BODY SIZE AND FLIGHT DISTANCE IN STINGLESS BEES (HYMENOPTERA: MELIPONINI): INFERENCE OF FLIGHT RANGE AND POSSIBLE ECOLOGICAL IMPLICATIONS

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ABSTRACT

We examined the spatial implications of maximum flight distance for several species of stingless bees. Data suggested that maximum flight distance in Meliponini is a function of body size, especially generalized wing size, which can be estimated through principal component analysis. For six species of stingless bees, flight distances and generalized wing sizes were highly correlated (r = 0.938). This indicates that species of Meliponini occupy an effectively larger area as body size increases, which has important implications in the spatial dynamics of local populations restricted to forest fragments. We also used the fitted linear regression model to estimate the maximum flight distance for 12 other species of Meliponini. The results of this research may provide insights for future studies of biological conservation.

Key words: flight distance, local populations, morphometry, multivariate analysis.

RESUMO

Tamanho do corpo em Meliponini (Hymenoptera: Apidae): inferência do raio de vôo e possíveis implicações ecológicas

Neste trabalho analisamos as implicações espaciais da distância máxima de vôo para algumas espécies de meliponíneos. Os dados sugerem que a distância máxima de vôo em meliponíneos está relacionada ao tamanho do corpo, especialmente ao tamanho generalizado das asas, que pode ser estimado utilizando análises de componentes principais. Uma análise utilizando seis espécies de meliponíneos evidenciou que o tamanho generalizado das asas está fortemente correlacionado à distância de vôo (r = 0,938). Isso sugere que espécies de meliponíneos ocupam área efetivamente maior quanto maior for o tamanho do corpo, trazendo importantes implicações para a dinâmica espacial de populações locais restritas a áreas fragmentadas. Neste trabalho, também utilizamos um modelo de regressão linear a fim de estimar as distâncias máximas de vôo para 12 outras espécies de meliponíneos. Esta pesquisa fornece subsídios para futuros estudos relacionados à conservação da biodiversidade.

Palavras-chave: distância de vôo, populações locais, morfometria, análise multivariada.

INTRODUCTION

Meliponini are eusocial bees which are abundant in subtropical and tropical regions of the world, and comprise one of the most diverse and important insect groups. The stingless bees have an important ecological role, especially in the pollination of a large fraction (40% to 90%) of the plants forming Brazilian forests (Kerr *et al.*, 1994).

Data of maxima flight distances of stingless bee workers are important for tropical ecosystems (Roubik & Aluja, 1983) and may even be used to formulate models of population dynamics of different species. Studies of flight distances, in conjunction with other studies of local populations, can generate important inferences on migration, colonization, forest fragmentation, and biodiversity conservation.

Flight distances have been studied for only a few stingless bee species and generally utilize indirect methods of release and recapture (Roubik, 1989). Apparently, there is no directional interference in flight activities, and the number of marked honey bees (*Apis mellifera*) collected declines linearly in relation to distance from the colonies (Paranhos *et al.*, 1997). There is an apparent positive correlation between body size, especially wing area, and flight distances (Casey *et al.*, 1985; Byrne *et al.*, 1988). Schwarz (1948) suggested that, because they strengthen wing stability, wing hamuli in greater number are associated with larger flight capacity.

Worker bee size reflects an adaptation to environmental conditions (Ruttner, 1988). A major part of the morphological variation in Meliponini occurs independently of phylogeny due to the fact that, for social bees, worker body size has been generally considered as an adaptation to foraging activity and floral resource exploitation (Roubik & Ackerman, 1987; Baumgartner & Roubik, 1989). About 75.5% of body size variation in Meliponini corresponds to adaptive factors associated with resource exploitation (Pignata & Diniz-Filho, 1996). Here we examine the spatial implications of maximum flight distance for several species of stingless bees.

MATERIAL AND METHODS

Variation in worker body size of six species of Meliponini was studied using principal component analysis (PCA) based on covariance matrices. The PCA uses the original variable set and performs an orthogonal analysis to transform it into a new non-correlated variable set, whose variances decline in each principal component, in such a way that the first principal component explains the major part of the variance present in the original characters (Reis *et al.*, 1988). A logarithmic data transformation is generally used to correct for nonlinearity produced by the allometry among differing morphological characters (Gould, 1966; Neff & Marcus, 1980). Species studied and their identification codes were: (Pb) *Plebeia droryana* Friese (1900), (Ts) *Trigona spinipes* Fabricius (1793), (Mc) *Melipona compressipes* Fabricius (1804), (Mq) *Melipona quadrifasciata* Lepeletier (1836), (Mm) *Melipona marginata* Lepeletier (1836), and (Cc) *Cephalotrigona capitata* Smith (1854), which were chosen because flight distances for these bees can easily be found in the literature.

