

GEOGRAPHIC VARIATION IN THE MORPHOLOGY
AND BEHAVIOURAL ECOLOGY OF A SPHECID WASP

Jaboury Ghazoul

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



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Behavioural Ecology of a Sphecid Wasp**

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Thesis submitted for the degree of Doctor of Philosophy,
University of St Andrews

February 1993



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This thesis is dedicated to my family, Ramez, Jemila, Rabab and Aysha. My biological career was launched at the age of six when I received the Hamlyns' Encyclopedia of Nature (not quoted in bibliography) from my mother and father, and ever since then my interest has been sustained through a constant flow of newspaper and magazine cuttings, books, and recorded nature programmes received from home. They can have this thesis in return.

"The next day was quite a different day. Instead of being hot and sunny, it was cold and misty. Pooh didn't mind for himself, but when he thought of all the honey the bees wouldn't be making, a cold and misty day always made him feel sorry for them."

The House at Pooh Corner

A. A. Milne

"One almost fancies that such happy things,
With coloured hoods and richly burnished wings,
Are fairy folk, in splendid masquerade
Disguised, as if of mortal folk afraid,
Keeping their merry pranks a mystery still,
Lest glaring day do their secrets ill."

John Clare (1793 - 1864)

Declaration

I, Jaboury Ghazoul, hereby certify that this thesis has been composed by myself, and that it is a record of my own work, and that it has not been accepted in partial or complete fulfilment of any other degree or professional qualification.

I was admitted to the Faculty of Science of the University of St Andrews under Ordinance General No. 12, and as a candidate for the degree of Ph.D., on 1 October 1989.

18 Feb. 1993.

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate to the degree of Ph.D.

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Geographic Variation in the Morphology and Behavioural Ecology of a
Sphecid Wasp

Abstract

A comparative study between populations of *Mellinus arvensis* (Hymenoptera: Sphecidae) was carried out in Britain. Large variations in size were found between populations and these were correlated with environmental, thermal, and biological factors. A latitudinal cline accounted for some of the variation, with larger wasps found at southerly locations. This was partially explained by climatic patterns and wasp warm-up rates. A hypothesis involving the interaction of environmental, behavioural and morphological factors was suggested to account for the remaining unexplained size variation between populations. It was found that at sites where the ground is compact and difficult to dig through, nests are more valuable in terms of time required to dig them. A strategy of searching for rather than digging a nest becomes viable. Wasps do not seem to be able to distinguish between occupied and abandoned nests, and aggressive interactions at nests occur between wasps searching for a nest and the nest residents. Aggression is more frequent at sites where pressure from searchers is greatest, that is, at sites where nest construction is most difficult and costly. Consequently, large wasps, which have greater success in aggressive encounters, are selected for at these sites. At sites where the ground is loose and easy to dig through, a more successful reproductive tactic appears to be maximisation of offspring number, resulting in many, small offspring.

Behavioural observations suggested that *M. arvensis* is capable of, at least, limited endothermy, although this could not be confirmed in laboratory experiments. Similar observations and results were obtained from several other sphecid species. However, endothermy was found in two sphecid species of the genus *Bembix* in Portugal, suggesting that endothermy may be more widespread than previously thought.

I'LL SAY! MY BOOK SAYS THAT
THIS ONE WASP LAYS ITS EGG
ON A SPIDER, SO WHEN THE
EGG HATCHES, THE LARVA EATS
THE SPIDER, SAVING THE VITAL
ORGANS FOR LAST, SO THE
SPIDER STAYS ALIVE WHILE
IT'S BEING DEVoured!



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In the past few years I have received help, support, and encouragement from such a large number of friends that to mention them all would require a task of similar magnitude to this thesis, upon which I am not prepared to embark. They know who they are.

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Chapter 1 Introduction

1.1 The Status of the Sphecidae Within the Hymenoptera

The order Hymenoptera is made up of the suborder Symphyta, the plant parasites; and the suborder Apocrita, the insect parasitoids (figure 1.1). The Apocrita is further divided into two series: the Parasitica, the larvae of which are parasitic on a wide range of hosts, and the Aculeata, the more familiar wasps, bees and ants. Five major superfamilies make up the wasps, of which the Sphecoidea is by far the largest (Evans & West-Eberhard 1973). This superfamily contains a single family, the Sphecidae. The majority of Sphecidae are solitary and dig nests in the ground and are thus called 'digger wasps', although a large number of species construct nests in twigs, mud, rotten wood or other materials. Sphecidae vary tremendously in their size and shape and also in their nesting behaviour.

Solitary wasp behaviour is consistent enough and rich enough to give abundant material for comparison within and between species. They display elaborate and relatively stereotyped behaviour patterns that are readily amenable to description and analysis. Furthermore, because a sphecid nest usually contains all the offspring of a single adult, their reproductive output is relatively easy to quantify. For these reasons evolutionary biologists have often turned to these animals when looking for trends in the evolutionary development of behaviour (eg, Evans 1962a,b; Evans 1966a; Alcock et al. 1978; Brockmann et al. 1979).

1.2 The Life History of Sphecid Wasps

The general pattern of a female sphecid's life (reviewed by Evans 1966a) involves the preparation of the nest by the adult and its subsequent provisioning with prey as food for the offspring. An egg is laid in each one of several cells that have been stocked with prey items, and the nest is sealed. When the larva hatches it feeds upon the stored food, pupates, and eventually emerges as an adult from the nest. The adult wasp mates and, if it is a female, prepares and provisions its own nest. There is a great deal of variation between the species in the details of this pattern.

Variation in behaviour can also be found within species where females may adopt any of a number of strategies in order to obtain a nest or provisions. Males of a species have been observed to adopt different strategies in gaining copulations, and mating behaviour may also be quite different between species. The following brief review of sphecid behavioural ecology has been divided into three sections. Firstly the nesting biology of sphecids, usually the first piece of complex behaviour undertaken by the adult female, is considered. Upon completion of the nest structure females start foraging and provisioning the nest and this is the subject of the second section. Thirdly, intraspecific interactions between females, and pre-adaptations to social behaviour, are discussed.

1.2.1 Nesting Behaviour of the Sphecidae

Within the Aculeata there seems to be a general evolutionary trend from no nests at all to simple and then more complex nests. The most primitive aculeate wasps do not build nests (eg, Bethylidae, Yamada 1955) while other species use crevices that are often closed over or modified (eg, some

Pompilidae, Evans & Yoshimoto 1962). More advanced aculeates (eg, many of the Sphecidae and Apoidea) dig nests in soil which vary from simple burrows to multicellular and complex nests. There have been reversals in this trend involving wasps that must once have made nests but now seek out, enter and lay their eggs in the cells of other wasps (eg, *Nysson* spp., Bohart & Menke 1976). Such parasitic behaviour has also been observed intraspecifically and this is discussed in Chapter 5. The construction and maintenance of nests is thought to be an important pre-adaptation for social life, which has attracted so much interest in these insects.

By far the majority of the Sphecidae are associated with the soil, although there are some groups that have taken to nesting above ground, digging nests in pith or rotten wood (eg, *Passaloecus* spp., Yeo & Corbet; *Ectemnius* spp., Field 1986), using hollow twigs (eg, *Crossocerus capitosus*, *Psenulus concolor*, Field 1986), or by making nests of mud (eg, *Trypoxylon politum*., Brockmann 1980a). Fossorial wasps usually dig nests in bare friable soil, but there are examples of species nesting in hard packed soil or soil covered by vegetation (eg, *Cerceris cribrosa*, Elliott & Elliott 1987; *Mellinus arvensis*, personal observation). However, ground nesters are largely confined to places where the soil is more or less bare and friable whereas aerial nesters are able to nest in a wide variety of situations not available to ground nesters (Evans & West-Eberhard 1973).

A completed nest consists of a burrow with either one (unicellular, eg, *Ammophila* spp., Evans 1959; *A. azteca*, Evans 1965; *A. pubescens*, Field 1989) or a number (multicellular, eg, *Cerceris* spp., Evans 1971; *Cerceris simplex*, Alcock 1975a; *Crabro* spp., Matthews et al. 1979) of cells branching off it. Burrows may be vertical (eg, *Ammophila* spp., Evans 1965; Field 1989) or oblique (eg, *Bembix amoena*, Evans & West-Eberhard 1973; *Sphex ichneumoneus*, Brockmann

1980b, 1985a) and there may be several side branches or none at all. The initial cell may be the deepest with additional cells being constructed back towards the entrance (eg, *Crabro* spp., Hamm 1926) or it could be the closest to the entrance with additional cells added by deepening the burrow (eg, *Cerceris* spp., Evans 1966a, 1971; *Philanthus* spp., Evans & Lin 1959). The majority of species use flat or gently sloping surfaces (eg, *Ammophila dolichodera*, Weaving 1989) while some nest only in steeply sloping banks (eg, *A. insignis*, Weaving 1989) and others in either vertical or horizontal surfaces (eg, *Mellinus arvensis*, personal observation; *Philanthus gibbosus*, Evans & Lin 1959).

The ground nesting wasps have developed a number of morphological features that facilitate the digging of soil to make nests. The three major digging organs are the mandibles, the legs and the pygidium. The mandibles are used for breaking up the soil and tend to be more robust in species that dig in more compacted soil (eg, *Ammophila pubescens*, Olberg 1959). They are also used for dragging pebbles and placing objects over the closed nest entrance (eg, *A. pubescens*, Olberg 1959; *A. azteca*, Evans 1965). The legs of many digger wasps have a series of stout spines on the front tarsus which forms, in effect, a rake and is used as such (eg, *A. pubescens*, Yeo & Corbet 1983; *Bembix amoena*, Evans & West-Eberhard 1973). This rake is referred to as a 'tarsal comb' or pecten. In the majority of sphecids it is only the front legs that are used for digging and so only these legs bear the spines. Other wasps simply back out of the burrow and push the soil behind them using a modified flat area on the dorsal tip of the abdomen called the pygidium (eg, *Cerceris californica*, Linsley & MacSwain 1956; *Cerceris arenaria*, Yeo & Corbet 1983).

The soil characteristics will often determine the method used to remove soil from the burrow (Olberg 1959; Yeo & Corbet 1983; Evans 1966a). Wasps

nesting in loose dry sandy soils are 'rakers' (after Olberg 1959) and use the two front legs to scoop particles from in front of the body to the rear (eg, *Bembix* spp., Evans 1966b) or 'pushers' which push the soil behind them using the strong pygidial plate (eg, *Cerceris arenaria*, Yeo & Corbet 1983). In heavy soils that form clumps, 'pullers' use the mouthparts to remove lumps of soil which are held between the head and front legs, and deposited close to the burrow (eg, *Mellinus arvensis*, Huber 1961). 'Carriers' are 'pullers' which carry the soil some distance from the nest before dumping it (eg, *Ammophila* spp., Powell 1964; *Sphex ichneumoneus*, Brockmann 1980b, 1985a).

While digging the burrow the mandibles break up the soil and a cylindrical bore is maintained through the twisting actions of the wasp inside the burrow (Evans 1966a). Loosened soil is removed from the burrow, although soil excavated from a new cell may be used to close off another completed cell in multicellular nests (eg, *Sphex ichneumoneus*, Brockmann 1985a). The ejected soil often forms a mound around the entrance hole (eg, *Cerceris californica*, Linsley & MacSwain 1956; *Crabro cribrellifer*, Wcislo et al. 1985) and many species will level the mound (eg, *Tachysphex pechumani*, Kurczewski & Elliott 1978) by scraping the sand away and turning from side to side. Location of the nest by predators, parasites or potentially usurping conspecifics is made more difficult through the dispersal of the mound (Evans 1966c; Wcislo 1986; Rosenheim 1987a,b).

After the cells are fully provisioned the nest is, in most species, sealed permanently. The wasp will first level off any accumulated sand at the entrance and will then scrape sand from the burrow walls and the periphery of the entrance and pack it down into the burrow. Upon completion of the closure the wasp will walk in irregular patterns over the entrance, kicking sand in various directions and leaving no trace of the burrow. Nest entrances

are often further hidden by the placement of sticks, leaves and other objects over the site (eg, *Chlorion laeviventris*, LaRivers 1945; *Ammophila beniniensis*, Weaving 1989). Most groups of the Sphecidae pack the soil down using the tip of the abdomen (eg, *Tachysphex antennatus*, *T. crassiformis*, and *T. krombeini*, Kurczewski & Kurczewski 1987) although the sub-family Sphecinae use the front of the head (eg, *Ammophila sabulosa*, Krombein 1955). *Ammophila pubescens* is unusual in that the females pound the soil with small pebbles held between the mandibles (Evans 1965; Brockmann 1985b). Many sphecid species will make a temporary closure which is simply a backscattering of sand into the open burrow entrance (eg, *Bembix multipicta*, Cane & Miyamoto 1979). Wasps will close the burrow in this way before departing to forage, but the nest is never left in this state for any great length of time. A temporary closure provides some sort of security during the day and only minimally delays a wasp returning with prey, the time at which the wasp is at its most vulnerable to parasites. Other wasps (eg, *Mellinus arvensis*, personal observation; *Cerceris halone*, Byers 1978; *Crabro cribrellifer*, Wcislo et al. 1985; *Tachysphex antennatus*, Kurczewski & Kurczewski 1987) leave the entrance open between foraging trips. Such behaviour might be in response to parasitic pressure from miltogrammine flies which generally oviposit on the prey of wasps as it is being carried into the nest. An open nest removes the cause for any delay at the nest entrance, allowing wasps to enter the nest with their prey rapidly, and in this way the risk of parasitism by these flies might be reduced (eg, *Cerceris australis*, Evans & Hook 1982a; *Crabro cribrellifer*, Wcislo et al. 1985).

In a number of sphecid species (eg, *Bembix texana*, *Philanthus lepidus*, *Sphex argentatus fumosus*, Evans 1966c) soil for nest closure is dug from one or a few spots close to the nest. These quarries are subsequently left open, and it has been suggested that they serve to divert the attention of parasites. Other

wasps dig 'accessory' burrows (Evans 1966c) before or after closure of the nest, which are never provisioned. These burrows are always left open and are maintained if they accidentally become filled. Again it is thought that these accessory burrows may serve to divert parasites, though female wasps have occasionally been seen to rest in them. There are now many observations of mutillid wasps and miltogrammine flies, nest parasites of sphecids, being attracted to these burrows (Evans 1964a, 1966c; Tsuneki 1963), and bombyliid flies have been observed ovipositing in the accessory burrows of some species (Evans 1966c).

Upon leaving the nest on the first foraging trip, wasps commonly make one or more orientation flights. During these flights the wasp learns visual cues which guide it back to the nest upon its return. Orientation flights vary in duration and number depending on the complexity of the terrain and the species concerned; but some species, such as *Mellinus arvensis*, tend to reinforce their recognition of the site by short orientation flights over the first two or three days (Evans 1966b). In the event of a major disturbance in the area a re-orientation flight is commonly undertaken.

Soil softness has been shown to be an important factor in nest initiation at least for some of the smaller sphecids, for example *Cerceris antipodes* which only starts digging nests when the soil is soft after a period of rainfall (McCorquodale 1989a). *Cerceris* (which are weak diggers compared to other sphecids such as *Bembix* and *Sphex*) and several other species often avoid digging through the hard surface crust by usurping the nest of another female (eg, *Cerceris arenaria*, Field & Foster, unpublished observations), remaining within the natal nest (*C. watlingensis*, Salbert and Elliot 1979), sharing a nest with another female (*C. arenaria*, Willmer 1985a,b; *C. antipodes*, McCorquodale 1988, 1989a,b) or using a pre-existing hole in the hard surface crust (eg,

Trypoxylon texense, Brockmann 1980a). These strategies avoid the costs of time taken to dig the nest and wear of the body parts such as mandibles, wings and the general surface of the cuticle.

The nests of solitary wasps are often not distributed randomly throughout a suitable habitat but are rather aggregated in a small area. It was previously assumed that nesting aggregations were a consequence of limited suitable nesting sites; however there are often no abiotic factors, such as soil temperature, hardness or percentage moisture, that correlate well with the distribution of nests. Michener et al. (1958) examined seven abiotic factors and showed that their variability had no influence on the distribution of solitary burrowing bees, and similar results were obtained from a study by Cane (1991) on 32 species of fossorial bees. Their explanation for the nesting aggregations was that females tend to return to their natal areas to nest. This conclusion offers no insights as to why nesting at these aggregated sites is successful, as it has to be if this behaviour is to be maintained by selection.

Parasite pressure has been suggested as an explanation for aggregation. A hypothesis proposed by Wcislo (1984) is that of the 'selfish herd' whereby the probability of a nest being parasitized is some increasing function of its nearest neighbour distance. The biotic interactions between wasp conspecifics as well as other species may reduce a parasite's efficiency in high density areas. High density nesting may give rise to a greater number of shared nests, possibly resulting in guarding of the nest by one of the females.

Outcrossing and mating between unrelated individuals is promoted in nesting aggregations (Lin & Michener 1972). This becomes especially important in primitively social Hymenoptera where nests are occupied by family units and outcrossing is important if variability is to be maintained.

Harassment of females by males has been suggested to be the cause of nest site changes in *Bembecinus quinquespinosus* which forms dense nesting aggregations at a different site each year (Evans et al. 1986). Emerging females apparently start nesting in the emergence area but due to continued male attention they abandon the site and search out a nearby suitable substrate where males are absent. Remaining females are somehow attracted to the new nesting site, perhaps by the visible swarming of females already present at the site (Evans et al. 1986).

Aggregating may result in factors favouring social evolution. The increased number of parasites at aggregations may lead to the evolution of defence mechanisms such as the occurrence of more than one individual in the nest and special guard castes. Decreased nesting space per female may also lead to nest sharing.

The evolution of diverse and complex nesting behaviours in the sphecid wasps reflects the ability of these animals to exploit different environments. The construction of deep and complex nests in the soil has permitted survival under rigorous environmental conditions (eg, deserts). The possession of a nest, the location of nests in nesting aggregations, and the occurrence of nest switching and usurpation are important pre-adaptations for the evolution of sociality which has led to an extensive diversification in the Aculeata.

1.2.2 The Foraging Behaviour of Sphecid Wasps

All solitary aculeate wasps (with the exception of the vespoid family Masaridae) are predators as adults. Predatory wasps have been termed by Evans (1966b) as 'predatoids' due to the unusual features of their predatory

behaviour, that is that the prey is primarily utilized as a larval food source and that predation is sex limited as it is part of the provisioning behaviour of the female.

The Sphecidae exploit adults and larvae of almost all pterygote insects as well as springtails and spiders (Evans 1966a,b). However, nearly all wasps exhibit some degree of host specificity (table 1.1) and their hunting and stinging behaviour is closely adapted to the type of prey. Specificity may be at the familial, generic or species level and prey type may often be used as a taxonomic character. For example, *Tracheloides* (Pate 1942) and *Aphilanthops* (Evans 1962a) attack only one or a few closely related species of ant, and only one sex and caste. Prey specificity should not be confused with a situation where a wasp may prey on a broad range of insects but, due to a local abundance of one prey species, catches a disproportionately high number of individuals of this species (Elton & Greenwood 1987).

Specialization of prey type may be due to resource partitioning resulting from inter-specific competition between two or more sympatric species (Muma & Jeffers 1945). Where several species occur together wasps may become specialists and divide up the available prey or become generalists by taking advantage of any prey in the surrounding area. In a study of the prey selection of sympatric species of the genus *Cerceris*, it became evident that some of the species were generalists while others were specialists (Evans & Hook 1986). It seems that hunting behaviour had become either directed to only one otherwise unexploited group, or was versatile that wasps were able to utilize a wide variety of prey that were sufficiently abundant so as not to constitute a cause of competition. A generalist strategy may be more successful in areas where prey species are kept low by other factors, or are highly variable from year to year (Evans & Hook 1986). Some wasps escape

direct competition by temporal or spatial displacement of foraging, for example *Bembix u-scripta* hunts at dusk and takes flies that rest on vegetation rather than on the ground (Evans & O'Neill 1986).

Odour stimuli received by the antennae probably play an important part in prey capture. Wasps are not deceived by visual mimics, for example fly predators often use flies which mimic bees while bee predators do not pursue such mimics (Hamm & Richards 1930). Tinbergen (1935) (quoted in Evans 1966a) found that *Philanthus triangulum* first approach potential prey from a downwind direction responding to visual cues. Odour becomes important from a distance of 10-15 cm and if the proper stimulus is received the wasp leaps on the prey. Stinging occurs only upon receipt of additional, probably tactile, stimuli.

Wasp prey are paralysed and often remain alive until consumed by the larvae, thereby insuring that the prey does not dry up or deteriorate (Rathmayer 1962). Prey immobilisation is achieved in most species by venom injected through the sting. The venom of *Philanthus triangulum* does not act as a neurotoxin but diffuses through the blood to the leg musculature (Rathmayer 1962). *Cerceris* which prey upon weevils and buprestids paralyse their prey by injecting venom into the thoracic ganglia which are fused or close together in these insects (Linsley & MacSwain 1956). This may explain why only a few insect families are suitable for *Cerceris* to collect and store (Linsley & MacSwain 1956). Predators on insect larvae (eg, *Podalonia*) sting the prey many times rather than once, probably because the locomotory organs are more widespread (Steiner 1983). Stings are concentrated at the location of the ganglia of the ventral nerve cord (Steiner 1983). *Passaloecus* does not sting its aphid prey but paralyses it by pinching the neck region with its mandibles (Yeo & Corbet 1983). This paralyses the prey but does not kill it. The aphid

remains fresh with its heart still beating. *Eumenes* (family Eumenidae) stings its prey but this is followed by a lengthy pinching in the vicinity of the nerve ganglia which may insure complete paralysis (Evans 1966b).

Primitive sphecids catch the prey before digging the nest (eg, *Podalonia*, Steiner 1983). The evolution of locality learning and orientation enables wasps to excavate the nest first and then stock the completed burrow. This avoids the risk of theft and parasitism of the provisions during nest excavation and also temporally separates nest digging, the stage that is most conspicuous to parasites, from nest provisioning, the stage most vulnerable to exploitation.

An interesting feature of wasp evolution is that of prey carrying mechanisms which have been extensively reviewed by Evans (1962b). Primitive wasps (*Ampulex*, *Sphex*, *Prionyx*, *Podalonia*) having been derived from parasitoids, utilize a single host specimen per offspring. The evolutionary trend has been towards the utilization of several or many smaller sized prey specimens to feed a single larva (table 1.1). The smaller the prey the easier it is to carry. Thus advanced forms of prey carriage have evolved in wasps that utilize smaller prey.

Evans (1962b) has classified three types of prey carriage, mandibular, pedal and abdominal. The first and most primitive method of prey carriage is with the mandibles. The mandibles must be used to unblock a burrow entrance that was previously closed, and consequently prey carried in the mandibles must be released (eg, *Ammophila pubescens*, Yeo & Corbet 1983). At this time the wasp is susceptible to parasites that oviposit upon the prey. An alternative strategy is to leave the nest entrance open (eg, *Mellinus arvensis*, personal observation), but this leaves the nest susceptible to attack by mutillid wasps and ants while the wasp is foraging.

At a more advanced level the prey is held further back by the legs (*Bembix* spp., Evans 1962b). Pedal mechanisms of prey carriage free the mandibles and the first pair of legs allowing wasps to enter the nest without letting go of the prey. A nest may thus be closed while the wasp is foraging and subsequently opened without releasing the prey. Pedal prey carriage also allows for the removal of impediments from the nest or driving away predators.

Abdominal carriage is effected by impaling the prey on the sting (*Oxybelus*, Evans 1973) or by the use of specially modified apical abdominal tergites functioning as a clamp in which the prey is held (*Clypeadon laticinctus*, Alexander 1986). This frees both the mandibles and all three pairs of legs, allowing wasps to provision the nest with minimal risk from parasites.

Abdominal prey transport allows the mandibles and legs to be used for other activities and does not impede flight.

Most wasp species fully provision the cell before laying the egg and closing the cell (Evans & West-Eberhard 1973). This is known as mass provisioning and is contrasted with progressive provisioning whereby the wasp provides the larvae with food according to their needs as they develop (eg, *Ammophila pubescens*, Field 1989b; *Bembix multipicta*, Cane & Miyamoto 1979). The latter type of provisioning results in contact between the mother and her offspring, providing a greater degree of protection for the young from parasites or predators. Any parasites in the nest will be discovered by the mother and removed. Up to several different nests containing offspring at different stages of development may be attended by a single mother. Progressive provisioning may also allow the overlap of generations which in turn may lead to the first steps towards eusociality (Evans & West-Eberhard 1973).

Adult wasps require liquid food periodically and nectar is the major source of nourishment. Some wasps feed on plant sap while others subsist on honeydew from aphids. Other wasps will rarely or never visit flowers but rather feed directly on or from insects. Wasps that hunt flower feeding insects may squeeze out the contents of their prey's crop obtaining liquid carbohydrates in this way (*Philanthus* spp. and *Bembix* spp., Evans 1966a). Some species of *Bembix* have been observed to stop on their way back to the burrow and feed from the oral opening of syrphid flies (Tsuneki 1956). Malaxation of prey and the lapping of haemolymph occurs in some sphecid species. The prey may be subsequently placed in a cell or discarded (eg, *Mellinus arvensis*, Evans 1966a).

1.2.3 Intraspecific Interactions among Sphecid Wasps and Pre-Adaptations for Sociality

Much work has been carried out on the evolution of sociality in the Hymenoptera which has given rise to highly complex and ordered 'insect societies' and which has evolved independently several times (Lin & Michener 1972). There exists a continuum in the Hymenoptera from those species that are purely solitary to those that are fully eusocial. The evolutionary steps taken from solitary wasps to the eusocial colonies may be elucidated by observing the behaviour of the species that represent the different stages along the continuum towards eusociality.

There are two theories that attempt to explain the evolution of complex social behaviour in the Hymenoptera. The first is the well documented genetic theory of social behaviour (Hamilton 1964) based on the haplo-diploid method of sex determination. While this is a widely accepted and plausible theory for the existence of non-reproductive castes, the theory rests upon a

number of assumptions whose validity is still somewhat uncertain (Alexander & Sherman 1977).

An alternative (but not mutually exclusive) hypothesis examines the possibility of sociality arising from mutualistic behaviour between individuals that may or may not be related (reviewed by Lin & Michener 1972). Co-operative defence of the nest against parasites or predators may, for example, increase the fitness of all members of the colony. Eusocial behaviour may have arisen from solitary behaviour via a 'semi-social' route where the individuals in the colony are unrelated, or a 'sub-social' route, where the colony consists of family units and kin selection. Described here are a number of examples of how eusociality may have arisen through social strategies between individuals.

In the sphecid wasps changes of burrow ownership are often observed. Alcock (1975a) frequently observed *Cerceris simplex* to enter the burrows of other females often for no apparent reason. In a number of other cases the home burrow of a wasp had been plugged by another female, and rather than unblock the nest entrance the resident wasp would then enter another nest. Intruders often entered a nest and were subsequently ejected upon discovery by the original occupant. Communal provisioning of nests was also observed where two or more females provisioned the same burrow for brief periods of time (two or three days).

Alcock (1975a) presented three possible advantages to a female to account for burrow switching and communal provisioning. By changing nest sites a female may avoid placing all her eggs in one nest, while at the same time avoid the costs of digging another nest. If a female oviposited in more than one nest, then in the event of a localised disturbance destroying the nest that a

female had constructed, there would be a chance that at least some of her progeny in other nests would survive (see also Elliott et al. 1981, with reference to *Cerceris zonata*).

Secondly, by usurping a nest a female may steal the provisions held within the burrow. Thus a female may save herself the time and energy of digging a nest and gain the added cache of prey that the original owner had collected.

Thirdly, if the would-be usurper fails to evict the original owner, both wasps may continue to provision the same nest and this may have advantages for both individuals. The nest would be occupied more often than if there were a single owner, thus reducing the chances of parasitism or takeover by a third conspecific. In such a situation, as long as both individuals bring in about the same amount of prey, and if the wasp that oviposits in a stocked cell is determined randomly, then both wasps may gain important advantages in nest defence.

McCorquodale (1989b) has recently shown that nest sharing results in improved nest defence in *Cerceris antipodes*, and the greater the number of females in a nest, the greater the degree of defence.

Salbert and Elliot (1979) observed nest sharing between individuals of *Cerceris watlingensis* where in each nest one of the females was older but all the females were active in provisioning. They suggested that due to the longer nesting season in the subtropical environments young females may emerge before the parent has left the nest. The emergent young females may remain in the nest and provision their own cells or aid the mother. This may represent the primitive steps towards eusociality following the sub-social route. It is of interest to note that presocial behaviour seems to occur more

frequently in the tropical species (Evans 1973) because the prolonged nesting season permits overlap of generations.

Two types of behaviour were observed by Alcock (1980) in females of *Cerceris antipodes* that were sharing nests. Females were either non-provisioning, and spent most of their time in the nest and at the nest entrance actively guarding the nest against ants, parasitic flies and mutillid wasps as well as conspecifics; or they were provisioners who would fly out and return with prey.

Individuals could switch between these two types of behaviour from day to day. In this species it is also likely that nest sharing females are relations that emerge in a staggered fashion over the nesting season - several nests upon excavation were found to contain pupae that were about to metamorphose into adult females.

Characteristic of the behaviour of wasps from subsocial colonies is the lack of aggression against nest mates and the intolerance towards strange females. The peaceful behaviour of *Cerceris antipodes* (McCorquodale 1989b) contrasts sharply with the aggressive behaviour of *C. simplex* (Alcock 1975a). The former nests communally and benefits from cooperation among relatives (subsocial), whereas nest sharing in the latter species is a consequence of one female forcing herself on the original owner. Initially there is much aggression between the two females until eventually the nest owner tolerates the successful intruder.

A further advantage to subsocial behaviour is that if a female provisioning the nest should die and leave a nest incompletely stocked, the prey need not be wasted as they would be used by a relative who could add a few more prey and then lay an egg. This would not be an advantage in semisocial colonies as the individuals are unrelated.

Communal nesting has been observed in genera other than *Cerceris*.

Philanthus gibbosus often live together, the newly emerged adults (both male and female) often remaining in the nest for several days before the females disperse to found new nests (Evans 1973). The presence of these young adults may have value as guards against mutillid wasps and miltogrammine flies. However this species is unusual in that communal use of the burrow is a temporary phenomenon occurring at the beginning of the season as the adults emerge.

The degree of soil softness may result in an increase or decrease of communal nesting. Nest initiation is costly if the ground is hard and it is therefore an advantage to join another nest (eg, *Cerceris antipodes*, McCorquodale 1989a). After periods of dry weather fewer nests and a greater proportion of shared nests would be expected. The nest digger may gain an advantage in improved nest defence through the acceptance of another female. There may indeed be an increase in parasite pressure during dry spells for the simple reason that there are fewer nests constructed and the number of parasites per nest therefore increases. A study to confirm this has yet to be carried out.

Wasps may gain advantages in foraging if two female of different size share a nest. *Cerceris arenaria* shows an increase in the incidence of nest sharing among adults during hot summers (Willmer 1985a). A single nest will often contain one small female and another much larger female. Willmer suggested that the reason for this is temperature constraints while foraging. Large females may forage earlier in the day and on cooler days, but during the hottest part of the day, or on unusually hot days, large females becomes heat stressed and have to remain in the burrow. It is during these periods of high temperature that small females may forage efficiently. By sharing a nest both females gain the advantages of co-operative provisioning. Both females will

also gain from reduced parasitism as the nest will be occupied by at least one wasp for most of the time.

Despite the potential benefits of burrow sharing for females, the number of communal nests is often a small proportion of the total. It is also surprising that so few cases of this behaviour have been recorded for sphecid wasps. The rarity of communal nesting suggests that there are some costs as well as benefits to this option. Miltogrammine flies do not seem to be deterred by nest guards and may in fact benefit from the delay caused to the prey-laden wasps entering the burrow due to the presence of guards (Alcock 1980). Populations of these parasites may build up over time in areas of communal nests. Individual wasps that disperse to dig nests in new habitats might be able to avoid these parasites more effectively. Dispersal to new areas may also provide individuals with patches of high prey density which have not been subject to resource depression (Alcock 1980).

More examples of communal nesting and cooperation between females are emerging from studies on sphecid wasps. Additional comparative studies will no doubt lead to an improved understanding of this and many other interesting aspects of sphecid behaviour.

1.3 A Brief Review of Thermoregulation in the Insects

The body temperature (T_b) of most small invertebrate animals corresponds closely with that of the environment. These animals used to be called 'poikilothermic', which implies an absence of regulation. Thermal control is not absent however, and is achieved largely through behavioural rather than physiological means. The term 'ectothermic' is for this reason preferred, as it

indicates that body heat is derived from environmental rather than metabolic sources.

Almost all animals can be said to regulate body temperature behaviourally. Terrestrial environments are highly heterogenous, and very few habitats are of uniform temperature throughout. Insects are aided by their small size in making use of these heterogenous environments, to maintain favourable body temperatures, and this is a major component of their behavioural thermoregulation.

Body temperature may also be affected by the internal generation of heat and this is known as endothermy. All animals produce heat as a by-product of metabolic processes, and as such may be labelled as 'endothermic'. In practice, however, the term endothermy refers to only those animals with unusually high metabolic rates that generate substantially more heat than is lost from the body, leading to an increase in body temperature.

In insects, thoracic temperature excesses of about 10 - 20 °C can be achieved by retaining some of the heat produced by flight muscle activity. The primary advantage of elevated body temperature is an increase in the power output and frequency of wingbeat, ultimately allowing the insect to remain active at cooler temperatures.

Irrespective of the principal mode of heat gain, thermoregulation is taken to be the ability of an animal to regulate body temperature in at least a portion of its body, either above or below ambient temperature, by behavioural or physiological means. The range in which T_b is regulated may be narrow or wide but it is implicit that variation in T_b is less than variation in ambient temperature (T_a) over the same range of environmental conditions.

Unlike most birds and mammals, no insect has yet been found that continuously maintains a constant T_b (homeothermy) and for this reason the term 'heterothermy' may be more accurately applied to at least some insects. 'Heterothermy' applies to animals that are capable of periodic endothermy. Endothermic insects regulate T_b only during certain periods of activity and each period of activity is preceded by a period of warm-up and followed by cooling.

Heterothermic insects gain several advantages by having a greater independence from T_a . They become able to occupy a wider range of habitats, and can extend their periods of activity to improve foraging (Chappell 1982) and reproductive success (May 1977; Chappell 1984; Stone et al. 1988). Additionally a high T_b may increase the speed of metabolic processes and might enable the insect to react more quickly to predators (Bartholemew & Heinrich 1973) or prey (May 1976a).

Heterothermy in the insects is now known to occur in at least eight insect orders: Odonata, Orthoptera, Neuroptera, Hemiptera, Lepidoptera, Diptera, Coleoptera and Hymenoptera. It is widespread in the Apoidea, both the social honeybees and bumble bees (Heinrich 1974, 1975, 1980) and the solitary bees (Stone 1989). Should endothermy exist in the Sphecidae, and there is no reason to assume that it does not, it may have a major influence on the ecology, behaviour and thermal physiology of the species concerned. Therefore any behavioural study would be improved with additional consideration of the endothermic capability of the animal under study.

1.4 Some Information on the Sphecid, *Mellinus arvensis*.

Much of the work in this study concentrates on the common ground nesting sphecid, *Mellinus arvensis* (figure 1.2), which has a geographical range that extends throughout western Europe. The taxonomic definition of *Mellinus arvensis* is outlined below:

| | |
|-------------|-------------------------------------|
| Order | Hymenoptera |
| Sub Order | Apocrita |
| Section | Aculeata |
| Superfamily | Sphecoidea |
| Family | Sphecidae |
| Sub-Family | Nyssoninae |
| Tribe | Mellinini |
| Genus | <i>Mellinus</i> (Fabricius) |
| Species | <i>Mellinus arvensis</i> (Linnaeus) |

There is much argument about whether the tribe Mellinini should be included in the subfamily Nyssoninae. Evans (1966b) would maintain that the genus be considered as a separate subfamily on the basis of larval structure and ethological grounds. But *Mellinus* does exhibit some specialized traits such as the nodose form of the first gastral segment, found in many other groups within the Nyssoninae (Bohart & Menke 1976). The classification followed is that of Bohart & Menke who treat the tribe Mellinini as an early branch from the Nyssoninae stem.

Of the nine species of *Mellinus*, three are Eurasian, three are Nearctic and three are New World Tropical. The two European species are the most abundant, particularly *Mellinus arvensis*, which is widespread and common

throughout the British Isles. The other British species, *Mellinus crabroneus*, is rare and may even be extinct in this country (Else, personal communication) though it is quite common in continental Europe.

There is a sexual dimorphism in this species, the females being larger and more robust than the males (figure 1.2). More specifically, males have bidentate mandibles, thirteen antennal segments, seven abdominal sclerites and the pygidial area is curved. Females have tridentate mandibles, twelve antennal segments, six abdominal sclerites and the pygidial area is flat and triangular (Bohart & Menke 1976). Both sexes are black in colouration with 2 - 3 (male) or 3 - 4 (female) yellow bands on the abdomen. The female has additional yellow markings on the collar of the pronotum and the scutellum. The clypeus and inner orbit of some individuals, both male and female, are also coloured yellow.

In Britain adults appear in mid July and remain active until mid October. Males emerge earlier in the season than females (protandry) and mate with the females soon after female emergence. Males search for females at the nesting area and at areas that females frequent for foraging (Huber 1961). Male *Mellinus arvensis* pounce upon any dark moving object of similar size to a female, and often mistake other males for females. As far as is known the females mate only once (Hamm & Richards 1930). There is no evidence to suggest that *Mellinus arvensis* is bivoltine (Paxton 1985).

Females appear to use just one burrow which is normally constructed in sandy habitats (Saunders 1886) to a depth of 30-50cm (personal observation, although Grandi (1954), suggests nest depths of up to 1 metre at a population in Italy). Beyond a depth of 20 cm individual cells are constructed at intervals and are attached to the main tunnel by side branches (Hamm & Richards

1930). Cells are constructed and filled one at a time and average 5-10 cells in every tunnel (Huber 1961). The lateral tunnels are filled with sand after the cell is sealed (Huber 1961).

The female hunts on the leaves of trees, on bare ground, at flowers, about dung and in almost any other area where flies are found in abundance (personal observation). The prey is stalked with the antennae stretched forwards and when the wasp is within two centimetres of the fly she springs onto the victim, bends her abdomen around, and stings the fly beneath its thorax (Huber 1961). With the sting still in place, the fly is turned over, its proboscis is gripped by the mandibles of the wasp, the sting withdrawn and the fly, which can be further supported by the wasp's front legs, is carried off to the nest. Thus a mandibular mechanism of prey transport is used (figure 1.3); the most primitive form in Evans' (1962b) classification.

The nest is stocked with a wide range of Diptera prey, especially from the sub-order Cyclorrhapha (Thornley 1932). Each cell is stocked with about 4-9 flies (Hamm & Richards 1930, but see Chapter 4) and an egg is laid on the ventral surface of the thorax of the last fly. Fly prey remain fresh for about two weeks (Hamm & Richards 1930). The full grown larva spins a light coloured parchment-like cocoon surrounded by a layer of sand grains and fly remains (figure 1.4).

Mellinus arvensis is a convenient wasp to work with as it is widespread throughout the British Isles, nests in large aggregations and has a body size that allows easy observation and facilitates marking. It can be handled with relative ease in the field without the need for anaesthetizing agents. Furthermore its abundance allows the removal of a number of individuals for laboratory studies without profoundly influencing the population structure.

1.5 The Aims of This Thesis.

Although the Sphecidae have a small number of relatively stereotyped behaviours there is a huge diversity in their nesting, foraging and reproductive ecology. The huge number of species (about 15,000 worldwide) attests to their great success in colonising and inhabiting a wide range of habitats throughout the terrestrial environment. The study of intraspecific variation may give us some idea as to how these many species arose. Individuals from populations of a single species that has a large geographical distribution could evolve a variety of behavioural and morphological differences. Intraspecific variation between geographically isolated populations is often considered to be the first step towards speciation. For this reason such work is interesting and of importance in evolutionary studies. Furthermore, the responses of conspecifics to different environmental conditions, together with interspecific comparisons, can provide information on the evolution of behaviour patterns, such as the evolution of sociality, along phylogenetic lineages and across taxonomic groups.

This thesis examines geographic variation in the nesting and foraging behaviours (Chapter 3) and the morphology (Chapter 4) of the sphecid wasp *Mellinus arvensis* across a number of populations within Britain. The first objective is to determine whether differences between individuals from different locations exist. Data on a variety of aspects of nesting and foraging behaviour are collected and variation within and between populations is compared. The role of environmental (Chapter 4) and biological (Chapter 5) factors are discussed in relation to the morphology and behavioural ecology of this wasp, and both adaptive and non-adaptive hypotheses are examined with a view to explaining the observed variation. In particular, latitudinal clines and the importance of temperature variation between sites is examined

(Chapter 4). The abundance and types of prey available to the wasps are considered as factors influencing behaviour and size (Chapter 4). In Chapter 5 two alternative hypotheses, linking nest site availability with intraspecific interactions, are proposed and discussed as an explanation for much of the observed variation in morphology and behaviour.

Endothermy has been shown to occur in many of the solitary and social bees (Heinrich 1972a; Stone & Willmer 1989a) as well as the Vespidae (Ishay 1972). At least one chrysidid species (*Stilbum cyanurum*, Bethyloidea) and one scoliid (*Scolia* sp.) are capable of endothermy (Stone 1989). As yet there have been no studies of endothermic ability in the sphecid wasps, and the second objective of this thesis is to examine and quantify warm-up rates from a number of species from this family (Chapter 6).

