A novel form of territoriality: daily paternal investment in an anthophorid bee

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Abstract. A solitary anthophorid bee (*Anthophora* sp. nov.) in the Sinai desert showed sexually dimorphic diurnal activity patterns, whereby males defended territories containing clumps of the flower *Alkanna orientalis* between 0815 and 1430 hours while females fed exclusively on these same flowers only in the early morning up to 0900 hours and from about 1400 hours with virtually no male–female overlap on any one particular plant. Thus males defended the floral resources through long periods when conspecific females were absent. Female nests were usually within the male territories, however, and females copulated mainly with resident males. This system therefore has some similarities to resource defence polygyny, with territoriality functioning for mating advantage. The male strategy, however, was inappropriate merely to secure matings, as these occurred principally in the early morning and thereafter territories could have been abandoned for the day without loss of copulations; but by maintaining patrols throughout the day, a male would additionally ensure that there were better quality floral reserves in areas where his own females would feed to stock that day's nest-cells, and thereby he achieved matings with better-resourced females. The behaviour of the male *Anthophora* is therefore a form of territoriality that achieves potentially larger offspring, thus serving as pre-zygotic paternal investment.

In many species, territoriality is a strategy used by males to obtain increased matings (Kaufmann 1983; Hixon 1987); examples from aculeate Hymenoptera are particularly well known (Alcock 1975; Alcock et al. 1978; Eickwort & Ginsberg 1980; O'Neill 1983). A distinction is usually made between males that hold territories and those that patrol a home range. Species with a home range follow a regular circuit, visiting a series of points along their flight path, but interactions with other males are rare and subdued (Alcock et al. 1978). By contrast, males of 'true' territorial species may or may not have patrol routes (some patrol, others merely wait or perch on site), but always actively exclude conspecifics from the area that is being defended. These territories are established in areas where females occur predictably, such as foraging sites and nesting aggregations, or in visually conspicuous areas such as 'hilltops' to which females have been attracted by scent-marking males (Kimsey 1980; Alcock & Smith 1987).

In the Apoidea (bees), male territoriality has been reported for many species, and from seven families. Territory size varies from the diameter of the opening of the emergence tunnel to an area of many square metres. The sites defended are commonly one of three kinds: (1) the plants at which females are feeding (e.g. *Anthophora plumipes*: Stone 1990; *Hoplitis anthocopoides*: Eickwort 1977); (2) the nesting aggregations of the females (e.g. *Lasioglossum rohweri*: Barrows 1976) and (3) more rarely, the emergence sites of the females (e.g. *Centris pallida*: Alcock et al. 1976). In the first two cases, repeated matings may occur, but bees that hold territories at emergence sites are usually those for which the first mating is the critical, and often the only, one. Aggression patterns for the males also differ according to site: interactions between male bees around defended flowers may involve active chasing and only brief physical contact, while at emergence or nesting sites male encounters commonly result in multiple fights around an intercepted female.

Territoriality is described here in *Anthophora* ? sp. nov. a possibly undescribed species, recently found elsewhere in the Middle East by D. Baker

(O'Toole, personal communication); each male holds a territory around clumps of *Alkanna orientalis* flowers in wadis (dry river valleys) of southern Sinai. This territorial system is unusually easily studied, as the patrolling male can be observed continuously through his entire daily activity, because of the relatively small territory sizes and the barren nature of the landscape. Territorial male interactions with male and female conspecifics can also be recorded with relative ease, so that the whole mating system and life cycle are amenable to analysis.

The territoriality and associated mating system discussed in this paper differ from all others of which we are aware in one crucial respect. Male *Anthophora* sp. nov. defend the flowers on which 'their' females will later feed, throughout long periods when the female is absent, and in advance of (though with a high chance of) securing paternity of the resulting egg. We believe that in effect the males are exhibiting a pre-emptive (and pre-zygotic) paternal investment in the resultant offspring, since the cells in which their young are going to be laid can be better provisioned as a result of the father's daily activities.

SITE AND METHODS

Site

This study was carried out in March–April 1992, in the wadis around the St Katherine Field Station of Suez Canal University, situated in the southern Sinai desert of Egypt (see Dewedar 1991). The plain of St Katherine lies at about 1600 m, and the surrounding wadis radiate between mountain ridges rising to about 2400 m, each wadi thus forming an isolated community.

Most observations of bee territoriality occurred in Wadi Arbaein, a moderately steep rocky gorge running for about 2 km, roughly south-east from the central plain, and to the south-west of Gebel Musa (Mt Sinai). The surrounding peaks produce deep shadow over the floor of the wadi, except between roughly 0800 and 1430 hours local time, profoundly influencing insect activity patterns within the valley. Three sites were used, at the mouth (1), the steep-sided middle area (2), and the somewhat more open upper end of the wadi (3).

Vegetation was extremely sparse, and the plant we studied, *A. orientalis* (L.) Boiss. (Boraginaceae), was the only plant in flower in any

abundance during this period. The plants were distributed among the rocks of the valley floor and up the lower slopes at the sides; each plant formed a discrete clump up to 1 m in diameter and bore up to 700 bright yellow flowers on any one day, though the majority of clumps were substantially smaller with around 10–60 flowers.

Materials and Methods

The two sexes of *Anthophora* sp. nov. are visually very distinct, males ($\bar{X} \pm \text{SD} = 83 \cdot 4 \pm 7 \cdot 5$ mg, $N = 7$) being grey-haired and females being larger ($123 \cdot 1 \pm 3 \cdot 3$ mg, $N = 8$) and with distinct brown hair bands on the abdomen. Since territories were quite small (about 5×5 m to 15×15 m), single observers, or more commonly pairs of observers, could readily score patrolling routes of individual males (even with unmarked bees), watching the bee travelling around groups of *Alkanna* plants through the full period of bee activity. These observations were repeated over several days for part or all of the bees' active periods (0700–1700 hours), and the data thus gathered were supplemented with detailed observations of male behaviour at other key periods. Some territory-holding male bees were marked early in the study with numbered plastic discs (E. Thorne (Beehives) Ltd, Wragbury, Lincoln, U.K.) on the thorax, so that the persistence of an individual bee on a territory could be assessed over several days.

Each male bee performed a variety of highly stereotyped patrol loops, designated A–X as required, so that each type of loop could be recorded unambiguously. All flight loops were two-dimensional and close to the ground, so we could calculate lengths of patrols and total trip distances. Patrol times were recorded with stopwatches. The number of flowers on each of the plants included in the territory was recorded each day. We noted the number of flowers actually visited at any one time on any particular plant by the patrolling bee, and by other bees, and the nature of the visit where possible (collecting pollen, nectar or both: see below).

The number of encounters of the territory holder with other male bees, and with females, was scored throughout each observation period, together with the nature of each encounter. Most male–male encounters involved chasing, the intruding male departing and the territory holder returning to his patrol; on some occasions

grappling and fighting occurred, with one or both males occasionally falling to the ground and requiring several seconds to recover. Male–female encounters sometimes involved a chase, and at other times included attempted or actual copulation. Non-copulating encounters involved fast approach from any angle with abrupt physical contact unless the female flew off, whereas males seeking copulations hovered behind a flower-feeding female and attempted to land on her more gently, in alignment, from the rear. Where actual copulation occurred, the pair remained joined for several seconds, usually falling from the flowers to the ground, and could be unambiguously scored as having mated.

