Original article

Drifting of workers in nest aggregations of the giant honeybee *Apis dorsata*

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Abstract – The extent of worker drifting between nests in aggregations of colonies of the giant Asian honeybee *Apis dorsata* was studied using DNA microsatellites. Four aggregations with three, six, seven and eight colonies were sampled. 1537 workers were genotyped using four loci. Maternity testing was used to separate drifted and natal workers, and to assign drifted individuals to their actual maternal colony. The proportion of drifted workers ranged from 0 to 6.25% with an average of 1.27% (sd = 0.245). No significant differences in rates of drifting were found between the four aggregations. There was also no correlation between the direction of the drift and the position of the nests relative to each other. These results show that in *A. dorsata*, a bee species that frequently nests in dense aggregations, the extent of forager drifting between colonies can be very low.

drifting / *Apis dorsata* / colony aggregation / honeybee

1. INTRODUCTION

Drifting of foragers and drones is a well-known phenomenon in *Apis mellifera* L. (e.g. Betts, 1932; Free, 1958). During drifting events, foragers return to the wrong colony due to orientation errors (Rauschmayer, 1928), where they must then be accepted by the guard bees. Acceptance rates vary. When colonies are nutritionally stressed, and robber bees are about, very few foreign bees are admitted to colonies, but when conditions are favourable, drifted bees are usually accepted (Downs and Ratnieks, 2000).

In apiaries of *Apis mellifera* the degree of drifting depends on a variety of environmental and apiary layout factors. Hive orientation with respect to the sun and prevailing wind can influence direction and level of drift (Jay, 1965, 1971; Moritz and Neumann, 1996). Placing colonies in long rows with little space between and few markings on or between colonies can cause confusion among returning foragers, a large proportion of which return to the wrong colony. Under these extreme circumstances, 50–90% of foragers can move from their natal nest to neighbouring nests, depleting the foraging populations from colonies situated in the

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middle of the rows, and greatly increasing those of the colonies located at the ends (Free and Spencer-Booth, 1961; Jay, 1965, 1966; Pfeiffer and Crailsheim, 1998). However, if colonies are arranged in small clusters around conspicuous land marks, with random entrance orientations, or other appropriate apiary layouts, rates of drifting are much lower – around 5% (Neumann et al., 2000).

Drifting of foragers between natural colonies is not expected because it is likely to reduce colony fitness (Jay, 1969a, b; Robinson, 1979; Goodwin et al., 1994). First, colonies that receive foragers from other colonies may become exposed to contagions from other colonies (Jay, 1968; Matheson, 1984; Sakofski, 1990; Boylan et al., 1991; Rath et al., 1991; Goodwin et al., 1993, 1994), though they may benefit from an increased forager force. Second, kin selection arguments suggest that it is mal-adaptive for workers to forage for unrelated colonies. Finally, honey bees frequently rob the colonies of their con-specifics. Thus there is a strong chance that a forager arriving from another colony will be mistaken for a robber and expelled or killed (Downs et al., 2001).

Taken together, it is somewhat surprising that *A. mellifera* foragers are so prone to drifting between colonies. This suggests that drifting is an artefact of artificial aggregations in apiaries. In the wild, colonies of *A. mellifera* are either found singly, or in loose aggregations in which colonies are separated by many meters both vertically and horizontally (Oldroyd et al., 1995; McNally and Schneider, 1996), suggesting that in the wild, foragers would rarely drift.

Unlike the rather loose aggregations sometimes found in *A. mellifera* the giant Asian honeybee *Apis dorsata* Fabr. regularly forms extremely dense aggregations of colonies. Up to 200 colonies may occur in a single tree (Oldroyd et al., 2000) and the combs are often separated by only a few centimetres. Despite observations of short range swarming – 'budding' – (Lindauer, 1956) and home site fidelity of swarms after their seasonal migration (Neumann et al., 2000; Paar et al., 2000) colonies within aggregations do not seem to be closely related (Oldroyd et al., 2000; Paar et al., unpublished data).

The single combs of *A. dorsata* are attached to tree branches, cliff overhangs or buildings and so are completely exposed on all sides. Thus *A. dorsata* colonies would appear to be particularly vulnerable to conspecific robbing, and to the spread of pathogens and parasites among nests. Additionally, *A. dorsata* colonies are regularly attacked by wasps, hornets and birds. When this happens, hundreds or thousands of bees leave their colony for defence in form of a mass attack, and these are often joined by bees of neighbouring nests (Kastberger and Sharma, 2000). This reaction, with large number of bees flying around the aggregation, would seem to increase the possibility of high rates of drifting.