Table 1.1 The Prey of Sphecoid Wasps

| | <u>Prey Type</u> | <u>No. of Prey per cell</u> | <u>Source</u> |
|-------------------------------|--|---------------------------------|----------------------|
| <u>Sub Family Ampulicinae</u> | | | |
| Ampulex | | | |
| -compressa | Orthoptera: Cockroaches | 1-2 | Williams 1942 |
| -amoena | Orthoptera: Cockroaches | 1-2 | Kamo 1957 |
| <u>Sub Family Sphecinae</u> | | | |
| Sceliphron | | | |
| -assimile | Arachnidae | several | Freeman 1973 |
| -spirifex | Arachnidae | 1-5 | White 1989 |
| -caementarium | Arachnidae | 1-5 | White 1989 |
| Chlorion | | | |
| -laeviventris | Orthoptera: Mormon cricket (<i>Anabrus simplex</i>) | | LaRivers 1945 |
| Sphex | | | |
| -ichneumonous | Orthoptera: Tettigonidae, Gryllidae and Gryllacrididae | 2+ | Brockmann 1985a |
| -pensylvanicus | Orthoptera: Tettigonidae | | Brockmann 1985b |
| -tomentosus | Orthoptera: Tettigonidae | 3-8 | Weaving 1990 |
| Palmodes | | | |
| -laeviventris | Orthoptera: Mormon cricket (<i>Anabrus simplex</i>) | 1-2 | Gwynne & Dodson 1983 |
| Prionyx | | | |
| -parkeri | Orthoptera: Acrididae | 1 | Evans 1958 |
| Podalonia | | | |
| -luctuosa | Lepidoptera: Noctuidae larva | 1 | Steiner 1983 |
| -occidentalis | Lepidoptera: Lasiocampidae larvae | | Krombein 1979 |
| -hirsuta | Lepidoptera: Gypsy moth larvae (<i>Lymantria dispar</i>) | | Krombein 1979 |
| -communis | Lepidoptera: Noctuidae larvae | | Evans 1970 |

| | | | | | |
|---------------------------|---|---------|--|-------------------------|--|
| Ammophila | | | | | |
| -procera | Lepidoptera: Notodontidae larvae | 1 | | Hager & Kurczewski 1985 | |
| -harti | Lepidoptera: Geometridae and Noctuidae larvae | 5-12 | | Hager & Kurczewski 1985 | |
| -azteca | Lepidoptera, Hymenoptera and occasionally Curculionidae larvae | | | Evans 1965 | |
| -aberti | Lepidoptera: Geometridae larvae | 5-10 | | Powell 1964 | |
| -placida | Lepidoptera: Hesperidae larvae | 3-5 | | Powell 1964 | |
| -junceae | Lepidoptera: Notodontidae and Noctuidae larvae | 1-2 | | Powell 1964 | |
| -urnaria | Lepidoptera: Noctuidae and Geometridae larvae | 1-6 | | Powell 1964 | |
| -aureonotata | Lepidoptera: Notodontidae larva | 1 | | Powell 1964 | |
| -nigricans | Lepidoptera: Noctuidae larva | 1 | | Powell 1964 | |
| -xanthoptera | Lepidoptera: Noctuidae larva (<i>Zale lunata</i>) | 1 | | Powell 1964 | |
| -pruinosa | Lepidoptera: Microlepidopterous larva | Several | | Powell 1964 | |
| -sabulosa | Lepidoptera larva | 1 | | Field 1989a | |
| -sabulosa nipponica | Lepidoptera: Noctuidae and Geometridae larvae | 1-5 | | Tsuneki 1968 | |
| -pubescens | Lepidoptera larva | 5-10 | | Field 1989b | |
| -dolichodera | Lepidoptera larva | 1 | | Weaving 1989 | |
| -ferrugineipes | Lepidoptera larva | Several | | Weaving 1989 | |
| -dysmica | Lepidoptera larvae | Several | | Rosenheim 1987b, 1988 | |
| -aemulans | Lepidoptera: Ceruridae larvae (<i>Gonoclostera timonides</i>) | 1 | | Tsuneki 1968 | |
| -pilosa | Lepidoptera: Lycaenidae larvae | Several | | Evans 1970 | |
| Sub Family Pemphredoninae | | | | | |
| Mimesa | | | | | |
| -unicincta | Hemiptera: Cicadellidae | | | Evans 1970 | |
| Mimumesa | | | | | |
| -mixta | Hemiptera: Cicadellidae | | | Evans 1970 | |
| Diodontus | | | | | |
| -ater | Hemiptera: Aphids | | | Evans 1970 | |
| -argentinae | Hemiptera: Aphids | | | Evans 1970 | |
| Passaloecus | | | | | |
| -tenax | Hemiptera: Aphids | | | Evans 1970 | |

| | Hemiptera: Aphids | 20-30 (104) | Yeo & Corbet 1983 |
|-----------------------------|--|-------------|---------------------------|
| -insignis | | | |
| <u>Sub Family Astatinae</u> | | | |
| Astata | | | |
| -boops | Hemiptera: Pentatomid nymphs | | Evans 1970 |
| -pinguis | Hemiptera: Pentatomid and Lygaeid nymphs | 1-4 | Evans 1970 |
| -nubecula | Hemiptera: Pentatomid nymphs | | Evans 1970 |
| Dryudella | | | |
| -montana | Hemiptera: Reduviidae, Scutelleridae and Cydnidae nymphs | | Evans 1970 |
| <u>Sub Family Larrinae</u> | | | |
| Larra | | | |
| -anathema | Orthoptera: <i>Gryllotalpha</i> spp. (Mole crickets) | | Steiner 1984a |
| - analis | Orthoptera: <i>G. hexadactyla</i> | | Steiner 1984a |
| -femorata | Orthoptera: <i>G. coarctata</i> | | Steiner 1984a |
| -luzonensis | Orthoptera: <i>G. coarctata</i> | | Steiner 1984a |
| -amplipennis | Orthoptera: <i>G. africana</i> | | Steiner 1984a |
| -carbonaria erebus | Orthoptera: <i>G. africana</i> | | Steiner 1984a |
| Liris | | | |
| -nigra | Orthoptera: Tettigoniidae | | Steiner 1962 |
| -argentata | Orthoptera: Tettigoniidae | | Steiner 1962 |
| -aequalis | Orthoptera: Tettigoniidae | | Steiner 1962 |
| Larropsis | | | |
| -capax | Orthoptera: <i>Ceuthophilus</i> spp. nymphs | | Evans 1970 |
| Plenoculus | | | |
| -davisi | Hemiptera: Miridae, adults and immatures | | Evans 1970 |
| Nitelopterus | | | |
| -evansi | Arachnids: Dictynidae (<i>Dictyna</i> spp.) | | Evans 1970 |
| Tachysphex | | | |
| -helveticus | Orthoptera | | Elliott & Kurczewski 1985 |
| -pompiliformis | Orthoptera: Acrididae nymphs | | Elliott & Kurczewski 1985 |
| -albocinctus | Dictyoptera: Mantidae (<i>Mantis religiosa</i> nymphs) | 3-4 | Elliott & Kurczewski 1985 |

| | | |
|-------------------------------|--|------------------------------|
| -consocius | Orthoptera: Acridinae nymphs (Orthoptera: Acrididae) (8) | Elliott & Kurczewski 1985 |
| -antennatus | Orthoptera: Acridinae nymphs (<i>Melanoplus</i> spp.) 3-9 | Kurczewski & Kurczewski 1987 |
| -semirufus | Orthoptera: Tettigoniidae | Kurczewski & Evans 1986 |
| -krombeini | Orthoptera: Tettigoniidae and Acrididae | Kurczewski 1971 |
| -apicus | Orthoptera: immature Phasmidae | Elliott & Kurczewski 1985 |
| -tarsinus | Orthoptera: Acridinae nymphs | Asis et al. 1989 |
| -nigrior | Orthoptera: Acridinae nymphs | Evans 1970 |
| -terminatus | Orthoptera: Acridinae nymphs | Evans 1970 |
| -linsleyi | Orthoptera: Acridinae nymphs | Evans 1970 |
| Palarus | | |
| -variegatus | Hymenoptera: bees and wasps | Rathmayer 1962 |
| Dineus | | |
| -pictus | Orthoptera | Evans 1970 |
| Tachytes | | |
| -sayi | Orthoptera: Acrididae | Evans 1970 |
| Trypoxylon | | |
| -politum | Arachnids | Brockmann 1980a |
| -palliditarse | Arachnids | Freeman 1981a |
| -frigidum | Arachnids | Evans 1970 |
| Sub Family <u>Crabroninae</u> | | |
| Lindenius | | |
| -columbianus | Small flies, sucking bugs and parasitic Hymenoptera | Miller & Kurczewski 1973 |
| Moniaecera | | |
| -abdominalis | Hemiptera: Cicadellidae (<i>Tylozygus bifidus</i>) | Evans 1964b |
| -asperata | Diptera and Hemiptera | Evans 1964b |
| Tracheloidea | Hymenoptera: Formicoidea | Pate 1942 |
| Crabro | | |
| -scutellatus | Diptera: Dolichopodidae | Bristowe 1948 |
| -peltarius | Diptera: Therevidae, Muscoidea, Stratiomyidae | Yeo & Corbet 1983 |
| -cribrarius | Diptera: Therevidae, Asilidae, Muscoidea, Empididae, Syrphidae | Yeo & Corbet 1983 |

| | | | |
|-----------------------|---|------------|----------------------------|
| -cribrellifer | Diptera: Asilidae | | Wcislo et al. 1985 |
| -hilaris | Diptera | 4-14 | Alcock 1981 |
| -argusinus | Diptera | 9-30, (92) | Alcock 1981 |
| -monticola | Diptera: Therevidae, and a few Tabanidae, Syrphidae and Calliphoridae | 1-7 | Alcock 1981 |
| Crossocerus | | | |
| -quadrimaculatus | Diptera: mainly Nematocera rarely Lepidoptera and Trichoptera | | Bristowe 1948 |
| -vagabundus | Diptera: Tipulidae | | Bristowe 1948 |
| -walkeri | Ephemeroptera: Baetidae | | Bristowe 1948 |
| -annulipes | Hemiptera: Typhlocybidae | | Bristowe 1948 |
| -maculiclypeus | Diptera: mainly acalypterates | (18) | Evans 1970 |
| Ecternius | | | |
| -chrsargyrus | Diptera | | Evans 1970 |
| -centralis | Diptera | 4-7 | Hook 1982 |
| Lestica | | | |
| -interrupta bella | Adult Lepidoptera (usually small moths) | | Peckham & Peckham 1905 |
| Belomicrus | | | |
| -forbesii | Hemiptera: Miridae (Orectoderus obliquus) | | Evans 1970 |
| Oxybelus | | | |
| -strandii | Diptera | | Evans 1966a |
| -sericeus | Diptera: Otitidae, Dolichopodidae | 3-14 | Evans 1966a |
| -emarginatus | Diptera: Nematocera | | Krombein & Kurczewski 1963 |
| -uniglumis | Diptera: mainly Rhagionidae | 4-8 | Evans 1970 |
| Sub Family Nyssoninae | | | |
| Melinus | | | |
| -arvensis | Diptera, esp. Cyclorhapha | 4-17 | Bristowe 1948; Huber 1961 |
| Gorytes | | | |
| -mystaceus | Hemiptera: Aphrophoridae (<i>Philaenus spumarius</i>) | | Bristowe 1948 |
| -canaliculatus | Hemiptera: Cicadellidae, mainly <i>Idiocerus</i> spp. | | Evans 1970 |
| Hoplicoides | | | |
| -spilographus | Hemiptera: Membracidae | | Evans 1970 |

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|---------------------|---|--|--------------|-----------------------|--|
| Stictiella | | | | | |
| -emarginata | Lepidoptera: Noctuidae adults | | | Evans 1970 | |
| Steniolia | | | | | |
| -obliqua | Diptera: Bombyliidae | | | Evans 1970 | |
| Harpactus | | | | | |
| -tumidus | Hemiptera: Cercopidae (<i>Aphrodes bicinctus</i>) | | | Bristowe 1948 | |
| Exeirus | | | | | |
| -lateritius | Orthoptera: Cicadas | | | Evans 1970 | |
| Sphecius | | | | | |
| -speciosus | Orthoptera: Cicadas | | 1 (m), 2 (f) | Lin 1979 | |
| -grandis | Orthoptera: Cicadas | | | Hastings 1986 | |
| Microbembix | Arthropods from 2 Classes and 10 orders of Insects | | | | |
| -sulfurea | Arachnids & insects from 5 orders | | | Evans 1966a | |
| -monodonta | Arachnids, centipedes, crustacea (isopods), insects | | | Evans 1966a | |
| Bembix | | | | | |
| -texana | Diptera: Cyclorhapha | | | Evans & Matthews 1973 | |
| -americana comata | Diptera: Cyclorhapha | | 1-48 | Lane et al. 1986 | |
| -americana spinolae | Diptera: Cyclorhapha | | | Evans 1970 | |
| -stenebdoma | Coleoptera: Chrysopidae | | | Lane et al. 1986 | |
| -mareeba | Diptera | | | Evans et al. 1982 | |
| -octosetosa | Diptera | | | Evans et al. 1982 | |
| -kamulla | Neuroptera: Myrmeleontidae and Diptera: Asilidae | | | Evans et al. 1982 | |
| -allunga | Neuroptera: Myrmeleontidae also Diptera and Odonata | | | Evans et al. 1982 | |
| -tuberculiventris | Hymenoptera: Euryglossine Bees (Colletidae: Euryglossinae) | | (46) | Evans et al. 1982 | |
| -flavipes | <i>Trigona essingtoni</i> (males only) (Apidae: Melliponinae) | | (25) | Evans et al. 1982 | |
| -musca | <i>Trigona carbonaria</i> | | | Evans et al. 1982 | |
| -kunumurra | <i>Metallea incisuralis</i> complex (Diptera: Calliphoridae) | | (10) | Evans et al. 1982 | |

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|--------------------------------|--|--|
| -wilcannia | Neuroptera (a single record) probably also Diptera | Evans at al. 1982 |
| -multipicta | Diptera: Tabanidae | Cane & Miyamoto 1979 |
| -dira | Diptera (14 families, >200 species) | Cane & Miyamoto 1979 |
| <u>Sub Family Philanthinae</u> | | |
| <u>Philanthus</u> | | |
| -triangulum | <i>Apis mellifera</i> (Apoidea) | Tinbergen 1932 |
| -crabroniformis | Halicid bees (<i>Dialictus laevisimus</i>) but also other Aculeates, eg honeybees and sphecids | Alcock 1974 Bohart 1954 Hilchie 1982 |
| -gibbosus | Halicid bees (<i>Dialictus</i> and <i>Halictus</i>) | Alcock 1974 |
| -flavifrons | <i>Apis mellifera</i> (Apoidea) | Bohart 1954 |
| -albopilosus | Eumenidae, Sphecidae, Colletidae Andrenidae, Halictidae | Hilchie 1982 |
| -lepidus | Halictidae | Evans 1964b |
| -pulcher | Apoidea and Sphecidae | Hilchie 1982 |
| -zebratus | Apoidea and Sphecidae | Hilchie 1982 |
| -pacificus | Apoidea and Sphecidae | Hilchie 1982 |
| -multimaculatus | Apoidea: <i>Halictus</i> , <i>Sphcodes</i> | Alcock 1975b |
| -binctus | Apoidea: <i>Bombus</i> spp. | Armitage 1965 |
| Aphilanthops | | |
| -frigidus | Formicoidea: <i>Formica fusca</i> (queens) | Evans 1962a |
| -subfrigidus | Formicoidea: <i>Formica neogagates</i> (queens) | Evans 1970 |
| Clypeadon | | |
| -laeticinctus | Formicoidea: <i>Pogonomyrmex occidentalis</i> (workers) | Alexander 1986 |
| -haigi | Formicoidea: <i>Pogonomyrmex barbatus rugosus</i> | Alexander 1986 |
| -sculleni | Formicoidea: <i>Pogonomyrmex maricopa</i> | Alexander 1986 |
| Listropygia | Formicoidea: <i>Pogonomyrmex</i> ants | Evans & Eberhard 1973 |
| Cerceris | | |
| -arenaria | Coleoptera: Curculionidae (<i>Otiorrhynchus singularis</i>) | Willmer 1985 |

| | | | |
|----------------|--|----------|-------------------------|
| -californica | Coleoptera: Buprestidae (<i>Acmaeodera</i> spp., <i>Agrilus</i> spp. and <i>Chrysobothris</i> spp.) | 5-14 | Linsley & MacSwain 1956 |
| -bupresticidus | Coleoptera: Buprestidae | 5-10 | Linsley & MacSwain 1956 |
| -megacantha | Leaf beetles, <i>Rhyparida</i> (Chrysomelidae: Eumolpinae) | 2-7 | Evans & Hook 1986 |
| -froggatti | Coleoptera: Leaf beetles (Chrysomelidae: Chrysomelinae) | 8-12 | Evans & Hook 1986 |
| -opposita | Leaf beetles, <i>Edusella</i> (Chrysomelidae: Eumolpinae) | 6-19 | Evans & Hook 1986 |
| -laberculata | (Chrysomelidae: Eumolpinae) <i>Collaspoides pallidula</i> (Chrysomelidae: Eumolpinae) | (21, 25) | Evans & Hook 1986 |
| -xanthura | Coleoptera: Curculionidae | 2-11 | Evans & Hook 1986 |
| -gilberti | Coleoptera: Chrysomelidae | 8-19 | Evans & Hook 1986 |
| -australis | Coleoptera: Melolonthinae (Scarab beetles) | 10-53 | Evans & Hook 1986 |
| -goddardi | Coleoptera: Chrysomelidae and Curculionidae | 6-11 | Evans & Hook 1986 |
| -eungella | Scarab beetle (single record) | | |
| -antipodes | Coleoptera: Chrysomelidae | | |
| | Coleoptera: Chrysomelidae 71% | | |
| | Curculionidae 15% | | |
| | Scarabaeidae 14% | | |
| | Dermestidae (single record) | | |
| -calida | Coleoptera: Chrysomelidae (Eumolpinae and Cryptocephalinae) | 8-18 | Evans & Hook 1986 |
| -armigera | Coleoptera: Chrysomelidae and Curculionidae | 6-8 | Evans & Hook 1986 |
| -unispinosa | Coleoptera: Curculionidae (<i>Mylocerus</i>) | 20-59 | Evans & Hook 1986 |
| -miniscula | Coleoptera: Curculionidae 66%, but also Phalacridae, Chrysomelidae, Artelabidae | 7-15 | Evans & Hook 1986 |
| -anthicivora | <i>Anthicus scutellatus</i> (Anthicidae) | (24, 28) | Evans & Hook 1986 |
| -windorum | Coleoptera: <i>Ataenius</i> spp. (Scarabaeidae: Aphrodiinae) | | |
| -praedura | Coleoptera: Dermestidae, Chrysomelidae, Bruchidae, Apionidae. | | |

| | | | |
|----------------|--|----------------|-------------------------|
| -halone | Coleoptera: Curculionidae (<i>Curculio</i> spp.) | 3-4(m), 5-6(f) | Byers 1978 |
| -walingensis | Coleoptera: Curculionidae and some Chrysomelidae | 6-13 | Elliott et al. 1986 |
| -zonata | Coleoptera: Chrysomelidae | 24-32 | Evans & Hook 1986 |
| -binodis | Coleoptera: Chrysomelidae | 8-9 | Evans & Hook 1986 |
| -rufimana | Coleoptera: Chrysomelidae | 3-15 | Evans et al. 1976 |
| -fumipennis | Coleoptera: Buprestidae | 30-39 | Linsley & MacSwain 1956 |
| -echo | Coleoptera: Phalacridae (<i>Olibrus</i> spp. and <i>Phalacrus</i> spp.) | 8 | Evans & Hook 1986 |
| -robertsonii | Coleoptera: Chrysomelidae | 8 | Krombein 1953 |
| -nigrescens | Coleoptera: Curculionidae | 14-30 | Krombein 1953 |
| -atramontensis | Coleoptera: Curculionidae | | Krombein 1953 |
| -tuberculata | Coleoptera: Curculionidae (<i>Cleonus ophthalmicus</i>) | | Linsley & MacSwain 1956 |
| -ferrei | Coleoptera: Curculionidae | | Linsley & MacSwain 1956 |
| -argyotricha | Coleoptera: Buprestidae (<i>Acmaeodera</i> spp.) | | Linsley & MacSwain 1956 |
| -tybiensis | Hymenoptera: Halictidae (<i>Halictus</i>) | | Linsley & MacSwain 1956 |
| Eucerceris | | | |
| -zonata | Coleoptera: Curculionidae | 3-5(m), 5-7(f) | Evans 1970 |
| -flavocincta | Coleoptera: Curculionidae | 6-7 | Evans 1970 |
| -fulvipes | Coleoptera: Curculionidae | 12-18 | Evans 1970 |

Bracketed figures indicate data from a single cell.

In the Sphecidae as a whole, subfamilies considered primitive on structural grounds (such as the Ampulicinae and Sphecinae) mostly prey on ancient groups of arthropods, while more advanced groups such as bees and flies, are preyed upon by the more advanced and recently evolved subfamilies such as the Nyssoninae and Philanthinae.

Figure 1.1 The Evolution Of The Major Groups Of The Hymenoptera

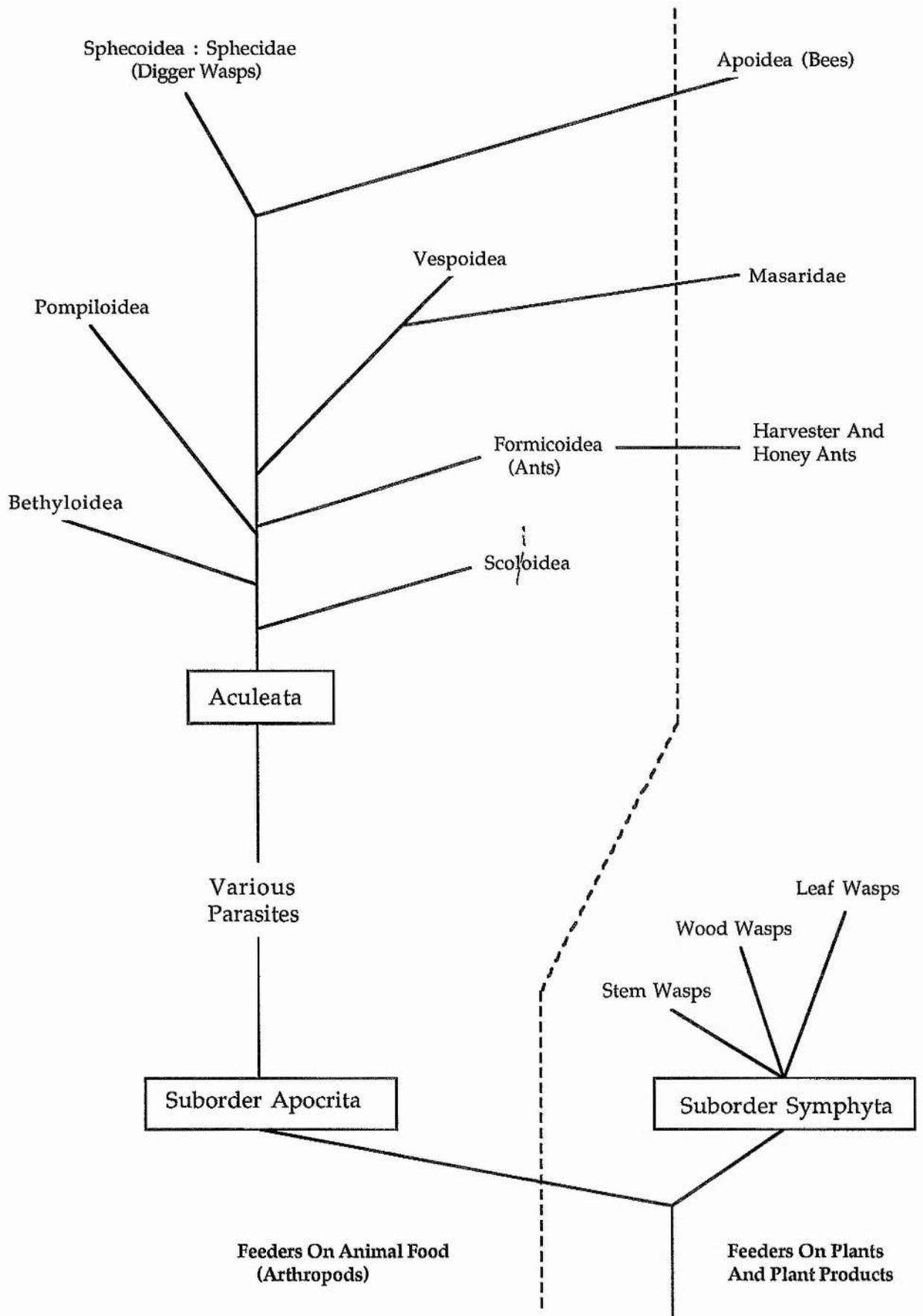


Fig. 1.1 The sphecid wasp, *Mellinus arvensis*.

Fig. 1.2 A copulating pair of *M. arvensis*. The male is the smaller individual above the female.



Fig. 1.3 Prey carriage in *Mellinus arvensis*.

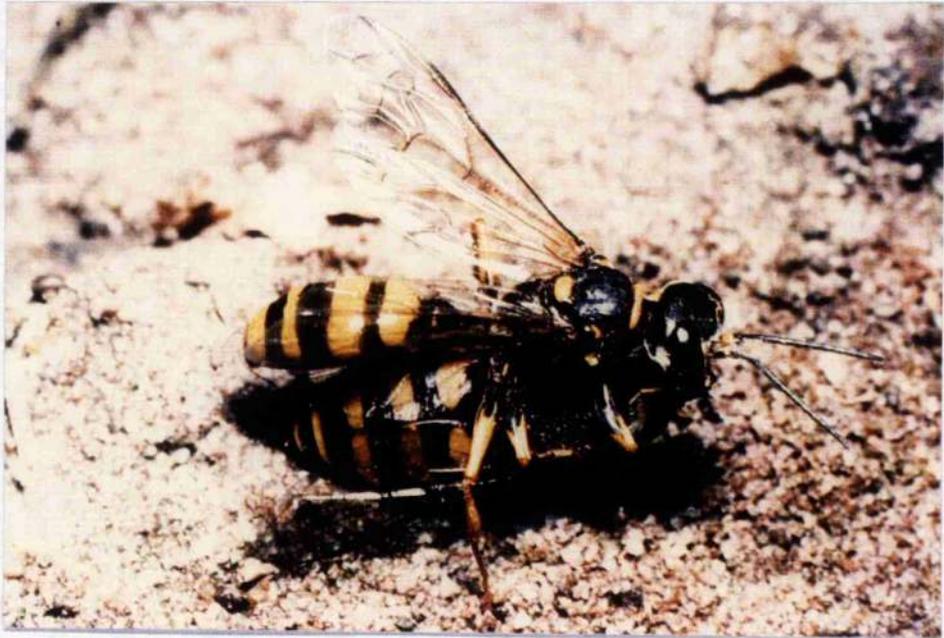
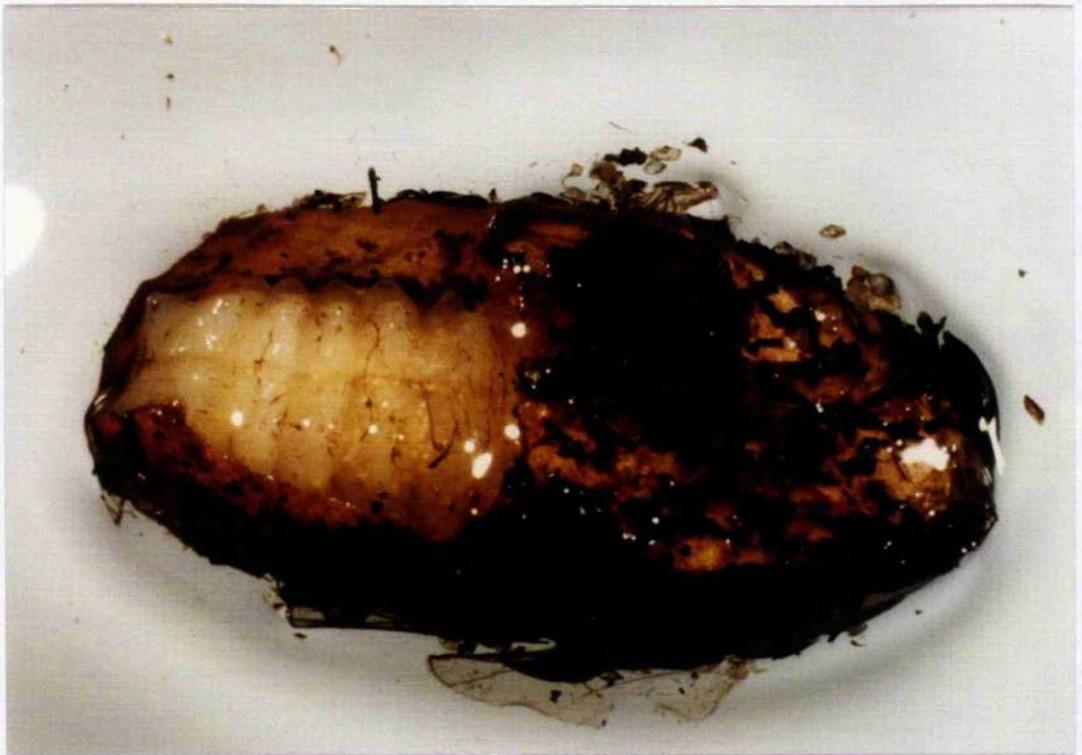


Fig. 1.4 The cocoon of *M. arvensis*, partially cut away to expose the pre-pupa.



Chapter 2 Sites, Materials & Methods

2.1 Research Sites

Data were collected from five 'primary' sites in Britain, chosen for their latitudinal location and the ease with which wasps could be observed. Some additional (but not behavioural) data were also gathered from three 'secondary' sites. The sites are described below in order of decreasing latitudinal position, and their location is shown in figure 2.1.

a) Findhorn Dunes, Grampian (latitude 58° 40', grid reference NJ 648 045, altitude sea level), is a coastal sand dune system with many horizontal and vertical bare sandy areas typically favoured by ground nesting Hymenoptera. The vegetation consists mostly of groundsels and ragworts (*Senecio* spp.); thistles (*Cirsium/Carduus* spp.); gorse (*Ulex* sp.); heather (*Calluna vulgaris*); and grasses and umbellifers. The majority of *M. arvensis* were found along a south facing, vertical sandy bank clear of vegetation, alongside a dirt road. The bank was not continuous for its entire length, and observations were made at only one section two metres long by fifty centimetres high. During periods of observation the number of active nests in this section varied between 10 - 30 nests, depending on the time of year. In addition to *M. arvensis*, *Crabro cribrarius* was also nesting in the same bank.

b) St Cyrus Nature Reserve, Tayside (latitude 57° 39', grid reference , altitude sea level), is another coastal sand dune system, the dominant vegetation being *Senecio* spp. and marram grass *Ammophila arenaria*. There are also several gorse bushes (*Ulex* sp.) nearby. The study site was an east facing vertical sandy bank, about 5 metres in length and between 30 and 50 centimetres

high. More than five hundred nest entrances were visible and it was estimated that about 250-300 wasps were active at the height of the nesting season. *Crabro cribrarius* and a solitary bee, *Halictus rubicundus*, were also found nesting in the same bank but *M. arvensis* was by far the most common resident.

c) A large population of *M. arvensis* was located in the sides of a dry drainage ditch (30 cm deep and about 150 metres long running north - south) along the boundary of a golf course at Alnmouth Common, Northumberland, (latitude 55° 23', grid reference NU 250 108, altitude sea level). This site is also coastal but the vegetation was different from the previous two sites, consisting primarily of bracken, *Pteridium aquilinum*, and bramble bushes, *Rubus fruticosus*, on one side, and the trimmed grass of the golf course on the other. *M. arvensis* was the only sphecid observed nesting in the drainage ditch. The number of nest entrances seen was in excess of 1000 along the entire length of the ditch, although the number of active nests seen during the period of observation (in September 1992) was considerably less and was estimated at about 200 for the entire site.

d) Alderly Edge, Cheshire, (latitude 53° 18', grid reference SJ 780 860, altitude 150 metres) is an inland woodland site straddling a geological fault line. At the fault line the land has slipped down some 80 metres exposing a steeply sloping area of boulders and soil mostly clear of vegetation and trees (figure 2.2). *M. arvensis* nesting aggregations are scattered in several locations in this area, mostly on vertical, or near vertical, surfaces. Heather, *Calluna vulgaris*, is the dominant plant in the clearing, but at the edges oak *Quercus robur*, beech *Fagus sylvatica*, and rowan *Sorbus aucuparia* trees predominate with an undergrowth of heather and grasses or bracken *Pteridium aquilinum*. Many other species of aculeate Hymenoptera are present in the area, the most

common being *Halictus rubicundus* and its parasite *Sphcodes marshamella*, and the sphecids *Crabro peltarius* and *Crossocerus quadrimaculatus*.

e) Thetford Warren, Norfolk, (latitude 52° 26', grid reference TL 843 840, altitude 35 metres) located in the centre of the Brecklands, is a heathland site surrounded by deciduous and coniferous woodland (figure 2.3). The dominant vegetation in the nesting site area is heather *Calluna vulgaris*, and small pedunculate oaks *Quercus robur* and silver birch *Betula pendula*. *M. arvensis* nests were found scattered throughout the site on sloping or vertical sandy surfaces. Besides *M. arvensis*, other Sphecidae (*Cerceris arenaria*, *Psen lutarius* and *Ammophila sabulosa*) and Apoidea (*Halictus rubicundus*, *Colletes succinctus* and its parasite, *Epeolus cruciger*) were nesting at this site.

The three secondary sites were an embankment running alongside the river Till in Northumberland, drainage ditches and paths at Strensall Common in Yorkshire, and another coastal sand dune system at Merthyr Mawr in south Wales.

Mellinus arvensis from the site at the river Till in Northumberland (latitude 55° 33', grid reference NV 062 285, altitude 47 metres) were nesting in the upper part of the vertical river clay embankment. The part of the embankment in which the nests of wasps were located was about 1 metre high and 9 metres long. The embankment was mostly facing south (6 metres) with the rest facing east (3 metres). By far the most common hymenopteran was *Halictus rubicundus* which had a nesting density of 25 nests per square metre (S. J. Potts, personal communication). Several vespids (*Vespula vulgaris*) were also seen.

Strensall Common, Yorkshire, (latitude 54° 03', grid reference SE 655 605, altitude 20 metres) is site of 690 hectares situated about six miles north-east of York. It is an area of lowland heaths through which many drainage ditches have been dug. The sides of the drainage ditches provide excellent sites for soil nesting aculeates (Archer 1988). *M. arvensis* nests were found in these drainage ditches and along sandy footpaths. Archer (1988) recorded a total of 78 aculeate species of which the most common were *Ectemnius continuus*, *Crossocerus quadrimaculatus*, *Nomada marshamella*, *Lasioglossum fratellum* and *M. arvensis*.

Merthyr-Mawr, Mid Glamorgan, (latitude 51° 29', grid reference SS 773 870, altitude sea level) is a south facing coastal region consisting of heathland and sand dunes. Nests of *M. arvensis* were found throughout the site but were never observed to form nesting aggregations as was usually seen at other sites. The most common sphecid species seen in addition to *M. arvensis* were *Crabro cribrarius*, *C. peltarius*, *Ammophila sabulosa*, and *Ectemnius cavifrons*.

Additional morphological data from a population of *M. arvensis* collected during the years 1981 - 1983 at Street sand-pit, Sussex (latitude 50° 55', grid reference TQ 148 349, altitude 53 metres) were obtained from Paxton (1985). This site was an area where sand was being excavated, resulting in large areas of sandy ground devoid of vegetation. *M. arvensis* were nesting along one edge of the sand pit, close to an area that had not been excavated and where plants were growing.

2.2 Behavioural Observations and Marking

Intensive observations were made on individually marked nesting females at each of the primary sites for several hours on a number of days throughout

each season (ie. late June to mid October, 1990 - 1993). Only provisioning females were selected for marking. It was assumed that a female returning with prey to a nest was provisioning that nest. Females to be marked were caught by placing a small glass vial over a nest entrance after a female carrying prey had entered. Upon emerging the wasp would fly into the vial whereupon the lid would be fastened thus trapping the wasp. The wasp was then anaesthetised by partially removing the lid and introducing a small amount of carbon dioxide from a CO₂ cylinder into the vial via a narrow plastic tube. The wasp was immobilised within a few seconds, at which time it was removed from the vial and marked with a small dot of enamel paint applied to the dorsal surface of the mesonotum (figure 2.4), using a mounted needle or a fine grass stem. Care was taken to avoid the spreading of paint to other body parts such as the tegulae, head or wings. Wasp head width was also measured at this time (see section 2.4, below). Wasps were then allowed to recover in a cool, shaded and sheltered area. About one minute after removal from the vial wasps began to start moving, initially starting with leg twitches, followed by abdominal pumping movements, walking and ultimately flying. Full recovery, assumed to be the time at which wasps flew away, usually took about 4 - 5 minutes, but occasionally lasted longer (up to 15 minutes). The nest was also marked with an individual letter on a small piece of paper attached just above the nest entrance by a pin. This method of nest marking was convenient and sufficient as a permanent marking system was not required. The majority of marked wasps were seen provisioning the same nest after a period of 24 hours, but some were provisioning a different nest to that from which they had emerged, some were no longer provisioning any nest and a very few were not seen again. Observations were made and data collected on some wasps that had not been marked, and these data have only been included in the analysis where it was certain (because of size or colour) that the wasps were not misidentified.

The behaviour patterns of individual wasps and intra- and inter-specific interactions were noted. The terms used in referring to particular behaviours are identified and defined below.

Foraging time - the time, in minutes, taken for a wasp to locate, subdue and return with a prey item, from the point at which the wasp leaves the nest entrance to the moment it enters with the prey item.

Time in nest - the period of time, in seconds, spent inside the nest entrance from the moment of entry to the time first seen at the nest entrance. Typical behaviour inside the nest may be manipulating the prey into the cell, ovipositing or excavating a new cell.

Time at nest entrance - time spent, in seconds, at the mouth of the nest from the time of first appearing, to the time of departure from the nest.

Prey items were separated according to size into one of three categories, small (dry weight corresponding to < 10mg); medium (dry weight 10 - 20mg); and large (dry weight > 20 mg).

All activity at a marked nest was noted whether it involved the resident wasp, other wasps, or parasites, with particular attention to aggressive encounters between wasps.

On some days overall levels of wasp activity in a marked area of 1 m² was recorded as number of male and female *M. arvensis* seen within the area in a period of one minute at 20 minute intervals.

In a small number of cases wasps were seen to return repeatedly to the same foraging site. When this happened observations of prey capture were made.

2.3 Measurement of Climatic Variables

During the periods of behavioural observation of wasps, climatic data were recorded at intervals of 20 minutes. All temperature measurements were recorded using a Type K thermocouple and Type K (P9005) thermometer (Portec Instruments, UK). Ambient temperature (T_a) was recorded in the shade at a height of 1 metre. Ground surface temperature (T_g) was obtained by lightly pressing the shaded thermocouple onto the surface of the ground in the vicinity of the nesting area. Nest entrance temperature (T_e) was obtained by holding the thermocouple tip in the middle of the entrance taking care to avoid contact with the sides of the burrow and keeping the thermocouple shaded. Cloud cover was estimated in eighths, 0/8 meaning no clouds, 8/8 indicating a totally overcast sky.

2.4 Measurement of Wasp Body Size

Wasp size was determined in the field for most wasps, and in the laboratory for wasps retained from grab and stab temperature measurements (see below). Head width was used as the indicator of size (Evans & Hook 1982a; O'Neill 1983a,b) as it could be easily and accurately measured in the field with minimum disturbance to wasps. Head width was measured to the nearest 0.01 mm using a hand held digital micrometer (Mitutoyo Corporation, Japan) while the wasp was under sedation (section 2.2, above). To test the accuracy of these measurements head widths of some wasps were remeasured twice at a later date under a binocular microscope (Meiji Techno Co. Ltd.), firstly using the same micrometer and secondly using a calibrated

graticule, at a magnification of 20x. The maximum discrepancy between measurements made in the field and those made at the laboratory was 0.02 mm, but the majority of readings were identical and some were different by only 0.01 mm, and there was no significant direction to the errors. The head width of all wasps retained from grab and stab body temperature measurements (see below) were measured using the micrometer with the aid of some magnification underneath the microscope.

The dry weight of 186 wasps ranging in head width from 2.31 mm to 3.47 mm was determined. There was a highly significant correlation between head width and dry weight (figure 2.5; $p < 0.001$, $t = 36.39$, d.f. = 184).

2.5 Estimation of Wasp Age

It was sometimes necessary to obtain an estimate of the relative ages of wasps. This can be done by measuring the wear of body parts such as mandibles (Evans & Hook 1982a) or wings (Southwood 1978; Allsopp 1985; Paxton 1985). A rough guide to the wasps age was obtained by assessing the damage to the wing margins (see Paxton 1985). The benefits of this technique were that wasp age could be easily and quickly estimated in the field without the need for magnifying equipment other than a hand lens, and with minimal disturbance to the wasp. Age was graded into three numbered wing wear categories. A value of 0 was assigned to wasps that had no visible damage to the wing margins; a value of 1 indicated some small tears at the wing edges; a value of 2 represented wasps with considerable wing tear (figure 2.6).

2.6 Analysis of Prey

A sample of the prey of *M. arvensis* were collected by taking prey directly from wasps, and by collecting prey items that had been caught but subsequently dropped by wasps in the vicinity of the nesting area. Prey were identified to family or sub family and, if intact (see below), dry weights were obtained. When prey items were taken directly from wasps, the size of the wasp was also measured. *M. arvensis* often dropped prey due to interactions with males and females, attention from parasites or difficulty in entering the nest. Furthermore prey were often caught not for nest provisioning but for nourishment, typically the head being punctured with the mandibles, the exuding fluid lapped up, and the fly then being discarded (Hamm & Richards 1930; Bristowe 1948; Paxton 1985; personal observation). Dropped or discarded prey were collected at the end of most days on which behavioural observation were carried out. Thus the prey sample represented the catch of *M. arvensis* from a large number of days throughout the season.

Random samples of Diptera were obtained by sweeping a hand net over vegetation occurring in the vicinity of the nesting sites. Yellow and blue water pan traps were used at Alderly Edge but these proved to be very selective in the insects they caught (primarily syrphids, calliphorids and muscids, but also bees and several *M. arvensis*). Consequently, data obtained from pan traps were not included in the analysis.

At the end of the nesting season in 1991 and 1992 some nests from St Cyrus, Alderly Edge and Thetford were excavated and the cell contents removed to determine the number and size of prey provisioned per cell. Some nests were filled with plaster of Paris which was allowed to harden before excavating the nest. The majority of nests were excavated, using a wallpaper scraper, by

carefully removing a layer of sand a few millimetres thick from the vertical face in which *M. arvensis* had been nesting, thereby exposing the cells.

2.7 Nest Depth and Distribution

Nest depths were obtained by feeding a thermocouple into the nest until resistance was felt. Bends could be negotiated by continuously twisting and rotating the thermocouple while pushing it into the nest. The tip of the thermocouple was found to be at the deepest point of all four nests that were subsequently excavated. After recording the temperature at the bottom of the nest the thermocouple was pinched between two fingers at the nest entrance and removed, and the depth of the nest was measured to the nearest centimetre by aligning the thermocouple to a tape measure.

Values of the mean nearest neighbour distances of nests at each nesting aggregation were measured. Distances between a nest and its nearest neighbour were made for a large number of nests, although no distinction was made between active and abandoned nests. Distances between nests were either measured in the field, or photographs of the nesting aggregation, including a scale, were taken and subsequently analysed in the laboratory (St Cyrus, figure 2.7).

2.8 Measurement of Soil Hardness

Soil hardness was determined using a penetrometer (McCorquodale 1989a) consisting of a wooden plate out of which three nails were protruding nine centimetres (figure 2.8). The nails were in the form of an equilateral triangle the sides of which were 6 centimetres. The other side of the plate was attached centrally to a one metre long rigid pole along which a weight could

slide freely. The weight was a 1 kilogram cylindrical object with a central hole to fit the diameter of the pole. The pole was marked at 50 centimetres from the point at which the pole was attached to the top of the plate. The device was placed with the points of the nails resting on the ground surface. The weight was aligned at the 50 centimetre mark then released. The force of the impact of the weight on the top of the wooden plate drove the nails into the ground. It was assumed that the depth of penetration was dependent on the height of the weight before release and the resistance of the soil. As the height of the weight was standard, depth of penetration represents a measure of soil hardness. The depth of penetration was measured to the nearest millimetre, and it is in these units that soil hardness is expressed. Therefore a compact, hard soil would have a low soil penetrability.

M. arvensis generally nest in vertical or steeply sloping ground, and because of this measurements of soil hardness could not be made in the immediate vicinity of the nest entrances. In such cases the penetrometer was used on the horizontal surface directly above the nests in an area free from vegetation. It was assumed that the soil penetrability would be the same at the horizontal surface as it was at the vertical surface.

2.9 Field Analyses of Thoracic Temperatures

Body temperatures of wasps in the field were measured using the 'grab & stab' method (eg, Heinrich 1979a; Louw & Nicolson 1983; Cooper et al. 1985; Heinrich & Buchmann 1986; Dyer & Seeley 1987; Stone & Willmer 1989b). Thermocouples consisted of a fine steel hypodermic needle (10 mm long, outside diameter of 0.5 mm, D05930, Gillette, UK) through which a 40 gauge insulated copper wire was threaded. The copper wire was soldered to the tip of the needle and a steel wire was connected to the base. These wires were

connected to a Type T P9005 thermocouple thermometer (Portec Instruments, UK). The errors associated with the grab-and-stab technique have been discussed by Stone & Willmer (1989b) and in accordance with that study I have assumed that they are small and can be ignored. A thermocouple was inserted dorsally into the thorax within 8 seconds of capture. This process was carried out in the shade and, to minimise delay, the wasp was not removed from the net. Ambient temperature (T_a) was recorded immediately after each measurement. The size of each wasp was determined later in the laboratory as outlined above (section 2.3).

2.10 Laboratory Investigations of Warm-Up Rates

Wasps used in experiments were captured and placed into a glass vial which was then put into the refrigerator within, at most sixty, and usually thirty, minutes of capture. Wasps were cooled to about 10°C. A hole was made mid-dorsally in the thorax with a brass insect pin. A thermocouple made from 40 gauge copper and constantan wires (The Scientific Wire Company, UK) was inserted as shallowly as possible (about 1 mm), so as to minimize internal damage, into the thorax. The thermocouple was secured to the thorax using a minimal amount of glue (Loctite Super Glue 3, Loctite, UK). The potential errors due to heat loss down the sensor wires are assumed to be small (Stone & Willmer 1989b). A second potential source of error stems from disturbance to the wasps' behaviour and physiology by damage to internal structures (Stone & Willmer 1989b). This was minimised by shallow insertion of the thermocouple. All wasps were capable of flight at the end of the experiments. The thermocouple was connected to a chart recorder (Gould BS 272) which recorded the temperature continuously.

When a chart recorder was not available (when working in the field in Britain and Portugal), thoracic temperature was recorded at 15 second intervals commencing from the insertion of the thermocouple. Wasps sometimes initiated warm up without stimulation, but often it was necessary to tap the antennae gently with a pair of fine forceps. The wasps were given a small piece of styrofoam to grip in their tarsi to prevent flight attempts before warm up was complete. Upon initiating flight, the styrofoam was dropped and was reintroduced to the wasp's tarsi as soon as wing movements ceased, or when thoracic temperatures had stabilised. If wasps did not initiate flight, or showed no signs of warm up, the styrofoam was removed to determine if they were capable of flight, and if so, the thoracic temperature reached during tethered flight. After the experiment the wasp was killed and head width was measured.

2.11 Measurement of Passive Warming and Cooling Rates

To assess the significance of body size alone on the rates of warming and cooling, dead and dried wasps of varying size were mounted with thermocouples shallowly inserted into the body as described above. The wasp was positioned ten centimetres in front of a 60 watt bulb so that the dorsal side was facing the lamp. The lamp was switched on using a socket switch located about 2 metres away from the experimental set up, thereby avoiding touching the lamp and minimising disturbances such as convection currents around the wasp. Temperature was recorded automatically and continuously by a chart recorder to which the thermocouple was connected. The dead wasps were allowed to warm up until temperature stabilised. After thermal equilibrium was reached, the lamp was switched off and the cooling rate was recorded. Room temperature during each experiment was monitored, and all recordings were carried out when room temperature was between 22-23°C.

2.12 Statistical Methods

When analysing the affects of one continuous variable upon another continuous variable simple regressions, or multiple regressions, have been used. The equation for the regression is given in the figure legend, together with a value of R^2 . When mean values have been used error bars have been included indicating ± 1 standard error. The sample sizes are not included in the legends, but the degrees of freedom ($n - 2$) are.

Differences between populations in continuous data are analysed with the use of t-test or analysis of variance using Minitab or by hand following procedures described in Sokal & Rohlf (1981). Further statistical details are described in the text and in Appendix 1.

Fig. 2.1 Location of study sites in Britain

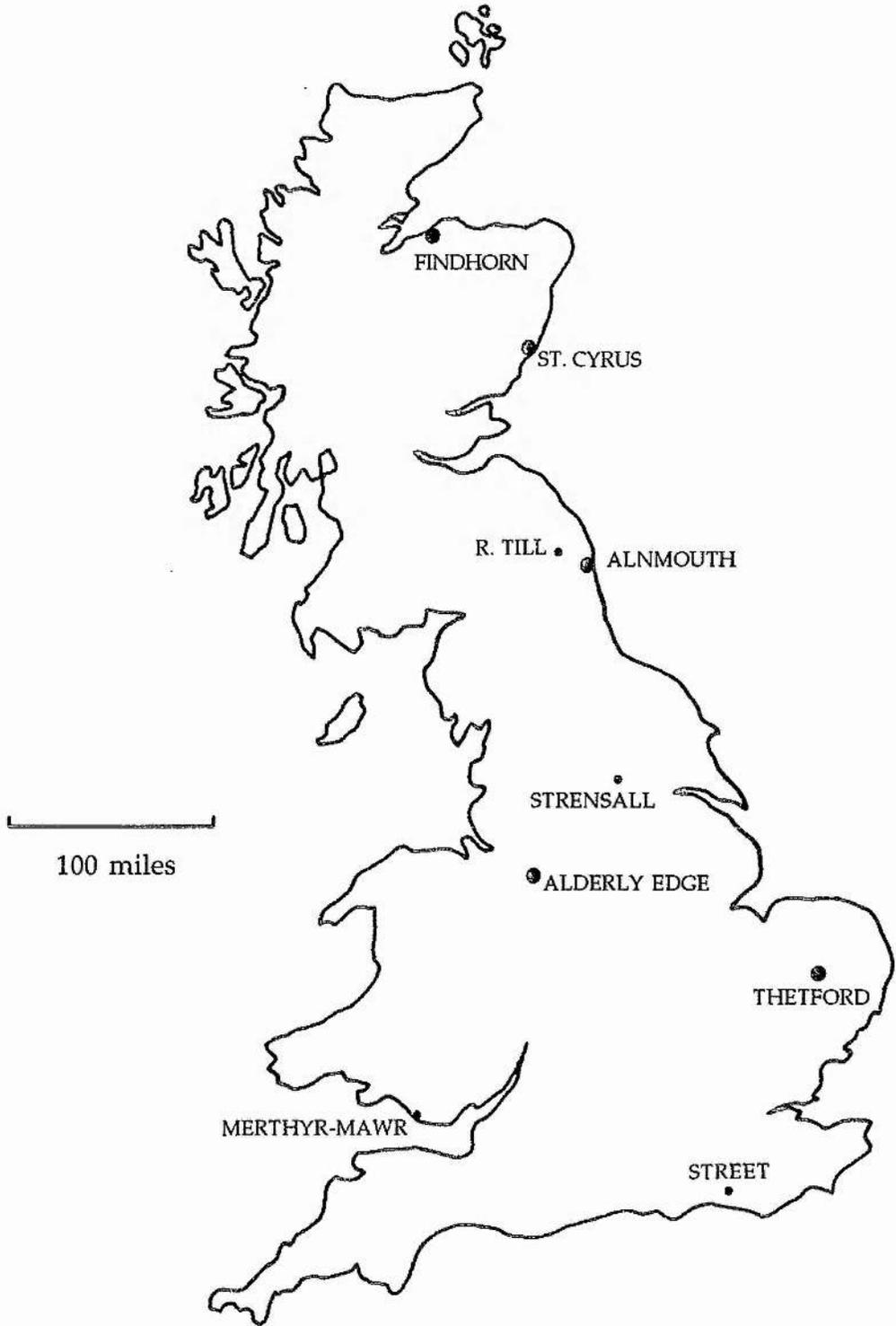


Fig. 2.2 The nesting area of *Mellinus arvensis* at Alderly Edge.

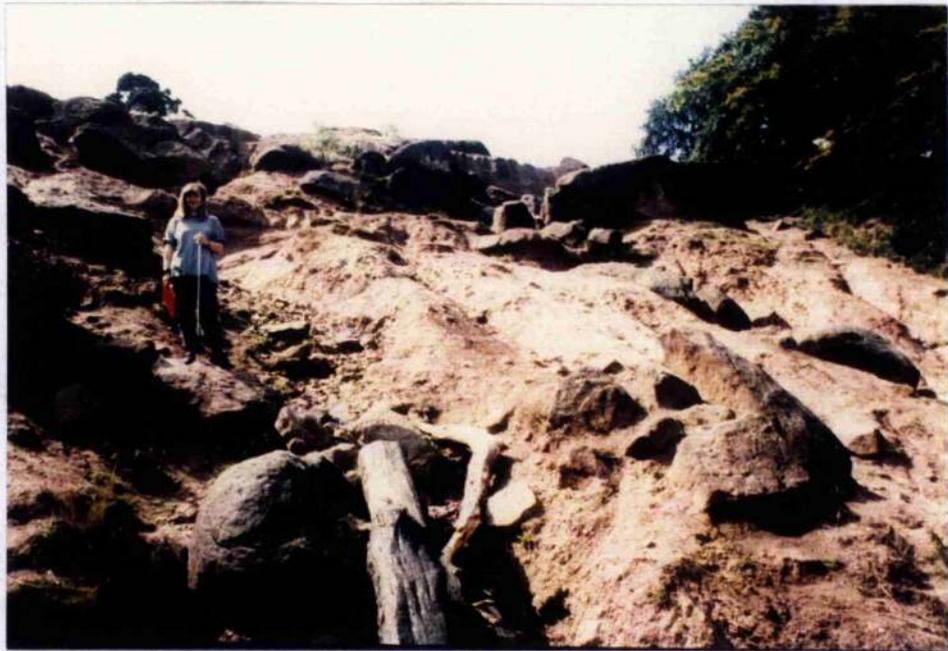


Fig. 2.3 The nesting area of *Mellinus arvensis* at Thetford.



Fig. 2.4 A female *M. arvensis* with yellow mark on thorax.



Fig. 2.5 The correlation between female head width and dry weight of *M. arvensis*. $y = -37.42 + 17.69x$, $R^2 = 0.878$; $p < 0.001$, $t = 36.39$, d.f. = 184.

