees are not familiar with the neighbourhood in which they are released, and the costs of reorientation are high.

The chance that a bee will accidentally reenter a familiar area depends on the search methods and orientation mechanisms it uses. Many animals ranging from isopods and ants to birds, and probably also bees, are known to explore their environment by 'random walks' (Waterman, 1989; Wehner et al, 1996). The relative importance of the various mechanisms used for orientation during the exploration may vary widely, depending on the availability and utility of specific cues in the environment.

The use of the polarisation of the sunlight (review by Wehner and Rossel, 1985) is of no use if the bee does not already know the direction from the place where it is released to her nest. If bees depend on visual cues in the landscape for their orientation, the percentage of returnees will decrease rapidly with increasing distance from the familiar area (Roubik and Aluja, 1983). A worker that finds itself outside its original foraging area may orientate herself with a familiar landmark inside this area. However, landmark orientation is limited by bee vision and memory (Gould, 1991; Dyer et al, 1993), and is not likely to be very successful over long distances in a dense and monotonous forest vegetation. Under such circumstances the use of odours (Lindauer and Kerr, 1960; Wenner et al, 1991) may be an important orientation mechanism.

The outcome of the capture–recapture technique is not only influenced by biological and physiological limitations of the bees, but also by characteristics of the experimental design. The percentage of bees recaught both by collecting metal marks with a magnet (Roubik and Aluja, 1983) and by capturing returning bees on a nectar source in front of the nest is between 60 and 70%. In contrast, the use of an empty 'trap'-nest was less efficient, probably because not all returning bees entered it. The first two methods are therefore preferable.

The other experiment, in which bees were trained at an artificial source, was likely to yield an underestimation of the natural flight range, because some bees were lost during the experiment because they could not relocate the source after it had been moved. The concentration of the provided sugar solution was chosen within the range of naturally collected nectar (Roubik et al, 1995), but a higher sugar concentration might have stimulated the foragers to continue source visitation over a longer distance. Moreover, the artificial source is visually much less attractive than a tree in full bloom. Therefore, the motivation to continue foraging will cease at a shorter distance.

In spite of the highly significant relationship, the variation between head width and the maximum distance of return in the various species studied is considerable. Especially *Ta* had a larger flight range than expected, whereas *Tc* had a relatively short flight range. Probably over a long distance, overheating causes a fall out among the returning foragers (Heinrich, 1980). The air temperature during the experiments reached about 35 °C. Possibly *Ta*, with its light body colour, was able to withstand the high insolation and air temperature for a longer time than the other three species, which all have dark coloured bodies (Willmer and Corbet, 1981).

Although the results are comparable, it must be stressed that the difference in vegetation between the experiment of Roubik and Aluja (1983) and our capture–recapture experiment may have influenced the spatial distribution of the returnees in different ways. As explained above, orientation may be more difficult in a forest because the orientation mechanisms the bees rely upon may be more restricted in a dense vegetation than in a more open landscape. On the other hand, overheating during flight caused by solar radiation is much less of a problem in a forest than in an open vegetation. If such differences had the potential to influence the results of the experiments, their influences have probably levelled off each other.

The relationship between head width and foraging range cannot be extrapolated to Apidae other than stingless bees. The foraging distances for several species of the genus *Apis*, inferred from dances for natural food sources, differ considerably from the distances expected from our experiments (Visscher and Seeley, 1982; Dyer and Seeley, 1991). No relation between body size and foraging distance was found in the comparison of four *Apis* species (Dyer and Seeley, 1991). The lack of a relationship in these two comparisons may be an effect of morphological or physiological features, such as a relatively longer wing length, a larger wing area/body weight ratio, and a higher wing beat frequency. These features, in interaction with the body size, define the maximum flight range of a species (Roubik, 1989, p 83).

Although the foraging range of a nest of stingless bees is limited, it competes for food sources with a number of neighbouring colonies. The number of intraspecifically competing colonies is difficult to be estimated for small non-agressive foragers, because they are randomly dispersed or even clumped (Roubik, 1991). However, the number of intraspecifically competing colonies can be estimated for species which are distributed uniformly. Such species most often use pheromone trails in their communication for food sources and aggressively defend sources (Hubbell and Johnson, 1977).

According to our calculations (fig 3), 95% of the foraging activity of the uniformly dispersed species observed by Hubbell and Johnson (which vary by a factor 1.4 in head width) occurs in an area of 2.9 km^2 (SD = 1.4; four species), the 95% foraging range for each species varying from 740 to 1 240 m. By using the colony densities measured by Hubbell and Johnson (1977), we calculated that in that area there will be several tens of competing colonies (average 54; SD = 31; four species) of the same species. The size of the home range of these species was positively related to the estimated colony weight (Hubbell and Johnson, 1977), and in a slightly lesser extent to bee weight (van Nieuwstadt, personal observation). Since the species with a larger flight range occur in lower densities, the calculated number of competing colonies within the 95% foraging range does not show a correlation with head width (Spearman rank correlation coefficient; $Z = -0.693$; $P = 0.49$; $n = 4$).