We hypothesised that unlike *A. mellifera*, *A. dorsata* would have evolved very efficient mechanisms to prevent drifting via accurate orientation of returning foragers or strong guarding abilities. To test this hypothesis we analysed samples of workers taken from colonies from four dense aggregations. The numbers of drifted bees were then quantified by microsatellite analyses. As this method does not interfere with the behaviour of the bees, it offers advantages over classical mark recapture experiments.

2. MATERIALS AND METHODS

2.1. Samples

Adult workers were collected from colonies at four different sites. Aggregation A, comprising six colonies attached to a house wall, was sampled in February 2000 in Nepal (Fig. 1). Aggregations B, C, and D were sampled in November 1998 in Assam, India. The first two with eight and seven colonies respectively were located in trees (Fig. 1). The three colonies of aggregation D were also attached to a house wall (Fig. 1).

All colonies were well established, and queen-right. Judging by the size of the nests and information provided by people living or working near the nests, we assume that all nests were older than seven weeks. At both sites we collected our samples during periods of major nectar and pollen production.

Samples were taken in the cool of the morning before bees had started to forage. Individuals were collected from the outer layers of the curtain, below
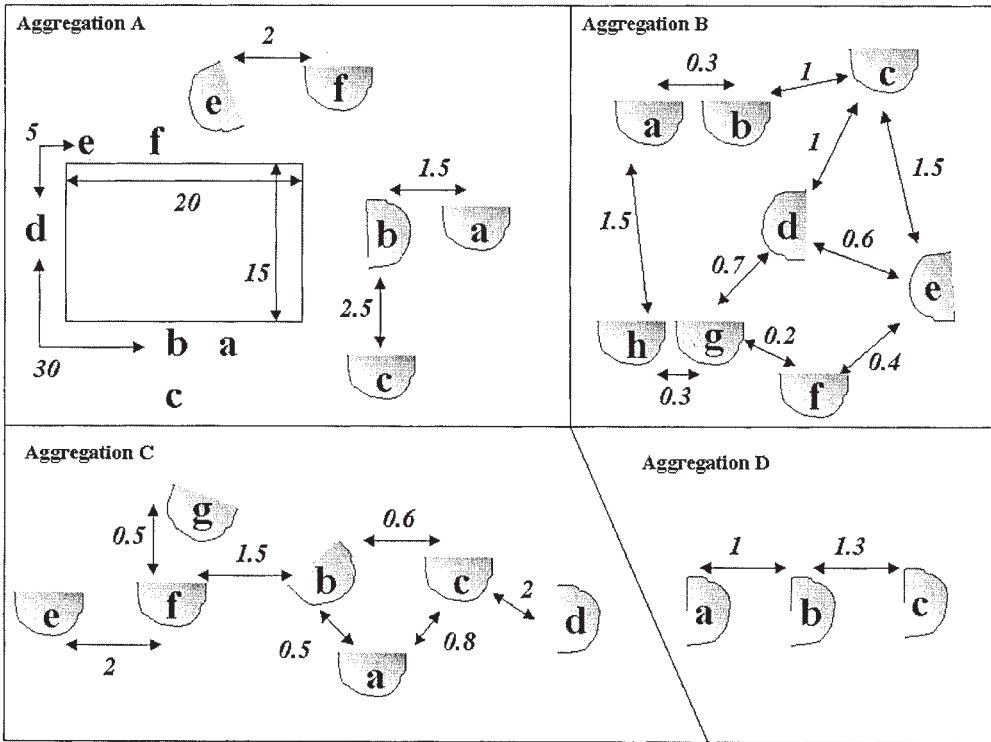
Figure 1. The four analysed aggregations of *A. dorsata*. Numbers indicate distances in metres.

the comb area to reduce the possibility of sampling a large number of young bees instead of foragers. Additionally, obviously callow workers were excluded from the sample. The sampled individuals were stored in 99% ethanol and kept frozen until further use.