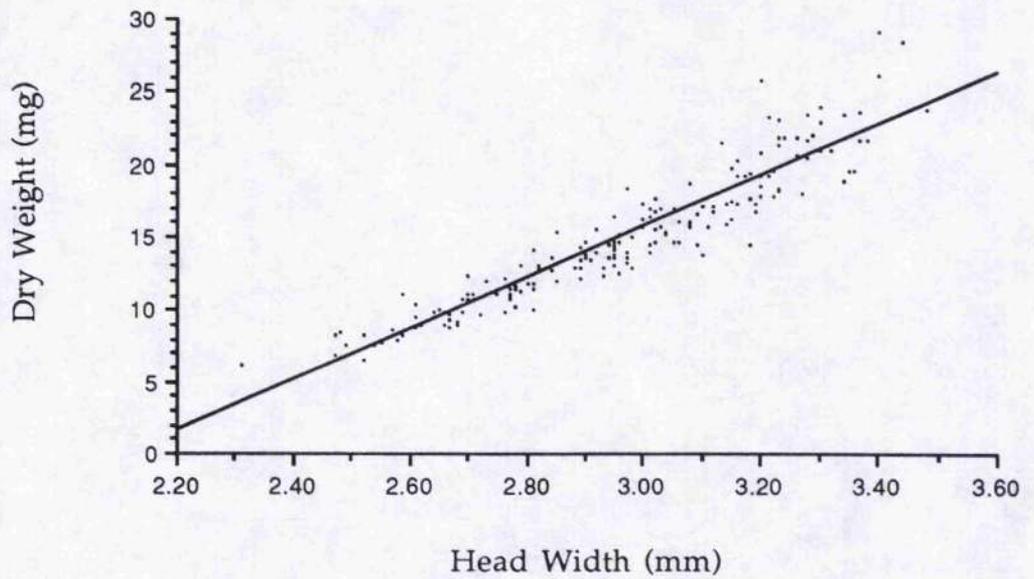


Fig. 2.6 Wing damage (coded 0 - 2) as a measure of wasp age. Wing wear code of 0 = no damage, recently emerged wasp; 1 = slight damage, middle aged wasp; 2 = much damage, old wasp.

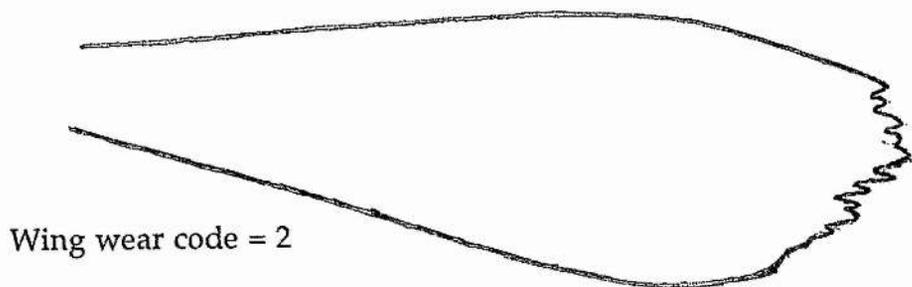
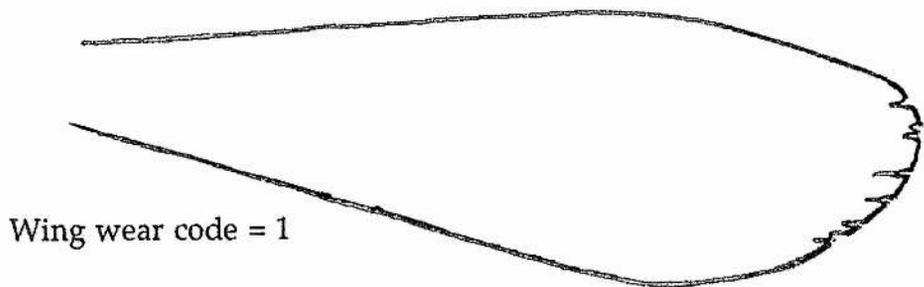
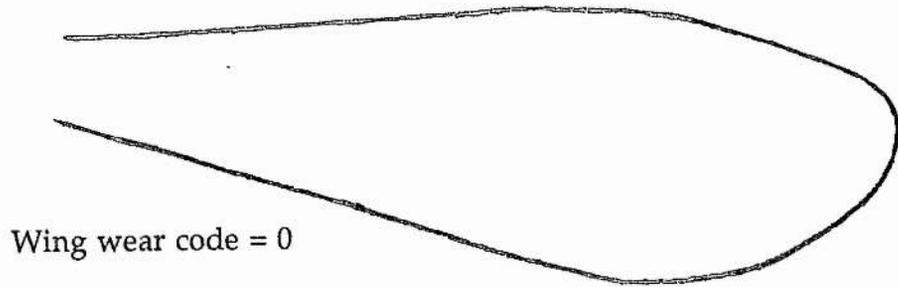


Fig. 2.7 Example of photograph of the nesting site of *M. arvensis* at St Cyrus used for analysis of nest density and distribution.



Fig. 2.8 The penetrometer, used for measuring soil hardness.



Chapter 3 The Behavioural Ecology of *Mellinus arvensis*

3.1 Introduction

The behavioural ecology of single populations of *M. arvensis* has been well documented at a number of sites in Europe (in Germany, Adlerz 1903 and Huber 1961; in Britain, Hamm & Richards 1930, Hobby 1931a, Bristowe 1948; in Italy, Grandi 1954, 1961). Much variation in behaviour is apparent between these widely separated populations although, as yet, no direct comparison has been made. This chapter considers a number of behavioural aspects of *M. arvensis* biology at each of the study sites in Britain.

3.2 Phenology

M. arvensis is one of the latest emerging species in Britain, usually appearing in mid July (personal observation). *M. arvensis* is protandrous, males emerging about a week before the females. The date of first emergence to the nearest week for all sites except Alnmouth, for which there are no data, is shown in table 3.1. *M. arvensis* from the two northern populations (St Cyrus and Findhorn) emerge earlier than the southern populations (Alderly Edge and Thetford Warren). However the season at St Cyrus reaches its end earlier also (in the first week of September) while the Thetford Warren and Alderly Edge populations are active until the second or third week of October (table 3.1). The length of the season during which adult females are active varies between ten and thirteen weeks.

3.3 A Brief Outline of *M. arvensis* Nesting Behaviour

Only female *Mellinus arvensis* were observed to dig nests, and these were located on vertical or steeply sloping bare ground, horizontal bare ground and horizontal ground covered with grass. Owing to the difficulty in finding nests hidden by vegetation, there is no quantitative data comparing the frequency of nests found in the above mentioned categories, but the vast majority of digging activity was observed to occur on vertical or steeply sloping bare ground at all sites. Nests were very rarely found within clumps of vegetation, and where the environment was heterogenous with respect to the angle of the ground (Alderly Edge and Thetford) almost all the nests were found in sloping ground.

A nest is started by loosening the soil crust with the mandibles, the soil debris being removed by gathering it into a lump, which is held between the head and front legs, and deposited a short distance away. *M. arvensis* will also remove soil from the nest by backing up the burrow using the abdomen to push the soil behind it. Soil debris usually accumulates at the nest entrance and periodically the wasp will get rid of this by backing out further than usual. A mound of debris often accumulates around the entrance of nests that are not located on steeply sloping ground, and this mound is usually scattered by wind or rain within twenty four hours. Mounds can persist for several days if the nest entrance is sheltered by the slope or surrounding plants and rocks. On one occasion only (at a small nesting aggregation at Nairn, ten miles west of Findhorn) was a wasp seen to dissipate a mound surrounding the nest entrance by walking backwards over the mound while dragging sand particles with its mandibles and fore legs. This was repeated several times, the wasp starting at, or very close to, the nest entrance and moving out towards the edge of the mound. A different direction from the

previous one was taken each time by the wasp. Such behaviour is complex in that the dissipation of the debris that forms the mound is carried out in a non random, efficient manner, indicating that this behaviour has evolved in response to some selection pressure. This in itself is not unusual as similar behaviour has been observed for several other species of sphecid wasp as a way to make nests less conspicuous to parasites (*Bembix alunga*, *B. atrifrons*, Evans et al. 1982). What is unexpected is that such apparently complex behaviour was only observed once out of more than 750 hours of observation, encompassing more than 200 different nesting individuals. Furthermore, such behaviour is not actually needed by the majority of wasps that nest on vertical surfaces where debris from nest excavation falls to the base of the bank. It is difficult to comprehend how this complex behaviour pattern evolved when it is superfluous to the needs of the majority of individuals, and why, having evolved, is it not observed more frequently in those wasps that do have a mound surrounding the nest entrance. One possibility is that wasps will only scatter the mound if the wind and rain do not do so first, and, in Britain at least, wasps will only carry out sand scattering behaviour if the mound persists for a period of time. A comparison of the incidence of this behaviour between populations in Britain with populations from sites in Europe where the dispersal agents of wind and rain are less severe would prove instructive on this point.

3.3.1 Time Taken to Dig a Nest

Unlike many other wasps (eg, > 2 days for *Philanthus triangulum*, Simon-Thomas & Simon-Thomas 1972; several days for *Philanthus bicinctus*, Gwynne 1981; 1-2 days for *Trypoxylon politum*, Brockmann 1980a; 2 days for *Cerceris cribrosa*, Elliott & Elliott 1987), the digging of a nest by *M. arvensis* was almost always completed relatively quickly and without interruption for feeding.

Because of the lack of interruptions it was possible to measure the time taken to dig a nest, assumed to start with the initial scraping at the ground surface and end with the time at which the wasp first appeared at the nest entrance prior to leaving the nest. Time for nest construction varied between individuals and populations (table 3.2). Wasps at Alderly Edge took a significantly longer time to dig a nest than wasps at St Cyrus (Alderly Edge 130 minutes; St Cyrus 76 minutes; $p = 0.003$, $t = 3.31$, d.f. = 21) or Findhorn (73 minutes; $p = 0.002$, $t = 3.59$, d.f. = 19). Variation between populations in the time taken to excavate a nest may be a result of differences in nest length, or may be due to environmental conditions such as soil structure and ease of penetration (see Chapter 4), soil moisture, or ambient temperature.

There is no correlation ($p > 0.4$) between the time taken to dig a burrow and the ambient temperature (figure 3.1). No nests were started when ambient temperature was below 19 °C, suggesting perhaps that at such ambient temperatures, temperatures inside the burrow are not high enough to permit digging behaviour. The duration of nest digging at ambient temperatures between 19.0 and 19.9 °C was low for all three observations recorded at this temperature. In these three cases the wasps might have been forced to cut short nest excavation due to low temperatures, and the recorded data would not therefore represent the time taken to fully excavate a burrow.

Unfortunately, no data on wasp body temperature while digging, or on burrow temperature, were obtained.

Due to this apparent temperature restriction, the cost in time for the completion of a single nest might be much greater than the actual time spent digging, as favourable temperatures for nest excavation may be brief or rare, delaying digging activity and therefore prolonging the time taken to complete a nest.

3.3.2 Nest Depth

Table 3.3 shows the mean depth of nests at the five primary sites. Nests at St Cyrus are the deepest of all sites, averaging 30 cm deep, and are significantly ($p < 0.05$) greater than the mean depth of nests at all other sites. Nests at Findhorn are the next deepest with a mean value of 23 cm, and are significantly deeper than nests at Alnmouth (mean depth = 18 cm; $p = 0.01$) and Alderly Edge (mean depth = 19 cm; $p = 0.023$), but not significantly different to the mean depth of nests at Thetford (21 cm). There are no significant differences between nest depths at Alderly Edge, Alnmouth and Thetford. Differences between sites might again be attributed to environmental factors such as soil moisture ^(Alcock & Khan 1973; Evans 1966; Brockmann 1980) with nests located in soils with high moisture retention being shallower than nests in drier sands (Linsley & MacSwain 1956; Hager & Kurczewski 1986), possibly because prey and larvae are susceptible to attack by fungus when humidity is high (Freeman 1982); or soil compaction or grain size which may prevent further deepening of the nest ^{* ~~Kistner 1953~~} (McCorquodale 1989a); or temperature, which, with increasing depth, might drop below the minimum temperature necessary to sustain wasp activity. The ease with which a soil can be penetrated by a wasp (soil hardness) might be expected to vary between soils of different characteristics, and the importance of this with respect to nest depth is discussed in Chapter 4.

The specific heat and thermal conductivity of soils vary greatly depending on soil moisture, porosity, organic matter, and density (Rosenberg 1974).

Therefore, a certain temperature will occur at different depths in different soil types. Nest depth between the different sites might vary according to the depth at which the critical minimum temperature required for wasp activity occurs. If this hypothesis is correct, the mean temperature at the bottom of

* Packard 1869; Peckham & Peckham 1898; Davis 1911; Hancock 1911; Law & Law 1918
Abbott 1931; Kistner 1953; Brockmann 1980.

nests should be similar among sites, and might represent the lower temperature limit for activity at which point wasps cannot continue digging.

Eight (5 in 1991, and 3 in 1992) wasps from St Cyrus, one from Alderly Edge (1992) and one from Alnmouth (1992) extended old burrows from the previous season rather than start new ones. This might be more likely to occur at sites where burrow entrances remain open throughout the winter season until the emergence of wasps the following year. Nests at Alnmouth, Findhorn and St Cyrus were located, on the whole, on vertical surfaces, and this may account for the fact that many entrances at these sites remained open to the following year. In contrast, nests at Alderly Edge and Thetford Warren were located on gradients that were only rarely in excess of 60° from the horizontal. A consequence of this is that nests became clogged and filled with debris from surface runoff. Additionally both Alderly Edge and Thetford Warren receive many human visitors who, by stepping on the nests, may cause the closure of many entrances before the start of the next wasp season.

A nest can also be used in a single season by two wasps consecutively. Where this occurs nest depth may exceed that expected as the second inhabitant extends the nest further into the ground. Fourteen nests being provisioned at St Cyrus on 19/6/92 were marked by pushing 11 cm nails into the sand above each nest. 44 days later one of these nests was being provisioned by a wasp. Due to the length of time between marking and observation (6 weeks & 2 days) and the average lifetime of an adult female *M. arvensis* in Britain (5 weeks, Paxton 1985) it is unlikely that the female provisioning the nest on 2/8/92 was the same as that observed on the earlier date. This is, however, the only occasion where a nest was assumed to be used by two individuals consecutively during the same season.

3.4 Temperature and Departure from Nests in the Morning

The first occasion on which wasps were seen at the beginning of each day was at the nest entrance, where they would remain, with only the head visible facing outwards, for several minutes before leaving the nest. During the day wasps were often seen pausing in such a position for variable periods of time (mean = 27 ± 2 seconds; range = 0 - 486 seconds; N = 457; data pooled from all sites and dates) before leaving the nest to resume foraging. These periods were significantly shorter than the first period of each day spent at the nest entrance (mean = 579 ± 98 seconds; range = 57 - 1333 seconds; N = 48; data pooled from all sites, $p < 0.001$, $t = 14.39$, d.f. = 503). The most likely function of sitting at the nest entrance, at least for the first time in the day, is behavioural thermoregulation, as nest entrance temperatures were always higher than ambient temperatures (table 3.4) and also, presumably, than the temperatures inside nests. When first emerging from the nest wasp body temperature is likely to be low since they are ectotherms (but see chapter 6), and the time required to warm up will be long, as the nest entrance temperature will also be low having as yet been exposed to the sun for only a short period. It is therefore not surprising, from a thermal viewpoint, that the first period of basking at the entrance is the longest. Later in the day when nest entrance and wasp body temperatures are higher, because of the warmer environment and heat generated from activity, basking periods at the nest do not need to be as long (section 3.9).

The soil surface at all sites attained a higher temperature excess over ambient than nest entrance temperature (table 3.4). Wasps basking on this surface would attain their required body heat more quickly than by basking at the nest entrance. Wasps were rarely seen basking on the sand and this was never observed in the morning at the time of first activity, though they were often

seen in this microhabitat while searching for, or digging, nests and while transporting prey to the nest. The nest entrance provides a certain amount of protection to the wasp, particularly in the cool mornings when they are least active and possibly most at risk from predators. A slight movement by the — observer at these times often resulted in the wasp rapidly backing down the burrow. Thus although nest entrance temperatures are lower than ground surface temperatures, wasps basking there do not risk predation.

The ambient temperature at which *M. ^{Spall}arvensis* was observed to leave the nest for the first time each day varied between 14 and 17 °C. Two female wasps at Alnmouth were caught outside the nest at 11 - 13 °C, but these individuals had very limited mobility, and no wasps at any site were seen flying or foraging at ambient temperatures below 14 °C. This was true irrespective of wasp size. Wasps caught as they emerged from the nest for the first time that day, at temperatures between 14 - 17 °C, had head width sizes ranging between 2.59 mm (Alnmouth) to 3.51 mm (Alderly Edge) (figure 3.2), and there was no correlation between ambient temperature at emergence and wasp size. However, there was a strong negative correlation between temperature at the nest entrance at first emergence and size ($p < 0.001$, $R^2 = 0.275$, $t = 4.267$, d.f. = 48, data taken from all sites) (figure 3.3) with the larger wasps of Alderly Edge emerging at lower nest entrance temperatures than wasps from St Cyrus. It therefore seems likely that time of emergence for a wasp is dependent on nest entrance temperature, rather than ambient temperature, with small wasps emerging at a higher nest entrance temperature than large wasps.

3.5 A Brief Outline of *M. arvensis* Foraging Behaviour

Upon completion of the nest, females begin to fill cells with prey for their offspring. Typically, a female sits at the nest entrance for a period of time and then leaves the nest in search of prey. Time spent away from the nest has been called foraging time, but includes searching for prey, location and handling of prey and transport of prey back to the nest, as well as periods of basking, feeding, or interactions with conspecifics. *M. arvensis* catch a wide variety of Diptera as provisions for the larvae and for their own nutrition (Thornley 1932; Huber 1961; and Chapter 4). *M. arvensis* carry a prey item underneath the body using the mandibles to grip the proboscis, and the first pair of legs to provide additional support. Upon returning to the nest the wasp lands at the entrance, turns around and enters the nest backwards, dragging the prey behind it. ^{(fig 3.4)?} When carrying large prey wasps would often land at the bottom of the slope below the nest and walk to the nest entrance with the prey still held by the proboscis underneath the body of the wasp. While inside the nest females presumably manipulate prey into the correct position in the cell, oviposit, excavate the tunnel, or eject intruders and parasites.

3.5.1 Hunting Site Fidelity

Although *M. arvensis* females prey upon a very wide range of Diptera species, individuals often returned with flies of the same genus, or even the same species, on several consecutive foraging trips. Observation of marked individuals revealed that *M. arvensis* would often return to the same flower patch or dung heap on each foraging trip. It seems likely that rather than specialising on a particular prey type females would simply catch the flies that were most commonly found at their preferred hunting site. One female (at Findhorn) caught three dung flies, *Scatophaga stercoraria*, at the same dog

Change subsequent fig. nos.

faeces, at intervals of 12 and 8 minutes between the first and second captures and the second and third captures respectively. Another female, hunting on a boulder at Alderly Edge, caught two bluebottles (*Calliphora vomitoria*) with an interval of 22 minutes between the prey captures. A further female also at Alderly Edge, searching among heather, caught three greenbottles (*Lucilia caesar*) at intervals of 9 and 18 minutes between captures. All the marked females observed at the foraging site had been marked at the nesting site on an earlier date.

Six females were caught and marked at a foraging site (a patch of heather at Alderly Edge) in an attempt to collect more data on this subject, but none of these females were seen again at the foraging site. This may be taken as evidence against fidelity to a foraging site, but a frequent problem, encountered again when marking usurpers (Chapter 5), was that marked females were rarely seen again at the same site for several hours after marking.

Evidence to suggest that wasps remember and return to the site of prey capture for additional prey exists for other sphecid species (*Bembix* sp., Evans & West Eberhard 1973; *Philanthus crabroniformis*, Alcock 1974; *Sphex ichneumoneus*, Brockmann 1985a; *Bembix rostrata*, personal observation).

3.6 An Analysis of Foraging Time

In table 3.5, foraging times, obtained over several days observation at each site, are shown. There are apparent differences between the means, but the only significant difference is between the sites Alderly Edge (26.0 minutes) and Alnmouth (16.7 minutes). The differences between Alderly Edge and St Cyrus (22.0 minutes), and Alderly Edge and Findhorn (19.6 minutes)

approach significance ($p = 0.062$ and 0.074). The longer foraging times at Alderly Edge may be due to fluctuations in local prey abundance, resulting in longer search times, or to climatic conditions, affecting the flying ability and speed of movement of wasps and prey. Owing to difficulties in accurately estimating prey abundance (see Chapter 4), it was not possible to collect data to test this factor, although local prey availability has been suggested to be a factor in determining the time spent on foraging trips (eg, *Tachysphex antennatus*, Kurczewski & Kurczewski 1987).

There is much variation of foraging time between individuals within populations (table 3.5). This variation may result from daily fluctuations in climate and prey availability for data collected at the same site but on different days. The size of prey caught, and the size of the wasp, will be factors in determining the handling time of prey capture and transport. Large prey might require more time and effort to subdue, and carry back to the nest. If wasp size is associated with stronger flight, large wasps would have shorter foraging times, being able to return to the nest with prey faster than a small wasp. A large wasp would also be able to catch flies that are beyond the upper size limit of other, smaller wasps; hence there is a greater range of prey items available to the large wasp.

3.6.1 Prey Size and Foraging Time

The size of prey caught by each wasp was classified into one of three categories, small, medium and large (see Chapter 2). In table 3.6, foraging times are separated according to prey size categories. Due to the division of the prey into three size categories, only data sets from Alderly Edge and St Cyrus, where the sample sizes are large, have been considered in this analysis. There are differences in foraging times for the different prey size

categories at St Cyrus but these are much less clear for *M. arvensis* at Alderly Edge.

Wasps at all sites were frequently seen to have difficulty in transporting and carrying large prey items when returning to the nest. In contrast wasps carrying small prey often flew directly to the nest entrance with little delay. Therefore the foraging times observed for wasps at St Cyrus are probably, in part, a consequence of the ease with which prey of differing sizes are provisioned. Small prey, being lighter in weight, could be carried in extended flights directly to the nest entrance. Larger prey were carried in a series of short flights, while the largest prey items were dragged over the ground with the wasp's wings being used for additional lift without actually achieving flight.

It is likely that the differences in foraging time between wasp prey size classes are particularly noticeable at St Cyrus because the wasp size to prey size ratio at this site is low (wasps at St Cyrus have a mean head width of 2.87 mm, and are smaller than wasps at Alderly Edge, which have a mean head width of 3.32 mm, see Chapter 4); hence the same prey item would be relatively larger to a wasp from St Cyrus as compared to a wasp from Alderly Edge. To a large wasp, there may be little difference between small and medium prey, in terms of time and effort needed for prey carriage. Thus larger wasps at Alderly Edge may be able to carry small and medium prey in one extended flight, but larger prey require more effort, and this is reflected in the increase of foraging times between the medium and large prey size categories. The wasps of St Cyrus, due to their small size, may need a relatively greater effort to return to the nest when laden with medium sized prey, and an even greater effort when carrying large prey. This, in turn, is reflected in the increase of foraging time between small-medium and medium-large prey categories (table 3.6).

Wasp size of *Clypeadon laticinctus* (Alexander 1986) was found to be positively correlated with provisioning rate, although no explanation was suggested.

Large prey may take longer to subdue than small prey which may add to the differences observed in table 3.6. Unfortunately, *M. arvensis* were rarely seen catching prey and consequently I have no data on this subject.

If large prey do require more time to subdue or transport to the nest, the difference between mean foraging times of Alderly Edge and St Cyrus may be explained by suggesting that wasps at Alderly Edge catch relatively larger flies than wasps at St Cyrus. A difference in the size of prey caught might be a result of differences in wasp size, large wasps preferentially catching relatively large prey, or a consequence of the abundance of flies of different sizes in the habitat, for example wasps at Alderly Edge may be forced to catch large flies because of a scarcity of small flies. Both these ideas are investigated in Chapter 4.

3.6.2 Prey Capture Rates and the Amount of Time Spent Foraging

The frequencies at which prey of different sizes (small, medium and large) were taken, and the rate of prey capture (which includes prey of all sizes) have been calculated (table 3.7). Wasps from Alnmouth have the fastest rate of prey capture (1.17 flies/hour of observation), and wasps from Alderly Edge have the lowest rate (0.73 flies/hr). This, in part, reflects the longer foraging times of wasps at Alderly Edge for all prey size classes (table 3.6).

A greater frequency of small flies are taken by wasps at St Cyrus (31%; mean dry weight of prey = 4.99 ± 0.16 mg, N = 431), Findhorn (39 %; no data for prey weight), and Alnmouth (50 %; mean dry weight of prey = 3.00 ± 0.27 mg,

N = 40), compared to wasps at Alderly Edge (8.9%^{space}; mean dry weight of prey = 12.79 ± 0.74 mg, N = 105) and Thetford (9.4%^{space}; mean dry weight of prey = 8.25 ± 0.49 mg, N = 81). As small prey are associated with shorter foraging trips, higher rates of prey capture are expected at sites where wasps catch smaller prey. Whether large prey are actively sought by *M. arvensis* females at Alderly Edge, or whether the frequencies observed are due to a naturally occurring greater abundance of larger flies is considered elsewhere (Chapter 4).

The total amount of time devoted to foraging behaviour (table 3.8), as opposed to other behaviours such as digging nests, basking and feeding, will also be an important factor in the consideration of prey capture rates. Rates of prey capture are a result of the mean time taken to catch each prey item (foraging time) and the amount of time devoted to foraging activity. The high rate of prey capture at St Cyrus (1.12 flies/hour) can be partially explained by the short mean foraging time observed at this site, and also by the relatively large amount of time devoted to foraging (40.9 %). Wasps at Alderly Edge devote the least amount of time to foraging (31.6 %) and take, on average, the longest time to catch prey. *M. arvensis* from Thetford have a short mean foraging time (20.77 minutes) but the rate of prey capture is lower than that of St Cyrus as only 35.2%^{space} of their time is spent foraging. The same is true of wasps at Alnmouth which have very short foraging trips (mean = 16.7 minutes) but only spend 32.6 % of their time foraging, resulting in a prey capture rate (1.17 flies/hour) only slightly higher than that of wasps from St Cyrus (1.12 flies/hour).

The amount of time devoted to foraging activity is dependent on environmental and biological factors. Climate will certainly be of importance, determining the amount of time in a day that wasps can undertake activity of

any kind. All the data presented in this section are based upon periods of observation when wasps were active, and thus when temperature was high enough to allow wasp activity. However, wasps might spend a greater proportion of time foraging when the temperature is high, allowing rapid movements and efficient flight needed for prey capture and transport. During cooler periods, wasps might remain at the nest entrance or on the ground in order to raise body temperature. Therefore it might be expected that the proportion of time spent foraging might be greater at southern sites, which are generally warmer, (Chapter 4, figure 4.2), as compared to northern, cooler sites. There is no such latitudinal trend in the proportion of time spent foraging (figure 3.4, $t = 0.944$, d.f. = 3, $p > 0.4$) suggesting either that climate is not an important cause of the variation, or that there is an adaptive trend in some other trait to compensate for the effects of climate. It is worth noting though, that the behavioural data on wasps from the population at Alnmouth were collected in the month of September (1992), while data from all other sites were obtained over several months (June to September for Findhorn and St Cyrus, and July to October for Alderly Edge and Thetford). September is a cooler month than June, July or August, and the low percentage of time spent foraging, compared to other sites, may be a result of these cooler temperatures. Furthermore, the length of periods on which data were collected varied among sites. Observations at St Cyrus and Alderly Edge were over a period of several weeks in the years 1990 - 1992; observations at Findhorn for four weeks in 1990 and three weeks in 1992; observations at Alnmouth for three weeks in 1992; and observations at Thetford for four weeks in 1992.

Due to variation in soil hardness between sites, wasps at some sites take longer to dig the nest than wasps at other sites (section 3.3.1). Other environmental variables such as the amount of space suitable for nesting

sites, or the frequency of disturbance, will influence the amount of time that is spent on activities other than foraging, such as nest building and upkeep, basking and feeding.

In addition to limitations imposed by the environment, there may be biological, and even adaptive reasons for the differences in the amount of time spent foraging. Variations in population density and parasite pressure between sites might cause differences in the amount of time set aside by each wasp for nest defense against intra- and inter-specific parasitism. Male *M. arvensis* were frequently seen pouncing upon nesting females, interrupting the latter's activity by up to several minutes (personal observation). Where male density is high, interruptions can be frequent (one female was pounced upon by males six times in 51 minutes), reducing the time available for other activities such as foraging.

Differences in climate cannot explain the differences in the proportion of time spent foraging between wasps from different sites, there being no significant correlation between this variable and latitude. A small amount of the variation will be due to differences between sites in the mean time taken to dig a nest, which is dependent on various environmental factors. These differences are not substantial enough to account for all the variation, some of which might be attributed to biological factors such as nest defense. The amount of time devoted to other behaviours, and the biological factors involved in determining this, are discussed in Chapter 5.

3.6.3 Ambient Temperature and Foraging Times

As ambient temperature increases, the duration of foraging trips decreases (data pooled from all sites), this being true for each prey size category (figures

3.5 - 3.7). This trend is significant for small ($t = 2.453$, d.f. = 90, $p = 0.02$) and medium ($t = 3.145$, d.f. = 111, $p = 0.01$) prey categories, and nearly so for large prey ($t = 1.842$, d.f. = 48, $p = 0.1$). As environmental temperature increases, temperate insects, including *M. arvensis*, become more active (Linsley & MacSwain 1956). Wasps can maintain higher body temperatures, increasing speed of flight and movement, and reducing flight times. As the prey become more active and abundant at higher temperatures, the number of encounters between wasps and flies will rise. This will reduce the time spent searching for prey, an important component of foraging time. However, as flies will become more rapid in movement, their chances of escape will be greater, which will act to decrease the rate of successful prey captures, and increase the length of wasp foraging trips.

The time of day has been suggested to be a factor that might be important in determining the length of foraging trips (eg, *Trypoxylon figulus*, Bristowe 1948). There is a significant decrease in foraging trip length with increasing time of day for *M. arvensis* ($p = 0.001$, $t = 3.42$, d.f. = 153; data from St Cyrus, medium sized prey only). However, a multiple regression of foraging time against temperature and time of day shows that temperature is the most important factor ($p < 0.001$, $t = 4.01$, d.f. = 153). After accounting for temperature the time of day still has a significant effect, foraging times decreasing with increasing time of day ($p = 0.038$, $t = 2.10$, d.f. = 153). It might be that wasp foraging time decreased as wasps gained experience from previous trips (Bristowe 1948; Linsley & MacSwain 1956). It has been observed that wasps are likely to return from several consecutive foraging trips with similar prey, indicating that they either develop a search pattern for a particular prey item (O'Brien et al. 1990), or that they repeatedly return to a particular hunting location where flies are presumably abundant (section 3.5.1). During the course of the day it might be expected that more and more

females find good sites at which to forage or become more efficient at locating, handling and returning with prey. In either case foraging times will decrease through the reduction of search times. A study of *Cerceris californica* (Linsley & MacSwain 1956) revealed no correlation between time of day and foraging time but there was a correlation between the length of foraging trips and the number of cells previously provisioned, suggesting that the experience gained from previous trips is used to reduce foraging times.

3.7 Time Spent in the Nest

Without the facilities to observe wasp behaviour inside the nest it is impossible to describe wasp activity beyond the burrow entrance. However, from observations of *M. arvensis* outside the nest, and from nest excavations, it is clear that prey taken into the nest are placed into a cell, that a single egg is laid upon the provisions, and that new cells are dug at intervals. In the majority (83%) of cases the time spent inside the nest between each foraging trip was brief (6 - 486 seconds) and probably involved no more than manipulating the prey into its correct position in the cell and possibly laying an egg on the provisions. Prolonged periods inside the burrow were usually associated with digging activity and encounters with intruding male or female conspecifics. After intruders were ejected from the nest the resident female would often remain in the nest for several minutes before appearing at the entrance.

There is no significant difference in the mean time spent inside the nest by wasps from each of the four sites from which data were collected (table 3.11; $p = 0.569$, $F = 0.67$, d.f. = 414). For this reason the data from all the sites have been pooled for the following analyses of the influence of wasp and prey size on the time spent inside the nest.

Two factors that may determine the time spent in the nest are prey size, large prey being more bulky and therefore requiring longer handling times; and wasp size, large wasps being able to handle prey items more quickly and efficiently, thereby reducing handling times. Figure 3.8 shows the mean time spent in the nest of the six possible combinations of wasp and prey size categories. Head width was used as the wasp size parameter: head widths less than 3.00 mm were defined as small; head widths between 3.00 - 3.20 mm were defined as medium; and wasps with head widths greater than 3.20 mm were considered large. Thus the category, Sw Mp, includes all small sized wasps carrying medium sized prey, and the category, Lw Sp, includes large wasps provisioning small prey. To maintain a statistically independent sample, thus avoiding individual biases, no more than one result, selected randomly, from each wasp was used.

There are trends, albeit non significant, of increasing mean time spent in the nest with increasing prey size, and with decreasing wasp size. Figure 3.9 plots the measured wasp head width against time in the nest. There is no significant relationship between these two variables ($t = 0.92$, d.f. = 105, $p > 0.2$), and less than one percent of the variance is explained by the correlation coefficient. Therefore, neither prey size nor wasp size, when considered alone, can account for the variation in the time spent inside the nest.

In figure 3.10, both wasp and prey size are considered together, each category being defined by wasp size and the size of the prey that the wasp was carrying. Large and small wasps show an increase in the time spent in the nest as prey size increases (although no small wasps carrying large prey were seen, so this category has been omitted). Medium sized wasps carrying small prey spend less time in the nest than wasps of similar size carrying medium or large prey. These categories can be rearranged in order of the time that

wasps might be expected to spend in the nest, on the basis of wasp and prey size. Thus a large wasp carrying a small fly would be expected to have the shortest handling time, while a small wasp carrying a large fly (if this ever happened) would be expected to spend the longest time in the nest. In order of increasing time spent in the nest, the categories would be sorted as follows: Lw Sp; Mw Sp = Lw Mp; Lw Lp = Mw Mp = Sw Sp; Mw Lp = Sw Mp. The observed results match, reasonably well, the expected order of the categories (figure 3.11), indicating that both prey and wasp size when taken together can explain some of the variability. Large wasps that are carrying small prey items spend the least amount of time in the nest, presumably because they have little difficulty in transporting and stocking such small flies. In contrast, wasps carrying prey of a size category larger than their own (although this does not mean that the prey is larger than the wasp as the wasp and prey categories are not defined using the same parameters) spend a long time in the nest, indicating that they might have some difficulty in handling these relatively large prey items. Wasps carrying prey items from the same size category show a trend of increasing time spent in the nest with increasing wasp and prey size, although these differences are unlikely to be significant from each other as indicated by the overlapping standard error bars (representing 1 S.E.). As some categories are considered equal in ranking, the data from these may be pooled into four groups. When the data from these groups are plotted (figure 3.12), there is a significant ($p = 0.023$, $F = 3.31$, d.f. = 3) trend that follows the predicted pattern of increasing time spent in the nest being with decreasing wasp, and increasing prey, size. It is likely that these differences will account for only a minor part of difference between the populations in the proportion of time spent foraging for prey (table 3.8) because the size of most prey taken by wasps is similar to their own body size (see Chapter 4) and differences in body size between populations will therefore not result in differences between the times taken to stock prey items.

Indeed a comparison between the mean time spent inside the nest after a foraging trip between two populations confirms this point, there being no significant differences (table 3.9).

Another variable, on which no data were collected, but which might affect the time spent in the nest is the depth of the nest, deeper nests presenting longer journeys to the wasps and so increasing the time needed to stock the prey. Data are available for mean nest depths from a sample of randomly selected burrows for each site (table 3.3), but the results do not show any relation to the mean time spent in the nest at these sites.

3.8 Time Spent at the Nest Entrance

It has been suggested that wasps pause at the nest entrance for reasons relating to thermoregulatory control (Willmer 1985a, Paxton 1985, and section 3.4). Burrow architecture does indeed result in an entrance temperature greater than ambient temperature, mean temperature excess varying between 1.6 °C and 8.6 °C between different sites (table 3.4), and wasps might use this microclimate to raise body temperature behaviourally. At low ambient temperatures wasps would be expected to spend more time at the nest entrance to achieve optimal body temperature for activity, whereas at high ambient temperatures shorter basking times would be needed, due to (probably) higher initial body temperatures and (certainly) faster warm up rates (Whitman 1988; O'Neill et al. 1990).

Ambient temperature (T_a) and time spent at the nest entrance are correlated ($t = 3.294$, d.f. = 225, $p < 0.01$) at St Cyrus, but the data could be misleading as there are only three results between 24.0 and 26.0 °C, the upper end of the temperature range (figure 3.13). Removal of these three results, however, does

not alter the trend or significance ($t = 3.234$, d.f. = 222, $p < 0.01$). Nest entrance temperature (T_e) is also correlated with the time for which wasps from the St Cyrus population remained at the entrance, after stocking a prey item (figure 3.14; $t = 2.103$, d.f. = 112, $p < 0.02$). However, this significance is lost upon removal of the single outlying result obtained at the lowest temperature ($t = 0.474$, d.f. = 111, $p > 0.5$).

M. arvensis females at Alderly Edge spend, on average, twice the amount of time at the nest entrance ^($\bar{x} = 42.0 \pm 6.1$; $0 - 486$; $N = 117$) as do females at St Cyrus ^(20.51 ± 1.8 ; $0 - 261$; $N = 237$) (data do not include periods at the nest entrance at first emergence in the morning). This highly significant difference ($t = 4.30$, d.f. = 352, $p < 0.001$) is the only significant difference observed between populations for this variable (table 3.11) and cannot be explained by responses to temperature, as neither T_a nor T_e are correlated with the time spent at the nest entrance by wasps at Alderly Edge (T_a : $p = 0.4$, $t = 0.963$, d.f. = 115; T_e : $p = 0.9$, $t = 0.013$, d.f. = 19). The absence of significant differences in other inter-population comparisons may be due to small sample sizes.

Wasps might remain at the nest entrance for reasons other than thermoregulation, one possibility being nest defense against conspecifics. Wasps were often seen at nest entrances, apparently about to leave, when approaching males or females caused them to retreat a short distance (typically 1 - 2 cm) into the burrow. Alternatively, upon the approach of a conspecific, a female at a nest entrance would orientate herself towards the approaching insect, watching but remaining motionless. When the wasp advanced to within about one body length of the nest entrance, the resident female would lunge at it and then return to the nest. Similar aggressive encounters were noticed between males and females. The frequency of all these encounters, and the amount of wasp activity in the vicinity of the nest,

may prolong the time spent at the entrance beyond what might otherwise be expected on the basis of thermoregulation alone. Where there is much activity, particularly of conspecifics, about the nesting site, time spent at the nest entrance by wasps is expected to be greater than in nesting areas with less activity. Overall activity is therefore expected to be greatest at Alderly Edge, the site at which female *M. arvensis* spend most time at the nest entrance. Aggressive behaviour, and how it relates to behavioural differences between wasps from different populations, are the subjects of Chapter 5 (but also see section 3.10, below).

The presence of an observer cannot be ruled out as a confounding factor in determining time of stays at nest entrances, as wasps might well have behaved differently due to my presence a few metres away from the nest. On a number of occasions my very slight movements were sufficient to cause the wasp to retreat into the burrow. It is possible that this same effect might also have extended the duration for which the wasp remained at the entrance. In the absence of any movement by the wasp it was impossible to judge whether the presence of the observer was a source of error.

3.9 The Pattern of *M. arvensis* Activity and Male Behaviour

The amount of male activity at the nesting site was measured on eleven days at St Cyrus (early August 1992) and seven days at Alderly Edge (mid September 1992). The number of wasps seen moving were counted within an area of the nesting site measuring 50 x 50 centimetres (0.25 m²). This was done for a period of one minute at intervals of twenty minutes, taking care not to count the same individual twice.

A similar pattern of male activity was observed at both sites (figure 3.15), with a rapid increase in the number of active males between 0800 and 1000, reaching a peak of about 5 males at St Cyrus and 7 males at Alderly Edge. This was followed by a gradual decline in the number of males seen at the nesting site, starting about 1100. After 1300 the number of males counted averaged between one and two. Because activity was measured by counting the number of individuals seen at the nesting site, it is not a measure of activity at other locations within the habitat. The apparent decline in male activity may simply reflect a shifting of the location of activity from the nesting site to the foraging site. Such a switch has been recorded for *Bembecinus quinquespinosus* (O'Neill & Evans 1983).

High male activity at the nesting site in the morning may be a strategy to intercept virgin females emerging from their natal nests or searching for a suitable nesting site. It has been noted for several species, including *Mellinus arvensis*, that virgin females emerging from their natal nests tend to do so in the morning rather than the afternoon (Huber 1961).

Males searched for females at the nesting site, often reacting aggressively towards other males encountered, although no territorial behaviour was observed. They were also seen to perform 'sundance' flights (Rau & Rau 1918) at prominent bushes or small trees within the foraging area. They often entered tunnels and were frequently seen at nest entrances but were ejected upon the return of the resident female. Males used visual cues to detect females over long distances and frequently mistook other males and even small dark inanimate objects for females. Males did not seem to be able to distinguish between receptive and unreceptive females, as they were frequently rejected by females which they had attempted to mount. Upon location of a female, the male would pounce upon the females back and

attempt to copulate. Such activity often attracted other males, frequently resulting in a mating cluster with up to four males attempting to couple with a single female. Mating clusters could persist for several minutes and ended only when the female escaped alone or when a male succeeded in coupling with her. Similar male mating behaviour has been observed in *Bembecinus quinquespinosus* (O'Neill & Evans 1983) and *Bembix rostrata* (Larsson 1989a; this thesis). In these species large males seem to have a competitive advantage in mating clusters. It was not possible to ascertain whether this was true for *M. arvensis*.

3.10 The Pattern of Female Activity, and Temperature as a Controlling Factor

There is little difference between Alderly Edge and St Cyrus in female activity (figure 3.16), measured in the same way as male activity. Activity gradually increases between 0800 and 1000, but there is little change beyond this time, with the average number of females never exceeding three wasps. Unlike the male activity pattern, females maintain the level of activity until 1700, after which there is a rapid decline with very little activity observed beyond 1800.

The gradual increase of mean female activity in the morning reflects an increase in mean ambient temperature (figures 3.17 & 3.18). There is little doubt that female wasp activity is dependent upon temperature, and when mean temperature is plotted against mean activity for each 20 minute interval (figures 3.19 & 3.20) the correlation between the two factors is high (St Cyrus: $t = 4.631$, d.f. = 26, $p = 0.001$; Alderly Edge: $t = 5.265$, d.f. = 26, $p = 0.001$). The increase in the number of wasps seen at high temperatures might be due to more wasps becoming active at these higher temperatures, or to an increase in the speed at which wasps move, increasing the rate of prey capture, and

therefore the number of visits to the nest, the measure of wasp activity. The upper temperature limit for activity of *Mellinus arvensis*, that is the temperature at which wasp activity ceases due to risk of overheating, is probably never, or very rarely, reached in Britain, and no decline in activity was observed at the highest temperatures, as has been observed with other sphecids (*Cerceris arenaria*, Willmer 1985a; *Bembix rostrata*, Larsson 1989a) and apooid species (Schaffer et al. 1979).

The number of active females is similar at Alderly Edge and St Cyrus (figure 3.16), although the number of nests enclosed within the 0.25 m² of nesting area (from which the data were collected) were different, the mean number of nests at St Cyrus being 37, and at Alderly Edge, 21. Therefore, the number of active females at St Cyrus is relatively low when the number of nests in the study area is taken into account (figure 3.21). Much of the observed activity may be due to females that were not nesting in the study area. There were many wasps flying over the nesting aggregations that were apparently without nests (Chapter 5), and these were included in the activity counts although unfortunately not distinguished from nesting females. These data might be explained by postulating a greater frequency of non-nesting females at Alderly Edge, which would increase the activity observed independently of nest number.

Non-nesting females account for much of the aggression between wasps at nest entrances (personal observation, see section 3.8). At Alderly Edge, where there are relatively few nests but similar wasp numbers, aggressive interactions may be more common, leading to an increase in the time spent at the nest entrance by nest owners, as predicted in section 3.8.

3.11 Discussion

There seem to be many differences in nesting and foraging behaviour between populations of *M. arvensis*. In Britain, activity in the north begins earlier in the year (late June/July) than in southern populations (early August) and also ends earlier, resulting in a season of 10 - 13 weeks. Variations in nest depth, and the time taken to dig a nest, exist between some populations, and this might be ascribed to temperature and other environmental factors such as soil moisture and hardness. Wasp size and the size of the prey taken by wasps can, to some extent, explain the differences in length of the foraging time and the time spent in the nest.

Not all of the variation between sites, such as differences in time devoted to foraging and the amount of activity in the nest vicinity, can be explained by environmental factors. The next chapter describes variation in body size between wasps from different populations, and discusses body size as being a cause (or consequence) of variations in the nesting and foraging behaviour of wasps.

While observing a nesting aggregation many non-nesting wasps were seen to investigate and enter nests, occasionally resulting in aggressive encounters between these "searchers" and the nest owners. So two alternative nesting strategies might be used by females: the first being that of "nesters", which dig and provision a nest, the subjects of this chapter; the other being that of searchers, which search for, enter, and subsequently use a burrow that may or may not be already occupied by another wasp. Differences in the behavioural ecology of wasps from several populations might be due the relative rates of success of these two nesting strategies at different sites, and this is the subject of chapter 5.

Thus differences in morphology, behaviour and edaphic factors will be investigated in an attempt to discover the underlying cause that might account for all variation between populations.

Table 3.1a The estimated date of the start of adult *M. arvensis* activity at four sites, (no data available for Alnmouth).

| Site | Season | Estimated Date of First Emergence * |
|--------------|--------|-------------------------------------|
| St Cyrus | 1991 | July, Wk 1 |
| St Cyrus | 1992 | June, Wk 3 |
| Findhorn | 1992 | July, Wk 1 |
| Alderly Edge | 1991 | August, Wk 1 |
| Alderly Edge | 1992 | July, Wk 4 |
| Thetford | 1992 | July, Wk 4 |

* Dates are estimates based on the first sightings of males (which are protandrous) and the number and behaviour of females. The presence of only a few females that have not yet started nest excavation or provisioning indicates the start of female activity.

Table 3.1b The estimated date of the end of adult *M. arvensis* activity.

| Site | Season | Estimated End of Season * | Length of Season (weeks) |
|--------------|--------|---------------------------|--------------------------|
| St Cyrus | 1990 | September, Wk 1 | - |
| St Cyrus | 1991 | September, Wk 1 | 10 |
| Findhorn | 1990 | September, Wk 2 | 11 |
| Alderly Edge | 1990 | October, Wk 2 | - |
| Alderly Edge | 1991 | October, Wk 3 | 12 |
| Alderly Edge | 1992 | October, Wk 3 | 13 |
| Thetford | 1992 | October, Wk 2 | 12 |
| Alnmouth | 1992 | September, Wk 3 | - |

* The end of the season was taken to be the last week on which wasp activity was observed.

(in minutes)

Table 3.2 The mean time taken for nest construction by wasps from four sites, (no data available for Alnmouth).

| <u>Site</u> | <u>Mean</u> | <u>S.E.</u> | <u>Range</u> | <u>N</u> |
|-------------|-------------------|-------------|--------------|----------|
| Alderly | 129.7 (\pm Se) | 14.1 | 84 - 211 | 10 |
| Thetford | 96.9 | 11.0 | 60 - 144 | 7 |
| St Cyrus | 75.9 | 9.2 | 38 - 145 | 13 |
| Findhorn | 72.7 | 8.0 | 41 - 134 | 11 |

Table 3.3 Depth and temperature of nests at different sites.

| <u>Site</u> | <u>Mean Depth</u> cm (\pm SE) | <u>Mean Nest Temp.</u> °C (\pm SE) | <u>N</u> |
|-------------|-------------------------------------|--|----------|
| Alnmouth | 18.25 (\pm 1.15) | 13.11 (\pm 0.33) | 20 |
| Thetford | 20.80 (\pm 2.06) | 17.90 (\pm 0.42) | 5 |
| Alderly | 19.10 (\pm 0.97) | 16.93 (\pm 0.37) | 21 |
| St Cyrus | 29.77 (\pm 1.34) | 19.11 (\pm 0.15) | 40 |
| Findhorn | 22.70 (\pm 1.18) | no data | 20 |

change to } Mean Ambient temp. (T_a), nest entrance temp. (T_e) & ground surface temp. (T_g) & the mean temp. excess of T_e & T_g over T_a .