Morphometric characters were measured using the criteria of Cunha (1973, 1991) and are given in Table 1, as well as the respective score for each of the six species studied.

Flight distance data were taken from publications which used mark-recapture methods. Roubik & Aluja (1983) used a magnetic recapture method and through regression analysis concluded that the maximum flight distance for workers of *Cephalotrigona capitata* was 1,650 m. In *Melipona marginata*, maximum flight distance is 800 m. (Wille, 1983). Kerr (1987) recorded a flight distance of 2,000 m for *Melipona quadrifasciata*; 840 m for *Trigona spinipes*; 2,470 m for *Melipona compressipes*; and 540 m for *Plebeia droryana*.

Two principal component analyses were performed. One analysis used generalized body size, employing all the morphometric variables; the other used only wing variables. First principal component scores, for each of these analyses, together with the flight distances for each species, were used to form two new matrices which were examined with a linear regression analysis (Zar, 1999). A third regression analysis was performed using log values of the number of wing hamuli for each of the six species studied in relation to their respective flight distances.

Upon fitting of the linear regression model, a new matrix was created with data from the 11 characters of the wing (characters number 18 to 28 of Table 1) of 12 other species of Meliponini. This new covariance matrix, following the same pattern as in the previous analysis, was converted into 11 log-transformed characters and subjected to a PCA.

TABLE 1
Measured morphological characters and their scores in the six stingless bee species analyzed (*P. droryana* – Pd, *T. spinipes* – Ts, *M. compressipes* – Mc, *M. quadrifasciata* – Mq, *M. marginata* – Mm, and *C. capitata* – Cc).

N	Character	Pd	Ts	Mc	Mq	Mm	Cc
1	Length of the antennal flagellus	1.125	1.825	3.100	2.835	0.975	2.425
2	Scape length	0.525	0.925	1.500	1.400	1.025	1.225
3	Mandibular length	0.525	0.925	1.575	1.550	1.025	1.175
4	Inter-malar distance	0.800	1.250	1.625	1.500	1.125	1.400
5	Glossa length	0.950	1.800	2.765	2.475	1.875	2.125
6	Distance between the central ocellus and the clypeus along the frontal line	0.850	1.550	2.500	2.375	1.625	2.200
7	Inter-ocular distance at the central ocellus	0.625	1.325	2.275	1.800	1.375	1.450
8	Inter-ocular distance along the frontal-clypeus suture	0.400	0.500	1.175	1.225	0.925	0.950
9	Clipeal length	0.200	0.350	0.575	0.475	0.325	0.450
10	Inter-alveolar distance	0.300	0.450	0.700	0.600	0.500	0.525
11	Distance between lateral ocelli	0.225	0.525	0.725	0.750	0.400	0.625
12	Distance between the lateral ocellus and the compound eye	0.950	1.800	2.800	2.125	1.625	0.875
13	Femur length	1.250	2.800	3.750	3.220	2.150	1.225
14	Tibial length	0.425	0.875	1.425	1.125	0.850	0.500
15	Maximum width of the tibia	0.650	1.125	1.950	1.625	1.175	0.475
16	Basitarsal length	0.275	0.575	1.000	0.825	0.550	0.275
17	Maximum width of the basitarsus	3.600	6.900	9.200	7.800	5.400	7.900
18	Maximum length of the fore wing	1.350	2.475	3.250	2.900	1.925	2.905
19	Maximum width of the fore wing	0.925	1.500	1.800	1.300	1.000	1.900
20	M nerve length	0.100	0.075	0.300	0.225	0.150	0.100
21	Rs nerve length	1.000	1.750	2.870	2.425	1.725	2.200
22	Anal nerve length	0.950	1.800	2.590	2.475	1.650	2.150
23	M + cubital nerve length	0.750	1.350	1.820	1.350	1.000	1.650
24	Cubital nerve length	0.225	0.375	0.550	0.475	0.325	0.450
25	Cubital transverse nerve length	0.100	0.200	0.350	0.300	0.175	0.200
26	Cubital + anal nerve length	2.695	4.600	6.600	6.000	3.950	5.500
27	Maximum length of the hind wing	0.675	1.150	1.775	1.450	1.000	1.225
28	Maximum length of the fore wing	0.125	0.125	0.350	0.250	0.250	0.200
29	Number of hamuli	1.050	1.750	3.150	3.080	2.000	2.400
30	Maximum length between tegula	0.975	1.375	3.150	2.940	1.825	1.775
31	Maximum length of the mesoscutum	0.300	0.575	1.050	0.375	0.625	0.550
32	Maximum length of the scutellum	1.119	1.390	3.867	3.320	2.340	2.907

The character scores of the first principal component were subjected to the same linear regression model as before, which was then used to estimate the maximum flight distance for each of these 12 species. Analyses were performed using SYSTAT, version 5.01 for Windows.