2.2. DNA extraction and PCR amplification

DNA was extracted using the Chelex® method (Walsh et al., 1991). The loci A14, A24, A88, A76, cloned from *A. mellifera* (Estoup et al., 1993) and Tc3-302 from *Trigona cabonaria* (Green et al., 2001) were amplified using the polymerase chain reaction (PCR). In each case the reverse primer had been labelled (Gibco BRL) with the fluorescent dye HEX. The PCR reactions were carried out in a total volume of 10 µl. Each reaction contained 0.4 µM of each primer, 100 µM of dNTP, 0.2 units of *Taq* polymerase, 1× reaction buffer, 1.2–1.7 mM of $MgCl_2$

and 2 µl of sample DNA. The PCRs were performed by denaturing the DNA for 4 min at 94 °C and then amplifying for 35 cycles of 30 s at 94 °C, 30 s at 55–58 °C and 10 s at 72 °C. The reaction was terminated by a 9 min elongation at 72 °C. The PCR products were electrophoresed on denaturing 6% polyacrylamide sequencing gels using an automated DNA fragment analyser (Corbett Research, Sydney).

2.3. Data analysis

Drifted individuals were identified using an iterative approach. First, for each colony, we inspected the genotypes of the workers. Under the assumption of monogyny (Oldroyd et al., 1996) all non-drifted workers will carry one of the two alleles carried by the queen at any given locus. Thus, with a large sample of workers, and low rates of drifting, queen genotype can be inferred from the worker sample by excluding any worker that does not carry a queen

allele. Second, having inferred the queen alleles, we classified any worker that did not carry a queen allele as a drifted worker. We also assigned drifted individuals to their most likely maternal colony based on their queen alleles.

Undetected drifted individuals might potentially bias the results. We therefore estimated the probability that a drifted bee could not be distinguished from the workers of the colony in which she was found. This depends on the allele frequencies of the host queen at each of the analysed loci. We calculated the probability P, that a random worker from the population would have an allele from the host colony's queen at all w loci by chance alone, as:

$$ P = \Pi \sum_{i=1}^{w} \left(\frac{f_{Q1} + f_{Q2}}{2} \right) $$

where: f_{Q1} = population frequency of queen allele 1 at locus l; f_{Q2} = population frequency of the queen allele 2 at locus l.

3. RESULTS

In total we genotyped 1537 workers. Nineteen individuals were identified as drifted (Tab. I) and these individuals were found in 41.6% of the 24 colonies examined. The proportion of drifted workers ranged from 0% to 6.25% with an average of 1.27% (sd = 0.245) per colony (Tab. I). Assuming that they did not come from remote colonies, all drifted workers could be unambiguously assigned to their maternal colony within the aggregation that they were found (Tabs. II, III). The probabilities that a random worker from the population had one of the two possible queen alleles at all four loci as any worker in a given colony, and therefore would not have been detected as drifted, were calculated from the queen allele frequencies of the sampled populations. The non-detection errors were $P = 0.016$ in aggregation A and $P = 0.00053$ for the population that included aggregations B, C and D.

No significant differences in the level of drift could be found between the four aggregations (ANOVA: $P = 0.96$). There was no significant correlation between the extent or the direction of drifting and the position of the colonies relative to each other (Tab. II; Fig. 1).

However, in 15 out of the 19 instances of drifting, bees drifted to colonies which were in the same horizontal plane as their maternal colony, regardless of the distance between the nests. Distances of drifting varied from 0.3 to 2.8 m. In aggregation A, one bee drifted to a new nest 5 metres around the corner of the house.

4. DISCUSSION

Our results show that in *A. dorsata*, a bee species that frequently nests in aggregations, the extent of drift between colonies is low. The 1.4% average incidence of drifting found in *A. dorsata* is less than 1/35th of the proportions of drifted workers found in *A. mellifera* apiaries with a similar dense arrangement of colonies. Even in apiaries with planned layouts designed to reduce drifting (Neumann et al., 2000), the average rates of drifting are more than three times higher in *A. mellifera* than in *A. dorsata*.

In another study (Paar et al., 2000) only 1.5% of the individuals were non-natal from a sample of 17 colonies with 30 analysed workers per colony (unpublished data). However, Moritz et al. (1995) genetically analysed a sample of 192 workers sampled from six *Apis dorsata* colonies. They found 22 non-natal (presumably drifted) individuals, equivalent to an average of 11.8%.

Recent history of the aggregation and the single colonies could be relevant for the interpretation of the levels of drifting. High rates of drifted workers may be related to previous, significant disturbances of the aggregation. Further, differences in the food availability at the time of three studies could have influenced the level of drift through changes in the guarding behaviour within the colonies (Downs and Ratnieks, 2000), though one might expect highest rates of drifting during copious nectar flows such as when we sampled.

Our results support our hypothesis that selection has acted to reduce rates of drifting in *A. dorsata* due to their habit of forming colony aggregations.