Table 3.4 Mean temperature excess of nest entrance (T_e) and ground surface (T_g) above ambient temperature (T_a).

| Site | T_a | T_e | T_g | T_e excess | T_g excess |
|--------------|-------------------|-------------------|-------------------|------------------|-------------------|
| Findhorn | 22.3 (\pm 0.5) | 31.4 (\pm 0.8) | 32.7 (\pm 1.0) | 8.6 (\pm 0.7) | 10.4 (\pm 0.7) |
| St Cyrus | 19.6 (\pm 0.2) | 26.4 (\pm 0.4) | 33.1 (\pm 0.7) | 6.7 (\pm 0.3) | 13.4 (\pm 0.5) |
| Alderly Edge | 20.0 (\pm 0.2) | 22.4 (\pm 0.4) | 23.5 (\pm 0.4) | 2.4 (\pm 0.4) | 3.5 (\pm 0.4) |
| Thetford | 19.0 (\pm 0.3) | 20.6 (\pm 0.2) | 26.7 (\pm 0.8) | 1.6 (\pm 0.2) | 6.1 (\pm 0.7) |
| Findhorn* | 19.3 (\pm 0.3) | 29.5 (\pm 0.7) | 26.8 (\pm 0.6) | 9.7 (\pm 0.6) | 7.4 (\pm 0.5) |

Although the climatic conditions under which these data were collected varied from day to day and between sites, because the sample sizes from each site were large (see below), variation due to factors such as insolation, wind and humidity was considered equal between sites.

Sample size for temperature data collected from each site.

| | <u>T_a</u> | <u>T_e</u> | <u>T_g</u> |
|--------------|-------------------------|-------------------------|-------------------------|
| Findhorn | 65 | 61 | 44 |
| St Cyrus | 116 | 109 | 113 |
| Alderly Edge | 144 | 142 | 134 |
| Thetford | 80 | 80 | 70 |

* Because the mean ambient temperature at Findhorn was a few degrees higher than at the other sites, the data for T_e and T_g at Findhorn could not be directly compared with data from other sites. Therefore, a sub-sample ($N = 16$) of the Findhorn sample was taken, and included all data where $18.0\text{ }^\circ\text{C} \leq T_a \leq 21.0\text{ }^\circ\text{C}$. Mean values of T_e , T_g and T_e and T_g excesses were calculated for this sub-sample, enabling a comparison between these data and similar data obtained at other sites.

Table 3.5 Mean length of foraging trips (per prey item) of wasps from five populations.

| <u>Site</u> | <u>Mean (\pm SE)</u> (minutes) | <u>Range</u> (minutes) | <u>N</u> |
|--------------|--|---------------------------|----------|
| Alnmouth | 16.70 (\pm 1.75) ^{1.26} | 2 - 56 | 40 |
| Findhorn | 19.59 (\pm 2.38) ^{1.79} | 2 - 67 | 34 |
| Thetford | 20.77 (\pm 2.64) | 3 - 59 | 26 |
| St Cyrus | 21.90 (\pm 1.15) | 1 - 120 | 355 |
| Alderly Edge | 26.02 (\pm 1.45) | 2 - 86 | 185 |

Significance between sites:

| <u>Site Comparison</u> | <u>Significance</u> | <u>t value</u> | <u>degrees of freedom</u> |
|------------------------|---------------------|-----------------|---------------------------|
| St Cyrus-Alderly | 0.062 | 1.87 | 474 |
| St Cyrus-Thetford | 0.800 | 0.25 | 376 |
| Alderly-Thetford | 0.194 | 1.31 | 148 |

what about Alnmouth & Findhorn. - need ANOVA & Tukey's

ANOVA (statworks: hilensme = forage Stats. all sites 9/92)

$$F = 2.63 \quad p = 0.034 \quad df = 4, 626, 639$$

| <u>t test</u> | | <u>p</u> | | |
|-----------------|--|---------------|------|-----|
| Alc : find. | | 0.065 | 1.85 | 217 |
| Alc : Alnmouth | | 0.004 | 2.94 | 223 |
| St.C : find. | | 0.539 | 0.61 | 387 |
| St.C : Alnmouth | | 0.134 | 1.50 | 393 |
| Thet : f | | 0.703 | 0.38 | 458 |
| Thet : Alnm. | | 0.128 | 1.54 | 64 |
| find : Alnmouth | | 1.35 0.182 | 1.35 | 372 |

Table 3.6 Mean foraging trip lengths for prey items from three size classes.

| | <u>Small</u> | <u>Medium</u> | <u>Large</u> |
|--------------|---|---|---|
| St Cyrus | 17.02 (^{space} ± 1.72) | 23.04 (^S ± 1.62) | 31.11 (^S ± 3.74) |
| Alderly Edge | 25.88 (^S ± 5.11) | 25.19 (^S ± 1.65) | 31.12 (^S ± 3.65) |

Foraging times in minutes (\pm standard error).

Table 3.7 The frequency of prey sizes caught by wasps from four sites (%), and prey capture rate.

| | <u>Small</u> | <u>Medium</u> | <u>Large</u> | <u>Prey No.</u> | <u>Hours</u> | <u>Rate</u> |
|----------|--------------|---------------|--------------|-----------------|--------------|-------------|
| Alderly | 8.9 | 75.9 | 15.2 | 270 | 369 | 0.73 |
| St Cyrus | 31.6 | 53.1 | 15.4 | 605 | 542 | 1.12 |
| Thetford | 9.4 | 71.7 | 18.9 | 53 | 52 | 1.02 |
| Findhorn | 39.1 | 52.7 | 8.1 | 74 | 68 | 1.09 |
| Alnmouth | 50.7 | 47.8 | 1.4 | 69 | 59 | 1.17 |

"Prey No.", is the total number of flies caught by all the wasps being observed.

"Hours", is the total hours of nest observation.

"Rate", is the mean number of prey caught per wasp per hour, or the rate of prey capture.

Table 3.8 The proportion of time spent foraging for prey*.

Underline →

get rid of space

| | <u>Mean Foraging Time (mins/prey)</u> | <u>Rate of Prey Capture (prey/hr)</u> | <u>% Time Spent Foraging</u> |
|----------|---------------------------------------|---------------------------------------|------------------------------|
| Alderly | 26.02 | 0.73 | 31.6 |
| Alnmouth | 16.70 | 1.17 | 32.6 |
| Thetford | 20.77 | 1.02 | 35.3 |
| Findhorn | 19.59 | 1.09 | 35.5 |
| St Cyrus | 21.90 | 1.12 | 40.9 |

* Calculated by multiplying the mean foraging time per prey item with the mean number of prey caught per hour (giving the number of minutes spent foraging in each hour).

10
 Table 3.9a The time spent inside the nest and prey size at St Cyrus.

| <u>Prey Size Category</u> | <u>Mean time in Nest (sec)</u> | <u>S.E.</u> | <u>Range</u> | <u>N</u> |
|---------------------------|--------------------------------|-------------|--------------|----------|
| Small | 83.24 (±SE) | 12.39 | 6-398 | 49 |
| Medium | 89.76 | 8.82 | 27-433 | 70 |
| Large | 106.67 | 22.66 | 8-436 | 18 |

10
 Table 3.9b The time spent inside the nest and prey size at Alderly Edge.

| <u>Prey Size Category</u> | <u>Mean time in Nest (sec)</u> | <u>S.E.</u> | <u>Range</u> | <u>N</u> |
|---------------------------|--------------------------------|-------------|--------------|----------|
| Small | 65.0 (±SE) | 15.1 | 23 - 150 | 10 |
| Medium | 70.2 | 5.96 | 16 - 368 | 122 |
| Large | 111.1 | 26.4 | 26 - 456 | 17 |

Table 9 3.10 The time spent in the nest - a comparison between sites.

| <u>Site</u> | <u>Mean time in Nest (sec)</u> | <u>S.E.</u> | <u>Range</u> | <u>N</u> |
|-------------|--------------------------------|-------------|--------------|----------|
| Alderly | 87.64 (± SE) | 6.76 | 17 - 456 | 125 |
| St Cyrus | 77.22 | 4.98 | 6 - 693 | 249 |
| Thetford | 69.62 | 9.12 | 29 - 151 | 26 |
| Findhorn | 84.36 | 9.42 | 25 - 184 | 25 |

Table 11 3.11 The time spent at the nest entrance - a comparison between sites.

| <u>Site</u> | <u>Mean time at Entrance (sec)</u> | <u>S.E.</u> | <u>Range</u> | <u>N</u> |
|-------------|------------------------------------|---------------|--------------|----------|
| Alderly | 42.01 (± SE) | 6.09 | 0 - 486 | 117 |
| St Cyrus | 20.54 | 1.82 | 0 - 261 | 237 |
| Thetford | 16.83 19.44 | 4.99 3.70 | 0 - 80 | 28 |
| Findhorn | 22.2 23.0 | 10.20 3.05 | 5 - 57 | 35 |
| Almuoth | 25.27 | 4.71 | 2 - 105 | 26 |

Fig. 3.1 The time taken to dig a nest by *Mellinus*¹⁵ *arvensis* 2 space? The time taken to dig a nest was taken from the time of nest initiation to the time at which the wasp was seen at the nest entrance prior to leaving on a foraging trip (defined as a trip which ended upon the return of the wasp with a prey item). $y = 19.68 + 3.20x$, $R^2 = 0.016$; $p > 0.4$, $t = 0.786$, d.f. = 38.

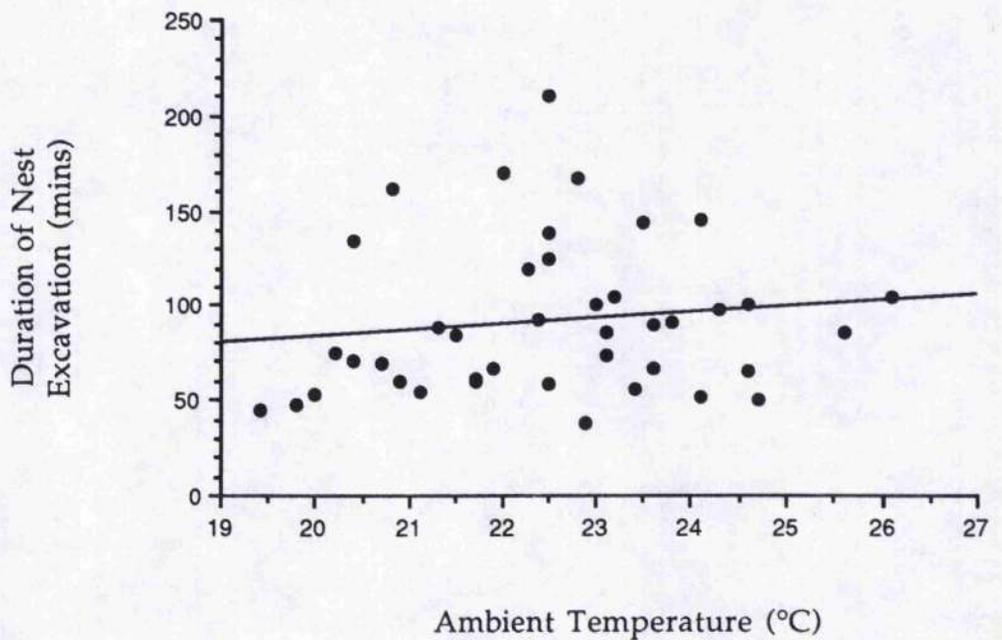
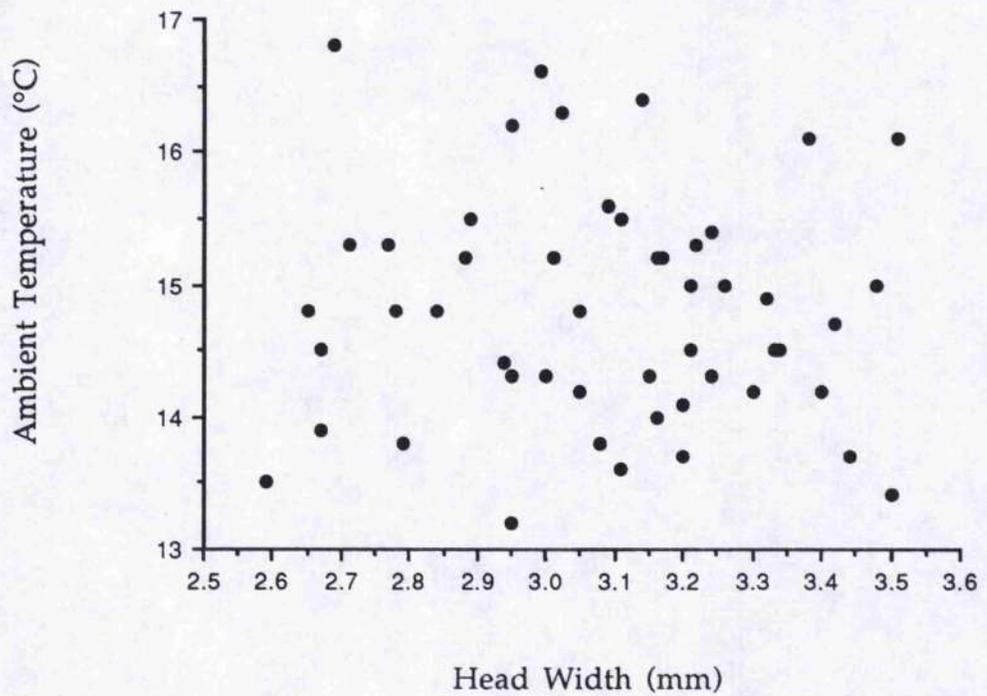
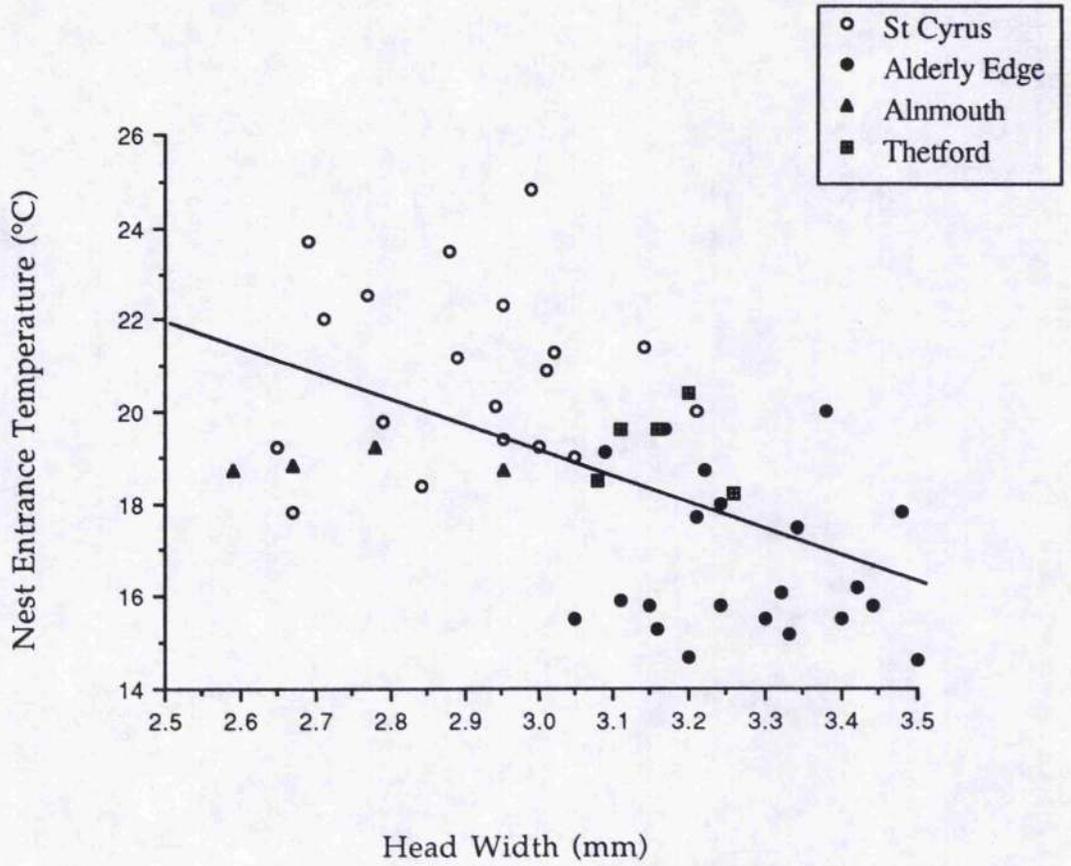


Fig. 3.2 The correlation between ambient temperature at time of first emergence of female *Mellinus arvensis* from the nest, and body size.



two to two decimal places
- t test ~~at sign~~

Fig. 3.3 The correlation between nest entrance temperature at time of first emergence of female *Mellinus arvensis* from the nest, and body size. $y = 35.11 - 5.30x$, $R^2 = 0.275$; $p =$, $t = 4.222$, $d.f. = 47$.



HW - 2 decimal places

Fig. 3.4 The proportion of time spent foraging by *Mellinus arvensis* from populations at different latitudes. The populations, in order of increasing latitude, are: Thetford; Alderly Edge; Alnmouth; St Cyrus; and Findhorn. Latitude has been converted into decimal units. $y = - 8.09 + 0.785x$, $R^2 = 0.229$; $p > 0.4$, $t = 0.944$, d.f. = 3.

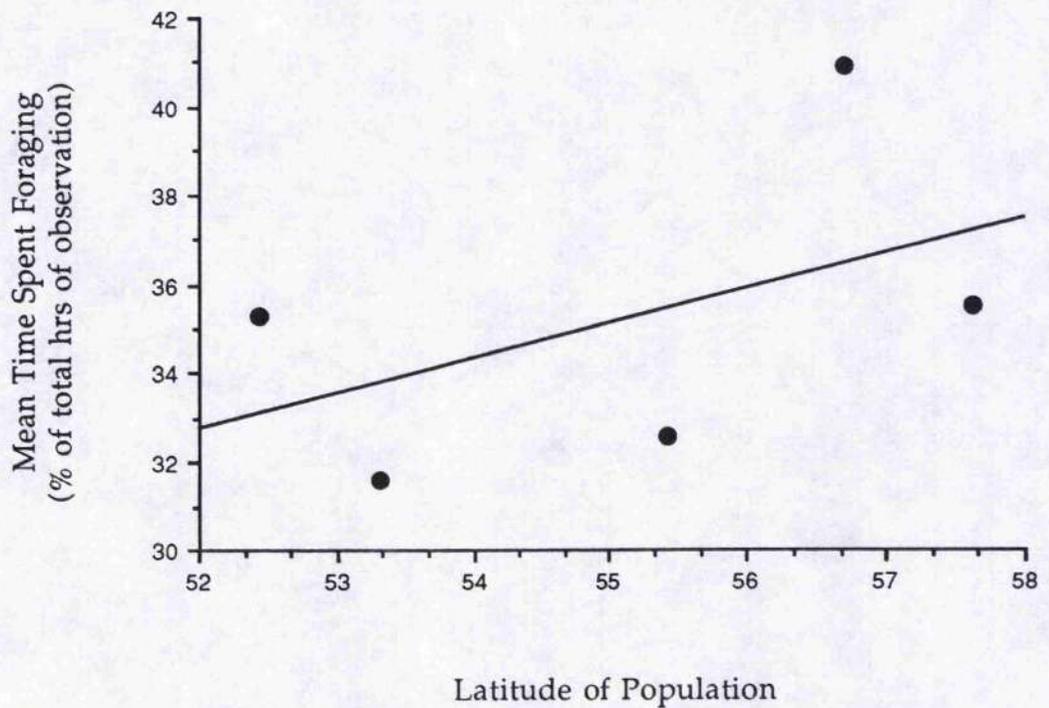


Fig. 3.5 The correlation between ambient temperature and foraging time of wasps carrying small sized prey (data pooled from all sites and years; only one randomly selected value from each individual has been used). $y = 67.05 - 2.588x$, $R^2 = 0.064$; $p < 0.02$, $t = 2.453$, d.f. = 90.

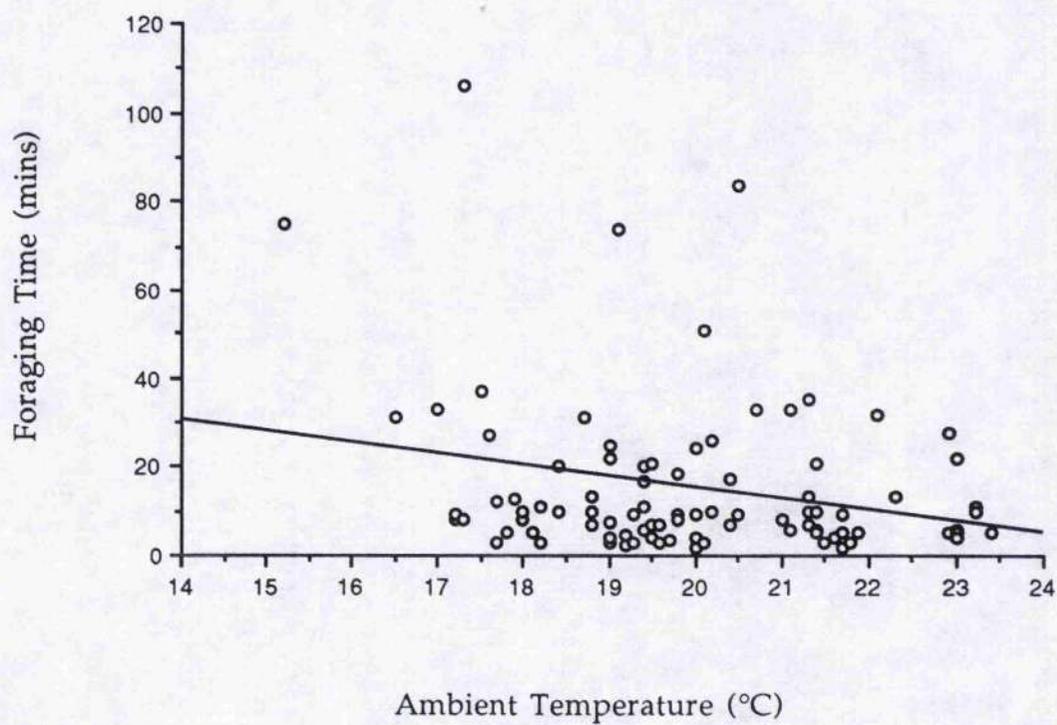


Fig. 3.6 The correlation between ambient temperature and foraging time of wasps carrying medium sized prey (data pooled from all sites and years; only one randomly selected value from each individual has been used). $y = 89.91 - 3.386x$, $R^2 = 0.082$; $p < 0.01$, $t = 3.145$, d.f. = 111.

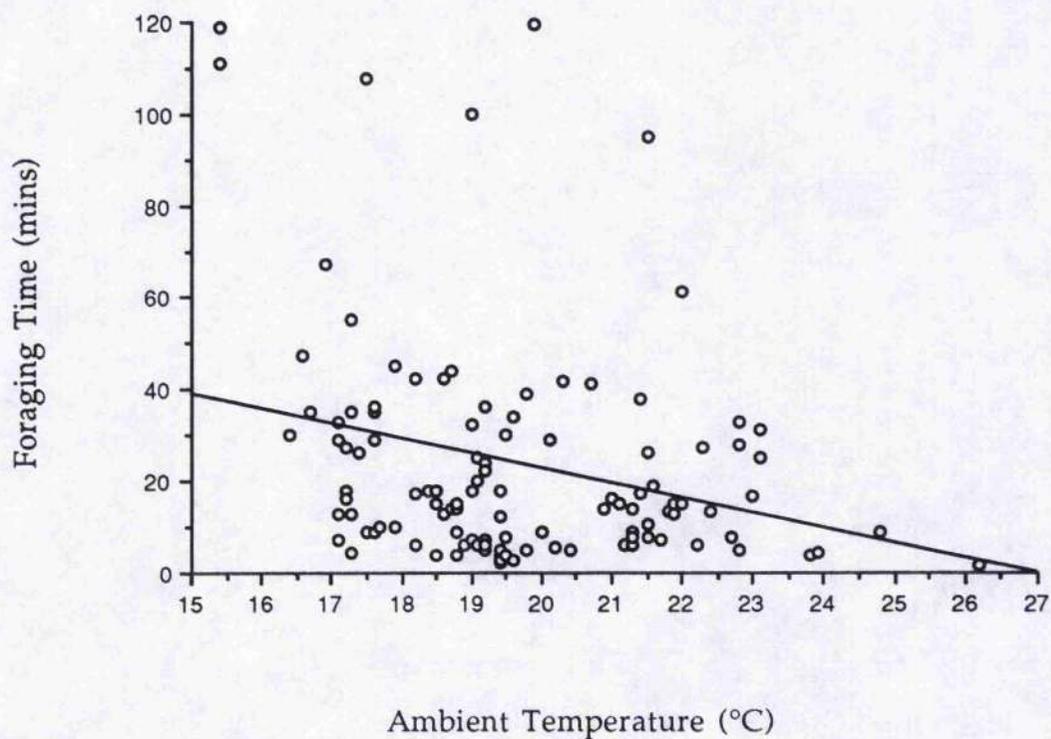


Fig. 3.7 The correlation between ambient temperature and foraging time of wasps carrying large sized prey (data pooled from all sites and years; only one randomly selected value from each individual has been used). $y = 85.61 - 3.087x$, $R^2 = 0.066$; $p < 0.1$, $t = 1.842$, d.f. = 48.

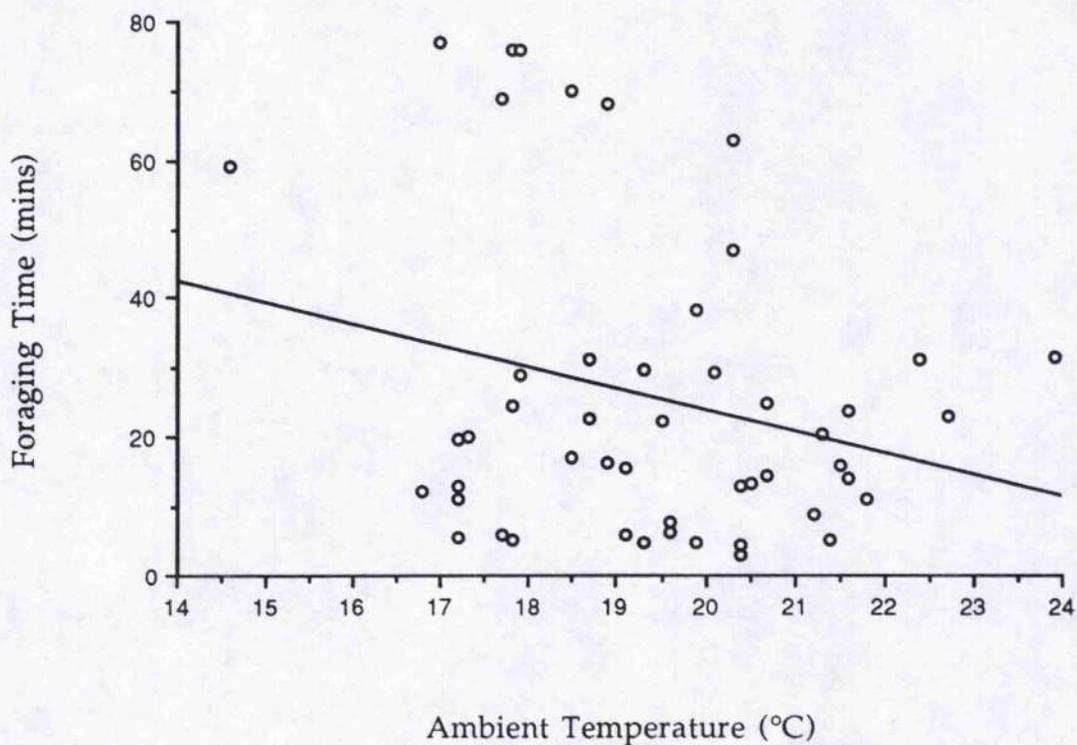


Fig. 3.8 The affects of wasp and prey sizes on the time spent in the nest by female *Mellinus arvensis* upon return to the nest from successful foraging trips. The prey size categories, defined on the basis of dry weight, are: small 0 - 5 mg; medium 5 - 10 mg; large > 10 mg. Wasp size categories, defined on the basis of head width, are: small < 3.00 mm; medium 3.00 - 3.20 mm; large > 3.20 mm.

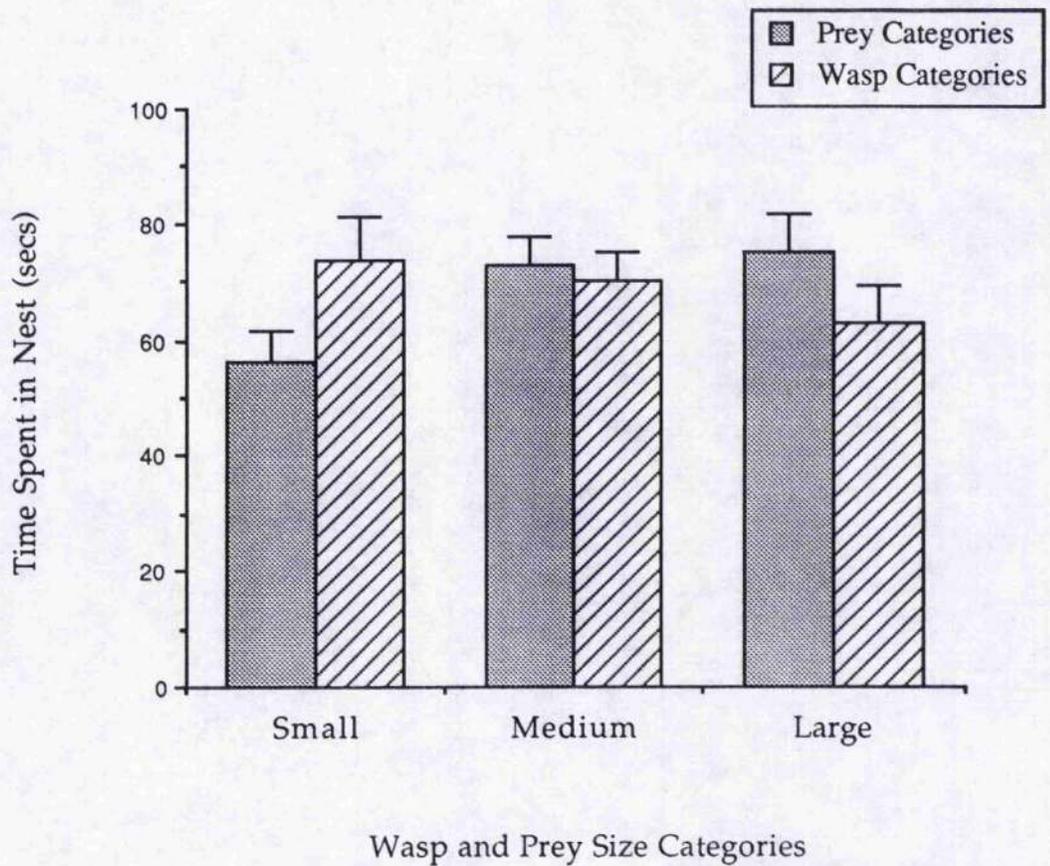


Fig. 3.9 The correlation between the time spent inside the nest upon return from a successful foraging trip, and wasp size. $y = 116.35 - 15.233x$, $R^2 = 0.008$; $p > 0.2$, $t = 0.92$, d.f. = 105.

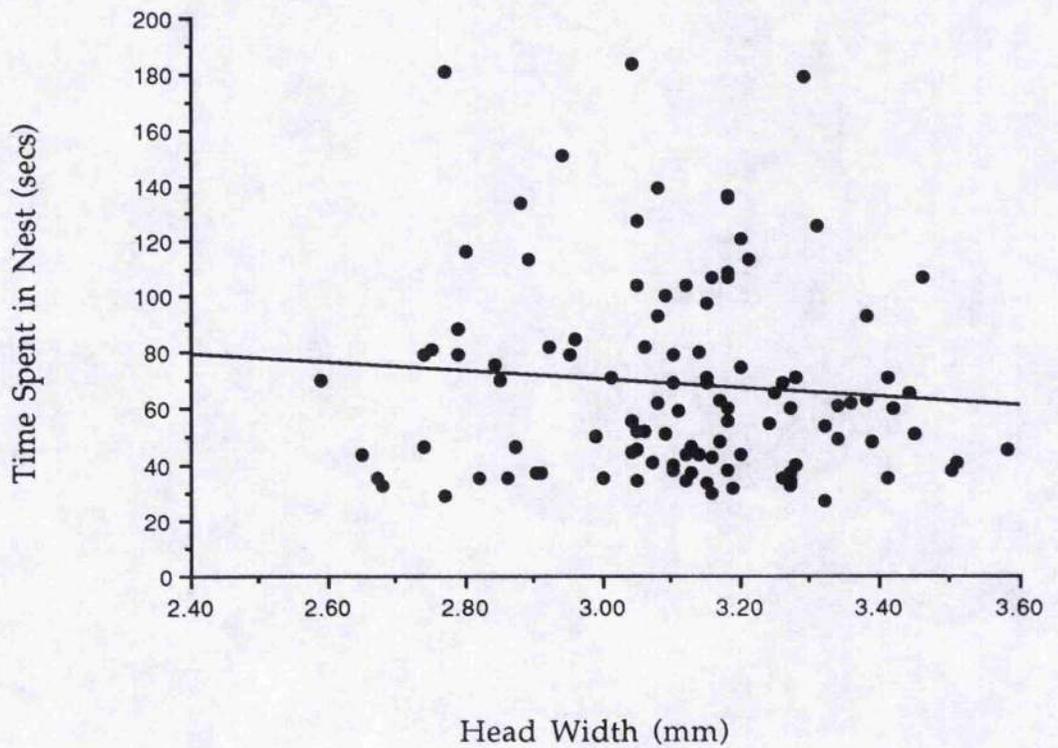


Fig. 3.10 The mean time spent in the nest upon return from a successful foraging trip of each wasp and prey size combination (excluding small wasps with large prey [SwLp] for which there are no data as no small wasps were observed to provision large prey).

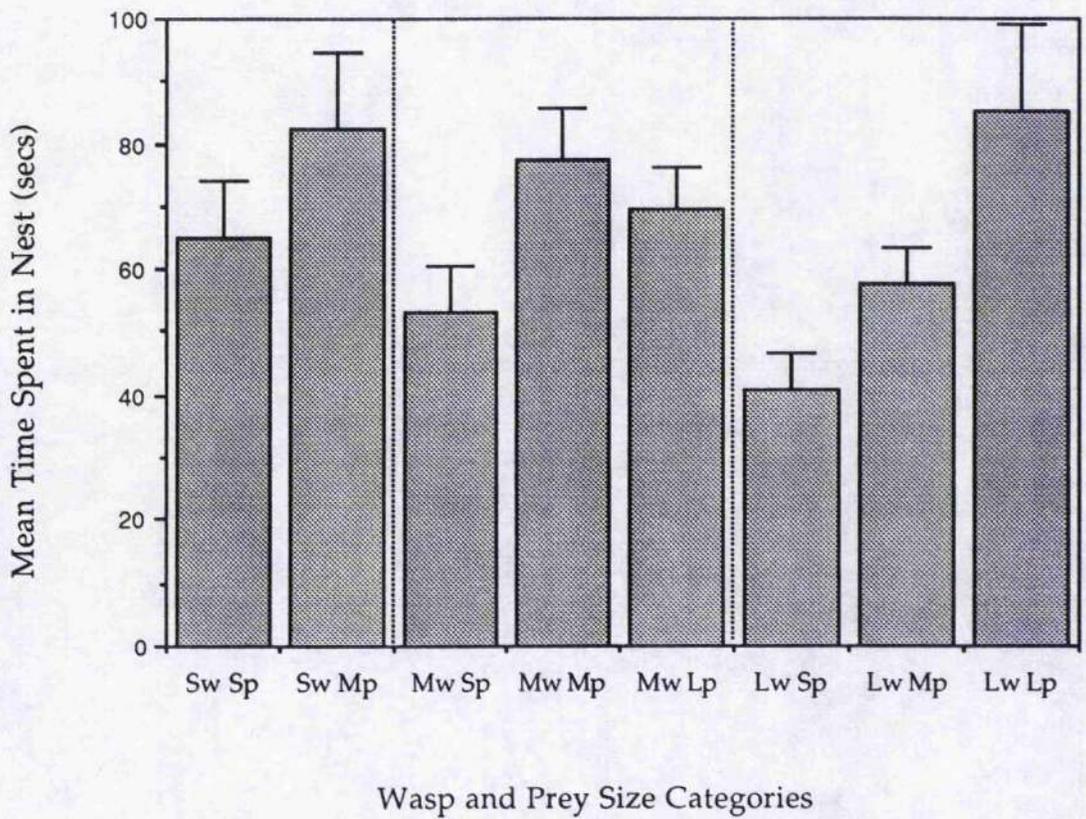


Fig. 3.11 The mean time spent in the nest by wasps upon return from a successful foraging trip, with wasp and prey size categories arranged in increasing order of expected time in nest (refer to text for explanation).

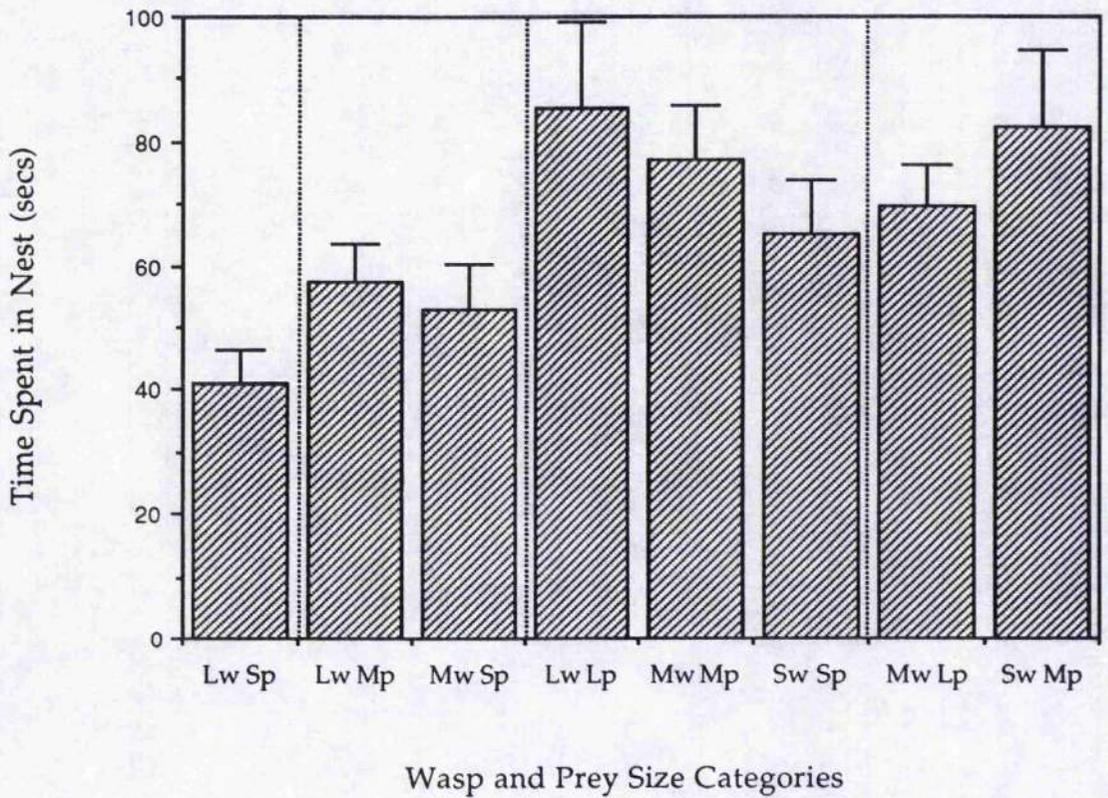


Fig. 3.12 The mean times spent in the nest upon return from a successful foraging trip of four pooled wasp and prey size categories, each containing categories of equal ranking (see text for details). ANOVA reveals a significant difference between the categories: $p = 0.023$, $F = 3.31$, $d.f. = 3$.

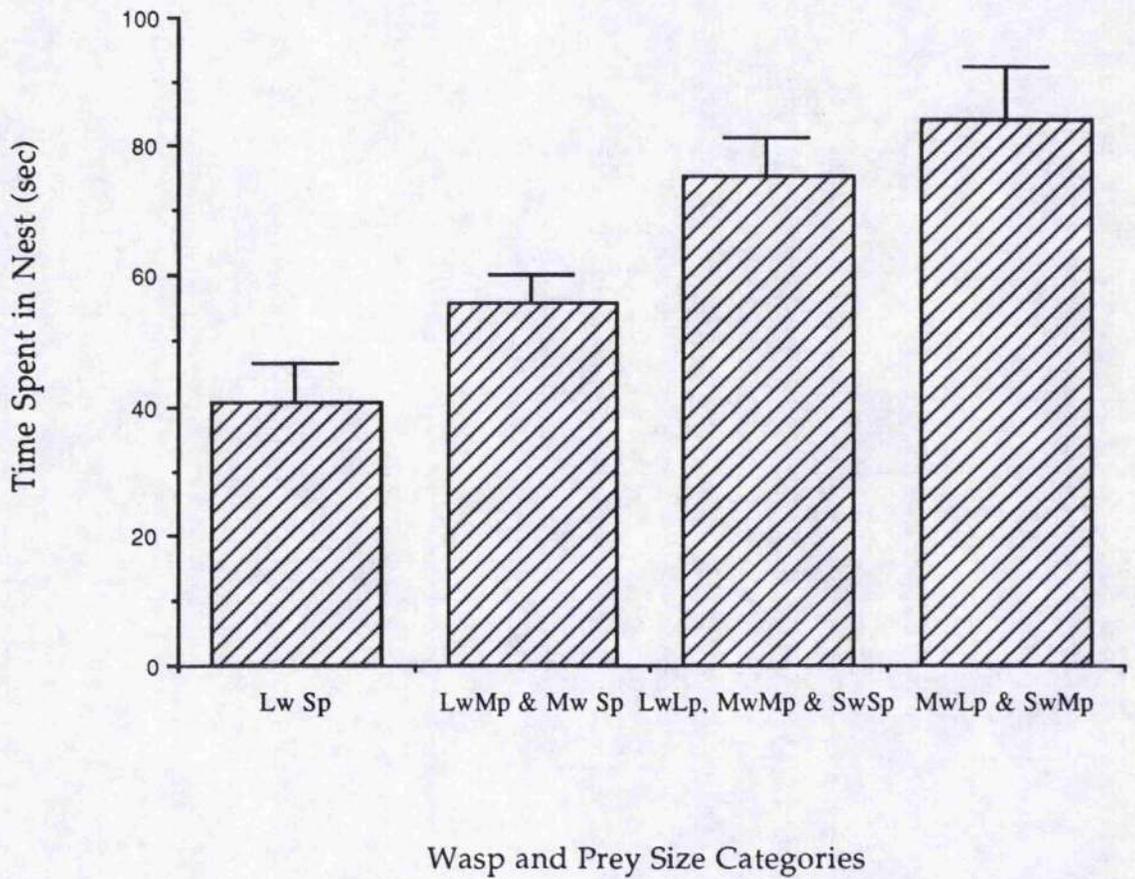


Fig. 3.13 The correlation between ambient temperature and the time spent at the nest entrance by female *Mellinus arvensis* (data from St Cyrus). $y = 76.20 - 2.893x$, $R^2 = 0.046$; $p < 0.01$, $t = 3.294$, d.f. = 225.

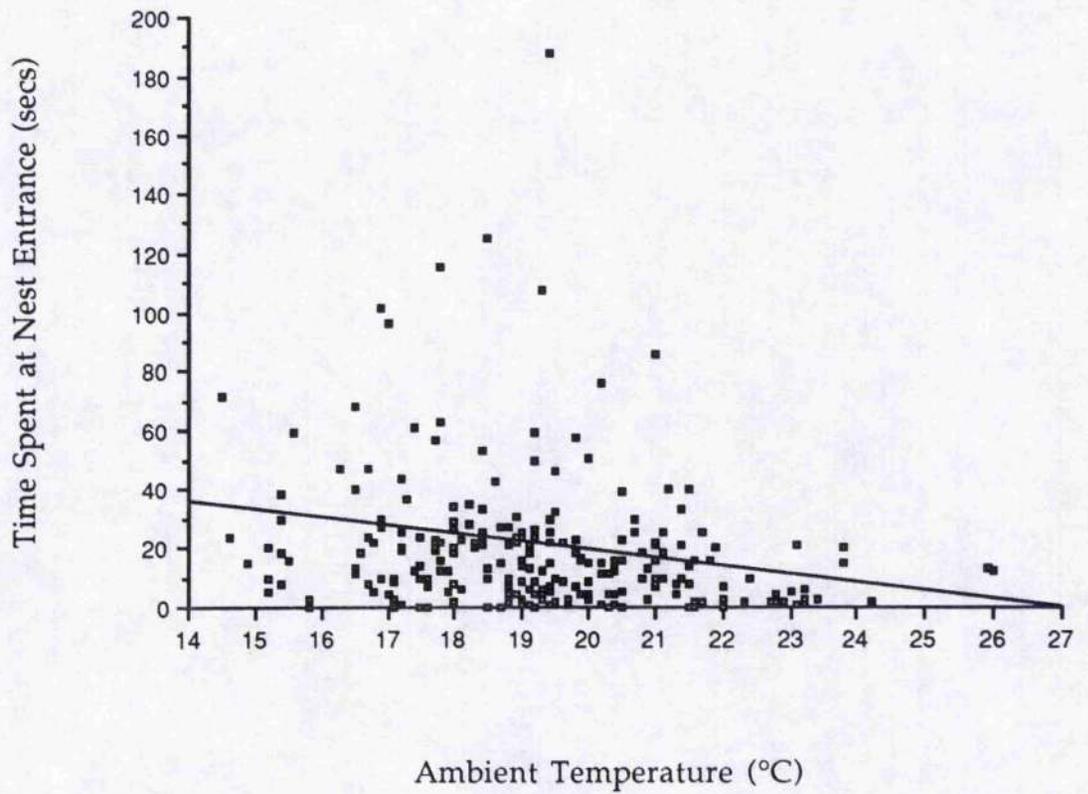


Fig. 3.14 The correlation between nest entrance temperature and the time spent at the nest entrance by female *Mellinus arvensis* (data from St Cyrus). $y = 83.38 - 2.397x$, $R^2 = 0.038$; $p < 0.02$, $t = 2.103$, d.f. = 112, (but see text).

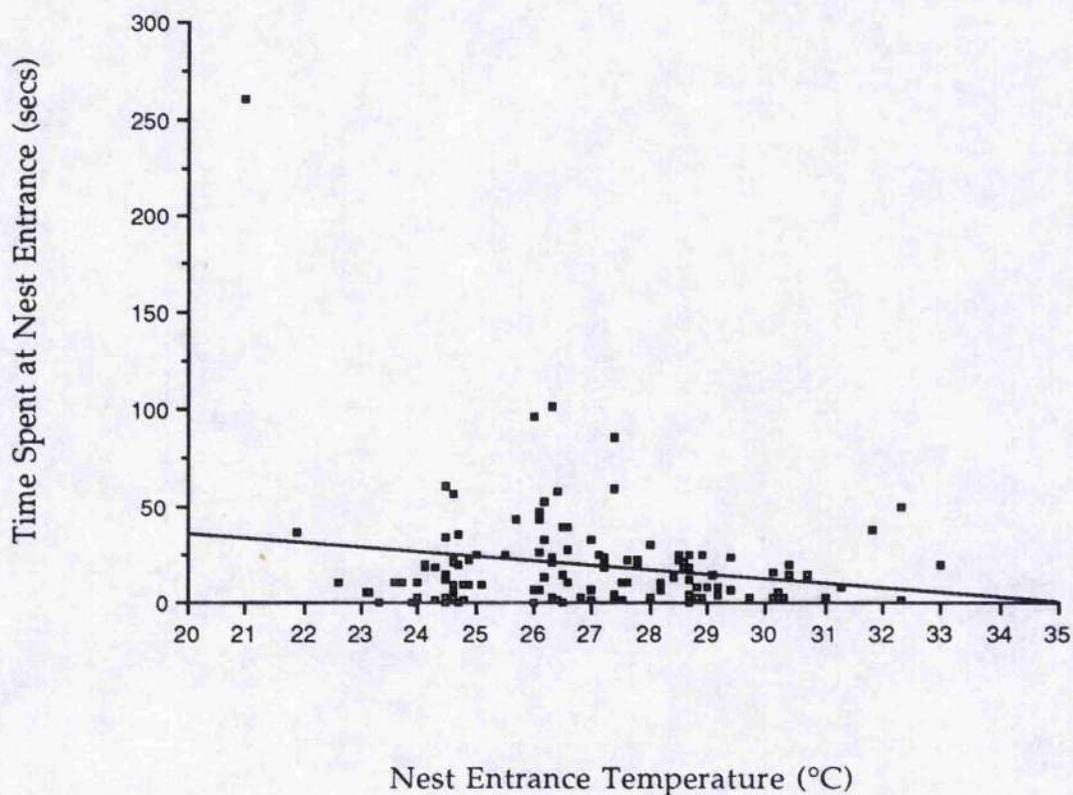


Fig. 3.15 Activity of males at St Cyrus and Alderly Edge. Standard error bars, which have been omitted for clarity, overlap between the two populations. Values for activity are means, and represent the number of individuals seen within a 0.25 m² area during a period of one minute.