Female behaviour patterns were scored by stationary observations of nesting sites, though we found relatively few of these; the nest entrances were under rocks or under flower clumps, within or immediately adjacent to the territorial zones of males. Departure and return times were recorded at the nest, together with the presence of full or part loads of pollen in the hind-tibial pollen baskets. In a few cases the females could also be watched throughout their foraging trips, as they exclusively used flower clumps adjacent to their nests. However, five females whose nests were not found were marked with numbered discs to give further indications of their foraging range.

We supplemented behavioural observations with repeated sampling of the floral rewards from *Alkanna* flowers, using 1 µl micropipettes (Drummond) to extract nectar from at least 10 flowers at each sampling time. Nectar volume was measured from the length of the column in the pipette, and concentration (as % sugar) was measured with hand-held refractometers (Bellingham & Stanley, Polyfract Works, Longfield Road, Tunbridge Wells, Kent, U.K.). Pollen availability was scored only crudely in the field, as the anthers of *A. orientalis* are positioned at two depths hidden within an elongate corolla (F. S. Gilbert, P. G. Willmer, F. M. M. Semida, J. Ghazoul & S. M. Zalat, unpublished data), but we checked timing and patterns of dehiscence more carefully under a binocular microscope, from recently picked flowers returned to the laboratory.

Ambient temperature and humidity (adjacent to the flowers) were recorded at regular intervals throughout all observation periods, using a Vaisala HMI 31 probe. Insolation or shading of particular flower clumps was also scored. We mapped representative areas of the upper, middle and lower wadi floors, recording each flower clump diameter and open flower number per clump, from which plant density and territory density could be established.

All data are given as mean ± 1 SE, with sample size in parentheses, unless otherwise stated.

RESULTS

Timing of Activity Patterns

Anthophora sp. nov. was the earliest bee to be present in any numbers in the wadis, in this as in other years (Zalat 1984), and was the only bee to coincide with the early flowering of *A. orientalis*. It was clearly protandrous; males were present at the start of the study (20 March 1992) in all wadi sites, while females first appeared 2–4 days later, somewhat earlier in the upper wadi site than in the two lower zones.

Figure 1 shows representative examples of the bee's diurnal activity patterns, recorded from pooled observations of several flower patches. Males were present at all times of day when the sun directly insolated the wadi floor, very predictably appearing within a few minutes of the sun striking a flower patch (0805–0820 hours), and disappearing almost equally synchronously in the early afternoon when shade again spread over the flower patches at about 1430–1440 hours. In the upper wadi where the valley walls were shallower and further apart the sun stayed on the valley floor somewhat longer, and the male bees persisted here until about 1500 hours.

Female bees had a very different activity pattern, with a peak in the early morning and relatively little activity through the warmer parts of the day. A further and more substantial peak of female activity occurred in the afternoon, with the first few female bees appearing during the last few minutes of male activity and then persisting in numbers through the shaded late afternoon, often until beyond 1700 hours. On any particular plant, males and females did not overlap by more than 10 min per day.

Throughout their active period, the majority of males performed distinctive patrol loops around specific sets of flower clumps, hereafter described as their territory. Most territories included one very large flower clump with over 100 open flowers, which received most visits by the male and
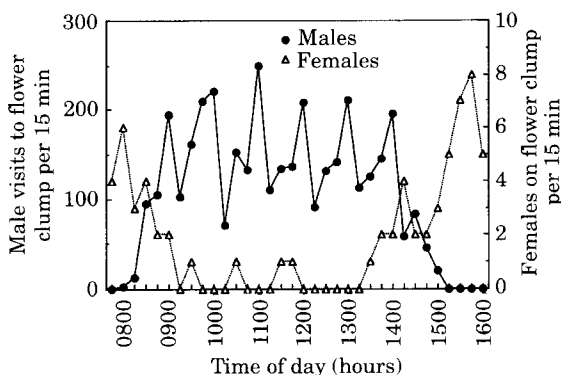
Figure 1. Visit frequency for male and female *Anthophora* on a group of *Alkanna* plants on 5 April 1992, showing the overall number of male visits to the plants (made up of repeated visits by the resident, plus some intruder visits) and the number of females present and feeding on the territory, per 15-min observation period.

where he commonly basked briefly between patrols, plus a number of other smaller clumps. Territories contained three to nine clumps, and an average of 297 ± 27 open flowers (range 217–469) on any particular day. The male territory holders interacted aggressively with most other bees encountered, and with flies, dragonflies or other insects seen nearby; and they fed only sporadically on the flowers, usually sampling between one and six flowers at a time on one specific clump only which was often the large 'base' plant.

Females when present in the early morning and again in the afternoon were invariably feeding on the flowers, usually visiting a high proportion of the open flowers on any one plant, very intensively, with often several hundred flower samplings on each visit to a large plant. They were not aggressive to passing males, or to any other species of insects encountered.

Pollen and Nectar Availability and Collection

Figure 2 shows representative daily patterns of floral nectar resources, for the three study sites within Wadi Arbaein. These data involve unprotected flowers, open to and receiving normal insect visits, and so represent the actual mean rewards available to bees. Nectar samples were fairly constant in concentration (Fig. 2a), with the mean at any one recording time varying from 32 to 47%; nectar was somewhat more dilute in the middle wadi site, where the valley floor was flattest and surface water may have been more readily available. There was no consistent diurnal pattern in any site. Nectar volumes did vary however, rising
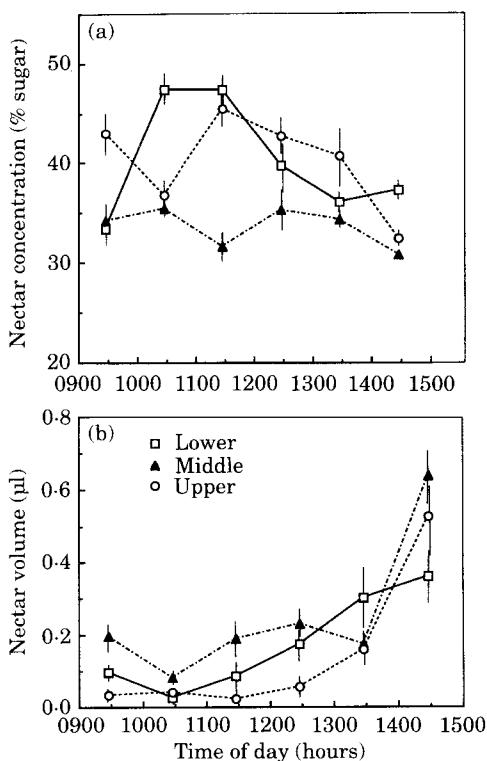