We suggest that the tendency for *A. dorsata* colonies to be highly aggregated may have selected for high levels of fidelity to the natal

Table I. Extent of drifting for the 14 tested colonies within two *A. dorsata* aggregations. (*N* = number of geno-typed individuals; *n* = number of drifted workers.)

Aggregation	Colony	N	n	Drift (%)
A	a	114	2	1.75
	b	120	-	-
	c	110	-	-
	d	60	-	-
	e	131	6	4.58
	f	144	1	0.69
		679	9	
	Mean			1.17
B	a	35	2	5.71
	b	40	-	-
	c	30	-	-
	d	26	1	3.85
	e	40	-	-
	f	40	-	-
	g	45	-	-
	h	45	1	2.22
		301	4	
	Mean			1.47
C	a	50	-	-
	b	40	-	-
	c	32	2	6.25
	d	40	-	-
	e	50	-	-
	f	35	1	2.86
	g	50	-	-
		297	3	
	Mean			1.30
D	a	80	1	1.25
	b	90	-	-
	c	90	2	2.22
		260	3	
	Mean			1.15

Table II. Origin and destination of drifted workers within four *A. dorsata* aggregations.

Aggregation	Adopted colony	Number of drifted individuals	Natal colony
A	a	2	b
	e	5	f
		1	d
	f	1	e
B	a	1	b
		1	h
	d	1	c
	h	1	g
C	c	1	b
		1	a
	f	1	b
D	a	1	c
	c	1	b
	b	1	c

nest, coupled with acute guarding behaviour. Aggregations increase the probability of con-specific robbing and transfer of diseases and pathogens, particularly of the mite *Tropilaelaps clareae* Delfinado and Baker. In support of this contention, our observations suggest that *A. dorsata* colonies attack workers from other nests with high frequency and ferocity.

A second mechanism that may contribute to natal colony fidelity by workers is that it arises from strong selection on queens and drones to return to their natal nests. *A. dorsata* queens mate at dusk and return to their nests after dark (Rinderer et al., 1993; Koeniger et al., 1994; Tan et al., 1999). If a queen returns to the wrong nest it is likely to be fatal to the queen and the severely reduce the fitness of its colony. Thus selection has probably fostered an acute ability to locate natal nests among returning queens, and this may have indirectly selected for the same trait in workers.

Our results may have underestimated actual rates of drifting if our sampling techniques favoured collecting workers of pre-foraging age. However, our techniques are similar to those used for sampling *A. mellifera* nests

Table III. Putative genotypes (length in base pairs) of the host colony's queen and the drifted individuals in aggregation A as an example.

Colony	a				e				f			
Locus	Tc3	A76	A14	A24	Tc3	A76	A14	A24	Tc3	A76	A14	A24
Queen's alleles of adopted colony	193	203	206	101	248	211	210	99	213	201	206	103
	193	189	212	105	221	201	214	103	219	207	208	105
Alleles of drifted workers	211	217	208	99	254	205	206	99	209	201	210	99
	222	201	214	99	213	201	208	103	248	209	214	103
	193	201	210	99	233	215	210	111				
	234	201	214	99	213	207	208	105				
					237	213	212	107				
					213	201	208	103				
					237	215	210	105				
					213	207	206	103				
					207	215	214	105				
					213	207	206	103				
					193	201	206	103				
					219	209	212	97				

(Neumann et al., 2000), and the relative rates of drifting should be comparable. The non-detection error for our study is low.

We conclude that *A. dorsata* shows very low levels of forager drifting compared to *A. mellifera*. Mechanisms seem to have evolved to prevent bees straying into non-natal nests. The high percentage of drifting foragers in apiaries of *A. mellifera* is probably an artefact of the unnaturally close proximity of hives in the domestic situation. Based on our hypotheses we make two testable predictions. First *A. laboriosa*, a bee species of the Himalayas that also nests in dense aggregations (Roubik et al., 1985), should show similarly low levels of drifting as *A. dorsata*, whereas other weakly aggregating species (*A. cerana*, *A. florae* Fabr., *A. andreniformis* F. Smith and *A. nigrocincta* Smith) should show *A. mellifera*-like levels of drifting if their colonies were placed in an apiary-type situation. Second, we suggest that *A. dorsata* and *A. laboriosa* F. Smith should show much more acute nestmate recognition than *A. mellifera* (Downs et al., 2001).