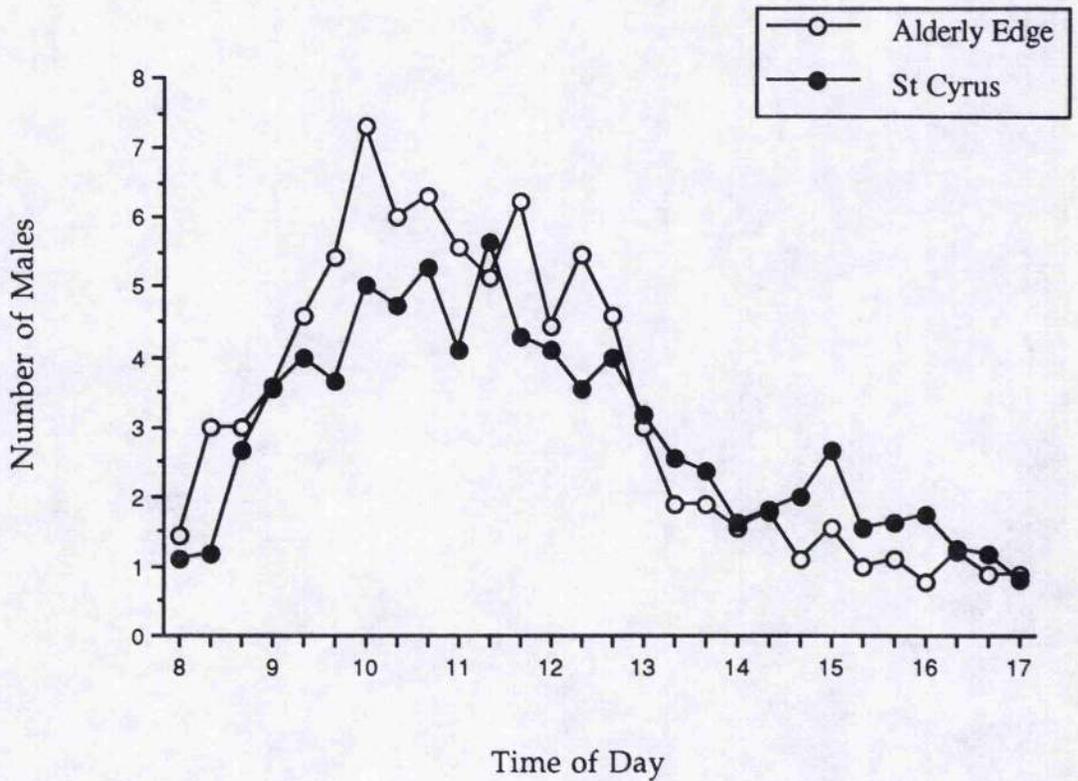
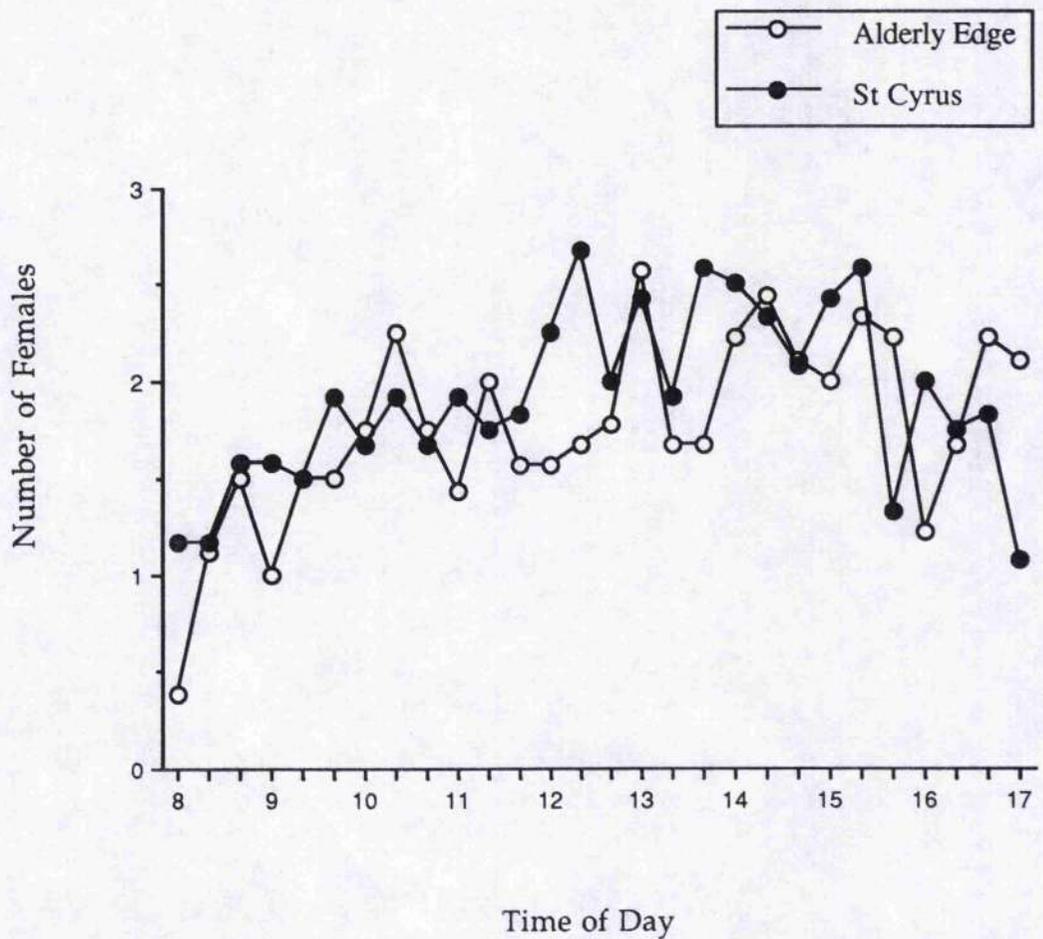


Fig. 3.16 Activity of females at St Cyrus and Alderly Edge. Standard error bars, which have been omitted for clarity, overlap between the two populations. Values for activity are means, and represent the number of individuals seen within a 0.25 m² area during a period of one minute.



Mean ♀ = *M. arvensis*

Fig. 3.17 Activity of female *Mellinus arvensis* at St Cyrus plotted against mean temperature.

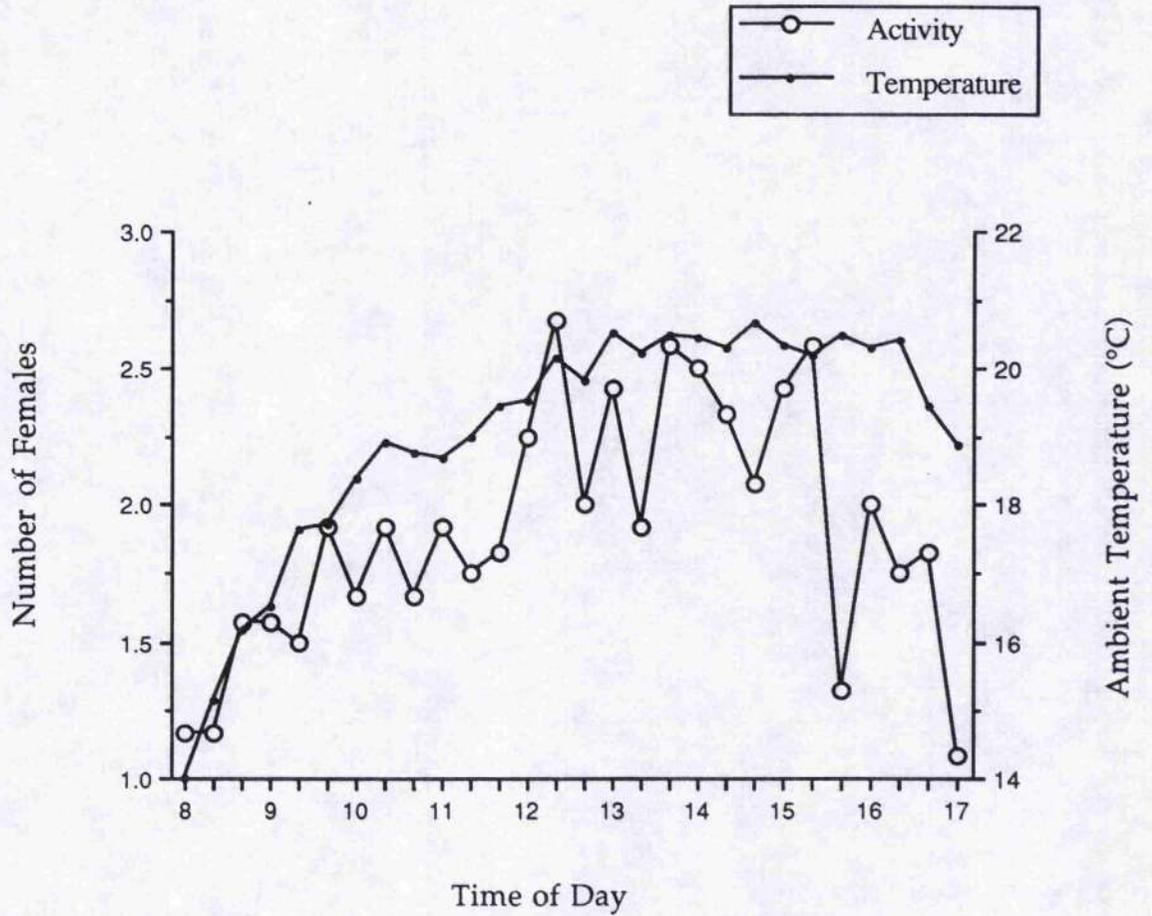


Fig. 3.18 Activity of female *Mellinus arvensis* at Alderly Edge plotted against mean ambient temperature.

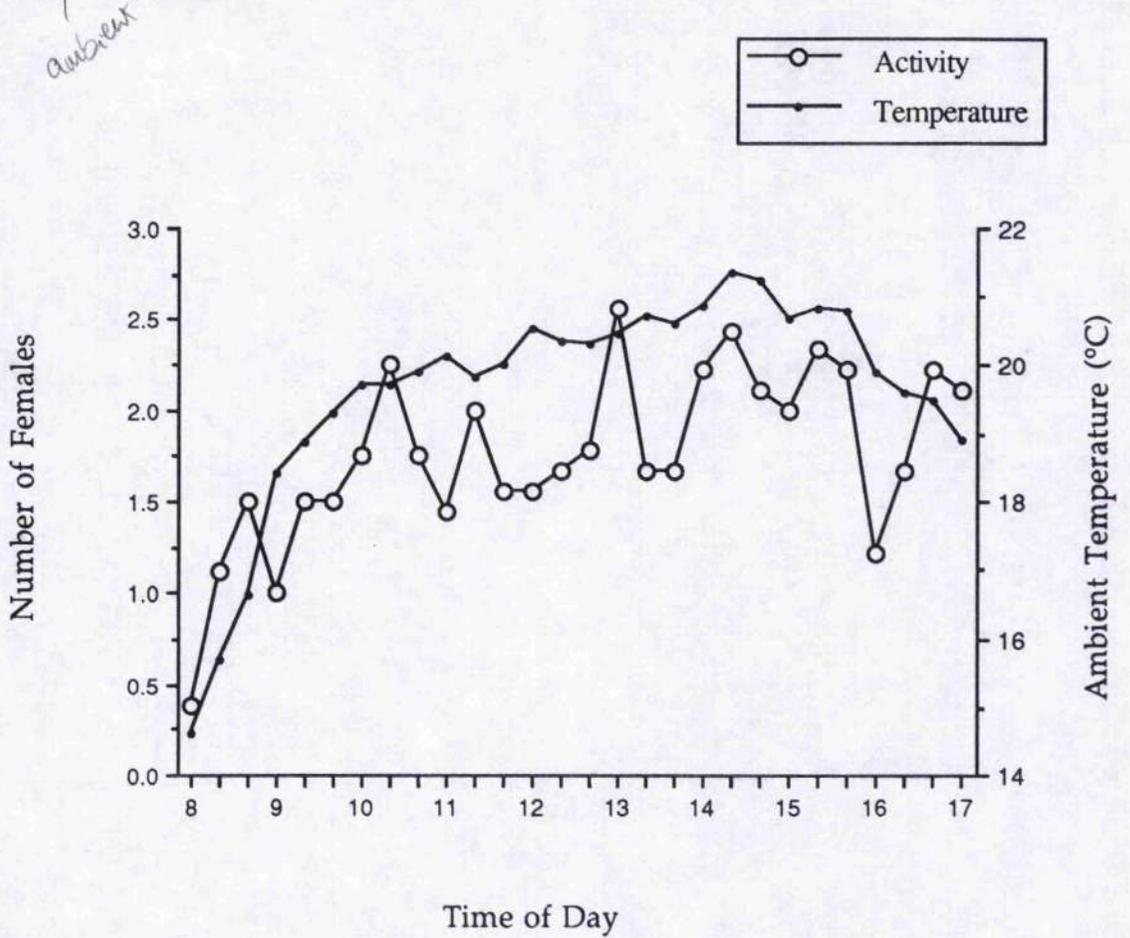


Fig. 3.19 The correlation between mean temperature and mean female activity at St Cyrus. $y = -1.369 + 0.172x$, $R^2 = 0.452$; $p < 0.001$, $t = 4.631$, d.f. = 26.

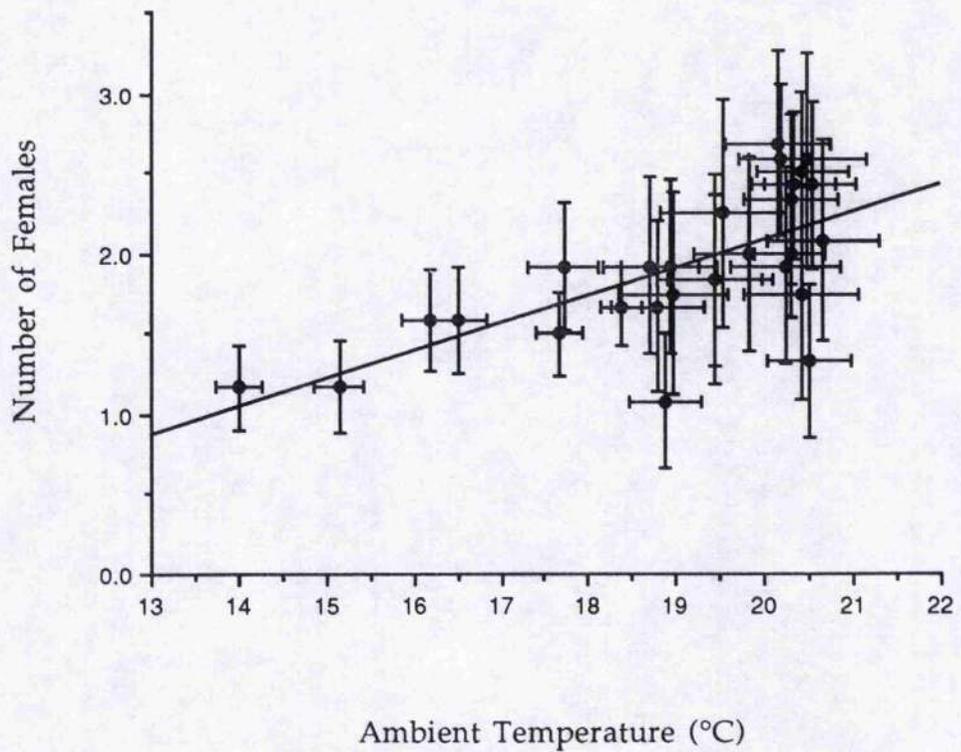


Fig. 3.20 The correlation between mean temperature and mean female activity at Alderly Edge. $y = -2.498 + 0.217x$, $R^2 = 0.516$; $p < 0.001$, $t = 5.265$, d.f. = 26.

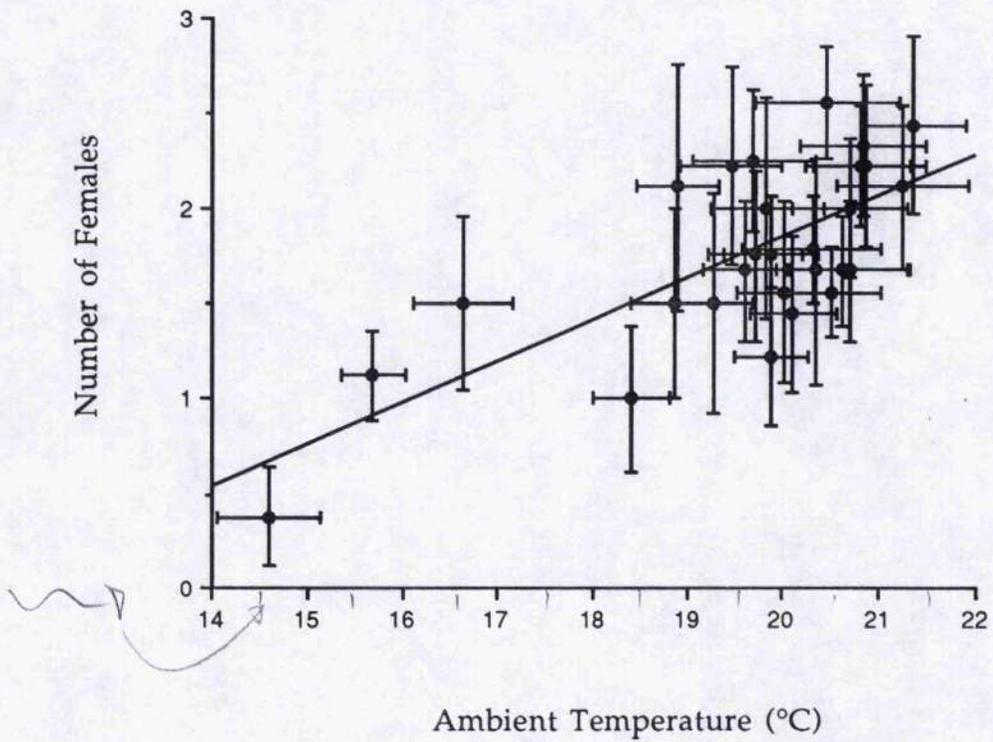
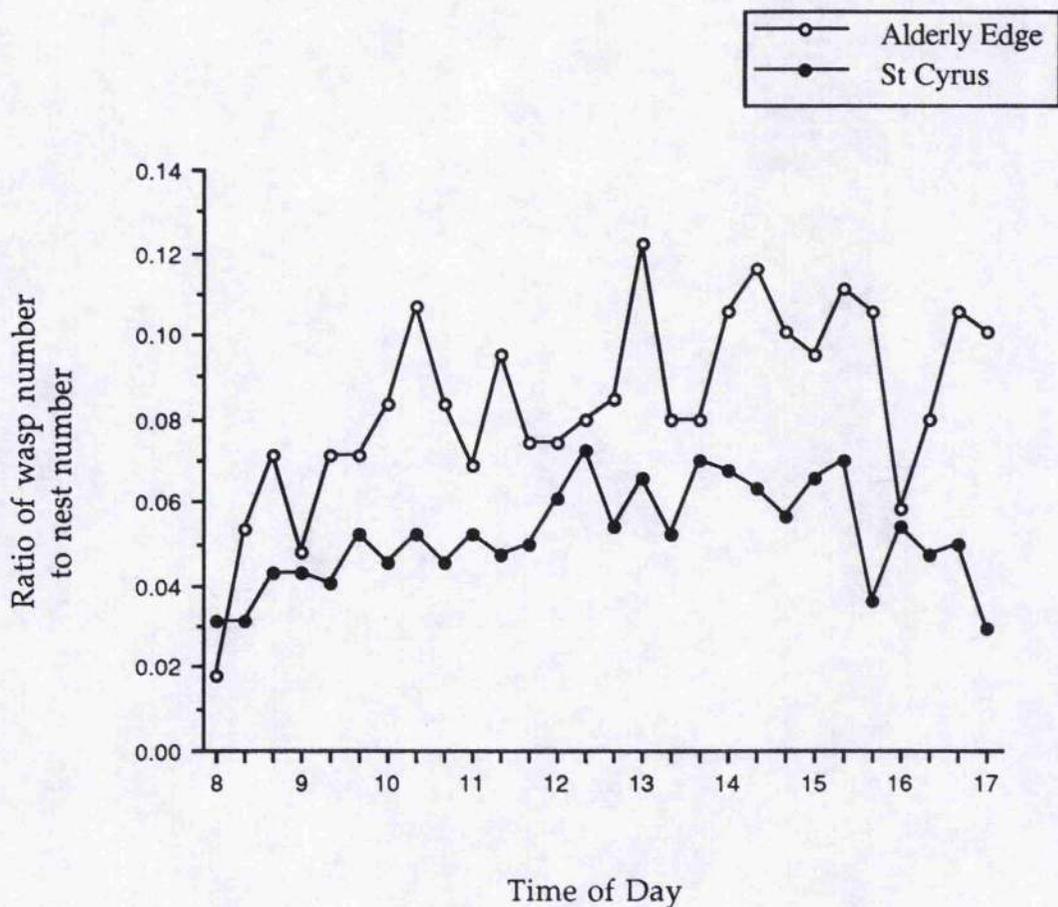


Fig. 3.21 The amount of wasp activity after correcting for number of nests in the observation area (see text for details). *Do standard error bars overlap??*



Chapter 4 Inter-Population Size Variation of *Mellinus arvensis*

4.1 Introduction

The study of the diversification of races and phylogenetic lineages, together with the associated changes in phenotypic traits, is a central theme of evolutionary biology. The evolution of body size has attracted much interest, because size of both fossils and living forms is easy to quantify, and is correlated with many attributes of ecology, morphology and physiology (Peters 1983; Schmidt-Nielson 1984; Maurer et al. 1992). Diversification in body size within taxonomic groups has occurred through evolutionary time and across geographical space. The apparent increase in body size within a taxonomic group over evolutionary time has been referred to as Cope's Rule (Stanley 1973). Specific advantages of large individuals have been used to explain this trend, such as the ability to tolerate short term variation in the physical environment, the capacity to extract energy from a wider variety of poorer-quality food, and the ability to avoid many kinds of predators (eg, Stanley 1973; Brown & Maurer 1986, 1987).

Two main patterns in the geographic variation of body size have been considered. Firstly, there is a tendency for body size of populations isolated on islands to rapidly diverge from their mainland relatives, with small species becoming larger, while large species become smaller (eg, Lawlor 1982; Lomolino 1985). Secondly, clinal trends in body size along geographical and ecological gradients have been documented in a number of groups of organisms (James 1970; McNab 1971). The subject of this study concerns the second of these patterns, describing trends in the body size of *Mellinus*

arvensis and suggesting adaptive processes that may be responsible for geographic variation in body size.

The diversity and variation in the body sizes of organisms has been explained in terms of either microevolutionary processes (natural selection due to differential fitness of individuals (eg, Wolda 1967; Boag & Grant 1981; Price et al. 1984)), or macroevolutionary processes (eg, species selection owing to the differential rates of reproduction of phylogenetic lineages (Gould 1982, 1988)). This study refers only to microevolutionary processes, as macroevolutionary processes within species are expected to be minimal, assuming reproductive rates of races are similar.

A small animal has, relative to its mass, a large body surface area. Heat loss and gain occur across the surface, and therefore, where there is a relatively large surface, heat gain and loss are rapid. This simple relationship has been well understood since the early part of the last century. In 1839, Rameaux and Sarrus emphasised that the heat loss from a warm blooded animal must be roughly proportional to its surface area and because a small animal has a relatively larger surface, it must also have a higher relative rate of heat production. This reasoning was adopted by Bergmann (1947) who stated that homeothermic animals in colder climates are of larger body size than their relatives in warmer climates (Bergmann's rule). The validity of this rule has been questioned (Scholander 1955) and caused much controversy (McNab 1971). The main point is that the law must be stated in terms of races or populations within a species, and then, as Rensch (1936, see McNab 1971) has shown for many bird species, as one travels north body size does increase (though this was severely criticized by Scholander 1955). Difficulties exist in other species, for example otters, pumas, and racoons, which display the reverse of the rule and become smaller at higher latitudes (Allen 1906).

Bergmann's rule has also been applied to endothermic arthropods, such as honeybees (Alpatov 1929; Daly et al. 1991), and ectotherms, such as marine and freshwater fish, frogs and toads, salamanders, snakes, lizards and turtles (Ray 1960, Lindsey 1966). Ectothermic insects are dependent almost entirely on ambient environmental conditions. Because of this dependence on external conditions it might be expected that body size is more finely tuned to climate in these small invertebrates. This chapter investigates differences in body size between several populations of *Mellinus arvensis*. Observed differences are correlated with latitude and environmental factors. Biological factors that may have influenced the evolution of body size are also suggested and discussed.

4.2 Latitudinal Variation in Body Size Between Populations

Head widths of *Mellinus arvensis* were measured from all the field sites (table 4.1a). There are large significant differences between the sites (table 4.1b) and considerable variation between individuals within populations. Due to the small number of populations included in this analysis, additional head width data were collected from museum collections (table 4.2) (Natural History Museum in London, Hope Entomological Collection at Oxford, University of Manchester Museum, Cambridge University Museum and the Royal Museum of Scotland).

Mean head width values of the wasp populations are correlated with latitude (figure 4.1). Despite considerable scatter about the regression line, there is a significant negative correlation between head width and latitude ($p = 0.001$, $F = 22.75$, d.f. = 35, $R^2 = 0.394$), the reverse of the positive correlation predicted for endotherms by Bergmann's rule. A climatic or thermal explanation for

size, which is intuitively suspected with any latitudinal clines, need not be rejected simply because the size trend is in the opposite direction of what might at first be expected. More complicated thermal explanations, that may not be immediately obvious, may account for this pattern.

Temperature data collected at field sites were too specific and temporally disjunct to be of use in the analysis of the effects of climate on wasp size. Therefore, meteorological data, from the Meteorological Offices in Edinburgh and Bracknell, were obtained for the closest weather stations to every field site (table 4.3). The climatic conditions recorded by the Meteorological Office at weather stations are assumed to be similar to those experienced at the associated field sites. Maps of mean monthly temperatures for the period 1941-1970 over the United Kingdom (Climatological Memorandum No. 73), (and maps of average monthly rainfall over the British Isles for 1941-1970 (Hydrological Memorandum No. 44), were obtained from the Meteorological Office in Edinburgh.)

Figures 4.2 - 4.4 present the mean daily temperature, the mean maximum and mean minimum temperature for the month of August for the years 1941-1970. August has been chosen for this analysis as all *M. arvensis* populations are active during this month throughout Britain. Females might emerge as late as mid July in southerly populations, while wasp activity at northerly populations is reaching its end in September. There is an obvious latitudinal trend in mean daily temperature in Britain, with higher means in the south (figure 4.2). There is a similar trend for mean daily maximum and minimum temperatures (figures 4.3 & 4.4). The higher temperatures experienced in the south presumably allow more time for wasp activity, with longer periods of thermally favourable temperatures at southern sites.

The Meteorological Office could not provide data on the confidence intervals associated with the average monthly temperatures for the years 1941-1970, and without these confidence intervals it is impossible to ascertain whether temporal variation of temperature from one year to the next is of greater magnitude than latitudinal geographic variation. Were this to be the case, with little geographic but much temporal variation in temperature, there would be a decrease in divergence of characters such as size due to the stochastic nature of the environment imposing stabilising selection (Levins 1968). However, if climate is more geographically variable and predictably so, size may indeed become tuned and adapted through evolutionary time to the local conditions. Figure 4.5 plots latitude against the mean daily temperature for the month of August in the years 1988-1992 for all ^{field} sites for which temperature data are available (see table 4.3), and for which confidence intervals can be calculated. A one way analysis of variance reveals that there are significant differences between the sites ($p < 0.001$, $F = 4.13$, d.f. = 43), and a regression on figure 4.5 shows that latitude accounts for 61.3% of the variance ($p = 0.013$, $F = 11.08$, d.f. = 8). We can therefore conclude that temporal variation in mean temperature is less than geographic temperature variation, indicating climate to be potentially capable of causing a divergence in wasp body size between sites. Furthermore, figure 4.5 proves statistically that temperature is indeed correlated with latitude.

When the mean temperatures for August (1988-1992) are plotted against head width for a number of sites, the resulting correlation is not significant ($t = 1.765$, d.f. = 7, $p > 0.1$), (figure 4.6). There is no significance either when head width is plotted against hours of sunshine ($t = 0.901$, d.f. = 7, $p > 0.2$), (figure 4.6). The absence of any significant correlation does not exclude climate as a factor in the determination of size; the sample is small ($n = 9$), and size may be determined by more subtle climatic variables.

Most of the sites in the north were coastal in location (Findhorn, St Cyrus and Alnmouth), there was little cover or shade, and the soils were sandy and relatively dry. Such conditions resulted in rapid warming of the ground surface when exposed to solar insolation (table 4.4). In addition to rapid warming, ground temperatures also reach a higher maximum temperature at these sandy coastal northern sites, favouring smaller wasps (table 4.4). Such microclimates that warm up rapidly and reach high temperatures may favour smaller wasps that can quickly adjust their body temperatures by moving between several microhabitats (see below). Larger wasps may also be subject to overheating on sand surfaces that typically exceed 40 °C, as often occurs at St Cyrus. Therefore, local environmental differences between sites, giving rise to thermal differences, might be the cause of some of the latitude related size variation between populations.

4.2.1 Temperature Fluctuation as a Determinant of Body Size

A site where temperature is warm enough for activity for long periods would favour large individuals, as large wasps maintain a higher temperature at thermal equilibrium, and lose heat more slowly than small wasps enabling them to continue foraging despite minor fluctuations in ambient temperature. Where the temperature fluctuates slowly but substantially between warm and cool conditions, neither small nor large wasps will have an advantage, although over time the population may become dominated by small individuals (small offspring requiring less foraging effort by the parent). If warm periods are frequent but very brief, small wasps might have an advantage because of their rapid warm up rates, being able to initiate activity sooner than large wasps that might not be able to attain a sufficiently high

temperature before the environment starts to cool. Small body size might therefore be an adaptation to make the best use of brief warm periods.

There is no direct evidence available to support this hypothesis, but data on the maximum daily temperature in the month of August for the years 1988-1992 were obtained for several sites (Kinloss weather station (WS) for Findhorn, Arbroath WS for St Cyrus, Boulmer WS for Alnmouth, Ringway WS for Alderly Edge and Honington WS for Thetford) and used as a measure of the length of thermally favourable periods for activity. The percentage of days having maximum temperatures of either 17.0 - 18.9 °C, or in excess of 19.0 °C, were calculated. These categories were defined on the basis of observed wasp activity, wasps being active but sluggish at temperatures between 17.0 - 18.9 °C, and very active at temperatures in excess of 19.0 °C (see Chapter 3). Thus, on days when the maximum temperature does not exceed 18.9 °C, thermally favourable periods are likely to be brief. Maximum daily temperature is not a direct measurement of the time duration of such periods, but in the absence of data collected specifically on this point, it is probably the best indication that is available.

When these data are plotted against head width, it is found that small wasps occur in areas where maximum daily temperature frequently falls within the lower temperature category (17 - 18.9 °C) and thus where temperature fluctuations about the lower temperature limit for activity are assumed to be greatest (figure 4.7). Large wasps occur at sites where maximum daily temperature is often in excess of 19 °C, and where favourable thermal periods are expected to be of a long duration (figure 4.8). Hence the thermal hypothesis discussed above does seem plausible. However, two points are located considerably above (Alderly Edge population) and below (Alnmouth population) the line in each graph. The presence of such outliers suggest that

the variation in body size cannot be explained solely in terms of climate, and other non-thermal factors might need to be examined.

4.2.2 Passive Rates of Warming and Cooling

To gain an indication of the relevance of body size to the warming and cooling rates of *M. arvensis*, rates of passive heat gain and loss of dead *M. arvensis* specimens of different sizes were measured, as described in Chapter 2. Half times of passive warming and cooling were positively correlated with wasp size (warming, $p < 0.01$, $R^2 = 0.814$, $t = 5.124$, d.f. = 6, figure 4.9; cooling, $p < 0.05$, $R^2 = 0.773$, $t = 2.722$, d.f. = 5, figure 4.10). Maximum thoracic temperature reached was also positively correlated with wasp size ($p = 0.01$, $R^2 = 0.696$, $t = 3.706$, d.f. = 6) (figure 4.11).

Large wasps have a higher thermal equilibrium temperature (that is, the point at which heat gain equals heat loss) at any given ambient temperature, than small wasps. Therefore the minimum temperature required for activity is expected to be lower for larger wasps. Despite the large differences in mean body size between sites, the actual minimum temperatures required for activity of individuals from four of the five primary sites was observed to be between 13 and 17 °C. Two wasps at Alnmouth were caught outside the nest at 11 - 13 °C but these had very limited mobility. Wasps caught as they emerged from the nest for the first time that day, at temperatures between 13 - 17 °C, were of head widths ranging between 2.59 mm (Alnmouth) and 3.51 mm (Alderly Edge) (Chapter 3, figure 3.2) and there was no correlation between ambient temperature at emergence and wasp size. However, there was a strong negative correlation between temperature at the nest entrance at the time of emergence, and size ($p < 0.001$, $R^2 = 0.274$, $t = 4.263$, d.f. = 48) (Chapter 3, figure 3.3). Time of emergence for a wasp may therefore be

dependent on the temperature at the nest entrance, small wasps emerging at a higher nest entrance temperature than large wasps.

Temperature differences between nest entrance and ambient temperatures have been shown to vary between sites (Chapter 3, table 3.4). These differences are probably a function of soil type, soil moisture, aspect of the ground and vegetation cover. At a particular ambient temperature, similar microhabitats, such as ground surface, have a higher temperature at St Cyrus than Alderly Edge. The difference in body size between these sites may be an adaptation to cooler conditions, large wasps being capable of initiating activity at lower temperatures. There is indeed a negative correlation between nest entrance temperature excess and mean head width for each population (figure 4.12) suggesting that small wasps are restricted to areas where nest entrance temperature is considerably greater than ambient.

Large size is likely to be an advantage where the climate is cool and uniform, so that the animal, once warmed up, can remain active for the duration of the day. A wasp of small size, and correspondingly rapid warm up rates, might be able to make use of brief hot periods that large wasps, due to low warm up rates, are unable to utilize effectively. Consequently, wasp size may have become adapted to different thermal regimes encountered at different sites. The temperature of the sandy ground surface at St Cyrus rises very rapidly upon insolation (table 4.4), quickly resulting in a large temperature excess between air temperature and ground temperature (table 3.4). The converse is also true, ground temperature dropping rapidly when shaded. Nest entrances at St Cyrus are also subject to rapid warming and cooling (tables 4.4 and 3.4). Small size might allow wasps to make best use of the rapidly changing temperatures in the habitat.

4.2.3 Latitude and Body Size Variation in Another Sphecid Wasp

Another sphecid that is common and occurs throughout the latitudinal range of Britain is *Crabro cribrarius*. This wasp is very similar to *M. arvensis* in its behaviour, often seen digging nests in the sand within an aggregation of *M. arvensis* nests and feeding on Diptera, although is somewhat larger (mean head width of *C. cribrarius* females = 3.67 ± 0.02 mm, N = 143; compared to *M. arvensis* females, mean head width = 3.02 ± 0.01 mm, N = 319). An important difference between the two species is that *C. cribrarius* rarely nests in large aggregations, as does *M. arvensis*, thus any variation in body size is more likely to be a result of environmental, rather than biological, factors, as encounters between *C. cribrarius* females, which are rarely found nesting in large aggregations, are likely to be far less frequent than for *M. arvensis* individuals.

Body size of *C. cribrarius* is not correlated with latitude (figure 4.13). Thus in this wasp, which is very similar to *M. arvensis* in nesting and foraging behaviour, body shape and colour, climate has not resulted in adaptation of body size to maximise activity periods. The larger body size of *C. cribrarius* may result in a greater degree of independence from climate (due to lower area to volume ratio), or alternatively, variation in body size may be predominantly a result of biological interactions between conspecifics, of which there are few in *C. cribrarius* and many in *M. arvensis*. Therefore it might be that body size in *M. arvensis* is due to factors other than, or in addition to, climate.

4.2.4 Non-Thermal Explanations of a Latitudinal Size Gradient

Small size at high latitudes might not necessarily be a thermal adaptation. Size of the adult wasps is determined by the amount of prey provisioned in the cell by the mother (Evans & Eberhard 1973). Thus a cell provisioned with fewer or smaller prey would result in a smaller adult, but would take a shorter period of time to provision. If large size does not confer a competitive or reproductive advantage then a strategy ^{of producing a greater no. of} pursuing more smaller, rather than few larger, offspring would be selected for.

Where prey are limited in numbers, small or difficult to locate, or where intraspecific competition for prey is high, small wasp size would be predicted as a strategy for maximising the number of offspring and making the best use of the available resources. In an area where egg or larval mortality is high (due to parasitism, fungal attack or predation), provisioning many cells with relatively few prey items increases the number of potential offspring thereby increasing the chance that at least some of them will complete development. Furthermore a cell provisioned with fewer or smaller prey remains open, and therefore exposed to risk, for a shorter period of time, thereby increasing the chances of survival. Another factor to be considered is the number of days available for foraging during the adult life of the wasp. This is dependent on the lifespan of the wasp and the local environmental conditions. If the number of days on which an adult can forage for prey is reduced, small offspring is again predicted as a strategy to maximise output when faced with a limited amount of time.

When climate is highly favourable for activity, and prey is not limiting, small size will not impart a reproductive advantage to the individual. The upper limit to the number and size of prey in a cell (and hence size of offspring),

imposed by the scarcity of prey and intra-specific competition, is raised as prey becomes plentiful and more readily found, allowing wasp size to increase without necessitating any particular selection pressure in that direction. The size increase may be accelerated if large individuals tend to provide a larger cache of prey per cell. Selection pressure in the direction of larger size will arise if, as in many aculeate and other species, size is correlated with increased fecundity (Darwin 1874; Leather 1988; Shine 1988), large females being capable of laying more eggs and leaving more offspring. Should large size also be correlated with a longer adult lifespan, selection will favour large individuals even more strongly.

Large body size may be advantageous in competitive and aggressive interactions between females, or where prey are of such a size that only large wasps are capable of subduing and transporting them. Aggression may arise between females at the hunting site (*Philanthus gibbosus*, Lin 1978) or the nesting site (*Ammophila campestris*, Baerends 1959; *Podalonia valida*, Steiner 1975; *Bembix cinerea*, Evans 1966b; *Cerceris halone*, Byers 1978). Aggression at the hunting site is unlikely for a species such as *M. arvensis* that preys upon a wide variety of flies that may be caught from many different hunting sites. Aggression at the nesting site is more likely as these wasps typically nest in large aggregations and there are many opportunities for encounters between females (Chapter 5). It might be expected that large aggregated populations are made up of wasps with larger mean size than populations where nests are more dispersed or where the population size is smaller.

The following sections consider the importance of prey in determining wasp body size. Detailed information was only collected from four study sites, Alderly Edge, Alnmouth, St Cyrus and Thetford. Differences in wasp body

size between these sites were pronounced, enabling useful comparisons to be made.

4.3 Prey Selection and Body Size

The body size of an adult wasp is largely dependent on the amount of prey consumed as a larva (Evans & Eberhard 1973). The amount of provisions available to a larva is determined by the parent's foraging and provisioning behaviour, which may in turn be influenced by factors such as prey availability and size. Differences in the type and size of prey caught, between both individual wasps and wasp populations, were apparent. These differences could result in the observed size variation between wasps, both within and between populations.

A complete study of the ecological factors controlling body size has to include an analysis of prey size, abundance, and prey selection preferences of wasps. Because of the difficulties encountered when attempting to measure prey abundance, (Chapter 2), only prey size, and selection of prey by wasps, can be considered in this study. But due to the wide range of flies taken by *M. arvensis*, and the large number of flies seen at each site, it has been assumed that prey abundance is of little or no importance in determining the foraging success of *M. arvensis*, and therefore, cannot explain the observed variation of wasp body size.

4.3.1 Wasp Size and the Size of Prey

The correlation between wasp size and the size of prey taken is not very convincing if data from each site (St Cyrus and Alderly Edge) are considered separately. The most likely reason for this is that the wasp size range at each

site is relatively narrow. If data from these two sites are pooled (figure 4.14), a highly significant correlation between wasp size and the size of prey taken emerges ($t = 6.169$, d.f. = 91, $p = 0.001$). It is only acceptable to pool the data if the coefficients for the populations are the same, the test for which is outlined in Appendix 1. In this case there is no significant difference between the coefficients ($z = 0.468$, d.f. = 39, $p > 0.5$) and the data can be legitimately pooled.

The scatter about the regression line confirms that *M. arvensis* takes prey from a wide size range. It appears that there are upper and lower limits to the size of prey taken for each wasp, both these limits increasing with increasing wasp size. It is likely that the upper limit is morphologically set, in that wasps do not have the ability to subdue or carry a prey item that exceeds this limit. Indeed, many wasps were often seen to be having difficulty in transporting large prey items to the nest. The lower limit may be economically constrained, flies below this limit not representing a large enough resource to overcome foraging costs in terms of energy, time, and risk of parasitism or predation.

4.3.2 The Types of Prey Caught

All the 1161 prey items collected from the four sites belonged to the order Diptera. Figure 4.15 describes the proportions of flies caught according to their major taxonomic categories (following keys from Colyer & Hammond 1968; Unwin 1981). By far the greater majority of prey belong to the sub-order Cyclorhapha (93.8%), with flies from the sub-order Brachycera accounting for 5.8% of the total, and only 0.4% represented by the Nematocera. Each prey item was further identified to the family level, and, in the case of flies belonging to the Muscidae, to the sub-family level. For all the sites, the relative abundance of flies taken by wasps from each family (or sub-family)

has been calculated as a percentage of the total number of flies in the prey sample from that site, and these values are shown in figures 4.16a - 4.19a. There is quite a large degree of variation between the sites in the types of flies most frequently taken by wasps. Phaoninae (a sub-family of the Muscidae) comprise more than a third of the total prey catch at Alderly Edge, whereas at other sites phaonines occur less frequently in the prey sample; 13% at Thetford; 7% at St Cyrus; and not at all at Alnmouth. The Scatophagidae were also commonly caught by wasps at Alderly Edge (20% of the prey sample) but were quite rare or absent in prey taken at other sites. Similarly, syrphids are caught by wasps on 35% of all prey captures at Thetford, while at other sites they only make up about 5 or 6% of the total prey capture. At St Cyrus the Mydaeinae (a sub-family of the Muscidae) account for 38% of flies in the prey sample but only 16% at Alnmouth, 8% at Thetford and 5% at Alderly Edge. Wasps at Alnmouth catch Anthomyiidae on one third of all successful foraging trips, while at St Cyrus this figure is 13%, only 3% at Alderly Edge, and not at all at Thetford. Similarities between sites were also evident; for example, Calliphoridae were found at roughly equal proportions in the prey of *M. arvensis* at all sites except Alnmouth, where they did not occur in the sample.

The observed variations in the prey taken may reflect differences between wasps in prey selection and preference. Alternatively, prey frequencies might simply reflect the natural abundance of Diptera families in the habitat (Hobby 1932). Random sweep net sampling of the vegetation (Chapter 2) provided data on the natural occurrence of flies at each habitat (figures 16b - 19b). Contrasting distributions were obtained from comparisons between random fly catches, and flies taken from wasps.

At St Cyrus (figure 4.16b), Mydaeinae are the most common flies in the random sample accounting for 33% of the total, and this proportion is similar to the proportion of Mydaeinae taken as prey by *M. arvensis* (38%) (figure 4.16a). With such data we have to conclude that there is no preference shown by *M. arvensis* for Mydaeinae. Similar results at St Cyrus are obtained for the families Calliphoridae, Syrphidae and Coenosiinae (Muscid sub-family) leading to the conclusion that wasps at St Cyrus show no preference for particular prey families, but rather the prey caught is a reflection of the natural abundance of the different families in the habitat. The Anthomyiidae may be the only exception, accounting for 23% of the flies from the random sample, but only 13% of the prey.

In contrast to the apparent lack of prey specialization by wasps at St Cyrus, a third of the prey caught by wasps at Alnmouth consisted of anthomyiid flies (figure 4.17a), which did not appear at all in the random sweep net samples from that site. Furthermore the sub-family Mydaeinae is under-represented in the prey catch (16%) when compared to its relative abundance in the habitat (38%) (figure 4.17b). The Mydaeinae that are taken by wasps have a mean dry weight of 4.25 ± 0.44 mg, compared to 7.17 ± 0.51 mg of Mydaeinae from the random catch ($p = 0.005$, $t = 3.14$, d.f. = 22). The mean weight of prey from the family Syrphidae (7.22 ± 0.83 mg), and the sub-family Coenosiinae (3.45 ± 0.87 mg), are also smaller than the corresponding values from the random sample (Syrphidae 11.67 ± 2.17 mg; Coenosiinae 4.69 ± 0.37 mg). This suggests that wasps are catching smaller individuals from these families. The abundance of Anthomyiidae in the prey catch may be due to their small size (mean dry weight of 1.95 ± 0.24 mg) and wasps may be preferentially seeking small prey, or may be limited in the size of prey they can handle. *M. arvensis* at Alnmouth are very small and may indeed be limited to catching small flies. This pattern

of small wasps catching small flies, and ignoring large flies, fits the data obtained in section 4.3.1.

The absence of Anthomyiidae from the random sweep net samples at Alnmouth (figure 4.17b) may simply reflect either, limitations in the technique used to catch flies, or, bias in the locations that were sampled. A large number of anthomyiid flies were caught at Alderly Edge, St Cyrus and Thetford using the same sampling technique, and it is therefore unlikely that this method is selective with regard to the types of flies caught. It is more plausible that the microhabitats sampled at Alnmouth were areas where anthomyiid flies do not occur. At Alnmouth, the majority of samples were taken from an embankment adjacent to a road in which *M. arvensis* was nesting. The vegetation on the embankment consisted of tall grasses, bracken and brambles, but much of it had recently been cut back artificially. Further up the embankment the vegetation was taller and thicker, but, due to the many bramble bushes on which the sweep net was snagged, it was difficult to sample this area. It is possible that Anthomyiidae are plentiful in the densely vegetated areas that could not be sampled. Anthomyiids are certainly common on umbels, brambles and foliage generally (Colyer & Hammond 1968) and several *Chirosia* spp. are very common in bracken, in which the larvae develop (Stubbs & Chandler 1978), so it would be very surprising to find that they are rare in this habitat. Anthomyiidae are therefore likely to be plentiful in the densely vegetated parts of the embankment, but absent in those areas that have been largely cleared of cover. Consequently, random samples from cleared areas are not representative of the natural abundance of flies at this site. The interesting point remains that the flies caught are significantly smaller than the mean size of the family to which the fly belongs. Whether wasps are actively selecting small flies, or whether they are restricted to small prey by their own body size, is discussed in section 4.3.1.

Phaoninae account for 35% of the prey caught by wasps at Alderly Edge (figure 4.18a). Scatophagidae are the next most frequently caught flies at 21% of the sample. The Phaoninae account for 10% of the random sample, while Scatophagidae are absent (figure 4.18b). In contrast, 33% of the random sample consisted of anthomyiids, which were rarely caught by wasps (3% of prey). These differences are, as for Thetford and Alnmouth, likely to be due to the microhabitats sampled. Most of the random sweep net samples were from low lying grasses and heather located within the nesting area. Wasps were often seen in these areas foraging for prey. Many wasps were also observed to fly up to the branches of beech and oak trees that surrounded the nesting area. Sampling of flies from this area was difficult due to the height and distribution of the branches. Phaoninae, which are often found in woodland localities, may therefore be under-represented in the sample, which consists primarily of flies from areas of low lying vegetation, lacking tree cover and leaf litter. Scatophagids are found on dung, of which there was much in the area from dogs and a nearby dairy farm. As this microhabitat was not included in the sweep net samples it is not surprising that scatophagids were not found. The Anthomyiids are probably over represented in the sample as a consequence of the under-representation of other dipteran groups.