Figure 2. Nectar concentrations (a) and volumes (b) in individual *Alkanna* flowers in Wadi Arbaein on 24 March 1992, at three sites. Values are means for at least 10 flowers at each sampling time, and error bars show ± 1 SE where this is larger than the symbol.

at all sites through the day (Fig. 2b) and with a substantial peak in the early afternoon coinciding with the beginning of female bee activity. The

Table 1. Diurnal patterns of patrol loops in a representative male *Anthophora*, on a single day

Time interval	No. of visits to base	Loop type*								Distance travelled (m)
		A	B	C	D	E	F	G	H	
0830–0845	22	19	—	—	1	—	2	—	—	378
0845–0900	24	21	—	—	3	—	—	—	—	438
0900–0915	24	14	4	—	6	—	—	—	—	508
0930–0945	40	11	21	—	—	—	3	2	3	1136
0945–1000	39	11	14	—	2	—	—	8	4	922
1000–1015	44	9	6	—	4	—	11	5	9	1080
1030–1045	36	3	8	—	5	—	10	5	5	1084
1045–1100	37	5	9	—	5	—	13	2	2	918
1130–1145	37	14	7	—	3	—	10	—	3	732
1145–1200	29	7	3	—	3	—	11	2	3	562
1230–1245	30	12	3	—	4	—	8	—	3	570
1245–1300	33	13	1	—	4	—	9	3	3	666
1330–1345	30	3	5	2	—	—	7	6	7	787
1345–1400	30	2	—	6	1	—	7	10	4	1065
1430–1445	31	2	—	9	—	1	4	8	7	1017
1445–1500	23	4	—	10	1	1	—	1	6	479

Total distance travelled in 4·0 h observation was 12·34 km. See Fig. 4 for further details.

steady rise in availability indicates secretion through the sunlit hours, with the afternoon peak further enhanced by new flower buds opening then (see below).

Nectar-collecting visits were made by both sexes, and were always short, averaging less than 2 s per flower and with no obvious diurnal variation in duration.

Pollen was probably available from at least some *Alkanna* flowers at all times of day, but was at a peak in the early afternoon when a new cohort of freshly opening buds was added to the flower population; the percentage of such freshly opened buds rose from 12 to 16% in the morning and at midday to about 25% after 1430 hours. Pollen was collected only by females, as in all bees, though it was the main resource 'guarded' by the activity of males (see below). Females collected pollen by a complex process involving 'buzzing' which they use for other Boraginaceae. They commonly buzzed at least once into a flower while hovering over it with the tongue inserted, and buzzing visits were especially common into young flowers just opening from the bud stage; around 90% of all visits to buds involved buzzing, while only a small proportion of mature flowers were buzzed (Fig. 3a). Each flower was commonly buzzed several times (up to 15), especially in the afternoon visiting peak

when new buds that would still have a full pollen store had just been recruited to the flower population. Figure 3 also shows the changing proportion of visits that were made to buds through the day, the proportion of visits involving buzzing at different tiumes, and (Fig. 3b) the variation in mean visit time per flower for pollen-collecting females. Pollen-gathering flower visits were short in the early morning, and were longest (up to 22 s being spent at certain young flowers) at the time when pollen availability was highest around 1400 hours. For most bees there were few if any pollen-gathering visits between 1000 and 1330 hours; the few records that contribute data for this period in Fig. 3a come from a tiny minority of bees (see below).

Patterns of Patrol Loops and Male Activity

Figure 4 shows a map of the territory and of the various routes around it, taken by one representative patrolling male on one day (29 March 1992) of intensive observation. Table I summarizes this male's behaviour, the loops used, and distances travelled in every 15-min interval. This particular patrolling male was chosen because his territory was of about average size and complexity and the patterns he showed through the day were typical of others observed; in addition we did not miss any trips that he made.
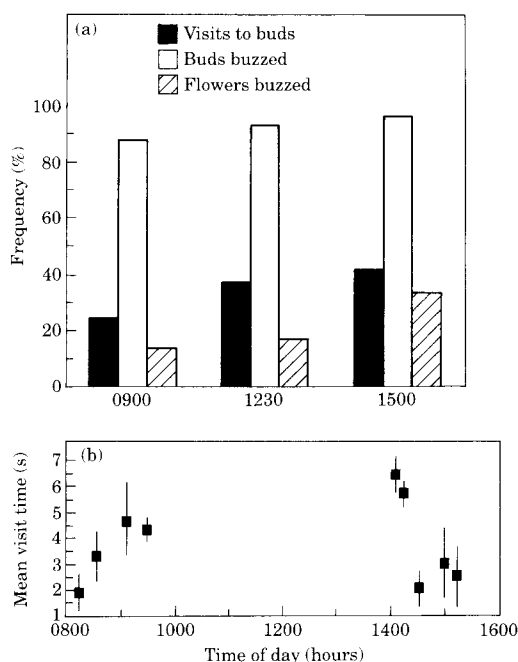
Figure 3. (a) The increasing percentage of all female *Anthophora* visits that were to just-opening buds throughout a day (4 April 1992) and the frequency of 'buzzing' (see text) at buds and flowers. (b) The resultant mean visit times per flower ± 1 SE. (There were insufficient visits through the midday period to give means, but those visits seen commonly took in excess of 15 s per flower.)

In the early morning the bee had a relatively simple patrol route, using loops A, D, F and later H. From about 0900 hours, when all female activity had ceased, he often incorporated into his patrol circuit side-loops (B) to a barren area which later proved to house at least two nest entrances. For nearly all circuits from 1330 hours these side loops were shortened (C and G) to include only flower clumps and not the nest sites. Thus the male bee patrolled all of his own flower clumps throughout his active period; he also checked the nest entrances during periods when females were inside and digging, but ceased to do so when the females were visiting flowers.

Total distances travelled per day per male, and mean trip lengths, can be calculated from these data, as shown in Table I. For this bee, and for other bees similarly observed, the distance travelled per 15-min interval was often in excess of 1 km, and varied with time, with longer trips generally occurring later in the day.

Changes in Patterns during the Day

Figure 5 shows examples of the frequency of visits by a resident male to his own largest 'base' flower patch, the number of visits he made to individual flowers, and his percentage time at the base flower patch, over his entire active period. All males showed a similarly clear peak of returns to the principal flower patch in the middle of the day. The percentage time that the base flower clump was attended by its resident territory holder was rather constant for all sites and individuals and at all times of day, values lying in the range 30–50%.

The data described so far concern only a few bees, each intensively watched. We examined the patterns of territory size and male patrol behaviour more quantitatively throughout the day on 26 March 1992, with observers assessing flower clump occupancy over large areas of the wadi floor at each of the three sites, classifying flower clumps broadly into three sizes, determining the territory to which they belonged, then timing and measuring the resident bees' circuits. Table II summarizes the findings for all times of day to show the very high incidence of patrolling, with around 80% of all large flower clumps (>50 flowers) incorporated into a territory. There are no significant differences in numbers of flower clumps per territory in the three wadi sites (Kruskal–Wallis test=1·7, NS), though the greater flower density higher up the wadi leads to a greater density of territories there.