Résumé – La dérive des ouvrières dans les agrégations de nids chez l'abeille géante, *Apis dorsata*. Contrairement à *A. mellifera* L. que l'on rencontre parfois en agrégations assez lâches, *A. dorsata* forme régulièrement des agrégations de colonies extrêmement denses. On peut trouver jusqu'à 200 colonies sur un seul arbre et les rayons ne sont souvent séparés que de quelques centimètres. L'étendue de la dérive des ouvrières entre nids de l'abeille géante asiatique, *Apis dorsata* Fabr., a été étudiée à l'aide de microsatellites d'ADN. Quatre agrégations de trois (A), six (B), sept (C) et huit (D) colonies ont été échantillonnées à Chitwan, Népal (Fig. 1). Le génotype de 1537 ouvrières a été déterminé à l'aide de quatre locus de microsatellites. Les abeilles qui ne portaient pas un des allèles de la reine à chaque locus ont été classées comme ayant dérivé et assignées à leur colonie maternelle réelle d'après les allèles de la reine (Tab. I et II). Le niveau de dérive des ouvrières était compris entre 0 et 6,25 % avec une moyenne de 1,27 % (0,25 %) (Tab. I). Les probabilités de ne pas détecter une abeille qui a dérivé ont été calculées d'après les fréquences des allèles portés par les reines (Tab. III). Les taux d'erreurs de non détection (c'est-à-dire la probabilité pour qu'une ouvrière prise au hasard puisse être classée uniquement par chance comme ouvrière de la colonie échantillonnée) étaient de $P = 0,016$ dans l'agrégation A et de $P = 0,0005$ pour les populations des agrégations B, C et D. On n'a trouvé aucune différence significative dans les taux de dérive entre les quatre agrégations (ANOVA : $P = 0,96$), ni aucune corrélation entre la direction de la dérive et la position des nids les uns par rapport aux autres. Nos résultats montrent que chez *A. dorsata*, espèce qui nidifie fréquemment en agrégations denses, l'étendue de la dérive entre les colonies est faible. Nous suggérons l'idée que la tendance des colonies d'*A. dorsata* à être fortement agrégées a sélectionné des niveaux élevés de fidélité au nid natal combiné à un comportement de garde développé.

Apis dorsata / dérive / agrégation de colonies

Zusammenfassung – Verflug von Arbeiterinnen in Völkeransammlungen der Riesenhonigbiene *Apis dorsata* (Fabricius). Mit Hilfe von DNA Mikrosatelliten wurde der Verflug von koloniefremden Arbeiterinnen bei der asiatischen Riesenhonigbiene *Apis dorsata* untersucht. Im Unterschied zu *Apis mellifera* zeigt *Apis dorsata* regelmäßig Ansammlungen von Kolonien. Bis zu 200 Nester können an einem solchen Aggregationsort vorkommen, oft mit den Waben nur wenige Zentimeter voneinander getrennt. Vier Aggregationen mit drei (A), sechs (B), sieben (C) und acht (D) Kolonien wurden in Chitwan / Nepal beprobt (Abb. 1) und davon von insgesamt 1537 Arbeiterinnen der Genotyp mit vier Mikrosatelliten bestimmt. Bienen, die nicht eines der beiden Königinnen – Allele an jedem Locus trugen, wurden als verflogen klassifiziert. In allen Fällen ließ sich die verflogene Arbeiterin auch der jeweiligen Mutterkolonie aufgrund ihrer Königin – Allele zuordnen (Tab. I, II und III). Das Ausmaß an Verflug variierte zwischen 0,00 und 6,25 %, mit einem Durchschnittswert von 1,27 ± 0,25 % (Tab. I). Die Wahrscheinlichkeit für eine Fehldiagnose (d.h. eine verflogene Arbeiterin wird nicht als solche erkannt und wird durch Zufall der beprobten Kolonie zugeordnet) war $P = 0,016$ für A and $P = 0,0005$ für B, C und D. Zwischen den Verflugraten in den vier Aggregationen gab es keinen signifikanten Unterschied ($P = 0,96$), und auch keinen Zusammenhang zwischen Verflughäufigkeit und der relativen

Lagebeziehung zwischen Mutter– und Ziel-Nest. Unsere Resultate zeigen, daß *A. dorsata* im Vergleich zu *A. mellifera* einen ausgesprochen niedrigen Verflug aufweist. Wir postulieren, dass *A. dorsata* während der Evolution der Kolonie-Aggregation auch Verhaltensweisen favorisiert hat, die es erlauben die Mutternester präziser wiederzuerkennen.

Verflug / *Apis dorsata* / Völkeransammlungen / Honigbiene

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