Selection of prey on the basis of size by wasps may be occurring at Alderly Edge. The wasps at Alderly Edge have the largest body sizes of the four sites, and the mean dry weight of prey taken was also the greatest. Due to their large size, wasps at Alderly Edge may be capable of taking prey of sizes that are beyond the upper size limit of smaller wasps. Additionally, they may be ignoring small flies that represent little reward for the effort involved in foraging and the associated risks. Anthomyiidae, although common, may be largely ignored by wasps for this reason. Indeed the Anthomyiidae that are taken by wasps have a significantly greater weight, 2.14 ± 0.36 mg, than those

from the random sample, 1.42 ± 0.10 mg ($t = 2.166$, d.f. = 32, $p = 0.038$). Phaonine flies taken by wasps are considerably greater in weight than phaonines in the random sample, the difference being highly significant (table 4.5). Curiously, the opposite is true for the Calliphoridae, although the significance is not high.

M. arvensis from Thetford take prey in roughly similar proportions to that found in the random fly samples. One clear difference again involves the Anthomyiidae, which are well represented in the random catch (27%), but do not feature in the prey sample. The Anthomyiidae from Thetford are small flies with a mean dry weight of only 2.60 ± 0.33 mg. The relatively large wasps of Thetford may ignore these small flies despite their apparent abundance, as the costs, in terms of energy, time or risk of parasitism, may exceed the gains, in terms of mass of prey for cell provisioning.

The second difference at Thetford is the absence of Phaoninae from the random sample when this muscid sub-family makes up 13% of the available prey (figures 4.19a & 4.19b). This result can also be explained by considering the location at which random sweep net samples were made. *M. arvensis* at Thetford were commonly seen to be foraging for prey among the heather and this is where sweep netting was carried out. Phaoninae, however, are typically found in wooded areas, leaf litter (Stubbs & Chandler 1978; Falk, personal communication) and decomposing fungi (Colyer & Hammond 1968). Deciduous woodland habitat surrounded the nesting site at Thetford, and wasps might easily have foraged in this area, although none were seen to do so. This habitat was not sampled for flies and therefore an unrepresentative sample might again have been obtained. It is worth noting that, unlike Alnmouth, there is little difference in the mean weights of Syrphidae, Mydaienae, and Muscinae, between the random sample and prey

sample. There is a difference between the two samples of Calliphoridae, calliphorids in the random sample being larger (16.01 ± 1.77 mg) than calliphorids caught by wasps (10.13 ± 0.79 mg; $p = 0.006$, $t = 3.48$, d.f. = 10). The mean dry weight of prey taken by wasps at Thetford is 8.25 mg and, like wasps at Alnmouth, there may be an upper limit to the size of prey taken. Large calliphorids may be beyond this limit, and therefore escape predation by *M. arvensis*.

Because of difficulties in obtaining an accurate estimate of the natural abundance of dipteran families at each site, there is not enough evidence to make conclusions regarding the existence of specialisation by wasps on the type of prey they catch, although such specialisation does seem unlikely (see also Hobby 1932). There are indications, however, that wasps select, or are restricted to, prey within a certain size range, that is dependent on the wasps' body size. Figure 4.20 reveals differences between the size of prey caught by wasps, and the mean weight of the flies from the random sample, at each site. Wasps at Alderly Edge prey upon larger flies than would be expected if no selection was taking place (figure 4.20). Wasps from Alnmouth show the opposite trend, preying upon smaller flies than expected. There is no significant difference between size of prey caught and the mean size of the random sample at either St Cyrus or Thetford. These patterns are interesting but should be considered carefully in the light of the limitations of the method used to sample flies from the habitat.

The random fly samples of all sites, except St Cyrus, have similar mean weights, and yet the mean wasp body sizes between the populations are significantly different. These facts indicate that the distribution of fly sizes at each site is not an important factor in the determination of wasp size. Wasps do, however, catch prey within a particular size range, according to the size of

the individual wasp. This may partially explain how wasp size is maintained over a number of generations at a particular site. Without selective forces acting upon body size, an increase in the wasp size range, due to stochastic factors, is expected, resulting in the gradual loss of differences in this character between populations. Differences in body size do exist though, implying that selective forces must be acting on the populations with regard to body size.

4.4 Cell Contents

In addition to the size of prey provisioned, the number of prey items in each cell must be measured to ascertain the amount of provisions available to the developing larva. Wasps at St Cyrus and Alnmouth catch small prey, but might provision each cell with many flies, thereby ensuring the larva receives a similar quantity of food to larvae from other sites. It has already been established that wasps foraging for small flies have shorter provisioning times, and therefore may make a greater number of foraging trips per day (section 3.6.1). Therefore it follows that wasps preying upon small flies can catch a greater number of prey items. A wasp provisioning a cell with small prey may increase the mass of provisions available to its larva by provisioning the cell with a greater number of flies. Thus at a site where the mean weight of available Diptera is low, it might be expected that cells contain a higher mean number of flies to offset a reduction in offspring size due to small prey.

Data on the number of prey items per cell were obtained from nest excavations at Alderly Edge and St Cyrus. Permission (from the Forestry Commission) was not granted to excavate nests at Thetford, and the location of the nesting aggregation at Alnmouth (by the side of a golf course)

prevented nest excavation. A useful comparison between Alderly Edge and St Cyrus can, however, be made, due to the considerable differences in wasp size, prey size and the dipteran populations at the two sites. Care was taken to avoid collecting data on more than one cell from each nest, thus maintaining statistical independence within each data set. Due to the proximity of nests to each other, each cell was excavated from a location far removed from the previous one, to satisfy this criterion. However, to minimise the extent of damage caused to the population, cells were excavated within a restricted area, and it is possible that a small number of cells included in the analysis were provisioned by the same female.

Another source of error arises from the impossibility of distinguishing between cells provisioned for males, and therefore containing less provisions in accordance with smaller male size, and cells provisioned for females, prior to pupation (Paxton, personal communication 1991). Data on the number of flies per cell were not divided into two disjunct groups, but rather formed a continuum, from the most meagerly stocked cell (presumably belonging to a male), to the most generously provisioned cell (presumably belonging to a female). For this reason, rather than attempting to separate the cells according to sex, it has been assumed that all cells have been provisioned for a single sex of offspring. Although this is clearly untrue, the error involved will be the same for both sites if a second assumption, that sex ratios are equal between sites, is taken to be true. No data on sex ratios at each site were collected, and should there be a significant difference between sites for this parameter, the conclusions reached in this section could be rightly questioned.

Cells contained either whole or partially eaten flies, flies consumed by fungus, or the cocoon of an unidentified parasitic fly. Wasp larvae only consumed the soft innards of flies, leaving the cuticle intact. The most

persistent part of the prey was the thoracic shell and it is these parts that were counted to obtain a value for the number of flies provisioned. Although some flies could be identified to family level, many others could not, due to the disintegration and dismemberment of bodily parts as a result of larval feeding and cell excavation. Any attempt to classify the prey into family groups would have led to biased results, as some flies (such as Syrphidae) are more easily recognisable than others and would be over-represented.

The number of flies provisioned inside cells at St Cyrus was greater than the corresponding value at Alderly Edge (table 4.6). The mean weight of cell contents has been estimated for both sites in table 4.7. It was also possible to measure the weight of contents of some cells from Alderly Edge directly (table 4.7), where flies were intact, the eggs not yet having hatched. The observed weight is somewhat lower than the estimated weight, but the two values are not significantly different, the higher value being within one standard error of the lower value. Direct measurements were not possible at St Cyrus, the season starting somewhat earlier, and all excavated cells containing developing larvae or cocoons.

The mean weight of cell contents at St Cyrus is not as high as at Alderly Edge (table 4.7), despite the greater number of flies provisioned. These values indicate that the size difference between the two populations is largely or entirely a function of prey available to the developing larvae, rather than principally a genetic trait. The ratio between mean cell weight at St Cyrus and Alderly Edge (1 : 1.44) can be compared to the ratio of mean female weight between the two populations (1 : 1.60). It seems, at first glance, that *M. arvensis* larvae from Alderly Edge utilise provisions more efficiently than larvae from St Cyrus, as they achieve a greater adult weight than would be expected on the basis of the weight of provisions available to them. However,

M. arvensis larvae consume only the soft parts of the dipteran prey, leaving the cuticle and wings. The surface area to weight ratio is lower for large animals, and therefore the amount of inedible cuticle is less, per weight, for a large fly than several smaller flies totalling the same weight. Thus a large fly affords a greater amount of edible material compared to several small flies of similar weight. Wasps at Alderly Edge catching larger prey need fewer flies per cell not only because the flies caught are larger, but also, and as a consequence of this, large flies provide more food per unit mass than small flies. To correct for this, fresh and dry weights of flies would need to be measured, from which a ratio of the relative amounts of edible material to total body weight, for flies of different body masses, could be obtained.

4.4.1 The Incidence of Cell Parasitism

Parasitism of cells is more frequent at St Cyrus (9.8 %) than Alderly Edge (2.1 %). Two parasites were observed to be active around nests at both sites, the chrysidid wasp *Chrysis ignita*, and a miltogrammine fly, the latter being seen far more frequently than the former. Tachinid flies have been reported to parasitise *M. arvensis* at Oxshott, Surrey (Hamm & Richards 1930), but were never seen in the nesting area at either site in the present study, although some tachinids were caught by wasps at St Cyrus. Other than *M. arvensis* cocoons, the only cocoons that were found in excavated cells were dipteran in shape and probably belonged to a miltogrammine fly.

It is difficult to judge whether the different foraging strategies employed by wasps from the two sites are a response to parasite pressure. Parasitism seems to be more intense at St Cyrus, but the concentration and number of nests at this site is far greater, perhaps leading to an increase in the concentration of parasites. Recent studies of digger wasps (*Crabro cribrellifer*) (Weislo 1984; —

Bembix rostrata (Larsson 1986) support the 'selfish herd' hypothesis (W. D. Hamilton 1971) which predicts a positive correlation between wasp nest density and visits by parasitic flies, but a decrease in average cell parasitism with increasing nest density. The data presented in this study do not agree with this hypothesis, there being a greater frequency of cell parasitism at the densely aggregated and populated nesting site. The density of nests may be a response to the large number of parasites in this location, and perhaps if nest density were less, the incidence of parasitism might be much greater.

Wasps at Alderly Edge may decrease the risk of cell parasitism by reducing the number of prey items per cell, thus providing fewer opportunities to miltogrammine flies, which oviposit on the prey as it is being carried into the nest. However, large flies are more cumbersome to carry, and wasps often require several attempts to enter the nest when so encumbered. Wasps at St Cyrus may have responded to parasite pressure by preying upon smaller flies, enabling cell provisioning with minimal delay at the nest entrance, where they are most likely to be observed by parasites. When carrying small prey, wasps were often observed to fly directly to the entrance with the prey, and enter with very little delay, minimising opportunities to parasites. *

Parasites were also seen to follow wasps carrying prey in flight. Wasps being pursued in this way, rather than flying to the nest, would undertake wide sweeping flights over the nesting area, presumably in an attempt to be rid of the attendant parasite. It might be expected that parasites are more successful at shadowing wasps carrying large flies, which are not only more visible, but also require more stops, and probably fly more slowly, than wasps carrying smaller prey.

* Unlike many other species of wasps, *M. areolaris* never closes the nest entrance. This may be an adaptive strategy to reduce the chance of parasitism by miltogrammine flies by avoiding delays at the nest when returning with prey. *Cercaris zonata* also leave the nest open as a way of avoiding parasites (Elliott et al. 1981).

Without data on the behaviour of wasps in response to parasites, and the degrees of parasitism on cells provisioned with different numbers and sizes of flies, it is not possible to assess whether size differences between wasps from different sites are a result of parasite pressure. However, parasitism accounts for less than 10% of the cells provisioned at St Cyrus and less than 3% at Alderly Edge, and although this is considerable, other factors may be more important in defining wasp body size.

4.5 Prey Selection and Climate - A Summary

There is not enough evidence to suggest that differences in wasp body size between sites can be attributed to the predominance of certain dipteran families, thereby restricting wasps to only large or small flies. Nor is the evidence substantial enough to suggest that wasps, as a population, show specialisation for a particular type of prey. Wasps often catch flies belonging to the same family, but this is more likely to be due to wasps repeatedly returning to the same foraging site than to active prey specialisation.

Climate accounts for 39.4% of the variance in body size between populations of *M. arvensis*, and is therefore an important factor in the evolution of body size differences. However much variance remains to be explained, and non-environmental factors must also be considered. The fact that *Q. ^{rubec}cribrarius*, occupying the same latitudinal range as *M. arvensis* but not nesting in large aggregations of interacting females, does not display a similar latitudinal trend in body size suggests further that other factors are important in the determination of this character. Therefore, an alternative explanation for wasp size variability between populations has to be sought. The following chapter describes a hypothesis that links body size with environmental and biological factors.

Little Wasps

Table 4.1a The Mean Size of *M. arvensis* from Several Populations in Britain.

| <u>Site</u> | <u>Head Width</u> (mm) | <u>N</u> | <u>SE</u> |
|--------------|---------------------------|----------|-----------|
| Findhorn | 2.75 | 21 | 0.05 |
| Alnmouth | 2.85 | 18 | 0.06 |
| St Cyrus | 2.87 | 132 | 0.02 |
| Strensall | 3.13 | 5 | 0.05 |
| Street* | 3.16 | 75 | 0.03 |
| Thetford | 3.17 | 15 | 0.04 |
| River Till | 3.21 | 7 | 0.03 |
| Alderly Edge | 3.32 | 82 | 0.02 |

* Head width data for this site were converted from wing length measurements of *M. arvensis* from Paxton (PhD thesis, 1985). The formula used was: $y = 0.0556 + 0.3046.x$, ($R^2 = 0.966$), where y = wasp head width, and x = wasp wing length. This formula was obtained from head width and wing length measurements of seventy *Mellinus arvensis* from a number of sites (Alderly Edge, Findhorn, Merthyr Mawr, St Cyrus, and Strensall) encompassing a head width range of 2.47 mm - 3.39 mm.

Table 4.1b - One way ANOVA on *Mellinus arvensis* head widths from several populations in Britain.

| <u>SOURCE</u> | <u>DF</u> | <u>SS</u> | <u>MS</u> | <u>F</u> | <u>p</u> |
|---------------|-----------|-----------|-----------|----------|----------|
| SITES | 7 | 13.7226 | 1.9604 | 45.08 | 0.000 |
| ERROR | 347 | 15.0892 | 0.0435 | | |
| TOTAL | 354 | 28.8118 | | | |

Tukey's pairwise comparisons

Family error rate = 0.05

Individual error rate = 0.00745

Critical value = 3.81

Confidence Intervals for the difference between column means and row means.

| | Alnmouth | St Cyrus | Strensall | Street | Thetford | R. Till | Alderly |
|-----------|-----------------|-----------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|
| Findhorn | -0.277 0.084 | -0.013 0.250 | -0.649 -0.090 | -0.543 -0.265 | -0.601 -0.221 | -0.702 -0.211 | 0.423 0.698 |
| Alnmouth | - | -0.119 0.163 | -0.557 0.011 | -0.455 -0.160 | 0.118 0.511 | -0.610 -0.110 | 0.317 0.610 |
| St Cyrus | | - | -0.507 0.005 | -0.367 -0.204 | -0.446 -0.140 | -0.556 -0.120 | -0.521 -0.363 |
| Strensall | | | - | -0.294 0.225 | -0.249 0.331 | -0.242 0.416 | -0.068 0.449 |
| Street | | | | - | -0.152 0.166 | -0.169 0.275 | 0.066 0.246 |
| Thetford | | | | | - | -0.303 0.212 | -0.009 0.307 |
| R. Till | | | | | | - | -0.118 0.325 |

If the confidence interval for the difference excludes zero (figures in bold), there is a significant difference between the sites

for site

Table 4.2 Mean head widths of populations of female *Mellinus arvensis* from specimens in museum collections.

| Site | Latitude | Head Width (\pm SE) | N | Museum Collection |
|---------------|----------|------------------------|----|-------------------|
| Dartmouth | 50.21 | 3.28 (\pm 0.10) | 6 | NHM |
| South Devon | 50.35 | 3.05 (\pm 0.11) | 4 | NHM |
| New Forest | 50.53 | 3.14 (\pm 0.05) | 24 | NHM, HEC |
| Somerset | 51.10 | 3.23 (\pm 0.04) | 20 | NHM, CUM |
| Shapwick | 51.10 | 3.30 (\pm 0.07) | 9 | NHM |
| SW London | 51.20 | 3.01 (\pm 0.04) | 21 | NHM, HEC |
| Chobham | 51.23 | 2.99 (\pm 0.03) | 6 | NHM, HEC |
| Oxford | 51.45 | 2.91 (\pm 0.11) | 24 | NHM, HEC, CUM |
| Suffolk | 52.04 | 3.20 (\pm 0.04) | 16 | NHM, HEC, CUM |
| Deventer | 52.15 | 3.00 (\pm 0.08) | 6 | NHM |
| Rothney | 52.38 | 2.83 (\pm 0.06) | 18 | HEC |
| Co. Claire | 42.45 | 3.31 (\pm 0.22) | 3 | NHM |
| Criccieth | 52.55 | 3.29 (\pm 0.08) | 3 | HEC |
| Wilmslow | 53.20 | 3.21 (\pm 0.08) | 26 | UMM |
| Wallasey | 53.26 | 3.15 (\pm 0.13) | 4 | NHM |
| Collingham | 53.54 | 2.82 (\pm 0.05) | 23 | HEC, CUM |
| Torrs Warren | 54.52 | 2.83 (\pm 0.12) | 4 | RMS |
| Colvend | 54.52 | 2.99 (\pm 0.08) | 9 | RMS |
| Southwick | 54.53 | 3.01 (\pm 0.05) | 4 | NHM |
| Carsethorn | 54.56 | 2.74 (\pm 0.05) | 4 | RMS, NHM |
| Tynefield | 55.01 | 2.91 (\pm 0.08) | 5 | RMS |
| Lochar Briggs | 55.06 | 2.91 (\pm 0.08) | 3 | RMS |
| Closeburn | 55.12 | 2.73 (\pm 0.26) | 3 | RMS |
| Longniddry | 55.58 | 2.81 (\pm 0.13) | 6 | RMS |
| Lawers | 56.34 | 2.89 (\pm 0.05) | 22 | RMS, CUM |
| Glen Muick | 56.58 | 2.95 (\pm 0.12) | 4 | RMS |
| Aberdeen | 57.10 | 2.79 (\pm 0.08) | 3 | RMS, HEC |
| Inverlair | 57.27 | 2.92 (\pm 0.03) | 29 | RMS |

NHM : Natural History Museum, London.

HEM : Hope Entomological Collection, Oxford.

UMM : University of Manchester Museum.

RMS : Royal Museum of Scotland, Edinburgh.

CUM : Cambridge University Museum.

Table 4.3 The Location of Meteorological Stations Used for the Climatological Analysis.

| <u>Field Site</u> | <u>Met. Station</u> | <u>Grid Reference</u> | <u>Distance from Site</u> (miles) |
|-------------------|---------------------|-----------------------|--------------------------------------|
| Findhorn | Kinloss | NJ 067 627 | 2 |
| St Cyrus | Montrose | NO 707 617 | 2 |
| | Arbroath | NO 649 411 | 13 |
| Alnmouth | Boulmer | NU 265 143 | 2 |
| Strensall | Leeming | SF 622 567 | 6 |
| Alderly Edge | Ringway | SJ 830 824 | 3 |
| Oxford | Oxford | SU 515 060 | 2 |
| Thetford | Honington | | |
| Merthyr Mawr | Swansea | SS 654 930 | 15 |
| Street | East Hoathly | TQ 512 165 | 10 |

Weather data were collected from the nearest meteorological station. Detailed information (max. and min. daily temperatures and sunshine hours) were not always available from the nearest station, and in such cases a second station is listed, from which the additional data were obtained.

Table 4.4 Warming and Cooling Rates of Ground Surface Temperatures.

| <u>Site</u> | <u>Warming Rate</u> (°C/min) | <u>Cooling Rate</u> (°C/min) | <u>Maximum Tg</u> (°C) |
|-------------|---------------------------------|---------------------------------|---------------------------|
| Findhorn | 0.301 (± 0.035) | 0.240 (± 0.033) | 38.90 (± 2.33) |
| St Cyrus | 0.295 (± 0.047) | 0.244 (± 0.046) | 44.07 (± 0.78) |
| Alnmouth | 0.204 (± 0.029) | 0.227 (± 0.031) | 36.41 (± 1.56) |
| Alderly | 0.145 (± 0.021) | 0.147 (± 0.024) | 31.50 (± 2.58) |
| Thetford | 0.164 (± 0.018) | 0.206 (± 0.028) | 34.33 (± 1.25) |

Warming rates were calculated for periods when the ground was exposed to solar irradiation, and where insolation was continuous for more than 60 minutes. Cooling rates were calculated for periods when there was a lack of solar insolation for a minimum of 60 minutes. The mean daily maximum ground temperature reached is recorded for the days from which warming and cooling rates data were obtained, and are different to those in table 4.5 as the sample sizes are very much smaller.

Sample sizes for each category:

| <u>Site</u> | <u>Warming Rate</u> | <u>Cooling Rate</u> | <u>Maximum Tg</u> |
|--------------|---------------------|---------------------|-------------------|
| Findhorn | 11 | 9 | 7 |
| St Cyrus | 17 | 10 | 11 |
| Alnmouth | 9 | 10 | 7 |
| Alderly Edge | 17 | 17 | 9 |
| Thetford | 15 | 11 | 9 |

Table 4.5 The Mean Dry Weight of Diptera Families, from Random and Prey Samples, at Aldely Edge

| <u>Family</u> | <u>Random</u> (mg) | <u>Prey</u> (mg) | <u>t</u> | <u>d.f.</u> | <u>p</u> | |
|---------------|-----------------------|---------------------|----------|-------------|----------|-----------|
| Phaoninae | 7.82 | 19.26 | 6.43 | 44 | 0.001 | P > R *** |
| Muscinae | 18.59 | 13.53 | 1.41 | 22 | 0.172 | n.s. |
| Calliphoridae | 14.86 | 9.47 | 2.35 | 28 | 0.026 | R > P * |
| Mydaienae | 7.56 | 6.88 | 0.35 | 13 | 0.735 | n.s. |
| Anthomyiidae | 1.42 | 2.14 | 2.17 | 32 | 0.038 | P > R * |

Table 4.6 St Cyrus and Alderly Edge Cell Contents

| | Mean No. of Flies/Cell (\pm SE) | N | Parasitised % (N) | Fungal Infection % (N) |
|--------------|---------------------------------------|----------|----------------------|---------------------------|
| St Cyrus | 7.00 (\pm 0.59) | 44 (51)* | 9.8 (5) | 3.9 (2) |
| Alderly Edge | 3.93 (\pm 0.27) | 46 (48)* | 2.1 (1) | 2.1 (1) |

* The figure outwith the brackets is number of cells containing intact or partially consumed flies and excludes parasitised cells and cells infected by fungus. The figure inside the brackets includes all the excavated cells from that site.

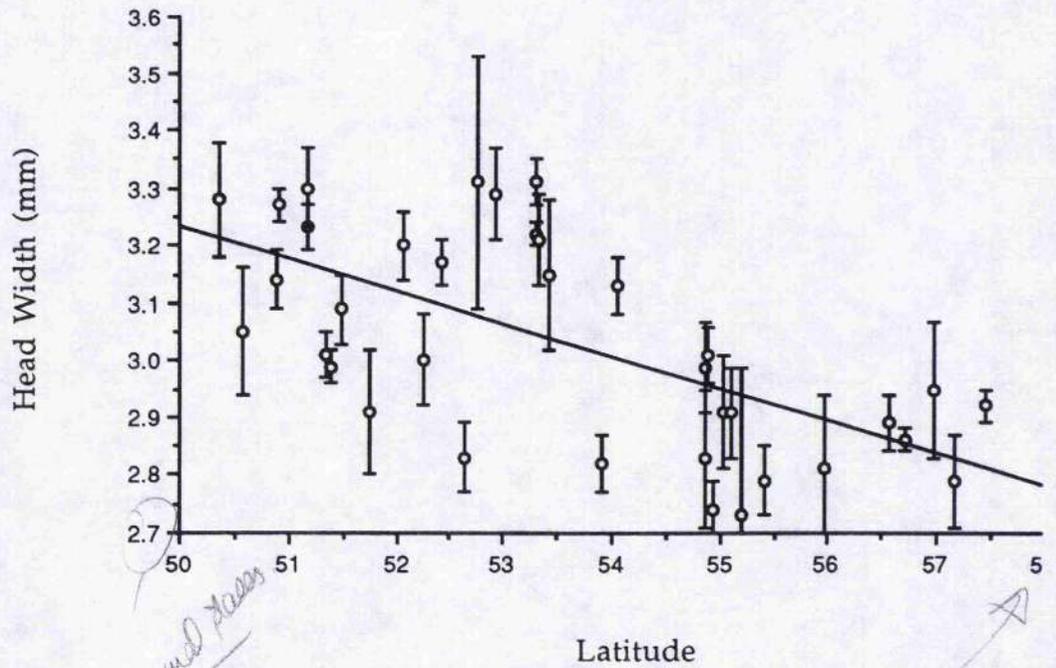
Table 4.7 The Weight of Cell Contents from Alderly Edge and St Cyrus

| | Mean Dry Wt. of Prey Items (mg) | Mean No. of Prey/Cell | Estimated Wt. of Cell Contents (mg) |
|--------------|------------------------------------|--------------------------|--|
| St Cyrus | 4.99 | 7.00 | 34.93 |
| Alderly Edge | 12.79 | 3.93 | 50.33 |

Observed weight of cell contents at Alderly* = 44.54 mg (SE = 7.72, N = 15)

* It was possible to weigh the cell contents of some of the cells from Alderly Edge where the flies were found intact (see text).

Fig. 4.1 The correlation between size and latitude for populations of *Mellinus arvensis* in Britain. Latitude has been converted to decimal units. $y = 6.045 - 0.056x$, $R^2 = 0.404$; $p < 0.001$, $t = 4.800$, $d.f. = 34$. ✓



Key for climatic graphs
Figures 4.2 - 4.4

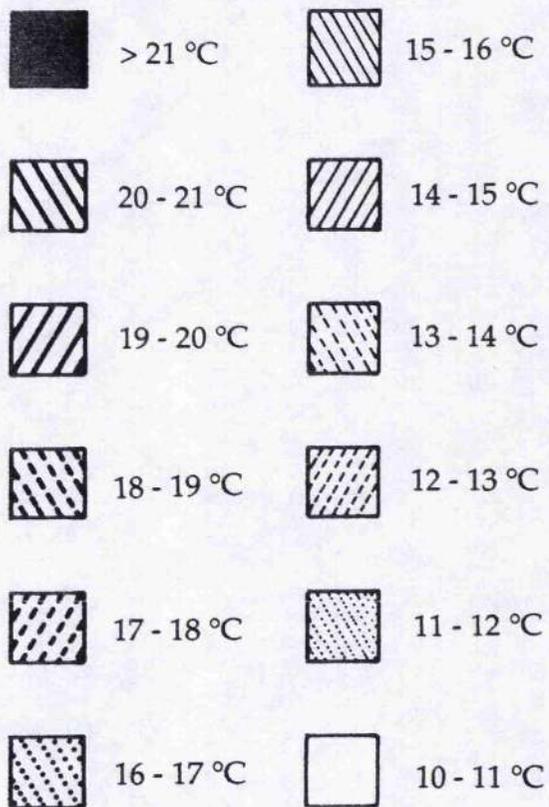


Fig. 4.2

Mean daily temperature $^{\circ}\text{C}$ 1941-70 August
Reduced to mean sea level $0.6^{\circ}\text{C}/100$ metres

redo.

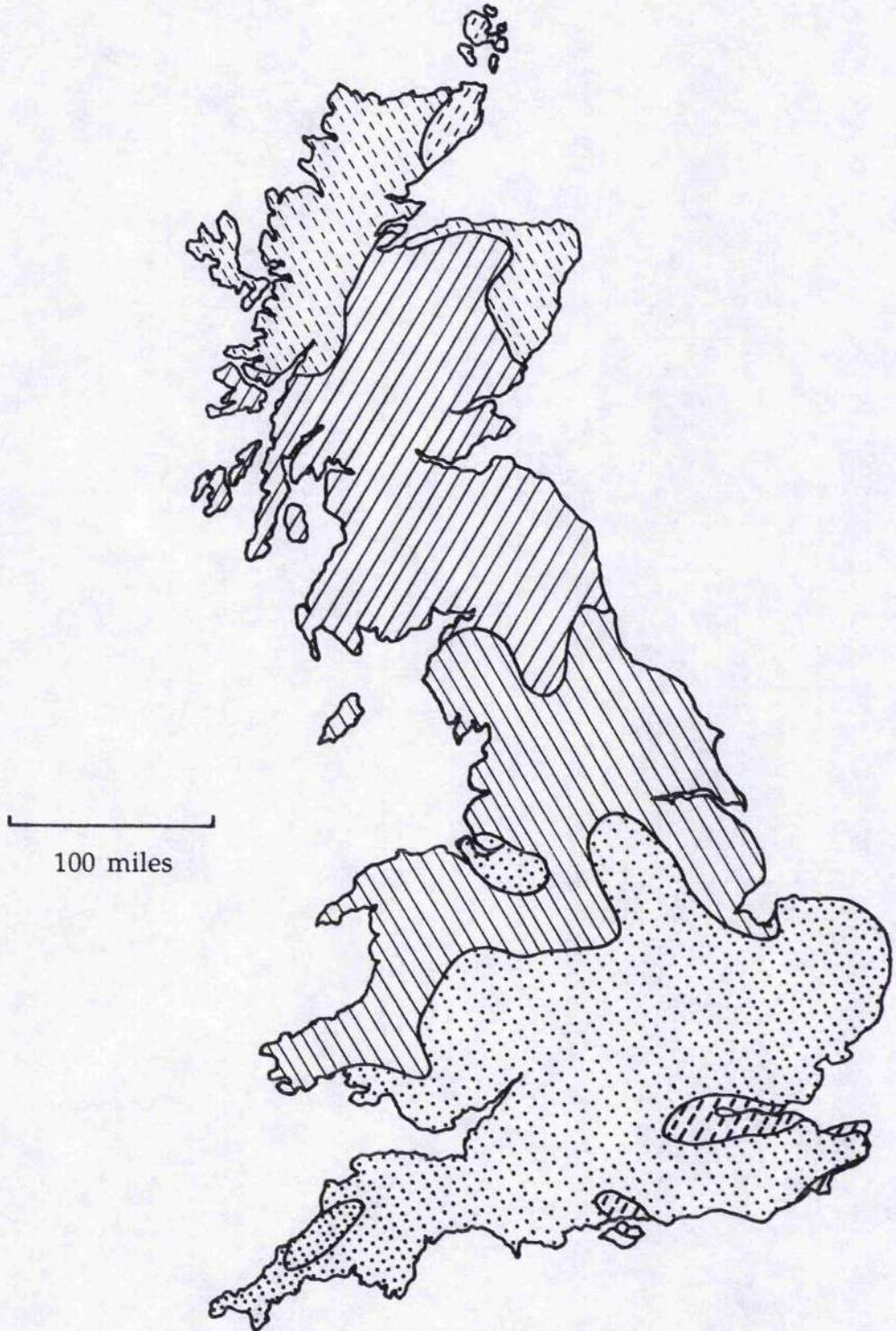


Fig. 4.3

Mean daily maximum temperature °C 1941-70 August
Reduced to mean sea level 0.7°C/100 metres

}redo

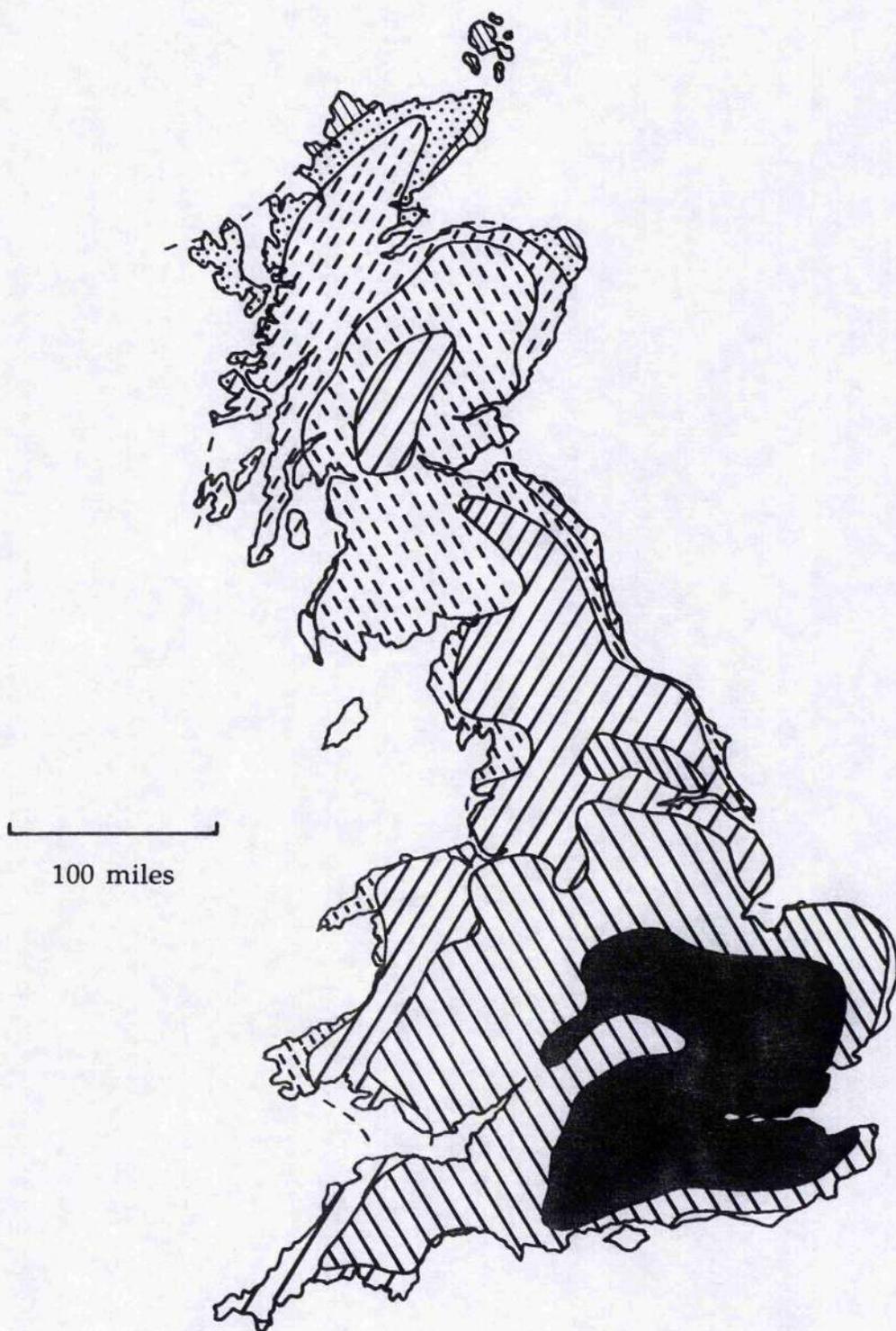


Fig. 4.4

Mean daily minimum temperature °C 1941-70 August
Reduced to mean sea level 0.5°C/100 metres

}redo

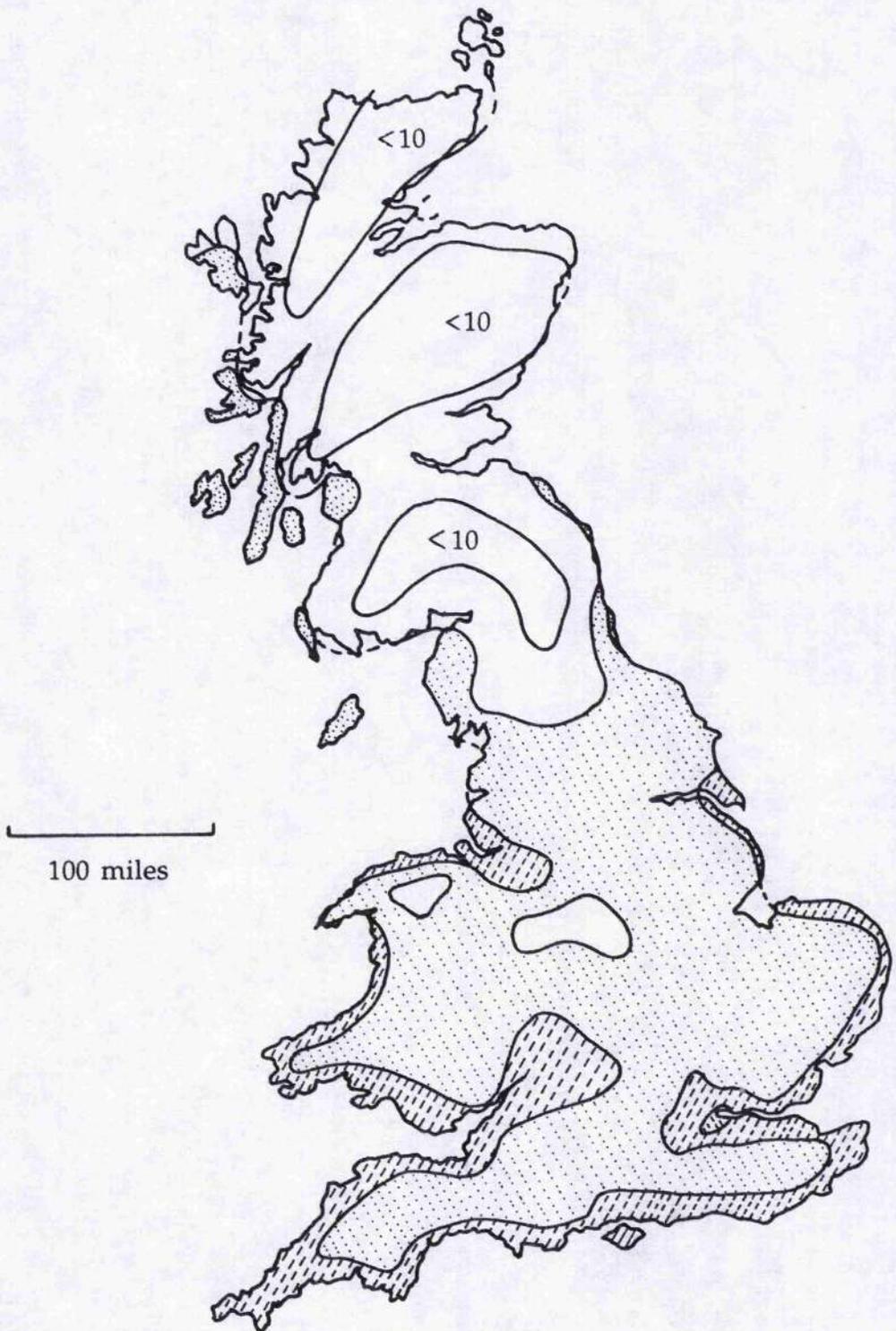


Fig. 4.5 Mean August daily temperatures (1988-1992) plotted against latitude of the weather station from which the data came. Latitude has been converted to decimal units. $y = 35.204 - 0.351x$, $R^2 = 0.619$; $p < 0.01$, $t = 3.372$, $d.f. = 7$.

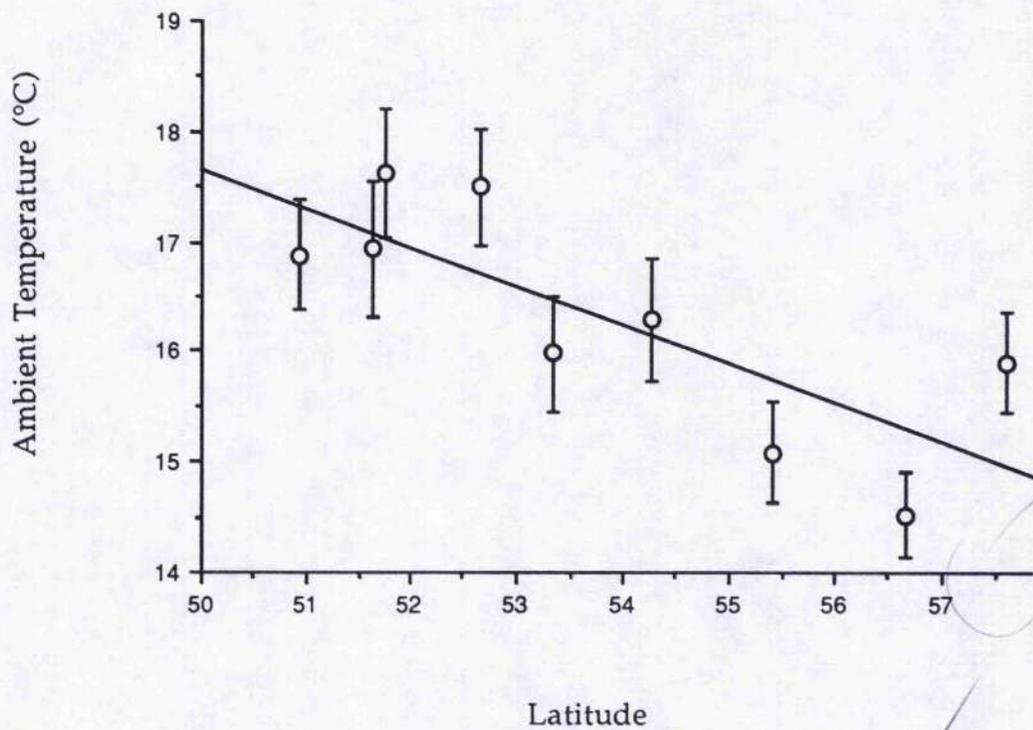
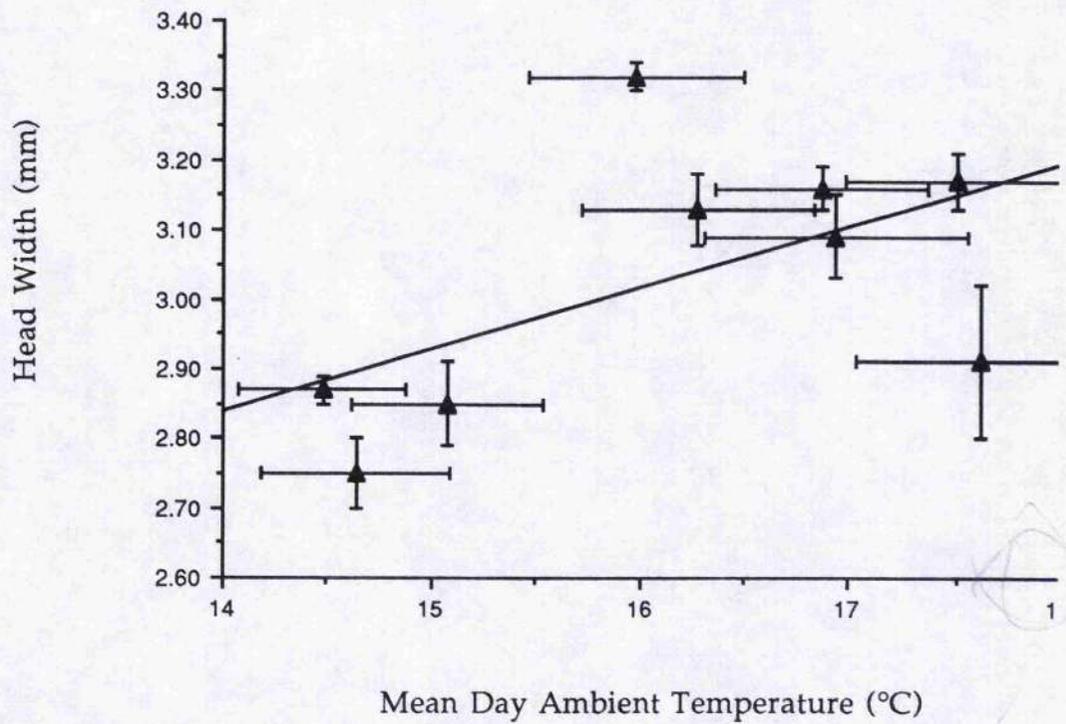


Fig. 4.6 The correlation between wasp size and mean day (0900 - 2100) ambient temperature for the month of August (1988 - 1992). $y = 1.609 + 0.088x$, $R^2 = 0.308$; $p > 0.02$, $t = 3.142$, d.f. = 7.



1.765

1

✓

Fig. 4.7 The correlation between wasp size and the frequency of days in the season where the maximum temperature reached is between 17 - 18.9 °C. $y = 3.409 - 0.016x$, $R^2 = 0.489$; $p > 0.1$, $t = 1.694$, d.f. = 3.

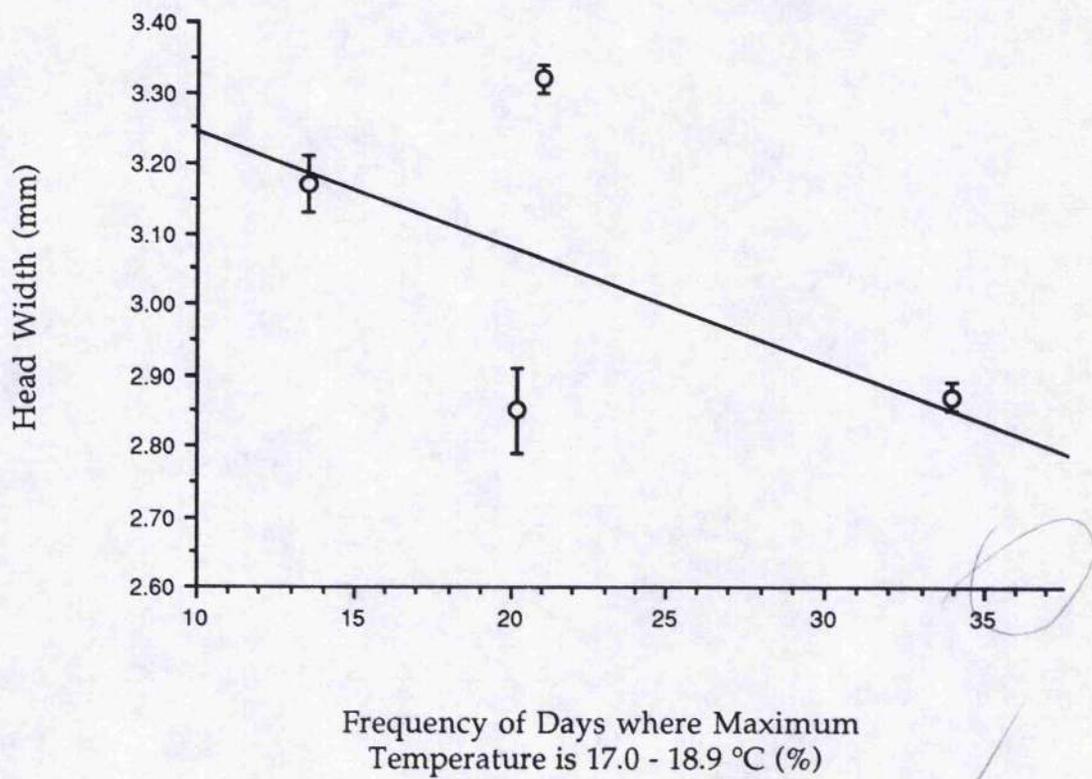


Fig. 4.8 The correlation between wasp size and the frequency of days in the season where the maximum temperature reached was greater than 19 °C. $y = 2.482 + 0.009x$, $R^2 = 0.566$; $p > 0.1$, $t = 1.978$, d.f. = 3.

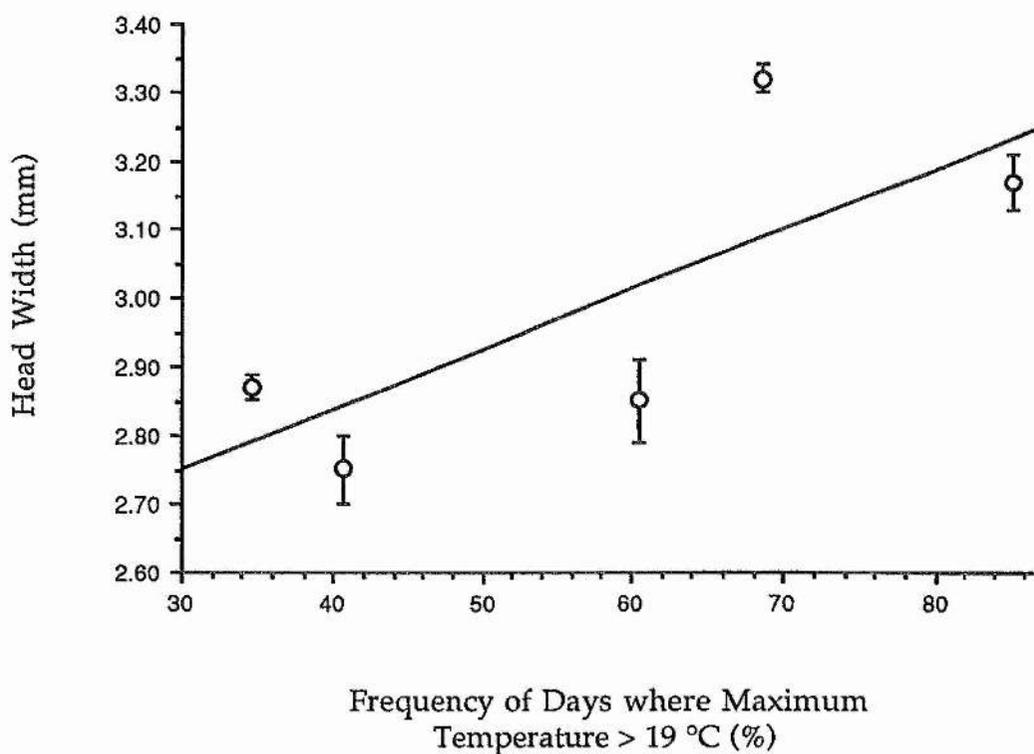


Fig. 4.9 The rate of passive warming of *Mellinus arvensis* (presented as half time to maximum body temperature, ie, the time taken to reach the mid point between initial and final (maximum) temperature). $y = - 4.204 + 2.836x$, $R^2 = 0.814$; $p < 0.01$, $t = 5.124$, $d.f. = 6$.