Figure 6 shows the patterns of territorial behaviour throughout the day, summed for a large number of bees (217 flower clumps, 150 bees) and for all sites. The number of flower patches in the territory of a male increased somewhat later in the day (Fig. 6a), from a mean of about 3·2 in the morning to 4·5 by the early afternoon, indicating territorial expansion out to nearby flower clumps for at least some males and an increased length of circuit (see also Table I). However, the mean flight speed of patrolling males also increased (Fig. 6b), so that even with larger territories the time to return to any particular flower patch actually declined substantially through the day (Fig. 6c), to be minimal at about the time that female activity resumed. This accords with the gradually increasing base-patch occupancy shown in Fig. 5c. From this larger data set, we could also calculate that the numbers of flowers visited by males always
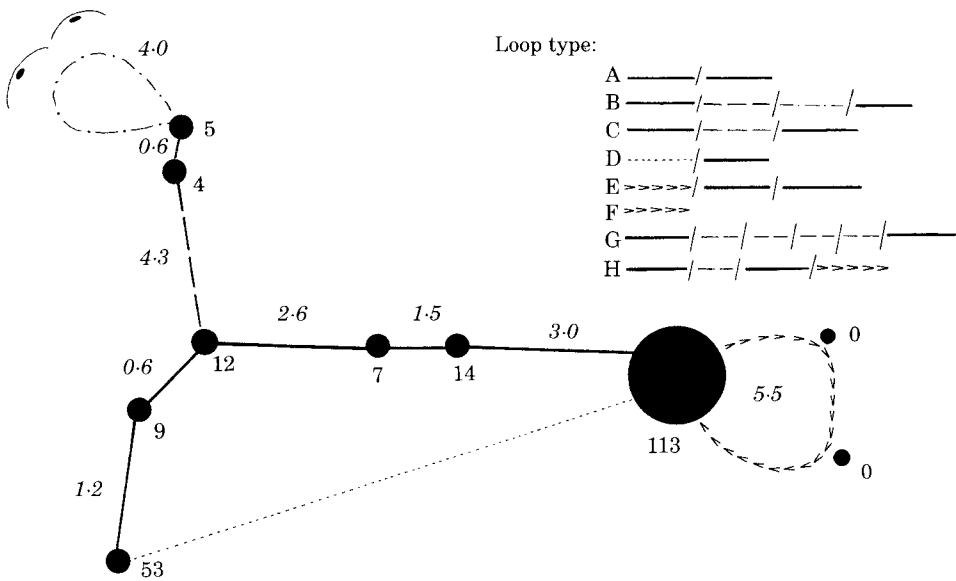
Figure 4. An example of a male *Anthophora* territory in the lower wadi site, showing flower clumps (with numbers of open flowers) and the patrol routes followed by the resident male. Not to scale; distances (m) between flower clumps are shown in italic. Upper left loop passes two female nest entrances. More details are given in the text.

tended to peak in the middle of the day, as shown for the single individual in Fig. 5b; but this number was always rather low, so that nectar availability still increased through the day as in Fig. 2.

In summary, the males of this anthophorid bee maintained territories of moderate size for 6–7 h each day, and defended the flowers against all comers, with the numbers of defended flowers increasing somewhat through a day. Each male supported this territoriality with just enough flower visits to fuel his own flight activity, with such visits commonest in the middle of the day when costs of flight may also be highest (cf. Willmer 1986). By flying faster as the day progresses he also achieved minimum return time to the prime flower clump within his territory, and thus maximum residency at this clump, at about the time that females began to visit it again.

Table II. Variations in territory size and frequency in different zones of Wadi Arbaein

		Zone 1, lower wadi	Zone 2, mid wadi	Zone 3, upper wadi
Percentage of flower clumps included in a territory	Small	47·0	53·8	52·9
	Medium	59·0	79·3	53·3
	Large	76·0	81·8	82·8
Clumps per territory	Small	4·2	5·6	2·7
	Medium	3·6	5·0	5·0
	Large	3·7	3·8	4·2
Time of circuit (s)	Small	18·8	24·2	18·5
	Medium	18·0	20·3	18·3
	Large	17·0	20·9	19·1
Overall density of territories/ha		48	85	151

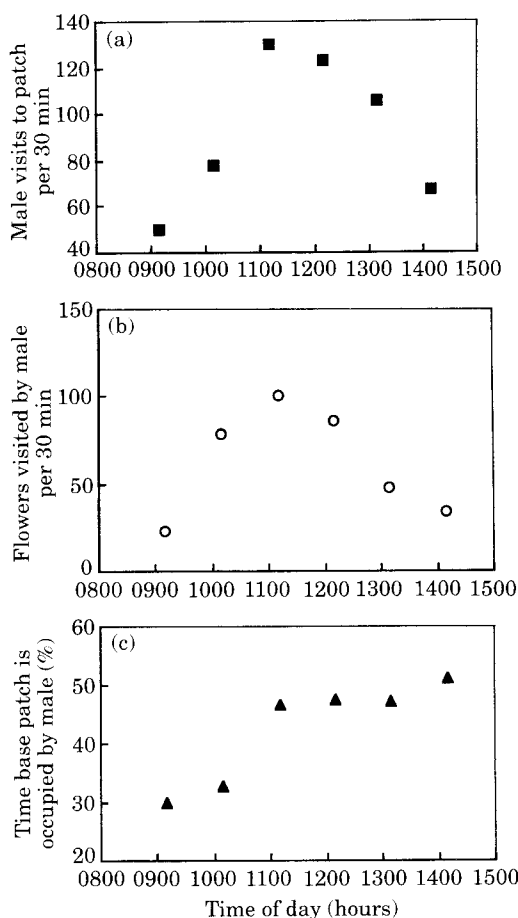Shown in relation to flower clump size: small=0–10 open flowers, medium=11–50, large ⩾ 50.

Figure 5. Behaviour of the male bee on the territory shown in Fig. 4 on 24 March 1992, showing (a) number of visits to main flower clump, (b) number of flowers visited and fed at, and (c) the percentage of time the male was present on main flower clump; all per 30-min observation period.
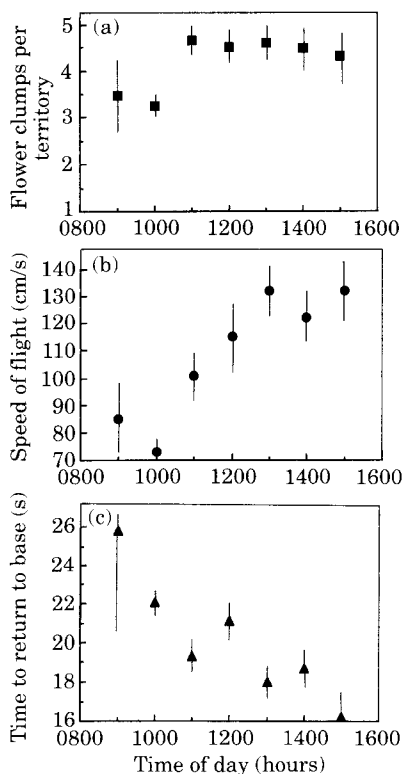

Figure 6. Mean values, for 150 bees summed for all sites, of (a) the numbers of flower clumps per territory, (b) the speed of flight of patrolling males, and (c) the time to return to the main clump. Error bars show ± 1 SE.