Because forager activity is highest in the vicinity of the nest, the intensity of competition between two colonies depends on the distance they are removed from each other (Roubik 1991). More than 75% of the foraging activity normally occurs within 40% of the maximum foraging distance (Roubik, 1991; van Nieuwstadt, unpublished data), while further away from the colony the forager density is low. It can therefore be concluded that for uniformly dispersed species only the ten (SD = 7) colonies that are on average present in that range should be considered as serious intraspecific competitors for the available resources.

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Résumé — Relation entre la taille et la distance de butinage chez les abeilles sans dard (Apidae, Meliponinae). Les distances de butinage chez les abeilles sans dard revêtent une importance capitale pour notre compréhension de la compétition entre colonies, l'influence de la déforestation sur la disponibilité des ressources et l'efficacité pollinisatrice dans les communautés végétales naturelles et les cultures. Il existe pourtant peu d'estimations de la distance maximale de butinage des différentes espèces et de la distribution de l'activité de butinage dans l'aire ainsi délimitée. Nous avons estimé les distances de butinage de quatre espèces néotropicales d'abeilles sans dard (Trigonini) à l'aide de deux méthodes expérimentales. Dans la première expérience nous avons utilisé la méthode de capture-recapture (Gary, 1971) : les abeilles, qui ont été lâchées à diverses distances du nid, sont recapturées près du nid. Le seconde méthode consiste à conditionner les abeilles à une source artificielle de nectar qui est ensuite éloignée progressivement du nid jusqu'à ce qu'il n'y ait plus de visites. Les distances qui délimitent l'aire d'où reviennent 95 % des abeilles dans l'expérience par capture-recapture varient de 623 à 853 m (fig 1, tableau I). Dans l'expérience par conditionnement, les distances qui délimitent l'aire dans laquelle 95 % de l'activité cumulée de butinage a lieu s'étend de 90 à 490 m (fig 2). Dans les deux séries d'expériences nous avons trouvé une relation positive linéaire entre la largeur de la tête des différentes espèces et la distance de butinage (fig 3). Mais les distances maximales de butinage trouvées par la méthode de capture-recapture dépassent d'environ 300 m celles obtenues par la méthode de conditionnement. On en conclut que les distances maximales atteintes par des colonies qui butinent naturellement se situent entre les chiffres donnés par les deux méthodes. Parce que la plus grande partie de l'activité de butinage a lieu dans un rayon égal à 40% environ de la distance maximale de butinage, on peut conclure qu'une colonie d'une espèce uniformément dispersée et de taille moyenne (largeur de la tête comprise entre 2,4 et 3,3 mm) entre en compétition avec environ dix colonies de la même espèce.

Apidae / Meliponinae / abeille sans dard / distance de vol / aire de butinage / taille corporelle /

Zusammenfassung — Relation zwischen Größe und Sammelflugweite bei stachellosen Bienen (Apidae, Meliponinae). Grundlegende Kenntnisse über den Bereich, den stachellosen Bienen mit Trachtflügen abdecken, sind für unser Verständnis über die Konkurrenz zwischen den Völkern, über die Folgen des Abholzens der Wälder für die Nutzbarkeit von Trachtquellen, über die Bestäubungsleistung in natürlichen Lebensgemeinschaften und über Ernteerträge wichtig. Es gibt jedoch nur wenige Schätzungen über die maximale Distanz der Trachtflüge von verschiedenen Arten und über die Verteilung der Flugaktivität innerhalb dieses Bereichs. Wir schätzten die Flugdistanz für 4 Arten neotropischer stachelloser Bienen (Trigonini) mit zwei verschiedenen Methoden. Im ersten Experiment benutzten wir die Wiederfangmethode nach Gary (1971): Die in verschiedenen Entfernungen vom Nest freigelassenen Bienen wurden wurden in der Nähe des Nestes wiedergefangen. Bei der zweiten Methode dressierten wir Bienen auf künstliche Futterstellen, die anschließend schrittweise vom Nest fortbewegt wurden bis die Bienenbesuche aufhörten. Die Entfernungen, die einen Bereich umgrenzten in dem 95% der Bienen den Weg zurück ins Volk fanden variiert zwischen 623 m und 853 m (Abb 1, Tab I). In Dressurversuchen, in denen zu 95% eine allmählich zunehmende Sammelaktivität auftrat, reichten die Entfernungen von 50m bis 490m (Abb 2). In beiden Experimenten fanden wir eine positive lineare Korrelation zwischen der Kopfbreite der verschiedenen Arten und der Reichweite ihrer Trachtflüge (Abb 3). Jedoch war bei der Wiederfangmethode die maximale Flugweite um 300m größer als die, die durch eine Dressur auf künstliche Futterstellen erreicht wurde. Es wurde daraus geschlossen, daß das Maximum der Distanz, die von natürlich sammelnden Bienen erreicht wird, zwischen den Entfernungen liegt, die durch die beiden Methoden gefunden wurden. Da die größte Sammelaktivität innerhalb von etwa 40% der maximalen Flugweite liegt, kann man schließen, daß ein Volk einer gleichmäßig verteilten, mittelgroßen Art (Kopfbreite von 2,4 - 3,3 mm) mit im Schnitt 10 Völkern der gleichen Art in Konkurrenz steht.