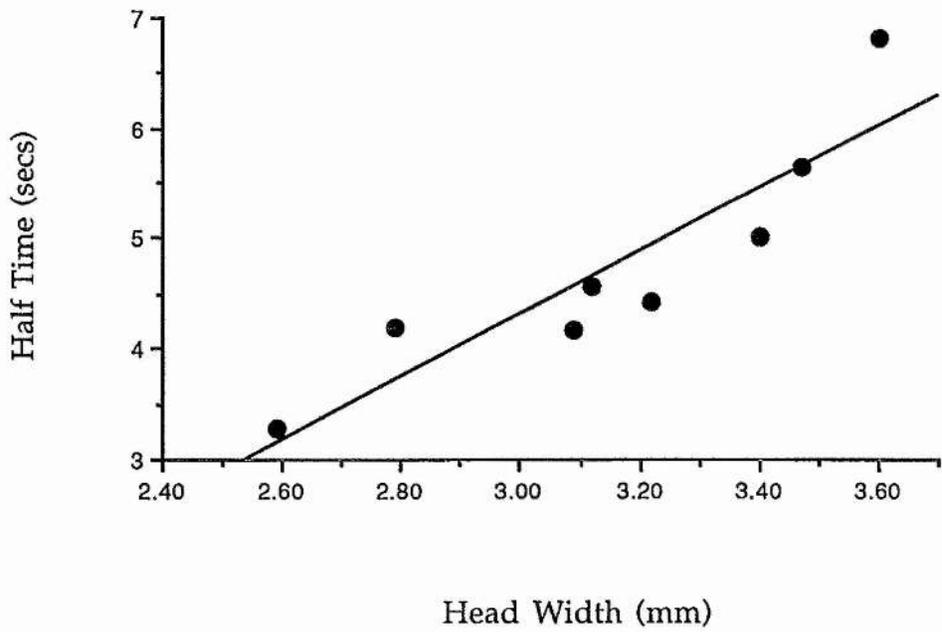


Fig. 4.10 The rate of passive cooling of *Mellinus arvensis* (presented as half time of the cooling curve, ie, the time taken to reach the mid point between maximum and minimum temperature). $y = -2.394 + 2.167x$, $R^2 = 0.772$; $p < 0.01$, $t = 4.507$, d.f. = 6.

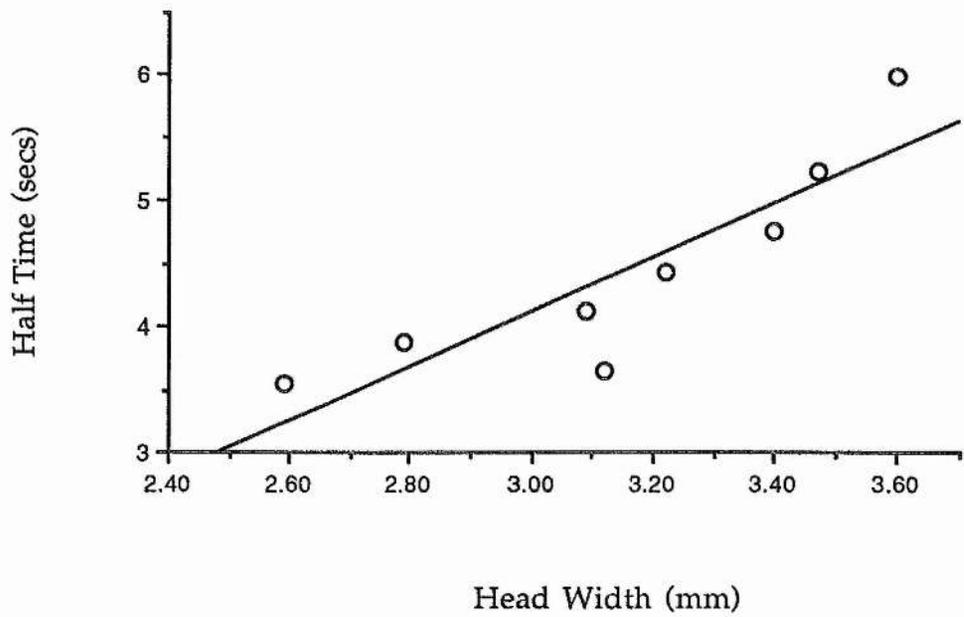


Fig. 4.11 The maximum thoracic temperatures (T_{th}) reached through passive warming of *Mellinus arvensis* of different sizes. $y = 5.815 + 11.427x$, $R^2 = 0.688$, $p < 0.05$, $t = 3.320$, d.f. = 6

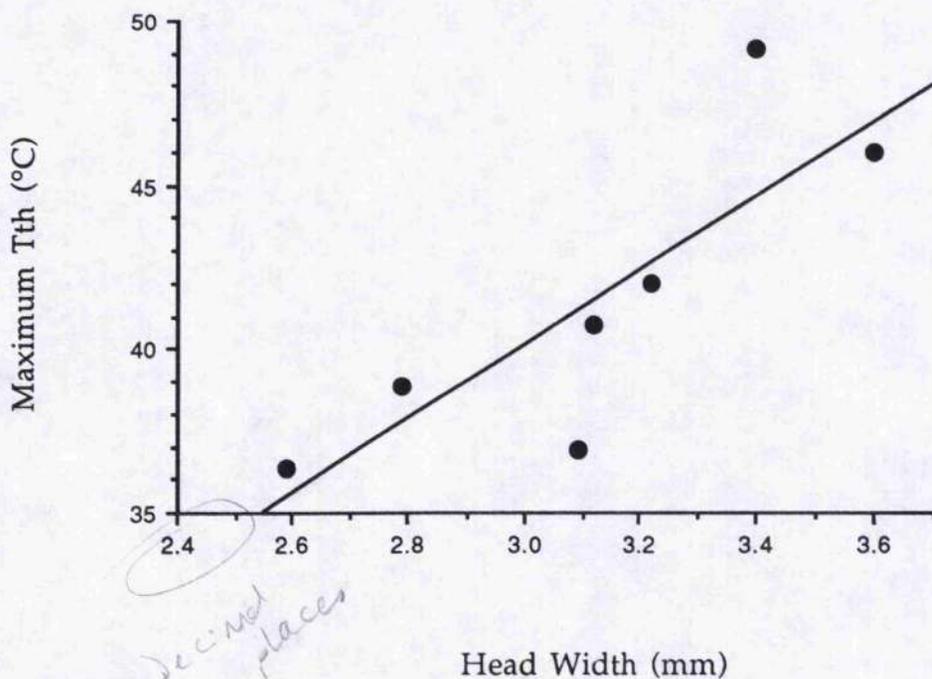


Fig. 4.12 The correlation between mean nest entrance temperature (T_e) excess at the time of first wasp emergence, and mean wasp size. $y = 41.898 - 12.235x$, $R^2 = 0.889$; $p < 0.1$, $t = 4.002$, $d.f. = 2$.

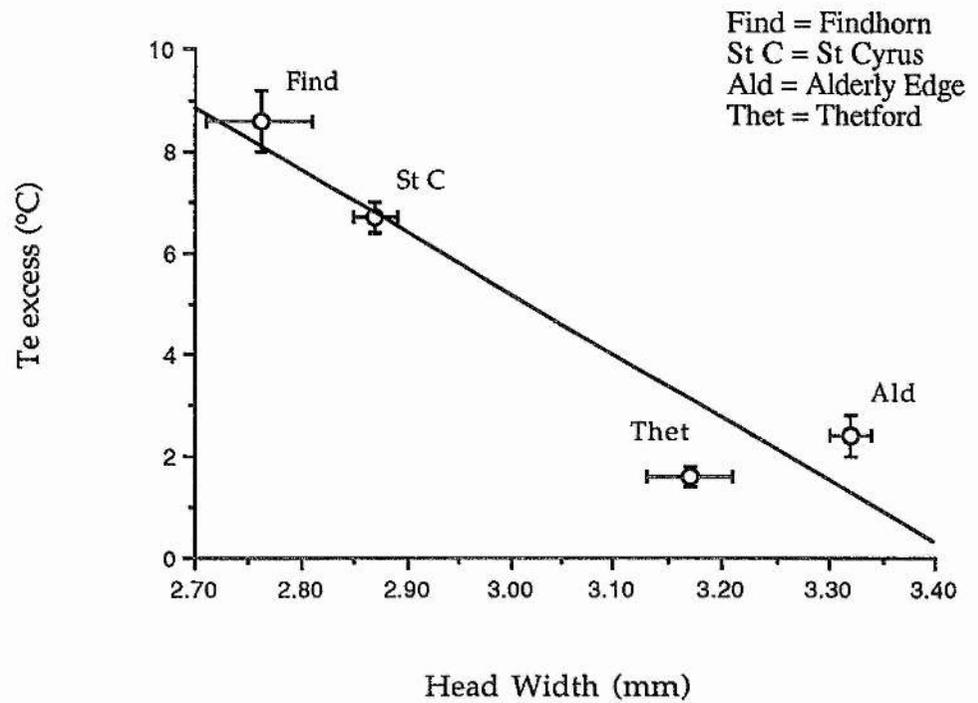


Fig. 4.13 The correlation between size and latitude for populations of *Crabro cribrarius* in Britain. Latitude has been converted to decimal units. $y = 3.61 + 0.0014x$, $R^2 = 0.001$; $p > 0.5$, $t = 0.145$, d.f. = 21.

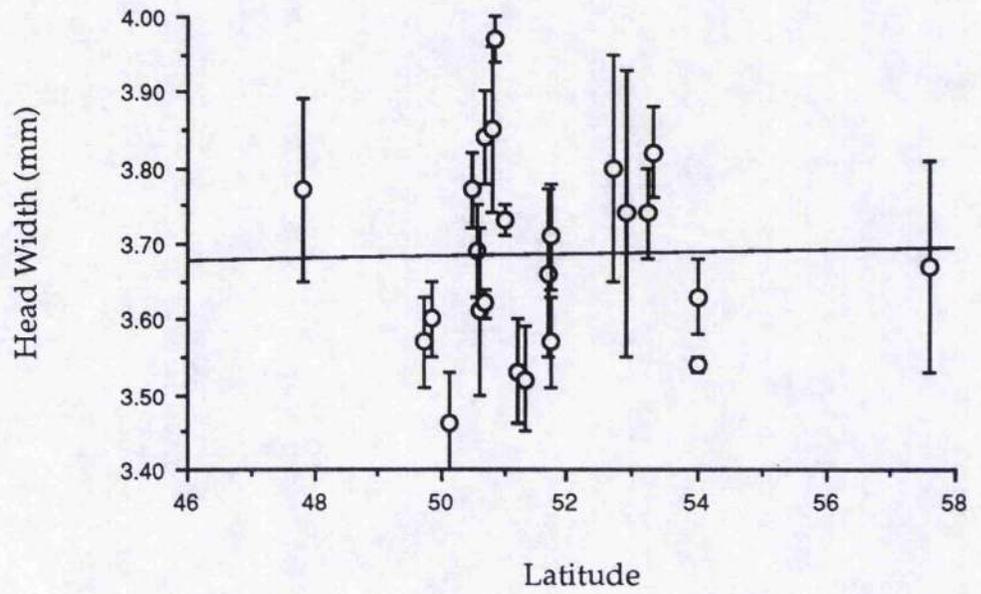


Fig. 4.14 The correlation between the size of wasps and the weight of their prey. $y = -34.46 + 14.34x$, $R^2 = 0.295$; $p < 0.001$, $t = 6.171$, $d.f. = 91$.

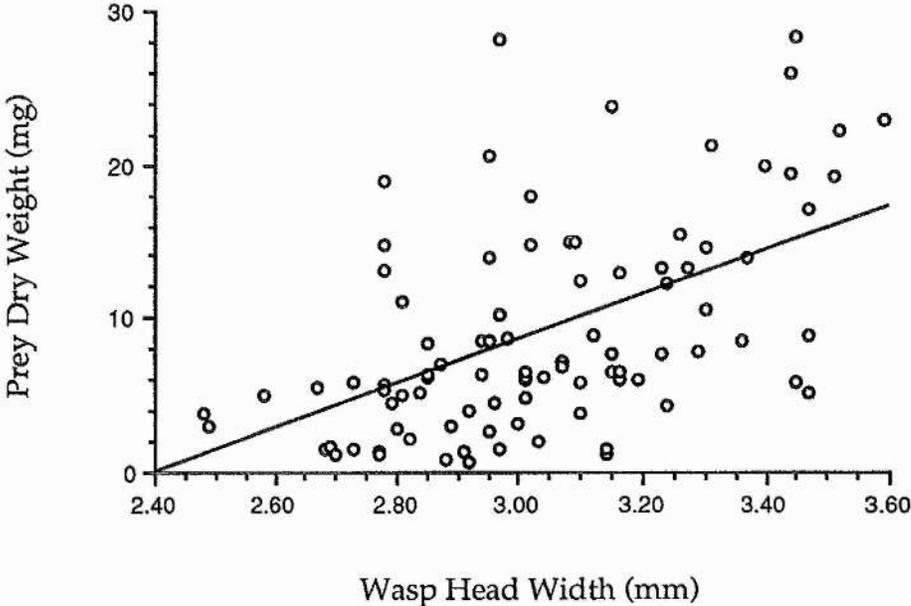
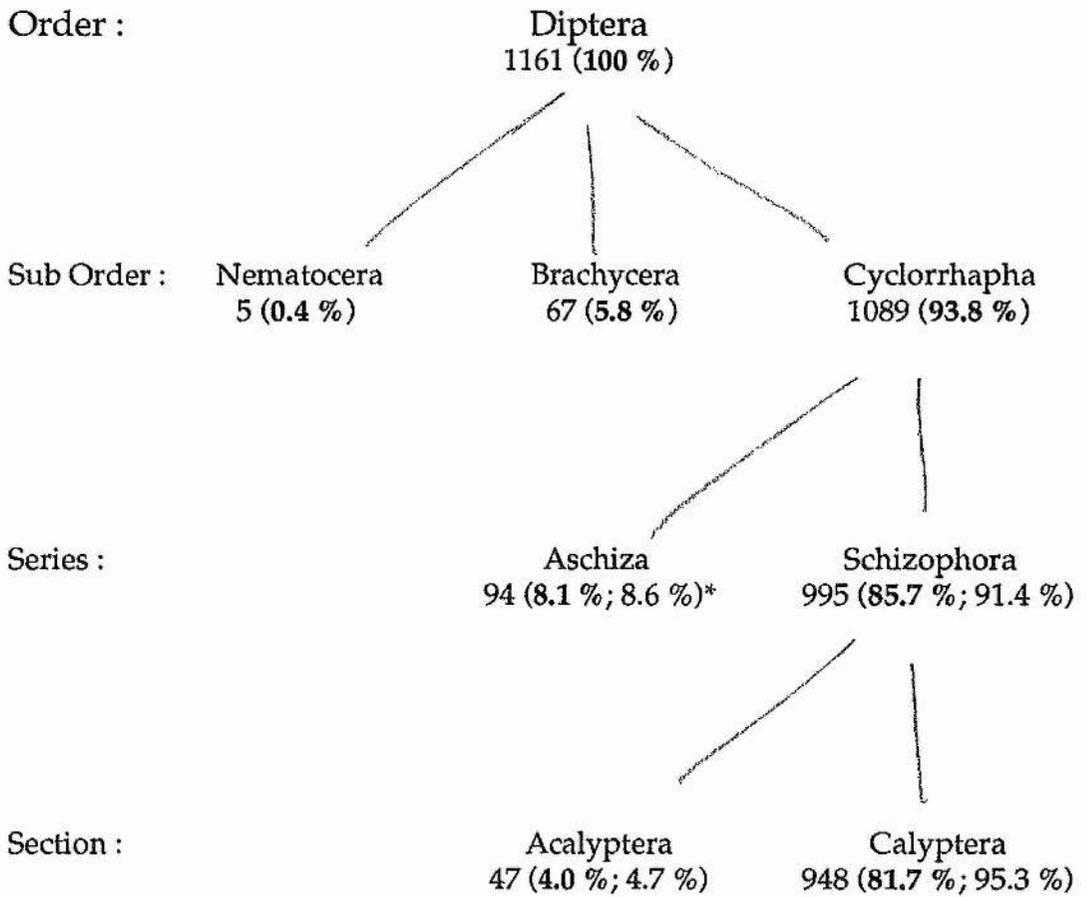


Fig 4.15 The number and relative proportions of prey caught by *Mellinus arvensis* at all sites.



* The first figure (in bold text) within the brackets is the fraction represented by the taxonomic group as a percentage of the total number of flies (1161) included in the analysis.

The second figure is the fraction represented by the taxonomic group as a percentage of the number of flies included in the preceding taxonomic group.

Fig. 4.16a The relative proportions of prey taken by *M. arvensis* at St Cyrus.

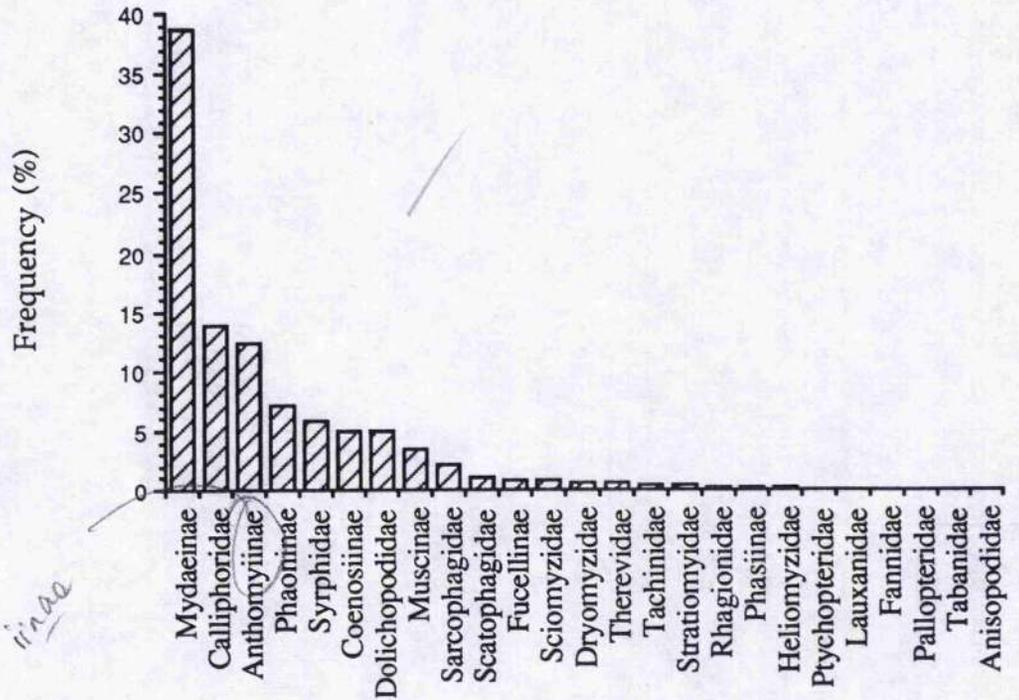


Fig. 4.16b The relative proportions of Diptera caught in the random sweep net samples at St Cyrus.

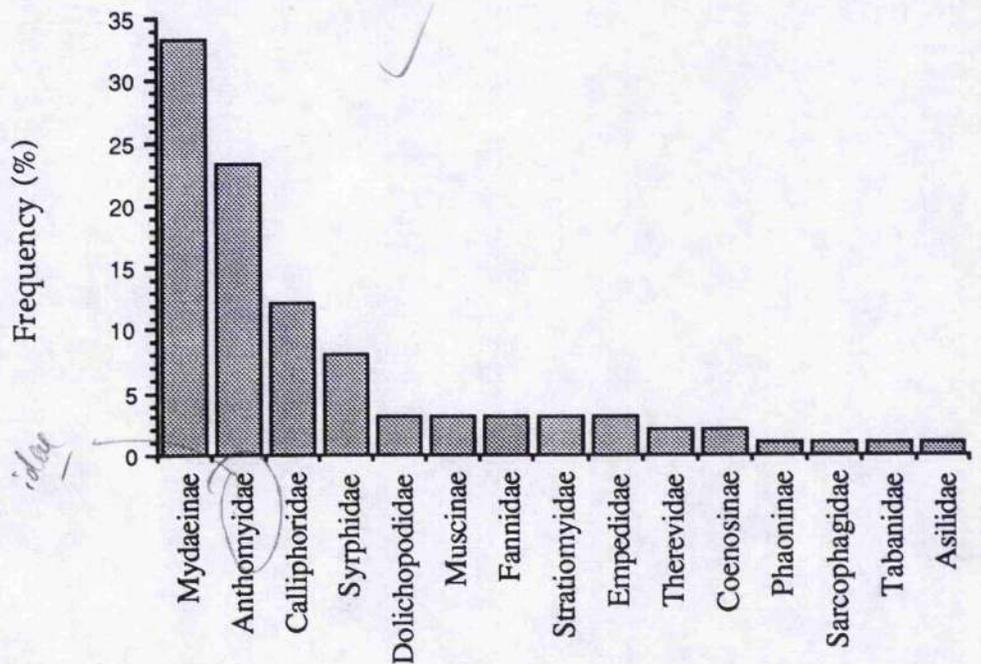


Fig. 4.17a The relative proportions of prey taken by *M. arvensis* at Alnmouth.

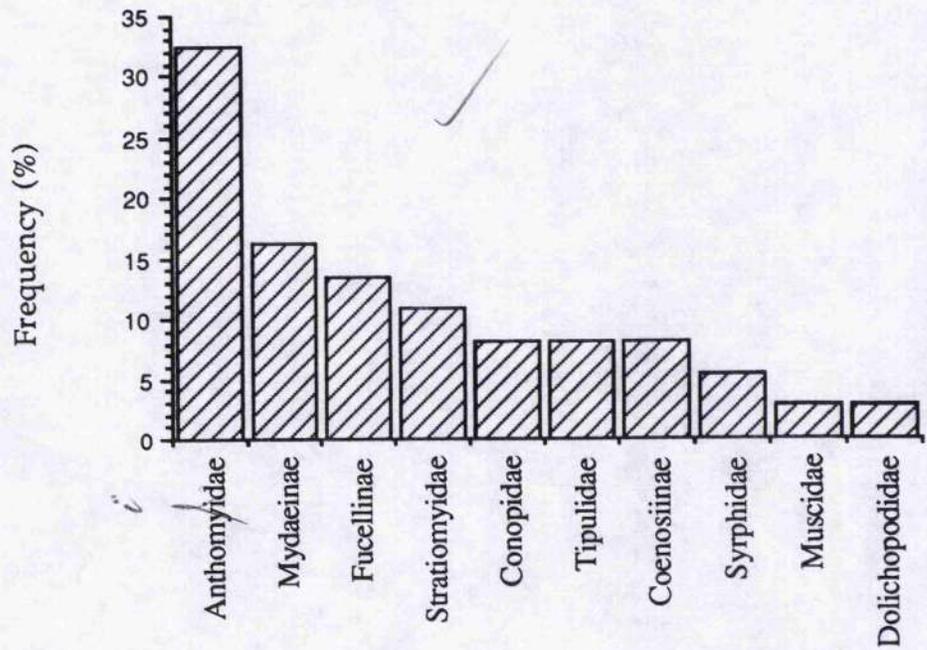


Fig. 4.17b The relative proportions of Diptera caught in the random sweep net samples at Alnmouth.

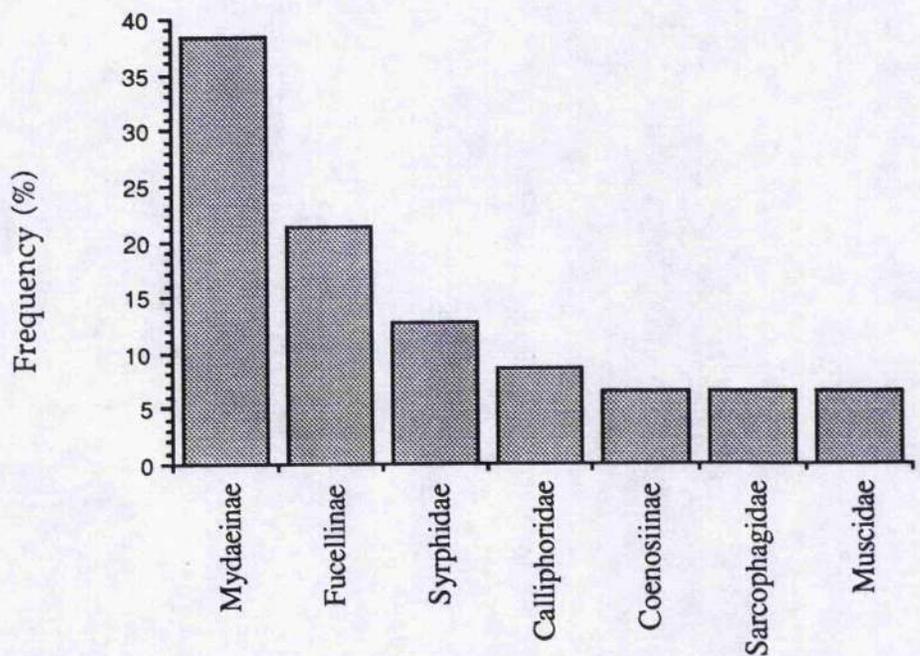


Fig. 4.18a The relative proportions of prey taken by *M. arvensis* at Alderly Edge.

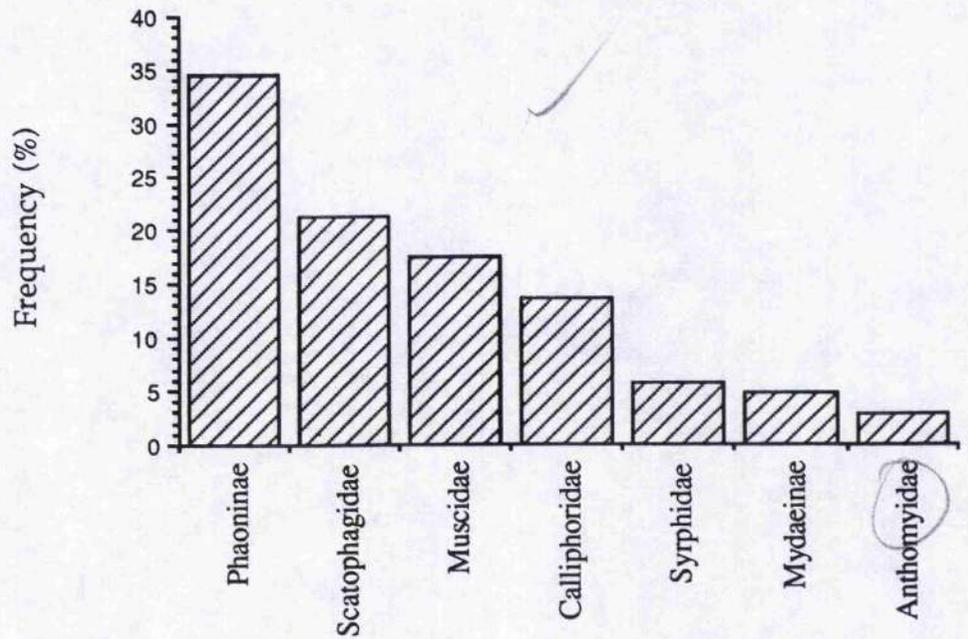


Fig. 4.18b The relative proportions of Diptera caught in the random sweep net samples at Alderly Edge.

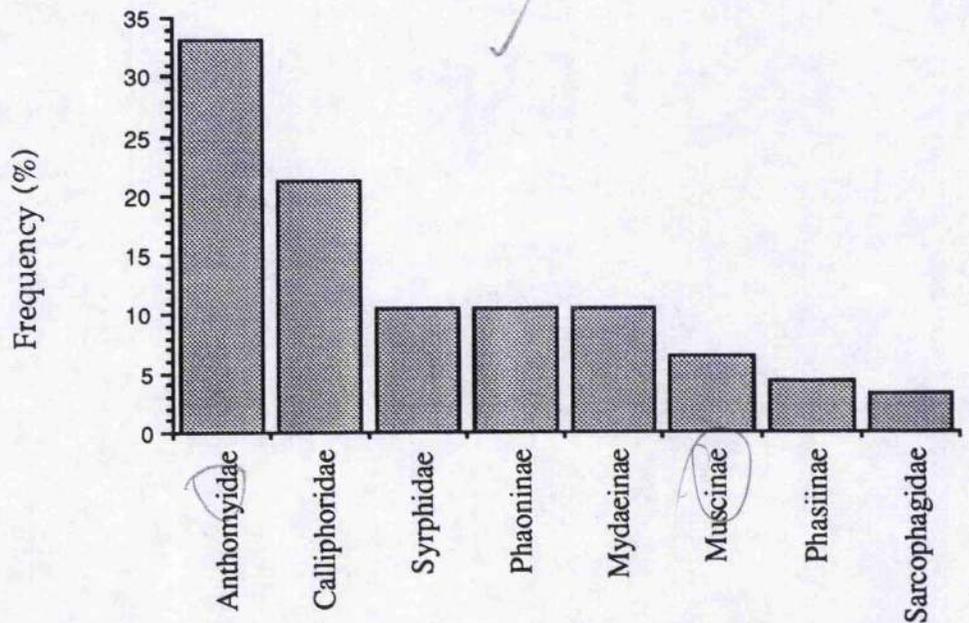


Fig. 4.19a The relative proportions of prey taken by *M. arvensis* at Thetford.

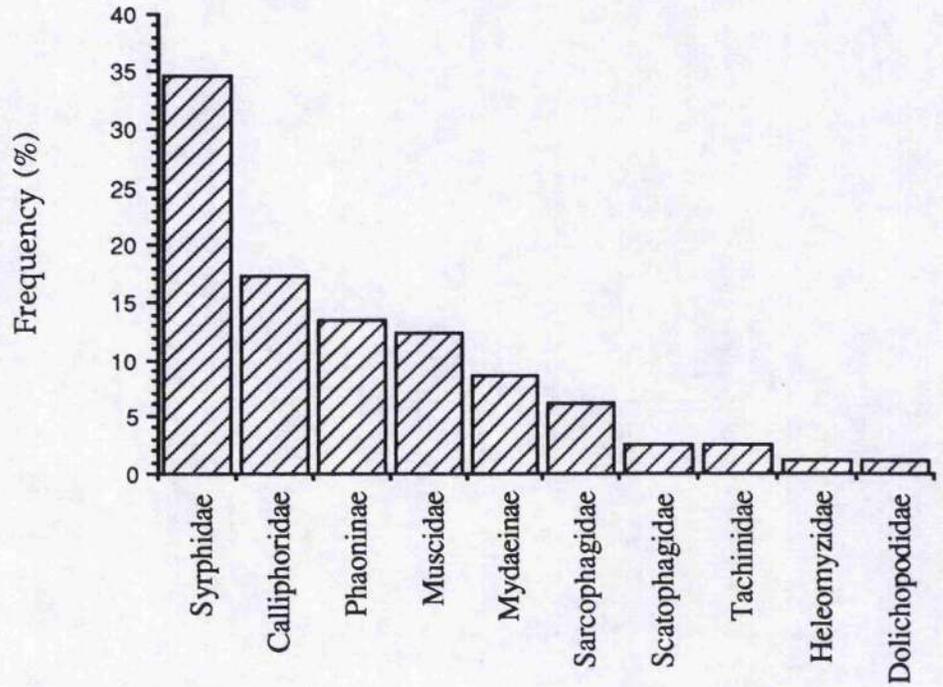


Fig. 4.19b The relative proportions of Diptera caught in the random sweep net samples at Thetford.

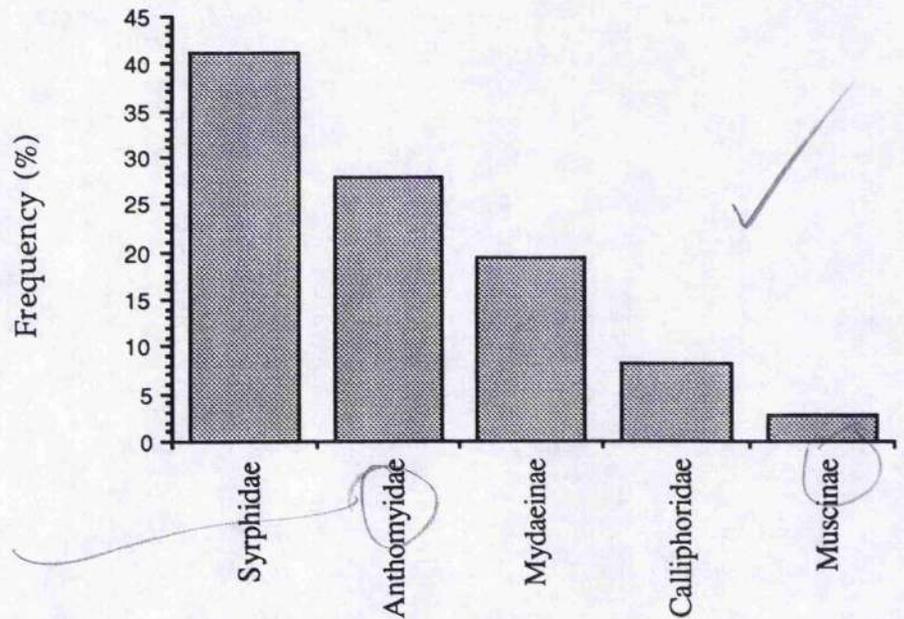
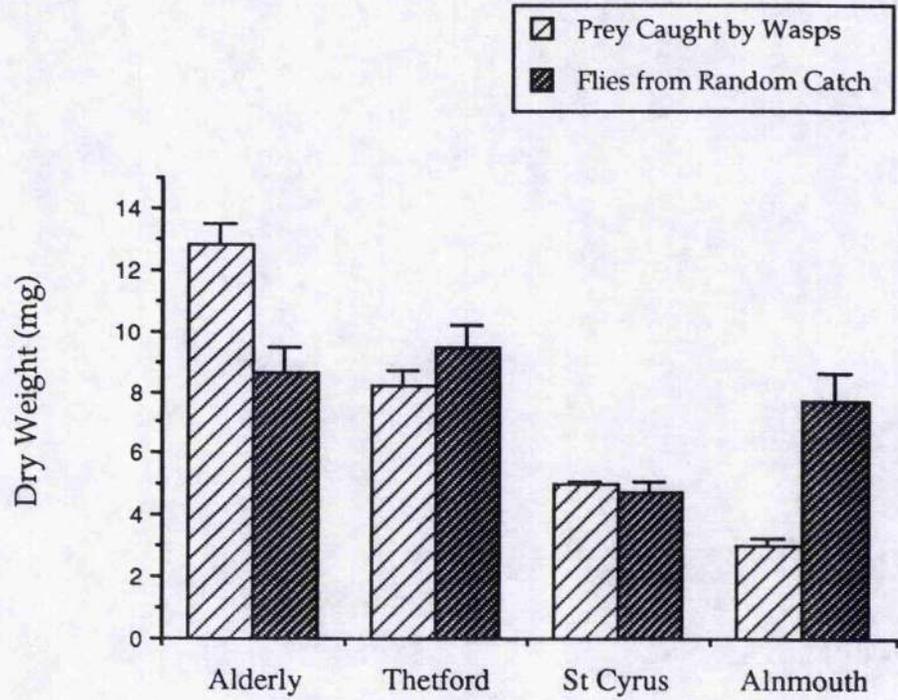


Fig. 4.20 Mean weight of prey caught by *Mellinus arvensis* and the mean weight of a random sample of flies from four widely separated populations. Populations are arranged in order of decreasing mean wasp size.



Chapter 5 - Usurpation and Aggression in *Mellinus arvensis*: an Explanation of Size Variation Between Populations

5.1 The Wasp Usurpation Hypothesis: an Introduction.

Intraspecific parasitism has been observed in a large number of aculeate genera (reviewed by Field 1992a,b). Six types of intraspecific parasitism have been defined according to resources lost to the host (Field 1992a,b), and gains to the parasite in terms of avoided costs. Cells may be brood parasitised, by replacing the host egg with one belonging to the parasite. Provisions may be stolen from cells, thus avoiding foraging costs, or alternatively, the nest itself may be stolen. Usurpation of nests among conspecifics has been reported in several sphecid genera, including *Ammophila* (Hager & Kurczewski 1986), *Crabro* (Alcock 1982), *Cerceris* (Alcock 1975a; Elliott & Elliott 1987; Field & Foster, unpublished observations), *Lindenius* (Miller & Kurczewski 1973), *Philanthus* (Gwynne 1981), *Sphecius* (Lin 1963; Pfennig & Reeve 1989), *Sphex* (Brockmann & Dawkins 1979; Brockmann 1985a), and *Trypoxylon* (Brockmann 1980a). Aggression between two females at a burrow has been reported for *Mellinus arvensis* (Hobby 1931b), and nest usurpation in *M. arvensis* has been observed by Bristowe (1948), Olberg (1959), Huber (1961), and, more recently, by Paxton (1985).

Through the usurpation of a nest, a wasp avoids the costs of finding a nest site and nest construction. The costs to a usurper, however, may be considerable in terms of injury to body parts, or risk of predation while searching for a nest. Therefore, usurpation is a strategy that is more successful in areas where the benefits of usurpation are great. Usurpation ceases to become viable when the costs involved outweigh the gains made. The value

of a nest to a wasp is determined by the time and energy expended in acquiring the nest, either by digging or usurpation, and the risks involved in doing so. Nest value will also increase if the number of nests, or suitable nesting sites, are limited (Cowan 1981) or if the time left for cell provisioning is low (ie. when it is late in the season). The time and energy invested in a nest may be dependent on environmental factors such as temperature (Brockmann & Dawkins 1979; Willmer 1985; Field 1989a) or soil hardness (Elliott & Elliott 1987; McCorquodale 1989a).

Most sphecid wasps dig their nests in the ground which can be subject to rapid heating and cooling. Wasps digging new nests in such conditions may risk overheating, and may have to limit digging activities to more thermally favourable times of the day (see section 3.3.1).

Soil density and surface compaction are known to influence nest site selection by *Sphex ichneumoneus* (Brockmann 1980b). Several species of *Cerceris* avoid digging through a hard surface crust by using a pre-existing holes in the crust (Tsuneki 1965), remaining in the natal nest (Evans & Hook 1986; Hook 1982), moving in with another female (Evans & Hook 1986; Hook 1982; Elliott & Elliott 1987; McCorquodale 1989a,b,c), or usurping the nest of another female (Elliott & Elliott 1987), all of which suggests significant costs for nest digging to *Cerceris* females. Nest initiation in *Cerceris antipodes* was more frequent after periods of rain when the soil surface was softer (McCorquodale 1989a). Costs to wasps of digging through hard soils could be increased time to dig the nest, and more wear to the body parts such as wings, cuticle and mandibles (Alcock 1980; Evans & Hook 1986).

At sites where the costs of nest construction are high, the benefits of nest usurpation increase, and hence aggressive interactions between nest

occupiers and searchers become more frequent. Where the amount of time available for wasp activity, and hence nest excavation, is limited, the construction of a nest would represent a high cost in terms of time. Wasp activity periods are a function of temperature, wasps requiring a minimum of 14 °C to be active (Chapter 3). It is unlikely that nesting activity is limited by high temperatures at British sites. Ground surface and nest entrance temperatures rarely exceeded 40 °C (Chapter 4), and the small size of *M. arvensis* minimises the risks of overheating. Minimum temperatures are of greater importance at British locations, limiting the amount of time available for nest construction or foraging. There is a trend of decreasing temperature with increasing latitude, and accordingly, the number of hours per day that ambient temperature exceeds 14 °C is less at northern sites (Chapter 4). It might therefore be expected that usurpation intensity increases with increasing latitude.

Soil type can influence the cost of nest construction, with hard compacted soils requiring more time and effort to dig through. Soil type, and therefore soil hardness and degree of compaction, is geographically variable. Because of this variation, nests dug at sites of a certain soil type might represent a greater investment of time and energy than nests dug at other locations, where the soil might be of a different, softer, type. If this is indeed the case, then aggression between wasps at sites where nests are difficult and costly to dig, is expected to be high.

The importance of size in influencing the outcome of an aggressive encounter between two individuals has long been known for vertebrates (Ghiselin 1974) but has been less well documented in invertebrates (Hamilton et al. 1976; Potter et al. 1976; Alcock et al. 1977; Borgia 1980; Severinghaus et al. 1981). There are only a few examples of a large size advantage in the Sphecidae and

these mostly refer to aggression between mate seeking males (eg Alcock et al. 1978; Alcock 1979; O'Neill 1983; O'Neill & Evans 1983; Thornhill & Alcock 1983; Larsson 1989a,b,c), rather than nesting females. The one clear example of a size advantage between female sphecid wasps is in *Lindenius columbianus errans*, where the winner of aggressive encounters between females over nest ownership was almost always the larger female (Miller & Kurczewski 1973). If a large size advantage does exist in sphecid wasps, encounters between wasps involving attempted usurpation should favour the larger female. Assuming all other factors are equal, in areas where pressure from usurpers is high, mean wasp size might therefore also be expected to be high.

A hypothesis can now be formulated that integrates body size, aggression and soil hardness. This hypothesis is based on the assumption that the value of a completed wasp burrow to a wasp is greater in areas where soil is difficult to penetrate. Nest usurpation attempts, and therefore the amount of aggression, at sites which have hard soil types will be high because of high nest values. If large wasps are favoured over small wasps in aggressive encounters, then there might be a selection pressure towards larger wasps at these sites. This selection pressure is countered by the number of offspring a wasp can provide for. A large offspring requires more food, and thus represents a greater investment of foraging time and energy by the adult wasp. It therefore follows that wasps provisioning each cell with many prey provision fewer cells, and leave fewer, although possibly fitter, large offspring. Where nest value is low there is no advantage to being large, and wasps might be reproductively more successful by provisioning many cells for smaller offspring. In such a case the selection pressure will be in the opposite direction, favouring females which maximise the number of offspring by reducing the amount of flies provisioned in each cell.

From this hypothesis a number of predictions can be made. Firstly, mean wasp size will be higher in areas where soils are harder. Consequently, nests will take longer to dig at these sites. Secondly, aggressive encounters, and the incidence of attempted usurpation, will be more frequent at sites where the mean body size is high. The validity of this hypothesis rests on the premise that there is a large size advantage in aggressive interactions between wasps. A size related advantage has been demonstrated in fights between *Stictia heros* females (unpublished data, Villalobos & Shelly) but this premise remains to be tested for *M. arvensis* females.

5.2 Geographical Variation of Soil Hardness

According to the above hypothesis, the mean body size of a population of *M. arvensis* is a function of soil hardness and the two factors must therefore be correlated. Measurements of soil hardness, made using a penetrometer (Chapter 2), were taken at all field sites (table 5.1). Figure 5.1 shows that soil hardness is correlated with wasp size, with large wasps found in areas where the soil is hard ($p = 0.028$, $t = 2.69$, $d.f. = 9$, $R^2 = 47.4\%$). This result confirms the first prediction made above, but it remains to be seen whether the mechanism by which soil hardness affects wasp size is aggression, as the hypothesis proposes. There is, however, an unusual result from Findhorn. Wasps at this site appear to be very much smaller than what might be expected on the basis of soil hardness. The site at Findhorn is the furthest north, and it may be that climatic effects have a greater influence on body size than soil hardness. Another possible explanation that is in accordance with the hypothesis described above is that the population size at Findhorn is small (about 30 nests at the height of the season), and the usurpation intensity is likely to be less, and thus no advantage is to be gained from large size.

Variation in soil hardness may explain the observed differences in nest depth and the time taken for nest construction between sites (Chapter 3, Section 3.1 & 3.2). Although there is no significant correlation between soil hardness and either time to dig a nest ($p = 0.251$, figure 5.2) or nest depth ($p = 0.643$, figure 5.3), there does seem to be a trend of an increase in the time taken to dig the nest with increasing soil hardness (figure 5.2), with an R^2 value of 56.1%. This trend indicates that hard soils do impose increased time, and probably energy, costs for nest construction. The premiss, vital to the overall hypothesis, that wasps nesting in hard soils invest more in nest construction than wasps in loose soil, is supported by these data. To ascertain the relative importance of soil hardness on this variable, more data need to be collected from several other sites, giving a larger sample size.

There is no indication of a correlation between soil hardness and nest depth, with the correlation coefficient explaining only 8.1% of the variance (figure 5.3). Nests at Alnmouth are shallow and occur in loose soils, suggesting that the mean time taken to dig a nest at this site is likely to be low (although no data for this were collected). If this is true, then nests at this site would represent a relatively small investment by the wasps, and accordingly nest usurpation is expected to be low. Where the frequency of usurpation is low, defense of the nest and thus female size is a low priority, and this is reflected in the small size of wasps at Alnmouth (mean 2.85 mm head width, see table 4.1a). Nests at Alderly Edge are also shallow (19.10 ± 0.97 cm), possibly reflecting the difficulty of digging in the hard substrate that occurs at this site, whereas in the soft soils of St Cyrus nests are deep (29.77 ± 1.34 cm). Presumably deeper nests represent a greater investment, and the most accurate measure of nest construction cost, given the available data, would be the rate of nest excavation through the soil, which takes into account both the depth of the nest and the time taken to dig it. As predicted, wasp size is

inversely correlated with the rate of nest excavation ($p = 0.059$, $R^2 = 88.6\%$, figure 5.4), supporting the idea that the evolution of large body size in *Mellinus arvensis*, regulated by the amount of intraspecific aggression, is linked to nest "value".

There is conflicting evidence to the importance of soil hardness on nest depth. Nests of *Bembix mareeba* were notably deeper (mean 87.5 cm, $N = 2$) in friable soil compared with nests from firm packed sand (mean 39 cm, $N = 5$) (Evans & Matthews 1973), whereas, in the same study it is reported that nests of *B. octosetosa* are shallower in more friable, loamy soil.

11 *Bembix oculata*.
Asis, Gayoto & Tomas
(1992)

5.3 Intraspecific Parasitism in *M. arvensis*

The central part of the hypothesis is the association of large body size with intraspecific parasitism and aggression. There are several types of intraspecific parasitism in the aculeate Hymenoptera (Field 1992a), some of which were observed in the behaviour of *Mellinus arvensis*. Observations of aggressive and parasitic behaviour at the nesting site totalled 1464 hours of nest observations (nest-hours) at four sites (Alderly Edge, Alnmouth, St Cyrus and Alnmouth). Aggressive and parasitic behaviours were classified into eight categories, and are listed in table 5.2.

The most frequently observed example of intraspecific parasitism consisted of wasps flying about the nesting site and looking into and entering nests. There was no evidence of any distinction being made between empty or abandoned nests, and nests that were occupied by females that were temporarily absent from the nest. *M. arvensis* females do readily use and extend old nests remaining from the previous year (Paxton 1985). There was much variation in the length of time spent inside the nest by a searching female, from a few

*

Also

M. areolaris lay a egg a last fly to be provisioned.

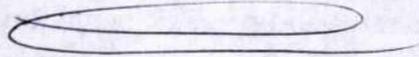
~~→ any wasp ~~lay~~ brood parasitizing~~

→ any egg that appears = an infested cell ~~is~~ can be removed by the resident

→ Brood parasitism is unlikely to be important
* perhaps this is why nest entrances are not closed.