Persistence of Territories

The patrol circuits of male bees were so consistent that it was often possible to identify the same male for several consecutive days from his circuit alone. To check, however, that the same male did indeed hold the same territory for more than 1 day, 16 territorial male bees were marked early on 30 March 1992, and their positions were checked later that day and then once a day for the following 8 days. We saw 14 at least twice more, six were still being resighted 5 days later, and two persisted on the same territory with similar patrol loops for the full 8 days. In all such studies, some marked

bees will always either lose their markings or fail to resume normal behaviour; and a small percentage of the male bees in the wadis were also lost naturally to spider predation, so accounting for some failure to persist on territories. The recovery rate of marked bees here is therefore rather high and must indicate a very good persistence of territorial males.

A few males (probably less than 10% of the population), however, were non-territorial, and these 'sneaker' bees tried on occasions to adopt territories; only one actual take-over was witnessed, so we know there were also very occasional failures of persistence resulting from usurpation. Non-territorial males flew with random flight paths around and between territories, sneaking occasional flower visits and being attacked by resident males. In the middle of the day these 'sneaking' males sometimes patrolled around the sites of known female
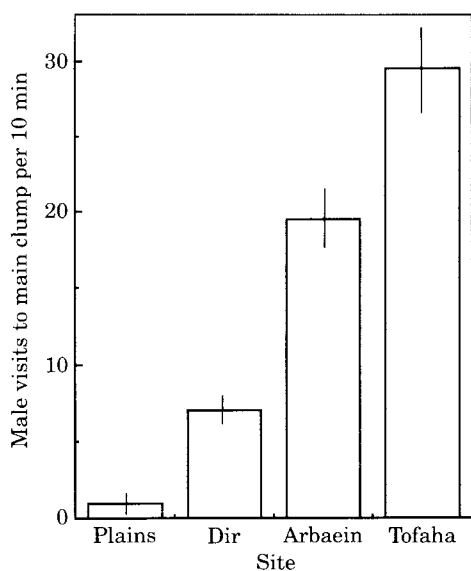
Figure 7. The variation in male patrol frequencies in sites with increasing bee density. Values are means for different recording times ± 1 SE.

nests, though they were never seen intercepting a female.

Territories in Different Sites

All the results quoted so far refer to bees resident in Wadi Arbaein. The same flower and the same bee, however, also occurred in other adjacent wadis, and in the main basin of St Katherine's valley, and here different patterns of territoriality occurred. The flowers in other sites proved to have very different characteristics of size, colour, density on the plant, and phenology, which were predictably linked with community isolation (F. S. Gilbert, P. G. Willmer, F. M. M. Semida, J. Ghazoul & S. M. Zalat, unpublished data). In association with these differences, territory-holding behaviour by male bees also varied (Fig. 7). It was most frequent and most intense in the most isolated wadis where bee numbers were high (Wadi Arbaein and Wadi Tofaha, steep and gorge-like, and with fewer and less showy flowers), moderate in the shallower and less isolated Wadi Dir, and non-existent in the open plains of the valley, where bees and plants were relatively scarce and flowers were larger and highly rewarding. Thus the territorial behaviour of this bee appears to be contingent upon the

circumstances of floral reward and/or bee density (which may themselves be linked).

Female Behaviour and Nesting Patterns

We observed only 10 female nests for appreciable lengths of time; Fig. 8 shows the patterns of trips out of the nest on a single day for three of these. Most of the observed females showed a similar pattern to bees 1 and 2, with a series of short foraging trips in the early morning, retirement to the nest from about 0930 to 1400 hours and a further series of trips in the later afternoon. Just two of the 10, and on just 1 day each, showed the other pattern (bee 3), with prolonged absences from the nest through the middle of the day. Thus the mean length for all trips up to 0930 hours was 21·9 ± 3·1 min, between 0930 and 1400 hours it was 83·7 ± 21·0 min, and after 1430 hours it was 12·5 ± 3·5 min.

Female bees must gather both pollen (the main food provided for their young, and on which the eggs are laid within individual cells) and nectar (to fuel their own flight and to mix with the pollen ball to provide the right moisture level and consistency). Most female trips involved some pollen collection; short trips in the later afternoon presumably reflect the abundance of young pollen-rich flowers then, while longer visits through the midday period may indicate pollen-depletion in the previous days' flowers with new buds not yet opened. For 1 day of intensive observation (4 April 1992) the numbers of visits involving nectar (N) or pollen (P) or both (NP) were as follows: 0800–0900 hours, N 14, P 2, NP 27; 1230–1330 hours, N 13, P 6, NP 6; and 1430–1530 hours, N 4, P 31, NP 29. This confirms the impression gained from the nesting behaviour that in the morning both resources are collected, while in the afternoons pollen gathering is predominant.

Male–Female Interactions and Function of Territories

Figure 9 shows the patterns of male–female interactions around the *Alkanna* flowers. Some males and females interacted quite aggressively at most times of day, except after 1500 hours when males had vanished and females worked the flowers largely uninterrupted, often several together on a flower clump. In the early morning and again in the afternoon, patrolling males
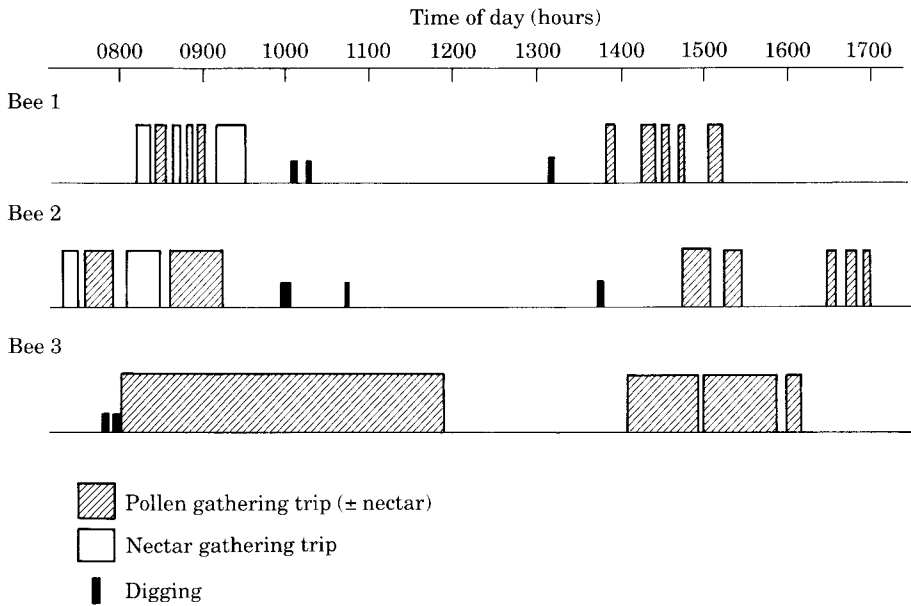
Figure 8. Three representative examples of diurnal activity patterns in female *Anthophora*, from observations of nest sites.