Apidae / Meliponinae / stachellose Biene / Flugdistanz / Körpergröße

REFERENCES

Dyer FC, Berry NA, Richard A (1993) Honey bee spatial memory: use of route-based memories after displacement. *Anim Behav* 45, 1028-1030

Dyer FC, Seeley TD (1991) Dance dialects and foraging range in three Asian honey bee species. *Behav Ecol Sociobiol* 28, 227-233

Free JB (1993) *Insect Pollination of Crops.* 2nd edition, Academic Press, London

Gary NE (1971) Magnetic retrieval of ferrous labels in a capture–recapture system for honey bees and other insects. *J Econ Entomol* 64, 961-965

Gould JL (1991) The ecology of honeybee learning. In: *The Behaviour and Physiology of Bees* (LJ Goodman, RC Fisher, eds), CAB International, 306-322

Heinrich B (1980) Mechanisms of body temperature regulation in honeybees, *Apis mellifera.* II. Regulation of thoracic temperature at high air temperatures. *J Exp Biol* 85, 73-87

Hubbell SP, Johnson LK (1977) Competition and nest spacing in a tropical stingless bee community. *Ecology* 58, 949-963

Kerr W E (1959) Bionomy of Meliponids -VI- Aspects of food gathering and processing in some stingless bees. In: *Symposium on Food Gathering Behaviour of Hymenoptera*. Ed at Cornell Univ, Ithaca, NY, USA, 24-31

Lindauer M, Kerr WE (1960) Communication between the workers of stingless bees. *Bee World* 41, 29-41, 65-71

Roubik DW (1989) *Ecology and Natural History of Tropical Bees*. Cambridge University Press, Cambridge

Roubik DW (1991) Aspects of Africanized honey bee ecology in tropical America. In: *The African Honeybee* (M Spivak , DJC Fletcher, MD Breed, eds), Westview Press, Boulder, CO, 259-281

Roubik DW (1992) Stingless bees: a guide to Panamanian and Mesoamerican species and their nests. In: *Insects of Panama and Mesoamerica* (D Quintero, A Aiello, eds), Oxford University Press, 495-524

Roubik DW, Aluja M (1983) Flight ranges of *Melipona* and *Trigona* in tropical forest. *J Kansas Entom Soc* 56, 217-222

Roubik DW, Yanega D, Aluja SM, Buchmann SL, Inouye DW (1995) On optimal nectar foraging by some tropical bees (Hymenoptera: Apidae). *Apidologie* 26, 197-211

Schoener TW (1979) Generality of the size-distance relation in models of optimal feeding. *Amer Nat* 114, 902-914

Visscher PK, Seeley TD (1982) Foraging strategy of honeybee colonies in a temperate deciduous forest. *Ecology* 62, 1790-1801

Waterman TH (1989) *Animal Navigation*. Scientific American Library, HPHLP, New York

Wehner R, Rossel S (1985) The bee's celestial compass - a case study in behavioural neuobiology. In: *Fortschritte der Zoologie* 31, *Experimental Behavioural Ecology and Sociobiology* (B Hölldobler, M Lindauer, eds), G Fischer Verlag, Germany, 11-53

Wehner R, Michel B, Antonsen P (1996) Visual navigation in insects: coupling of egocentric and geocentric information. *J Exp Biol* 199, 129-140

Wenner AM, Meade DE, Friesen LJ (1991) Recruitment, search behavior, and flight ranges of honey bees. *Am Zool* 31, 768-782

Willmer PG, Corbet SA (1981) Temporal and microclimatic partitioning of the floral resources of *Justicia aurea* amongst a concourse of pollen vectors and nectar robbers. *Oecologia* 51, 67-78