RESULTS

Estimated flight distances for the six species of Meliponini and the scores of the principal component analysis were used to form two new matrices. Scores from the first principal component for the 32 morphological characters represented the species-specific generalized body size, which was highly correlated with data of flight distances (r = 0.897). A linear regression analysis indicated that more than 75% of the variation in the maximum flight distance could be attributed to generalized worker body size (adjusted $R^2 = 0.755$). We then examined the log-transformed values of the number of hamuli, which produced a fit with maximum flight distance similiar to that obtained for generalized body size (adjusted $R^2 = 0.757$). These results are, however, congruent with the suggestion of Schwarz (1948) that a greater number of wing hamuli is associated with larger flight capacity. However, when we performed a linear regression analysis using only scores of species-specific generalized wing size, these were highly correlated with maximum flight distance (r = 0.938) (Fig. 1). Therefore, more than 84% of the maximum flight distance variation can be explained by generalized wing size (adjusted $R^2 = 0.849$). This suggests that, as in the Euglossinae (Casey *et al.*, 1985) and in Homoptera (Byrne *et al.*, 1988), Meliponini wing size explains a large fraction of maximum flight capacity.

Using the fitted linear regression, maximum flight distance = 1,383.333 + 645.185 (generalized wing size) + error, we estimated the maximum flight distance for 12 additional species of Meliponini from their generalized wing size. For small bees *Tetragonisca angustula* Latreille (1836), *Scaura latitarsis* Friese (1900), *Plebeia poecilochroa* Moure & Camargo (1993), and *Nannotrigona testaceicornis* Lepeletier (1836), maximal flight distances ranged from 621 to 951 m (Fig. 2). Maximal flight distances for medium-sized species *Trigona hypogea* Silvestri (1902), *Trigona recursa* SMITH (1863), *Geotrigona inusitata* Moure & Camargo (1991), *Frieseomelitta varia* Lepeletier (1836), *Partamona cupira* Smith (1863) and *Scaptotrigona postica* Latreille (1807) ranged from 1159 to 1710 m (Fig. 2). Estimated flight distances for larger bees *Melipona bicolor* Lepeletier (1836) and *Melipona scutellaris* Latreille (1811), were greater than 2 km (Fig. 2). It should be pointed out that each estimated value represents a mean expectation of the maximum flight distance for each species, with an associated error.

DISCUSSION

These data suggest further need for research of the spatial dynamics of local populations of Meliponini. Paranhos *et al.* (1997) observed that colonies of *Apis mellifera* show no directional interference in flight activities. This indicates that each colony occupies a central position in relation to flight radius, defining an effective area corresponding to the circumference described by the medium flight radius in their components.

Our results also suggest that stingless bees occupy a maximum effective space proportional to body size, especially with wing dimensions, which might constitute strong constraints on local populations restricted to forest fragments. Habitat fragmentation occurs when a large continuous area is reduced, creating one or more habitat fragments (Lovejoy *et al.*, 1986; Wilcove *et al.*, 1986). These fragments of the original habitat are frequently isolated by degraded and highly modified areas. When a habitat is fragmented, dispersion and potential colonization is frequently reduced. Many species of birds, mammals, and insects of the interior forest will not cross small distances of open areas (Lovejoy *et al.*, 1986; Bierregaard *et al.*, 1992).

In the Meliponini, genetic drift is an extremely important factor in the isolation of small local populations. Araújo (2000) suggested that populations of Melipona are particularly sensitive to the effects of genetic drift due to homozygosity in the Xo sex determination locus. Carvalho *et al.* (1995) documented the loss of alleles and the extinction of local populations due to low population number. Kerr & Vencovsky (1982) estimated that a Meliponini population should contain a minimum of 44 colonies to lower the risks of rapid extinction.

Our results suggest that the risk of extinction is greater for smaller stingless bees. Colonies of *Plebeia droryana* would be effectively isolated if inter-fragment distances were greater than 600 m. On the other hand, larger species, such as *Melipona compressipes* and *Melipona quadrifasciata*, would be effectively isolated if forest fragments were greater than 2 km apart. However, larger species theoretically have a greater capacity to migrate between forest fragments, but would also depend upon larger areas to persist.

In the stingless bees, body size could act as a limiting factor in maximum flight capacity. Nevertheless, it is possible that many species in fact occupy an effectivly smaller space, depending on the influence of other variables such as: foraging behavior related to specialization in the search for specific floral resources, manners of orientation and trail laying, localization and abundance of food resources, and availability of nest sites, among others. Swarming activity in Meliponini could also act as a limiting factor of the spatial distribution of nests, since a new colony of meliponins is strongly dependent on the parental nest from which stingless bees generally provide the new nest with food and materials (Nogueira-Neto, 1997). Therefore, maximum flight distance, conditioned by body size, must have a direct influence on the dispersion capacity of the population.