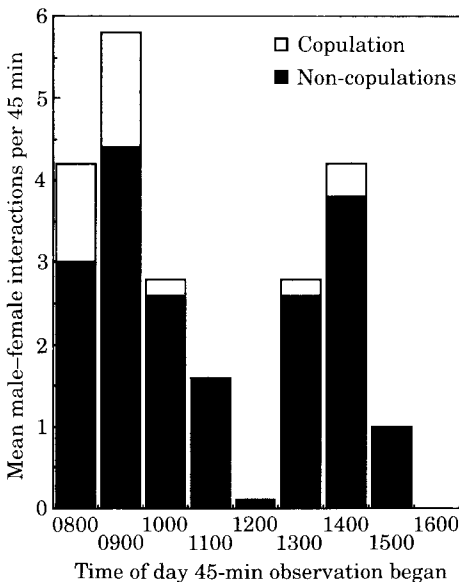clearly attacked certain females and left others alone, but since females were not marked we

Figure 9. Mean numbers of male–female interactions, scored over several days with 45 min of observation per h, and corrected to a norm of 5 days observation. Encounters involving copulation are scored separately, most others being aggressive chases or fights.

cannot be sure that it was the same females (or 'home range' females) that were allowed to feed freely. The few females working flowers around midday were particularly likely to be attacked indiscriminately by males, and their lengthy trips to the rather depleted flowers were probably made longer by the activities of the males.

Only in the early hours of the day were copulations common, with 13 out of 17 clear sightings occurring before 0945 hours, and with up to one-third of all male–female encounters before that time involving clear attempts at mating. During this early morning period, we just once saw a female mated by a non-resident male, and in this case the intruder was rapidly chased off and the female re-mated by the resident. Thus mating is predominantly a morning phenomenon and is secured in almost all cases by a territory-holding male.

DISCUSSION

There are a number of general features of the territorial system described here that should be emphasized as differing from the classic 'resource defence polygyny' systems described elsewhere (e.g. Alcock et al. 1978; Thornhill & Alcock 1983; Sandell & Liberg 1992).

(1) The most obvious curiosity is the precisely patterned male and female behaviour cycles that serve to prevent males and females meeting for all but the most transient period. The males appear as the early morning female activities cease; and they disappear sharply when the sun leaves the flowers and as females resume flower visits to gather provisions for a new cell. Male territoriality thus seems devoted to defending the resource in the absence of females, presumably enhancing future floral rewards (especially pollen) for the females.

(2) Other examples of aculeate territoriality generally involve systems where males are relatively scarce, and where the female emergence, nesting or feeding sites are clumped (Alcock et al. 1978), so that male–female encounters are facilitated. Neither of these criteria really applies to the *Anthophora* system described here, where males and females are spatially closely associated and males occur at high density with contiguous territories involving most of the available plants. The female nests were often actually within the male's territory, and were checked by him at regular intervals through the day though he never met the females at the nest sites. This 'checking', possibly linked to female nest-marking pheromones, could have allowed a male to be sure that each of his females was still active, or even more specifically that she was still digging new cells and so would be laying an egg that day. There are few records of territorial systems where the female 'home ranges' are included within male territories, so that the same males and females meet repeatedly, but this may be a factor promoting tightly clustered male territories and also a small proportion of roaming males (see Sandell & Liberg 1992). Ims (1987) argued that temporal patterns in the occurrence of receptive females may promote particular male spacing patterns in rodents, and the same feature may be promoting territoriality with these *Anthophora* bees (and with other bees where the females' diurnal activity cycle is tightly patterned).

(3) Duration of territory ownership in many bees is inversely related to competition (Eickwort & Ginsberg 1980), with many species showing fairly rapid turnover and high rates of usurpation; but the males of *Anthophora* sp. nov. commonly hold the same territories over successive days, even at such high densities and high levels of male–male interaction. In many bees, territories are held at least in part by scent-marking, males

using pheromones to stake out their area (Kimsey 1980; Marshall & Alcock 1981); but we saw no evidence of behaviour that could result in scent-marking of territories in Wadi Arbaein. *Anthophora* males nevertheless seem to find and retain the same few plants and thus the same few females over many days. This may indicate that they stay on or near their territories during their inactive hours, perhaps resting within plants or in sleeping-holes. We did not see the males leave the site when their activities ceased, and certainly in the mornings they appeared to begin activity 'instantaneously', without flying in from elsewhere. If they do sleep on site, the persistence of the unusually strict spatial patterns of territories held by the same males becomes more explicable.

(4) *Anthophora* sp. nov. females clearly mated repeatedly, perhaps once (at least) for each egg laid; although, as in the majority of solitary bees (cf. Danforth 1990), it is very likely that just one cell was provisioned and thus one egg laid per day by each female. In many bees females mate once only on emergence, though some are mated repeatedly by as many males as can get at them during flower visiting or around the nests. Polyandry is reasonably common in some bee families, though apparently infrequent in the Anthophoridae. It has been observed however, in *A. plumipes* in Britain (G. N. Stone, personal communication) and in Portugal (F. S. Gilbert, personal observation), and is strongly implied for *A. occidentalis* (Esmaili 1963), so may well be commoner than the available literature implies. In *Anthophora* sp. nov. copulations appeared to occur every day during the brief male–female overlap times, so that each egg laid could be fertilized by the sperm of a separate mating. Each territorial male encountered only his 'own' females, and must have achieved most of the matings with them; it presumably paid off for him to mate each female each day to ensure paternity of that day's eggs, and thus reap the rewards for his energetic territory holding. Each female, while she may occasionally have been mated by a sneaker male, was very much more likely to be mated last, day after day, by whichever male had held the territory around her nest site, and thus frequently by the same male. It seems most unlikely that she could not fertilize each day's eggs with sperm stored from previous matings, as in other bees (cf. Michener 1974); however, by allowing a further mating she could on occasion secure

paternity from an even stronger male who had usurped the previous holder. An alternative explanation for her acceptance of repeated matings is of course the standard one of avoiding the strife of trying to resist further matings from persistent males (cf. Alcock et al. 1977, 1978), though this is less plausible when many females must have mated peacefully only once per day.

Despite these strange features, *Anthophora* sp. nov. also bears significant similarities to other territorial bees. For example, the species shows alternative mating tactics (cf. *Anthidium manicatum*: Alcock et al. 1977; Severinghaus et al. 1981; *Eulaema meriana*: Stern 1991), in this case with a low frequency of 'sneaker' or 'satellite' males avoiding the costs of holding territories but ranging more widely over many other males' territories and presumably seeking surreptitious matings. The presence of a fairly small cohort of 'sneakers' is a rather common occurrence in insect mating systems in general, resulting in two or more alternative strategies (Willmer 1991). In some cases the two alternative types of behaviour are correlated with male size, or the frequency of each is related to male density. In this study the former seems unlikely, as non-territory holders (though not measured separately) were certainly not visibly different from those patrolling the *Alkanna*, but there may be a relation between frequency of satellites and male density, since in some parts of the habitat the roving non-territorial mating strategy became the norm, indicating a substantial ability to change the mating system with circumstance (cf. *A. manicatum*: Alcock et al. 1977). The most important parameter here is presumably the resource density (*Alkanna* plants), but probably taken in relation to bee density. A similar versatility in male strategy has been observed for the bee *Xylocopa sulcatipes* in desert sites in Israel relating to plant and bee density (Velthuis & Gerling 1980), and in other bees switches of this kind occur as the season progresses and bee density increases (e.g. Eickwort 1977). The stable balance between two such strategies has been modelled by Sandell & Liberg (1992).

It is also worth stressing the contingent nature of this territorial system, similar to that in other bee studies. First, the presence of territorial behaviour in the males is highly seasonally dependent on the presence of females, so that in the lower wadi males did not bother to set up patrol

systems until slightly later in the season once females began their nesting cycle. (It would be helpful to know whether male territory size, or patrolling effort, was also contingent upon the number of female nests in that territory, and whether male effort does indeed affect female reproductive success; but unfortunately many nests were very hard to locate, and most would be impossible to dig up to assess cell or offspring number and size.) Second, there was a clear contingency of territorial patterns in relation to either floral resource or overall bee density or both, with no territoriality in the plains area and reduced frequencies of territories in wadis with a less dense resource. Both of these features are to be expected in a system where the males are specifically using territoriality based on resource defence polygyny to secure (albeit somewhat indirectly) matings with females.

Explaining the Territorial Patterns

In some ways the system described here can be explained as straightforward resource defence polygyny as defined by Alcock et al. (1978). A number of factors, however, point to the male behaviour as a rather more unusual case of prezygotic male investment in future offspring quality, in a sense somewhat different from the usual forms of insect paternal investment where there is courtship feeding of various kinds (Thornhill 1976; Zeh & Smith 1985; Gwynne 1986). The problem lies in distinguishing clearly between these two phenomena, and a number of points are pertinent here.

First, the level of aggression by territory holders to other males and other nectar feeders in this bee is striking, though not entirely unusual as aggressive chasing of any intruder non-selectively has been recorded for other male bees (Alcock et al. 1978). Eickwort & Ginsberg (1980) suggested that this is not merely a bee mistaking other moving objects for intruding conspecific males, but involves the male protecting the food resource for himself and especially for his females, which would accord with the paternal investment idea of territory function.

Anthophora sp. nov. shows further similarities to certain other bees and wasps in that male territoriality occurs only at particular times of the day or season. For example, in the sphecid *Philanthus bicinctus* males are territorial only

during the early mornings, and only in the early part of the season, while females are digging their nests; and all copulations observed also took place during this period (Gwynne 1980). In all such systems, however, the timing of territoriality is such as to ensure that males coincide with female presence: we can find no other system where most male territoriality is organized to occur at times of female absence.

Territorial defence in advance of the expected benefit is not unknown: a territory being maintained because it will be useful later makes sense if, once given up, it will be difficult to regain. Certain birds may hold territories in this fashion: for example, pied wagtails, *Motacilla alba*, make long-term optimal compromises in territorial behaviour (Davies 1976). It is doubtful, however, whether this could evolve specifically in relation to paternal investment. It is in any case unlikely that territories are very hard to regain for the anthophorid considered here; and aggressive encounters were apparently principally with the sneaker males rather than with adjacent territory holders, the proportion of sneakers being quite small.

For these reasons it is hard to explain this bee's territoriality as simple mating investment. If matings occurred primarily in the afternoon male–female overlap period, there would be less of a problem, and the situation might be comparable to that of the wagtails with males establishing a territory because receptive females would come to it later that day. In fact, though, if mating were the only function of their territoriality, and with mating timed as it is, the males would only need to set up their territory early in the morning, mate their females in the critical hours up to 0900 hours, and retire again until the next morning. We have unpublished data showing that this bee, like others (Stone & Willmer 1989; Stone 1993), is capable of endothermy, so that males could indeed warm up to be active at such times, yet this capability is apparently rarely if ever used by *Anthophora* sp. nov. despite air temperatures often below 8°C in the early mornings.

Nevertheless, it is possible that the system described here for *Anthophora* may have evolved originally as territoriality to secure matings, in the more conventional manner (cf. Wickler 1985; Gwynne 1986; Sakaluk 1986), but has shifted ground functionally because of strong local selection pressure (F. S. Gilbert, P. G. Willmer, F. M. M. Semida, J. Ghazoul & S. M. Zalat, unpub-

lished data). Selection could have pushed the diurnal patterns of bee activity or of the flowers' presentation of rewards, or both, in directions that have uncoupled the male and female bees' activities. *Alkanna orientalis* is the first flower to open in the Sinai wadis, and is very difficult for insects to visit; it requires diligence to extract pollen by buzzing repeatedly while hovering, and the plant has well-defended sticky leaves that deter landing. As soon as other flowers are available, the bees switch preference and stop visiting the *Alkanna* (F. Semida, unpublished data). One line of speculative reasoning might be that *Alkanna* has been selected to flower increasingly early to achieve effective pollination, avoiding competition from other more accessible flowers. Thus it would encounter lower daily temperature regimes, so that dehiscence (strongly susceptible to thermal cues) would move to a midday period. The associated anthophorids, also emerging earlier in the season, would then have flower resources available at times inappropriate to the normal female nesting and foraging cycles; females would not encounter fresh pollen in their early morning visits. This would explain the discrepancy of timing between pollen presentation and pollen collection. It might also leave the males' normal flower-patrolling behaviour (strongly tied to the thermal regime in the local habitat) out of synchrony with the plant and the females. Thus the males persistently hold territories and preserve floral resources, to be gathered later by the surrounding females, while the latter are digging their new cells. Male activity may have originally been needed for only a small part of the day when females could be encountered, but now it is necessarily extended over many hours, looking like (and indeed functioning as) pre-zygotic paternal investment.

As such the system might become susceptible to 'cheating'. It could suffer invasion by 'lazy' males, who warmed up enough endothermically to gain some matings before other 'resident' males re-established yesterday's territories, taking advantage of the females feeding on the protected resources and then retiring for the day leaving the cuckolded males to husband some further well-filled flowers. However, we saw no evidence of this occurring, and in any case once the territorial male had re-established his patrols he could presumably re-mate any of his females before they retired for the day. A somewhat similar possibility

for cheating is that a male could mate 'his' females in the morning and then allow some other male to guard her flowers through the day (though he could not then be sure that the flowers had indeed been guarded and the offspring well-resourced); in practice this is unlikely, as we would presumably then have scored the latter male as a 'resident' and the former as a satellite, and we only once witnessed a satellite mating. The system might therefore be relatively immune to cheating and could become stably established in its present form.