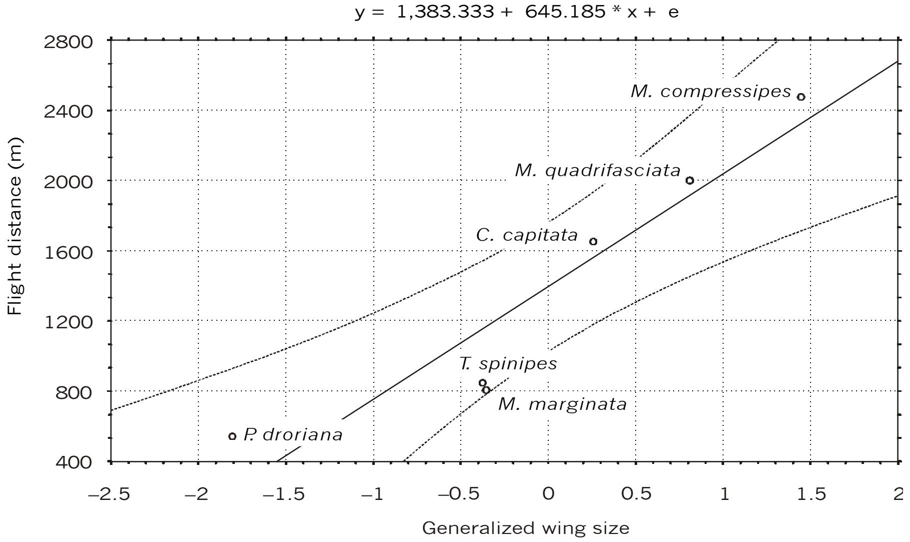

Fig. 1 — Linear regression of generalized wing size (from the first principal component) against maximum flight distance for several species of stingless bees. Dotted lines represent confidence intervals (α = 0.05).

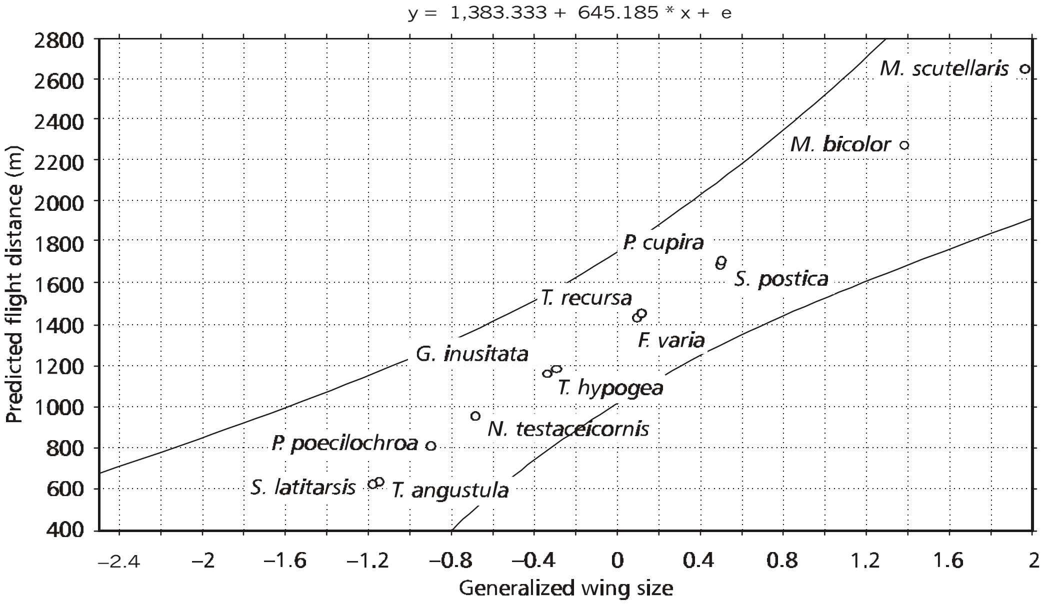

Fig. 2 — Maximum flight distances for 12 species of Meliponini estimated using a linear regression model. Dotted lines show the confidence interval (α = 0.05), based upon the linear regression of six documented species (Fig. 1).

With respect to biodiversity conservation in tropical forest fragments, the differential extinction of stingless bee species, due to physical limitations of dispersion constrained by body size, could lead to a change in plant abundance and diversity because stingless bees are one of the principal pollination agents of tropical forest species. Velthuis (1997) estimated that 33% of plant species in the Atlantic rainforest are exclusively pollinated by Meliponini. In spite of the fact that stingless bees are not specific pollinators, pollination tendencies exist for specific species and there is even a clear distinction between species that pollinate different forest strata (Velthuis, 1997). Within this context, the fact that a strong correlation exists between body size and flight distance in Meliponini can be of use in working to conserve tropical biodiversity.

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