We can find no alternative explanation of the apparent 'mismatch' of male and female activities in this bee, and our interpretation of paternal investment rather than mere mating investment as the function of this territorial system does account for the various peculiarities of behaviour exhibited by the male bees. Whether the syndrome originated as conventional simple investment to secure matings is perhaps less important; its present effect, for females and for offspring, seems clear.

REFERENCES

Alcock, J. 1975. Territorial behaviour by males of *Philanthus multimaculatus* (Hymenoptera, Sphecidae) with a review of territoriality in male sphecids. *Anim. Behav.*, **25**, 889–895.

Alcock, J., Jones, C. E. & Buchmann, S. L. 1976. Location before emergence of the female bee *Centris pallida* by its male (Hymenoptera: Anthophoridae). *J. Zool., Lond.*, **179**, 189–199.

Alcock, J., Eickwort, G. C. & Eickwort, K. R. 1977. The reproductive behaviour of *Anthidium manicatum* (Hymenoptera: Megachilidae) and the evolutionary significance of multiple copulations by females. *Behav. Ecol. Sociobiol.*, **2**, 385–396.

Alcock, J., Barrows, E. M., Gordh, G., Hubbard, L. H., Kirkendall, L., Pyle, D. W., Ponder, T. L. & Zalom, F. G. 1978. The ecology and evolution of male reproductive behaviour in the bees and wasps. *Zool. J. Linn. Soc.*, **64**, 293–326.

Alcock, J. & Smith, A. P. 1987. Hilltopping, leks and female choice in the carpenter bee *Xylocopa (Neoxylocopa) varipuncta. J. Zool., Lond.*, **211**, 1–10.

Barrows, E. M. 1976. Mating behaviour in halictine bees: II Microterritorial and patrolling behaviour in males of *Lasioglossum rohweri. Z. Tierpsychol.*, **40**, 377–389.

Danforth, B. N. 1990. Provisioning behaviour and the estimation of investment ratios in a solitary bee, *Calliopsis (Mypomacrotera) persimilis* (Cockerell) (Hymenoptera: Andrenidae). *Behav. Ecol. Sociobiol.*, **27**, 159–168.

Davies, N. B. 1976. Food, flocking and territorial behaviour of the pied wagtail (*Motacilla alba yarelli*) in winter. *J. Anim. Ecol.*, **45**, 235–254.

Dewedar, A. 1991. *The Sinai Desert Training Centre. Reports 1–4*. Cairo: Foreign Relations Coordination Unit, Supreme Council of Universities.

Eickwort, G. C. 1977. Male territorial behaviour in the mason bee *Hoplitis anthocopoides* (Hymenoptera: Megachilidae). *Anim. Behav.*, **25**, 542–554.

Eickwort, G. C. & Ginsberg, H. S. 1980. Foraging and mating behaviour in Apoidea. *A. Rev. Entomol.*, **25**, 421–446.

Esmaili, M. 1963. Biological studies on *Anthophora occidentalis* Cresson. (Hymenoptera: Anthophoridae) and its natural enemies in Utah. Ph.D. thesis, Utah State University.

Gwynne, D. T. 1980. Female defense polygyny in the bumblebee wolf *Philanthus bicinctus* (Hymenoptera: Sphecidae). *Behav. Ecol. Sociobiol.*, **7**, 213–225.

Gwynne, D. T. 1986. Courtship feeding in katydids (Orthoptera: Tettigoniidae): investment in offspring or in obtaining fertilizations? *Am. Nat.*, **128**, 342–352.

Hixon, M. A. 1987. Territory area as a determinant of mating systems. *Am. Zool.*, **27**, 229–247.

Ims, R. A. 1987. Male spacing systems in microtine rodents. *Am. Nat.*, **130**, 475–484.

Kaufmann, J. H. 1983. On the definitions and functions of dominance and territoriality. *Biol. Rev.*, **58**, 1–20.

Kimsey, L. S. 1980. The behaviour of male orchid bees (Apidae, Hymenoptera, Insecta) and the question of leks. *Anim. Behav.*, **28**, 996–1004.

Marshall, L. D. & Alcock, J. 1981. The evolution of the mating system of the carpenter bee *Xylocopa varipuncta* (Hymenoptera: Anthophoridae). *J. Zool., Lond.*, **193**, 315–324.

Michener, C. D. 1974. *The Social Behavior of the Bees.* Cambridge, Massachusetts: Harvard University Press.

O'Neill, K. M. 1983. The significance of body size in territorial interactions of male beewolves (Hymenoptera: Sphecidae, *Philanthus*). *Anim. Behav.*, **31**, 404–411.

Sakaluk, S. K. 1986. Is courtship feeding by male insects parental investment? *Ethology*, **73**, 161–166.

Sandell, M. & Liberg, O. 1992. Roamers and stayers: a model on male mating tactics and mating systems. *Am. Nat.*, **139**, 177–189.

Severinghaus, L. L., Harris, B. H. & Eickwort, G. C. 1981. The reproductive behaviour of *Anthidium manicatum* (Hymenoptera; Megachilidae) and the significance of size for territorial males. *Behav. Ecol. Sociobiol.*, **9**, 51–58.

Stern, D. L. 1991. Male territoriality and alternative male behaviors in the euglossine bee *Eulema meriana* (Hymenoptera: Apidae). *J. Kans. Entomol. Soc.*, **64**, 421–437.

Stone, G. N. 1990. Endothermy and thermoregulation in solitary bees. D.Phil. thesis, Oxford University.

Stone, G. N. 1993. Endothermy in the solitary bee *Anthophora plumipes*; independent measures of thermoregulatory ability, costs of warm-up, and the role of body size. *J. exp. Biol.*, **174**, 299–320.

Stone, G. N. & Willmer, P. G. 1989. Warm-up rates and body temperature in bees: the importance of body size, thermal regime and phylogeny. *J. exp. Biol.*, **147**, 303–328.

Thornhill, R. 1976. Sexual selection and paternal investment in insects. *Am. Nat.*, **110**, 153–163.

Thornhill, R. & Alcock, J. 1983. *The Evolution of Insect Mating Systems*. Cambridge, Massachusetts: Harvard University Press.

Velthuis, H. H. W. & Gerling, D. 1980. Observations on territoriality and mating behaviour of the carpenter bee *Xylocopa sulcatipes. Entomol. Exp. Appl.*, **28**, 82–91.

Wickler, W. 1985. Stepfathers in insects and their pseudo-parental investment. *Z. Tierpsychol.*, **69**, 72–78.

Willmer, P. G. 1986. Foraging patterns and water balance: problems of optimization for a xerophilic bee, *Chalicodoma sicula. J. Anim. Ecol.*, **55**, 941–962.

Willmer, P. G. 1991. Thermal biology and mate acquisition in ectotherms. *Trends Ecol. Evol.*, **6**, 396–399.

Zalat, S. M. M. 1984. Survey and ecological studies of bees and wasps (Hymenoptera) in southern Sinai. M.Sc. thesis, Suez Canal University.

Zeh, D. W. & Smith, R. L. 1985. Paternal investment in terrestrial arthropods. *Am. Zool.*, **25**, 785–805.