- Alternative idea is that ~~wasps~~ parasitic flies are more important ~~than~~ the brood parasitic conspecifics
→ wasps do not close brood entrance so to avoid

delays when returning with prey



seconds to 36 minutes, and the significance of this variation is not known. When wasps entered the nest for short periods only it might be that the nest was not suitable, possibly being collapsed, excessively humid, or occupied by woodlice (Alnmouth), earwigs (St Cyrus), or other similar animals. Longer periods in the nest may be cases where the wasp was brood parasitising the cell of the previous nest resident, and the additional time spent in the nest might be required to dig through a filled lateral tunnel leading to a cell, the removal of an egg, and replacement with an egg of its own. In 55% of cases the entering female remained within the nest for less than five minutes (figure 5.5), but without data on the periods of time spent inside non-active nests it is not possible to determine whether entering wasps show any degree of preference, or indeed even an ability to detect differences, between active and non-active nests.

-- Note: If this was true there would be strong selective pressure to close nest entrance before ~~after~~ leaving for a foraging trip. *

Instances of repulsion by nest residents of potential usurpers were also frequently observed (N = 165). A wasp approaching the nest entrance would be repulsed by the resident which would lunge at the intruder from just inside the nest entrance and then quickly retreat back into the burrow. The intruder would almost always move away to investigate other nests, but sometimes (8.4 % of all incidents from all sites) the wasp remained close to the entrance which either elicited another attack from the resident (5 out of 6 cases), or was ignored (1 out of 6 cases). No physical contact was made between the two wasps during such an incident.

Some intruding females were ejected from inside the nest upon being discovered by the returning resident female. As behaviour beyond the nest entrance could not be observed, there was no way of telling what method was used to eject the intruder.

On a number of occasions visible fights occurred between two females. Fights were always between an intruder and a resident female and followed either the attempted entry of an occupied nest by an intruder ($N = 24$), or the discovery of an intruder inside a nest by the returning nest owner ($N = 4$). In the latter case, intruders were chased out of the nest by residents and fights would often take place at nest entrances or outside the nests. Fights were brief, usually lasting only a few seconds, but occasionally being much longer (mean 8.6 secs, range 3 - 32, $N = 21$). During a fight two wasps bit and grappled, often falling from the nest onto the sand below where they continued to fight. At the end of the fight one of the females returned to the nest entrance and successfully repelled any further attempts by the loser to enter. The number of observed fights was probably an underestimate of the true number as it was not possible to observe wasp behaviour within a nest, where fights may also have occurred.

Some unusual and rarely observed instances of intraspecific parasitism were the theft of prey from the nests of conspecifics. The stolen prey was either malaxated by the wasp ($N = 7$), discarded ($N = 4$), or provisioned in the parasite's own nest ($N = 1$, but see below). Wasps often caught flies that they did not provision but rather chewed, starting with the head capsule which was repeatedly punctured using the mandibles, and the fluids released were consumed. The thorax, and often the abdomen also, were consumed in a similar way, the mascerated body then being discarded with only the chewed cuticle and wings remaining. Thus 58% of the flies that were stolen were treated in this manner.

It is not clear why a wasp should discard flies from a cell partially provisioned by the host, although such behaviour has been associated with usurpation of the host nest (*Ammophila harti*, Hager & Kurczewski 1986; A.

dysmica Rosenheim 1987b). One possibility might be to make sure that no host egg remains in the cell attached to one of the prey items. This requires that wasps are either unable to locate, or remove, or destroy, host eggs. This seems unlikely as brood parasitism, requiring the removal or destruction of the host egg, has been reported in many Pompilidae and Sphecidae (eg, *Anoplius viaticus*, Olberg 1959; *Episyron arrogans*, Endo 1981; *Podalonia luctuosa*, Newcomer 1930; *Ammophila sabulosa*, Field 1989a; *A. atripes*, Krombein 1984; *A. aberti*, Parker et al. 1980; *A. urnaria* and *A. kennedyi*, Kurczewski et al. 1992; *Trypoxylon politum*, Brockmann 1980). Indeed, the sphecid wasps *Ammophila sabulosa*, *A. urnaria*, *A. kennedyi*, and *Trypoxylon politum* show both brood parasitism and discarding of flies are observed (Field 1989a; Kurczewski et al. 1992; Brockmann 1980a) indicating that the discarding of flies cannot be due to an inability to locate the host egg. Furthermore, in all four cases, the nests from which the prey were taken and discarded were not subsequently used by the usurpers. No explanation has been suggested for this behaviour.

There was only one occasion (at St Cyrus) when a fly was stolen from one nest and used to stock a cell in another nest. Theft of provisions from other nests might be expected to be more common: nests are aggregated and are therefore easily found; there is no temporary nest closure while the resident is away from the nest, allowing rapid and easy access; and there is no nest guarding while the resident is foraging. Furthermore, foraging trips, and therefore the time nests are left unattended, often last many minutes (means varying between 16 and 26 minutes for the four sites; section 3.6) giving plenty of opportunity for theft. The fact that prey theft was observed only once in 1464 nest-hours of observation suggests that intraspecific parasitism in this species is almost exclusively for the nest structure rather than prey items.

The number of successful usurpations observed was surprisingly small (table 5.2). Alderly had the largest number of successful usurpations, although as a proportion of total observation time, the frequency of successful usurpations at Thetford was about twice as great (figure 5.6). Due to the small number of successful usurpations observed and the relatively few hours of observation at Thetford, these data have to be interpreted with caution. The frequency of successful usurpations was very low at St Cyrus, and was absent at Alnmouth. These data are in accordance to what was predicted by the soil hardness-aggression model, although the results for Thetford are higher than expected. However, the very low incidence of successful usurpations at all sites suggests that usurpation of the nest structure, as a strategy, is not successful and therefore unlikely to be happening. This is discussed further below.

Figure 5.6 shows the relative frequency of the four most common types of aggressive or parasitic interactions at each site. The hypothesis predicts that the greatest amount of parasitic pressure from conspecifics will be at sites which have the hardest soils, and this is confirmed by figure 5.6, with only one result contrary to expectation, that of the frequency of repulsions at Thetford being greater than at Alderly Edge. This may be explained by the shorter foraging times of wasps at Thetford (20.8 mins compared to 26.0 mins at Alderly Edge), resulting in residents spending a greater proportion of their time at nest entrances where they may encounter nest searching conspecifics. By summing the frequencies of all categories for each site, overall measures of intraspecific parasitism pressure are obtained, and these can be plotted against the mean head width of each population (figure 5.7). There is little difference in parasitic pressure from conspecifics between Alderly Edge and Thetford (figure 5.7), although it should be noted that the hours of observation at Thetford were relatively few. Nevertheless, the trend is as

predicted by the hypothesis, with large wasp sizes at those populations where pressure from usurpers is high ($p = 0.031$, $t = 5.50$, $R^2 = 93.8\%$).

5.4 Is There a Large Body Size Advantage in Aggressive Encounters?

The proposed hypothesis assumes that large individuals are more successful in aggressive encounters. The validity of this assumption is crucial to the explanation linking body size variability with soil hardness. The assumption was tested by catching non-nesting females involved in fights and recording the head width ($N = 2$ from Thetford; $N = 6$ from St Cyrus; $N = 26$ from Alderly). The head width of the resident female in each case was already known, these females having been measured and marked at the beginning of the observation period. The individual that won the fight (usurper or resident) was also noted. In this way the mean head width of winners and losers (table 5.3a), as well as the mean head width of searchers and residents, could be compared (table 5.3b). Only 11 out of 34 fights (32%) were won by the smaller wasp. The mean size of winners (3.22 mm) was greater than losers (3.16 mm), the difference being significant (paired t test: $p = 0.024$, $t = 2.37$, d.f. = 33). This result confirms that there is a large wasp size related advantage in fights.

Residents are not significantly different in size to searchers (both groups have a head width of 3.19 mm, $p = 0.969$, $t = 0.04$, d.f. = 66) but they win the majority of fights (50/58 = 86%). Wasps that are in possession of a nest have more to lose in a fight and might therefore be more persistent. This might lead to small residents winning fights with larger adversaries, thereby reducing the importance of large size. Indeed every searcher that succeeded in winning a fight was larger than the resident, and the mean of the difference in head width between wasps in fights won by searchers was higher (0.17 mm

± 0.03 ; $N = 6$) than the size difference between wasps in fights won by residents (0.04 ± 0.03 ; $N = 28$). This difference is almost significant ($p = 0.053$, $t = 2.01$, $d.f. = 32$) and indicates that searchers need to be very much larger than residents to be successful in usurping a nest.

In most cases it was not known whether a nest resident excavated the nest itself (digger) or found/usurped the nest (searcher). To compare the sizes of wasps following each strategy, ie. digger or searcher, it was necessary to measure head widths of females that were seen to be digging nests. A comparison between the mean sizes obtained for wasps following each strategy is presented in table 5.3c. There is no significant difference between the means indicating that the type of strategy followed is not size related.

In conclusion, the assumption that large wasps have an advantage in aggressive physical encounters due to greater body size, is upheld, but its importance in affecting the outcome of a fight is reduced by residency, nest residents having an advantage over non-residents.

5.5 Regulation of Intraspecific Parasitism in *Mellinus arvensis*.

Intraspecific parasitism is always one of two or more alternative reproductive tactics, at least one of which must be non-parasitic. In the Hymenoptera, as in birds (Davies 1988), there is no evidence of discontinuous genetic polymorphisms resulting in obligate parasitic and non-parasitic types (eg, Brockmann & Dawkins 1979; Field 1989b). The existence of alternative tactics implies that individuals have to make decisions based upon environmental or phenotypic conditions. Thus a conditional strategy is a rule of behaviour which is followed only in particular circumstances (Brockmann 1980a). This is different to a frequency-dependent strategy where the relative proportions of

the two strategies are regulated by their own frequencies. This section discusses some of the conditional circumstances that might determine, or at least influence, the ^{nesting} strategy followed by *M. arvensis* individuals. ^{Females.}

Nest site availability has been shown to be sometimes limiting for many aerial nesters that utilize pre-existing cavities or plant stems (Danks 1971), and when all available nest sites became occupied Cowan (1981) found that female eumenid wasps would usurp the nests of other females. Nests were never seen to be limiting at nesting aggregations of *M. arvensis* as at every site empty nests comprised a substantial proportion of the total nest number. It is very unlikely therefore that usurpation is a conditional strategy dependent upon the availability of suitable nesting sites.

Thermal constraints have been observed to influence the nest digging behaviour of *Ammophila sabulosa* (Field 1989a). In *Mellinus arvensis* ambient ^{p. 44.} temperatures below 19 °C seem to preclude digging behaviour (section 3.3.1), although wasps are capable of making foraging trips and flying over the nesting area at temperatures between 14 - 19 °C. Temperature might therefore regulate the benefits of usurping versus digging, by affecting the time costs involved in nest construction. At high temperatures, when nest construction is possible, the bare sand surface might be too hot for females to spend long periods searching for the nests of other females. A conditional strategy, based upon temperature, is therefore possible.

In many species, size is often the condition that determines the strategy that is followed. In some bees large males pursue one highly profitable mating pattern while smaller males pursue other less successful ones (eg, Alcock 1979a; Alcock et al. 1976, 1977a,b 1978). In some eumenids and sphecids large females nest non-parasitically at a higher frequency than smaller, brood

parasitising, females (eg, Cowan 1981; Freeman 1981b; Hastings 1986; Pfennig & Reeve 1989). Prey theft outside the nest usually involves fighting, which might favour larger females (unpublished data, Villalobos & Shelley) but whether or not larger females are therefore more likely to attempt theft is not known. In *M. arvensis* females there is no difference in size between nest diggers and nest usurpers (table 5.3c). These data form additional evidence against the hypothesis stating that non-nesting females are true usurpers, for to be successful, usurpers need to be considerably larger than the nest owners (section 5.4).^{p. 106} In such a case small sized wasp would be more successful by following a digging strategy, which guarantees the possession of a nest for at least some time, rather than a usurping strategy which, at best, will result in much time lost, and at worst injury or even death, as a result of many lost fights. However, females of all sizes were seen to follow both strategies, supporting a "search" rather than "usurp" hypothesis (see section 5.6).^{p. 111}

There is contrasting evidence on the effect of female nesting density on the frequency of parasitic tactics (Eickwort 1975; Brockmann & Dawkins 1979; Field 1987; Villalobos & Shelly, unpublished data). The nesting density of *M. arvensis* aggregations was measured by nearest neighbour analysis, and the results ^{have been} plotted against the overall intraspecific aggression for each site (figure 5.8). There is no significant correlation between nesting density and usurper pressure ($p < 0.2$, $t = 2.820$, d.f. = 2), although results are available for only four populations. Furthermore, the trend is in the opposite direction to that which might be expected if some wasps were nest usurpers, suggesting that nesting density is, for *M. arvensis*, not directly responsible for regulation of the frequency of tactics adopted by wasps.

A usurpation strategy might be followed upon the loss of the nest to another wasp. In some species a knock-on effect is observed when a nest is usurped

with the expelled wasp searching for and usurping another nest, ultimately leading to a series of usurpations (eg, *Lindeni* *columbianus*, Miller & Kurczewski 1973; *Crabro monticola*, Alcock 1981; *Cerceris arenaria*, Field & Foster, unpublished observations). Due to the very small number of observed usurpations, this factor is unlikely to be of major influence in the regulation of the frequency of usurpation behaviour in *M. arvensis*.

Several sphecid species have been observed to abandon nests that they were provisioning and start provisioning a new nest (eg, *Sphex ichneumoneus*, Brockmann & Dawkins 1979; *Trypoxylon politum*, Brockmann 1980a; *Crabro monticola*, Alcock 1981; *Ammophila sabulosa*, Field 1989a). Alcock (1975a, 1981, 1982) suggested that this might be a form of risk spreading by having a wider distribution of offspring; however modelling by Bulmer (1984) suggests that the benefits of risk-spreading are very small, and are likely to be outweighed by the costs of nest abandonment (ie. usurping or digging a new nest). Further observations may reveal more obvious explanations for nest abandonment, such as the frequency of parasites or interactions with conspecifics, that will indirectly influence the frequency of usurpers. No voluntary nest abandonments were observed in *M. arvensis*, although, due to the nature of the observations made, the possibility that they occur cannot be ruled out. Three females at St Cyrus and one at Alderly Edge that had been marked while provisioning a nest, were on a later date (St Cyrus: 6, 7 and 14 days after marking; Alderly Edge: 18 days after marking) found searching for another nest. However it is not known whether these females were forced out of their nests by a conspecific, or whether they left voluntarily.

It is also possible that as wasps get older they become less efficient diggers due to wearing of the mandibles (eg, *Cerceris australis*, Evans & Hook 1982a), and the nesting strategy pursued by a wasp might therefore be conditional on

age. The ages of several diggers and usurpers were estimated by grading the damage to the wing margins (Chapter 2). Differences in this character between searchers and diggers were not significant (wing wear of diggers 0.50 ± 0.16 ; wing wear of searchers 0.53 ± 0.13 ; $p = 0.883$, $t = 0.15$, d.f. = 46).

Thus little evidence can be found to support the idea that usurpation is a purely conditional strategy, or a polymorphism. Nesting strategies could be frequency dependent, as part of a mixed evolutionarily stable strategy (Brockmann et al. 1979), with the fitness of each behaviour increasing as its frequency decreases. With such a model the final frequencies of the strategies at the evolutionarily stable state will be similar across populations unless the costs and benefits of a strategy are affected by factors such as soil hardness or climate, making it a partially conditional tactic. Furthermore, there is some evidence to the contrary of the usurpation model, such as the absence of a link between size and the nesting strategy employed, and in the next section a modified hypothesis, that does not infer the occurrence of true usurpation, is proposed.

5.6 Does usurpation exist as an alternative nesting strategy?

Soil hardness, intraspecific parasitism and wasp size seem to be correlated with each other as the hypothesis predicts. But despite the relatively high frequency of aggression and nest entering by non-nesting conspecifics, the number of cases observed where a parasite gained something (8 cases of prey theft and 8 cases of nest usurpation in 1464 nest hours of observation) was very low. So it seems that there is a paradoxical situation in that attempted usurpation is a frequently observed, but unsuccessful, strategy, and as such would not be expected to persist through evolutionary time.

5.6.1 The "Searching" Model: an Alternative to Usurpation.

A possible explanation to the apparent contradiction mentioned above may be that usurpation as a strategy does not actually exist, but rather it is an unintentional product of searching for and entering abandoned nests. Thus a wasp may either dig a new nest, or it may enter an abandoned nest. If wasps cannot distinguish between nests that have been abandoned and nests that are occupied (eg, *Sphex ichneumoneus* Brockmann & Dawkins 1979; *Trypoxylon politum*, Brockmann 1980a), then they are likely to enter occupied nests in the same frequency as that in which they occur. Upon the discovery of the new tenant by the original owner, aggression between the two is likely to occur, and occasionally the original resident loses the nest, resulting in a "usurpation". However, these instances of usurpation result from a "decision" to search and enter nests which might be empty, and not from a positive "decision" to usurp (Brockmann & Dawkins 1979). The amount of aggression will therefore depend upon the proportion of empty nests, and where nest construction is difficult due to soil hardness, the number of nests excavated will be less, and where the nest structure is quickly destroyed the number of empty nests will also be fewer. Table 5.4 lists the percentage of inactive nests at the four sites. Incidence of aggression and usurpation is more intense at sites where the numbers of abandoned or empty nests are less ($p < 0.05$, $t = 5.699$, d.f. = 2, figure 5.9) and this evidence supports the idea that aggression is dependent on the frequency of empty nests in the vicinity.

According to this model, the proportion in which the two strategies of "search" and "dig" occur in a wasp population is dependent ultimately upon the hardness of the soil. When there are many wasps digging nests, there are many burrows that are made available for wasps that follow a search strategy. This means that searching for and using empty nests becomes more

profitable. As entering existing nests becomes more common, and empty available burrows become increasingly less abundant, the costs of searching due to time and energy expended increases, and profitability of this strategy decreases. The frequency of digging relative to searching is thus held in balance by nest availability which is frequency-dependent. The equilibrium point, at which the net gains of both strategies are equal, is not fixed as it is affected by soil hardness which increases or decreases the costs of nest construction. In areas of soft soils the cost of digging are small and the balance will be tipped towards an increased number of digging females, thereby reducing the pressure from searchers, and hence reducing intraspecific aggression. The equilibrium point is therefore different for each site depending on soil hardness, and the persistence of nests from one season to the next.

This hypothesis rests on the assumption that wasps cannot distinguish between empty and occupied nests, for if they could there would be few, if any, instances of wasps entering nests being provisioned by other wasps, as the strategy being pursued is one of finding an empty nest, not an occupied one which may lead to costs due to fighting. Several species have been shown to be unable to distinguish between abandoned nests and active nests from which the owner is temporarily absent (eg, *Sphegichneumon* Brockmann & Dawkins 1979; *Trypoxylon politum*, Brockmann 1980a). However, Pfennig & Reeve (1989) found that *Sphecus spheciosus* females could distinguish between active and abandoned burrows, were more likely to enter active burrows, and furthermore preferred burrows that contained prey to burrows that were empty. A recent review by Wcislo (1992) concluded that there was little supporting evidence for olfactory nest recognition in the Sphecidae, in contrast to bees. In a study on the nesting behaviour of *M. arvensis* at Street, Paxton (1985) found that females show no preference between artificially

created tunnels and tunnels that were dug by other conspecific females, suggesting either that there is no olfactory cue at nests, or if there is females do not use it to distinguish between active and non-active nests. This study also showed that females at this site preferred to use pre-dug tunnels rather than dig their own tunnels ($p < 0.001$) indicating that the cost of digging a tunnel was greater than the cost of searching for and reusing a previously existing tunnel.

It might be somewhat surprising that wasps are unable to discriminate between occupied and non-occupied nests as there should be strong selection pressure in favour of such discrimination. Selection might favour wasps that advertise their occupancy of a nest (see Albans et al. 1980, with reference to anthophorid bees) so that searching wasps are dissuaded from entering the nest. However, such ^{chemical} markers might also attract the attentions of parasitic flies, cuckoo wasps and velvet ants. These parasites might have led to selection favouring wasps that did not advertise the occupancy of a nest.

To test this assumption for *M. arvensis* data are needed on the frequency of visits to empty and occupied nests, which, if the assumption is true, should equal the frequencies with which empty and occupied nests occur at each site. The collection of such data would require the identification of those nests being provisioned and those which are empty, and observations of known, marked searchers over a period of time, recording the number of visits made to nests of each type. Collection of such data would be difficult with large aggregations as nests change status from being empty to occupied and vice versa. Therefore each nest would have to be periodically checked to determine whether it had since been abandoned or occupied.

5.7 Seasonal Changes in Intraspecific Aggression

The number of newly emerging females is not constant throughout the season (figure 5.10, data from Paxton 1985), and there is a gradual increase in female emergence, peaking midway in the season, followed by a gradual decrease. Therefore the number of active females varies throughout the season and this might influence the amount of intraspecific aggression observed. Intraspecific aggression might be expected to increase with increasing population numbers through the season. However, when the first females emerge the number of available empty nests will be high (nests remaining from the previous season) and the number of females low. Consequently there will be little competition for nests and almost all females would be expected to follow a search strategy. As the season progresses, and more females emerge, the number of empty nests decreases, leading to increased competition for nests between searchers. As competition for nests increases the digging strategy becomes more profitable, and this will reduce the number of searchers, thereby reducing competition. In this way levels of aggression are likely to remain constant throughout the season, irrespective of population size. This was tested simply by comparing the amount of aggressive interactions between two months (August and September) within the same season (1992) at Alderly Edge, for which most data were available. Data from Paxton (1985) shows that the peak of female emergence at Street, and presumably the greatest competition for nests, was during August, with very few females emerging in September (figure 5.10). This curve should probably be moved forward in time by two weeks as the first females at Alderly Edge were seen at the beginning of August rather than the middle of July. There was no significant difference in the amount of aggression between the two months ($p = 0.237$, $\chi^2 = 1.320$, d.f. = 3) indicating no change in the proportion of

searchers through the season, as might be expected of an evolutionarily stable strategy.

5.8 The Influence of Nest Longevity

The depth of nests has been observed to differ between sites and explanations that have been suggested include soil moisture and compaction. Another possible cause for differences is the frequency of repeated burrow use by wasps, leading to ever deepening extensions of the burrow. At sites where the nest structure persists from one year to the next, wasps from the following generation can use and extend a burrow that was constructed one or more years previously. The longevity of nest structures will undoubtedly affect the proportions of empty burrows that may be used by searchers. Nest longevity is likely to be dependent upon soil characteristics, rainfall, disturbance by animals and humans, and the age of the population. On the basis of nest depth, nests at St Cyrus might be expected to have the longest "life expectancy", while those at Alderly have the least, resulting in differences of proportion of empty nests. While no data were collected on this issue, visits to Alderly Edge and St Cyrus during the winter months revealed that many (in excess of 200) nest entrances at St Cyrus remained open and nests were easily found, while at Alderly Edge only very few (less than 20) nest entrances were found, and these were located under overhangs where they were protected from erosion and trampling.

5.9 Conclusion

Several predictions were made by the usurpation ^{spaces}soil hardness ^{spaces}wasps size hypothesis. Correlations between soil hardness, aggression, and body size were as predicted suggesting that variation in body size between sites is a

result of soil hardness which exerts its influence through aggression brought about by defense or usurpation of nests. However, one problem with this theory is that successful usurpation of a nest was very rarely observed. If nest usurpation were a functional alternative to nest digging then the two strategies should be, on average, equally successful (Maynard Smith 1974). I was not able to collect data on the reproductive success of individuals pursuing the two strategies, but in view of the very low frequency of usurpations, it seems very unlikely that usurpation has the same success as nest digging.

A modified hypothesis was therefore proposed that replaced the strategy of usurpation of occupied nests with a strategy of searching for empty nests. This hypothesis rests on the assumption that wasps are unable to distinguish between nests that are in use and nests that have been abandoned. No data were collected that could support or reject this assumption, although it seems to be true for two other sphecids species (Brockmann & Dawkins 1979; Brockmann 1980a,b). Thus the two strategies are either dig a new nest, or search for and occupy an empty nest. Aggression between individuals results from a wasp entering an occupied burrow while in search of an empty burrow. The amount of aggression at each site is a factor of the proportion of empty nests in the nesting aggregation, which is in turn dependent on soil hardness.

There is indirect evidence for this modified hypothesis such as the lack of successful usurpations, and the fact that *M. arvensis* does not fill the entrance to the nest before departing on a foraging trip, as do many other sphecids in which true usurpation, and other forms of intraspecific parasitism, are commonly observed (*Ammophila sabulosa*, Field 1989a; *Passaloecus corniga*, Corbet & Backhouse 1975; *Stictia heros*, Sheehan 1984; *Trigonopsis cameronii*,

Eberhard 1974). As yet no direct evidence has been collected in support of this theory, although much of the evidence for the first hypothesis equally applies to this one. Such evidence might be difficult to obtain as the intensity of aggression between wasps is dependent upon the frequency of empty nests, which is not a product of whether wasps are true usurpers or passive searchers, but rather a result of competition for nest sites, which in turn is dependent on soil hardness and the number of wasps that dig, and subsequently abandon, nests. These two theories can be interpreted in diagrammatic form (figures 5.11 & 5.12), which illustrate the numerous negative feedback loops that characterise an evolutionarily stable strategy (Maynard Smith 1974, 1976; Parker 1978; Dawkins 1976, 1980).

The evidence that is available suggests that a searching strategy is frequency dependent (the fitness of the behaviour will increase as its frequency decreases), but also a partially conditional tactic, with factors such as soil hardness and climate influencing the final frequencies of the strategies at the evolutionarily stable state.

Table 5.1 Soil Hardness of field sites

| <u>Site</u> | <u>Soil Hardness</u> | <u>S.E.</u> | <u>N</u> |
|--------------|----------------------|-------------|----------|
| Alderly Edge | 3.08 | 0.34 | 16 |
| St Cyrus | 5.41 | 0.31 | 11 |
| Findhorn | 3.84 4.08 | 0.17 | 10 |
| Thetford | 4.66 | 0.25 | 11 |
| Alnmouth | 5.82 | 0.19 | 11 |
| River Till | 3.02 | 0.29 | 10 |
| Merthyr Mawr | 4.45 | 0.12 | 13 |
| Street | 3.99 | 0.23 | 13 |
| Ainsdale | 4.16 | 0.29 | 13 |

Soil hardness was measured using a penetrometer (Chapter 2). The units are in centimetres and represent the depth to which the device penetrated the soil, giving a value for soil compaction or hardness. Thus a hard soil has a low value and a soft soil has a high value.

If adult lifespan is assumed to be three weeks.

$$** \text{ no. of usurpations / nest / hour} = \frac{5}{505} = 9.9 \times 10^{-3}$$

then no. of usurpations expected during a single adult lifetime

$$= (9.9 \times 10^{-3}) \times (21 \text{ days} \times 10 \text{ hours})$$

$$= (9.9 \times 10^{-3}) \times 210 = 2.08$$

\Rightarrow a wasp at Ardeley would expect to be usurped twice during its lifetime

| | | |
|------------|----------|------|
| Values for | St Lys | 0.52 |
| | Armadale | 0 - |
| | Thelford | 4.04 |

If a nest is usurped, the leaving wasp may lose a minimum of time taken to construct a new nest.

Could lose maximum of an provisioned cell.

If time taken to search for & dig a new nest = 1 day,

& if this is taken to equal time taken to dig a cell & provision it with ~~off~~ prey. - ~~the time taken to~~

then a minimum of 1 cell & maximum of 2 cells may be

lost if the nest is usurped. If this occurred twice = adult lifetime

then it represents mean of 3 cells lost = $\approx 15\%$ of wasp products ~~of nest~~

observed

Table 5.2 The types of aggression or parasitism and their frequency observed between *Mellinus arvensis* females.

Single
spaced

| <u>Types of Aggression or Parasitism</u> | <u>Alderly</u> | <u>Thetford</u> | <u>St Cyrus</u> | <u>Alnmouth</u> |
|--|----------------|-----------------|-----------------|-----------------|
| Wasp enters < 1 min | 66 | 5 | 45 | 5 |
| Wasp enters > 1 min | 94 | 5 | 53 | 4 |
| Wasp Repulsed | 146 | 19 | 44 | 1 |
| Fight | 48 | 2 | 8 | 0 |
| Mastication of Prey | 2 | 1 | 4 | 0 |
| Discarding of Prey | 2 | 0 | 2 | 0 |
| Provisioning of Prey | 0 | 0 | 1 | 0 |
| Successful Usurpation | 5 | 1 | 2 | 0 |
| No. of Nests Observed | 112 | 14 | 187 | 22 |
| Nest-Hours of Observation | 505 | 52 | 814 | 93 |

if there is no way of telling whether a nest is occupied until entering the nest may be a way of gaining information regarding this.
 i.e. if the entering wasp finds a half provisioned cell then the nest is not empty & is being actively provisioned => they leave

Table 5.3a The mean head width of winners and losers in fights between *Mellinus arvensis* females.

| <u>Winners</u> (mm) | <u>Losers</u> (mm) | <u>t</u> | <u>p</u> | <u>d.f.</u> |
|------------------------|-----------------------|----------|----------|-------------|
| 3.22 (\pm 0.03) | 3.19 (\pm 0.03) | 2.37 | 0.024 | 33 |

Table 5.3b The mean head width of nest residents and searchers involved in fights.

| <u>Residents</u> (mm) | <u>Searchers</u> (mm) | <u>t</u> | <u>p</u> | <u>d.f.</u> |
|--------------------------|--------------------------|----------|----------|-------------|
| 3.19 (\pm 0.03) | 3.19 (\pm 0.03) | 0.04 | 0.969 | 66 |

Table 5.3c The mean head width of diggers compared with usurpers.

| <u>Diggers</u> (mm) | <u>Searchers</u> (mm) | <u>t</u> | <u>p</u> | <u>d.f.</u> |
|------------------------|--------------------------|----------|----------|-------------|
| 3.17 (\pm 0.04) | 3.19 (\pm 0.03) | 0.31 | 0.758 | 57 |

Table 5.4 The proportion of empty nests at each site.

| <u>Site</u> | <u>% Empty Nests</u> | <u>Total Number of Nests</u> |
|--------------|----------------------|------------------------------|
| Alderly Edge | 29 | 249 |
| Thetford | 30 | 54 |
| St Cyrus | 50 | 647 |
| Alnmouth | 69 | 395 |

Fig. 5.1 Wasp size and the hardness of the soil (measured as depth of penetration into the soil by a penetrometer). $y = 3.686 - 0.143x$, $R^2 = 0.474$; $p = 0.028$, $t = 2.685$, $d.f. = 8$.

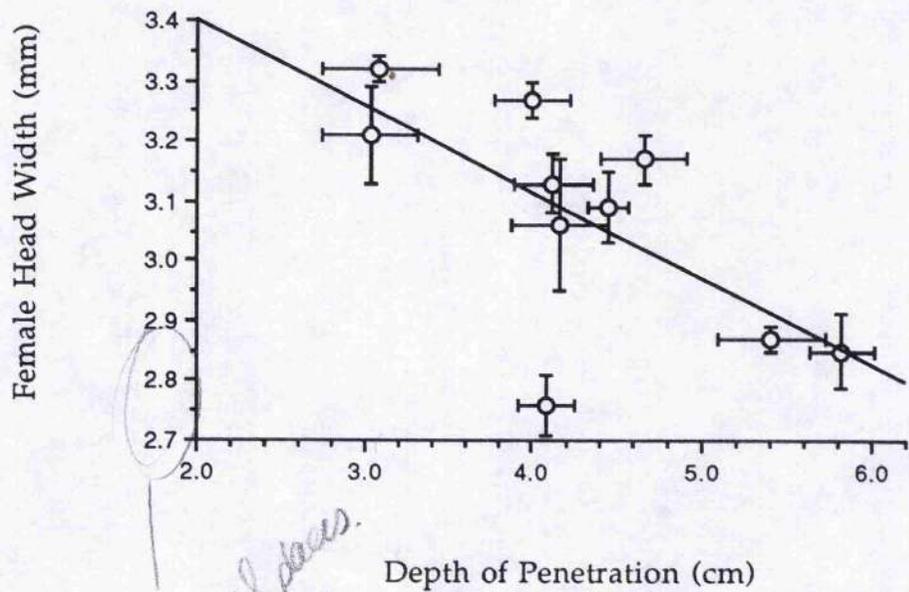


Fig. 5.2 The correlation of the mean time taken to dig a nest by *M. arvensis* at four sites and soil hardness. $y = 179.87 - 19.98x$, $R^2 = 0.561$; $p = 0.251$, $t = 1.599$, d.f. = 2.

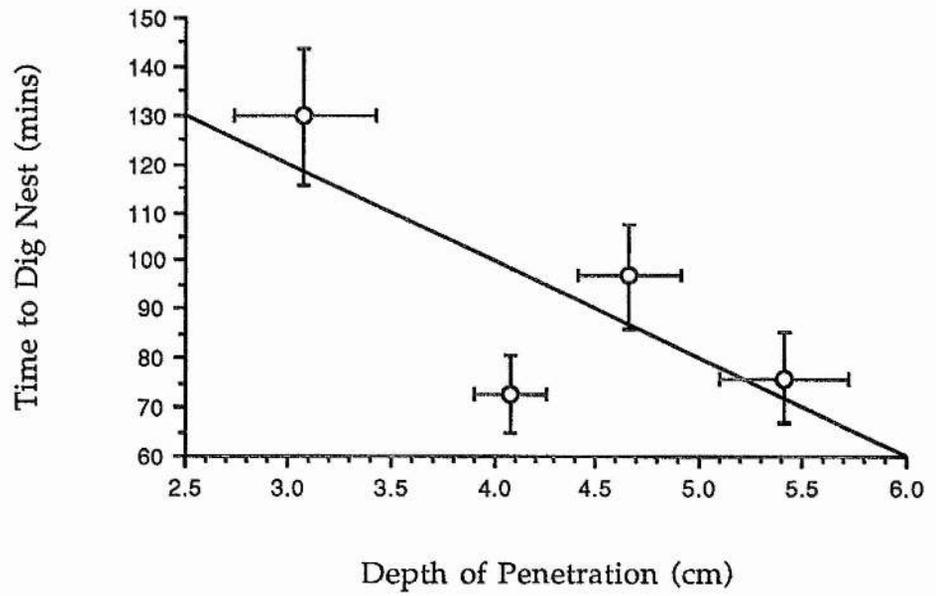


Fig. 5.3 The mean depth of nests excavated by *M. arvensis* from five sites and soil hardness. $y = 16.582 - 1.20x$, $R^2 = 0.081$; $p = 0.643$, $t = 0.420$, d.f. = 2.

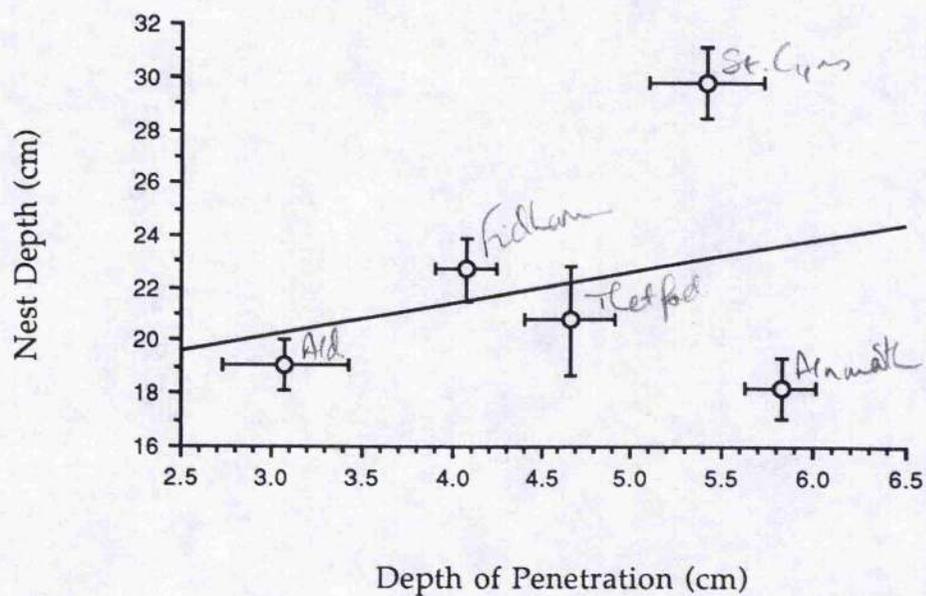


Fig 5.4 The rate of nest excavation and mean *M. arvensis* body size at four sites. $y = 13.553 - 3.596x$, $R^2 = 0.886$; $p = 0.059$, $t = 3.943$, d.f. = 2.

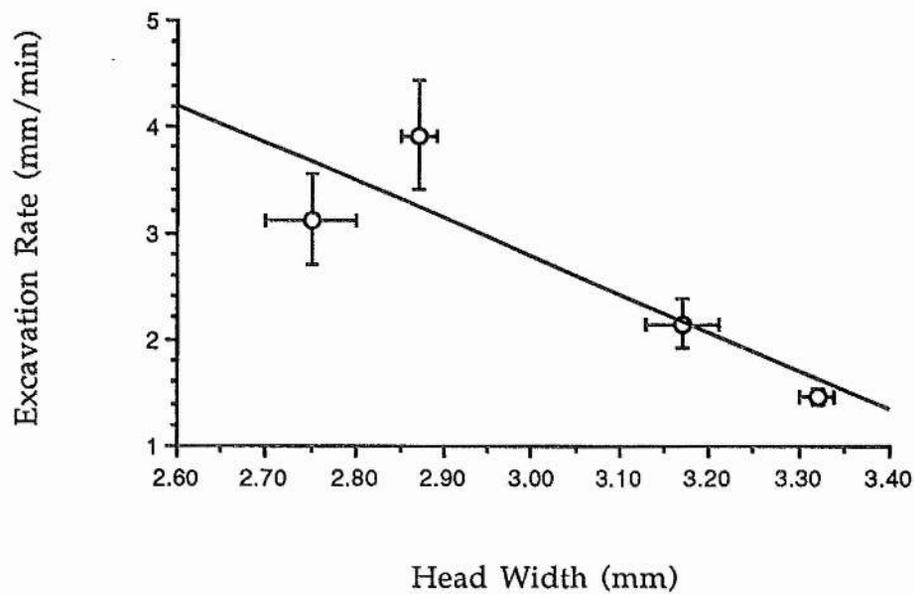


Fig. 5.5 The frequency of length of time spent inside the nest of a conspecific by a nest searching female *M. arvensis*.

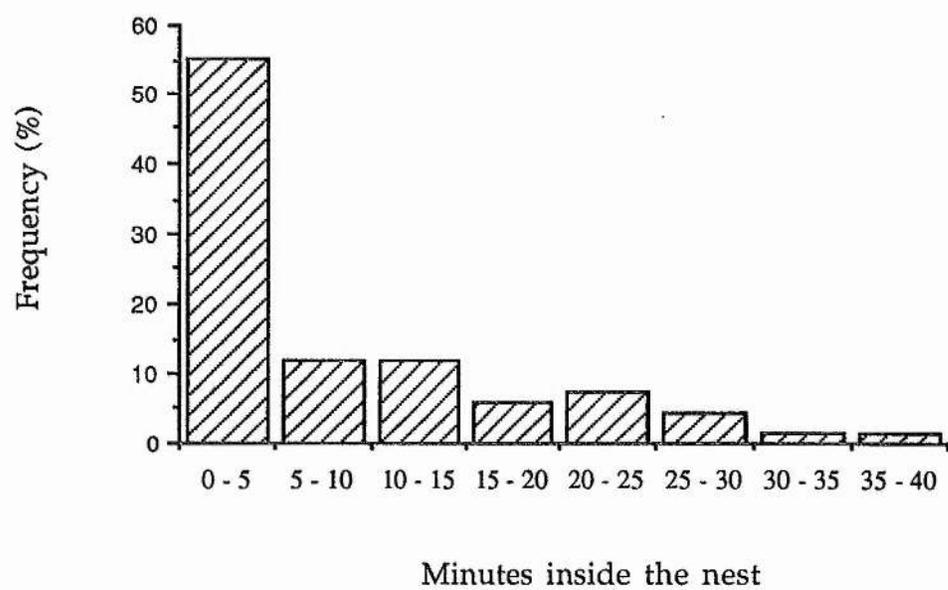


Fig. 5.6 The frequency of intraspecific parasitism and aggression in *M. arvensis* from four sites. The four categories are: "In < 1 min" - a foreign female entered and remained inside the nest for less than 1 minute; "In > 1 min" - a foreign female entered and remained inside the nest for more than 1 minute; "repulsion" - a foreign female was expelled from the vicinity of the nest by the resident female; "fight" - a fight, involving several seconds of contact, occurred between the resident and the foreign female. Frequency of encounters are given as incidents observed for each hour of observation of a single nest.

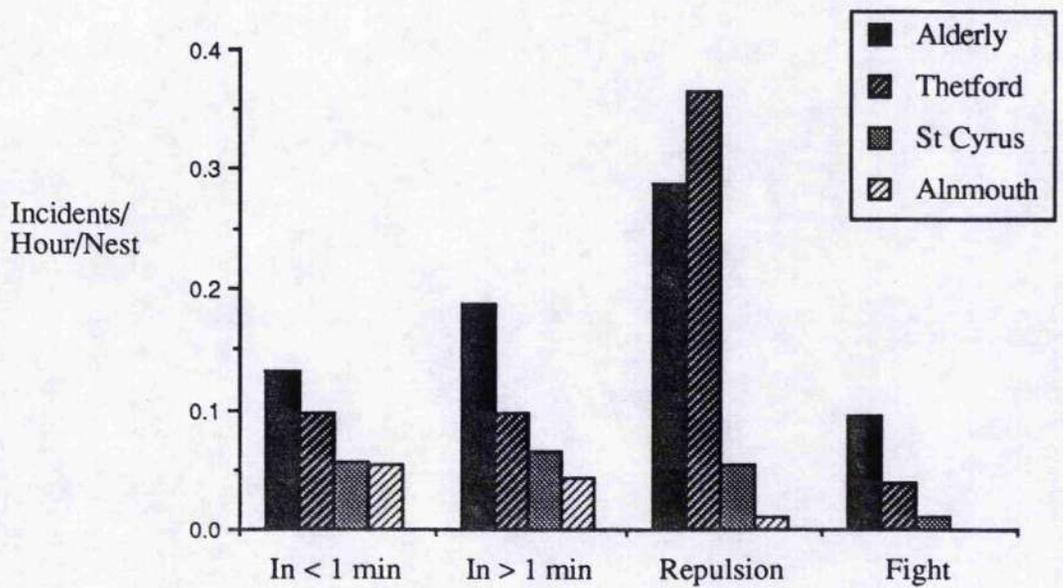


Fig. 5.7 Overall intraspecific parasite pressure and mean size of four populations of *M. arvensis*. $y = -3.667 + 1.34x$, $R^2 = 0.938$; $p = 0.031$, $t = 5.501$, d.f. = 2.

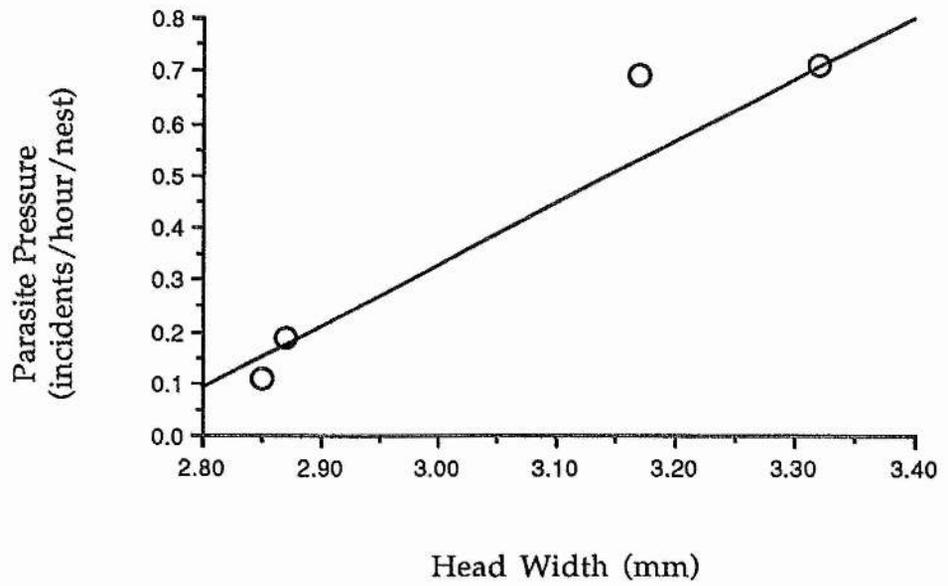


Fig. 5.8 The effect of nesting density on intraspecific parasite pressure. Nesting density is expressed as the mean nearest neighbour distance between nests. Parasite pressure is the overall number of incidents for each hour of observation of a single nest. $y = -0.184 + 0.070x$, $R^2 = 0.799$; $p < 0.2$, $t = 2.820$, d.f. = 2.

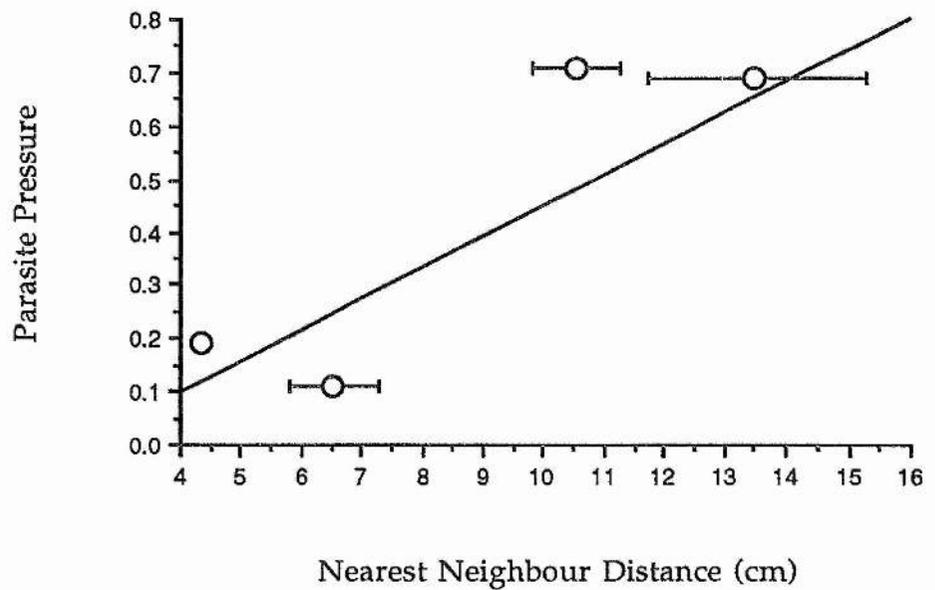


Fig. 5.9 The correlation between the probability of entering an empty (non-active) nest and the proportion of empty nests in the nesting aggregation at four sites. $y = -3.734 + 1.419x$, $R^2 = 0.942$; $p < 0.05$, $t = 5.700$, d.f. = 2.

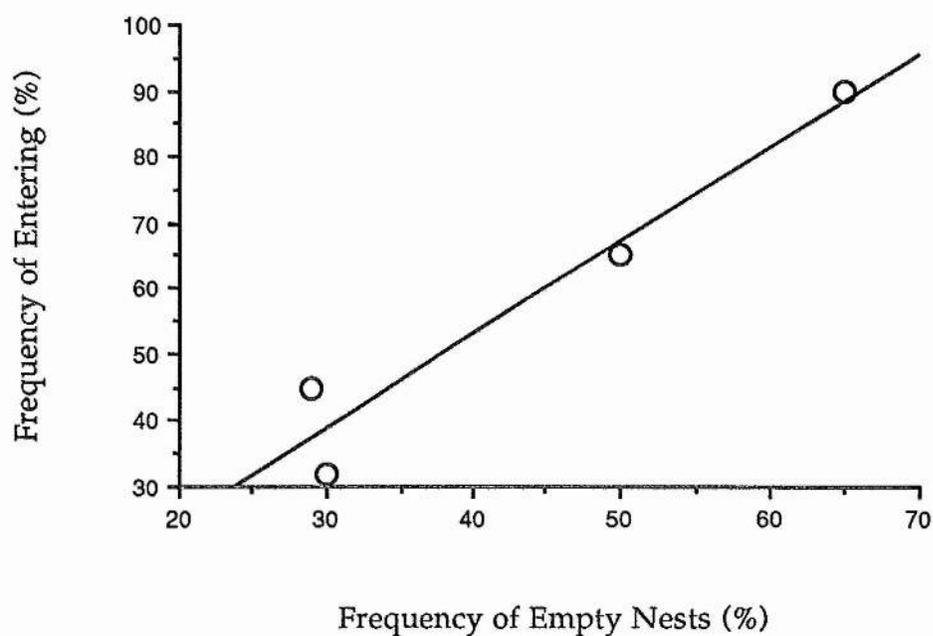
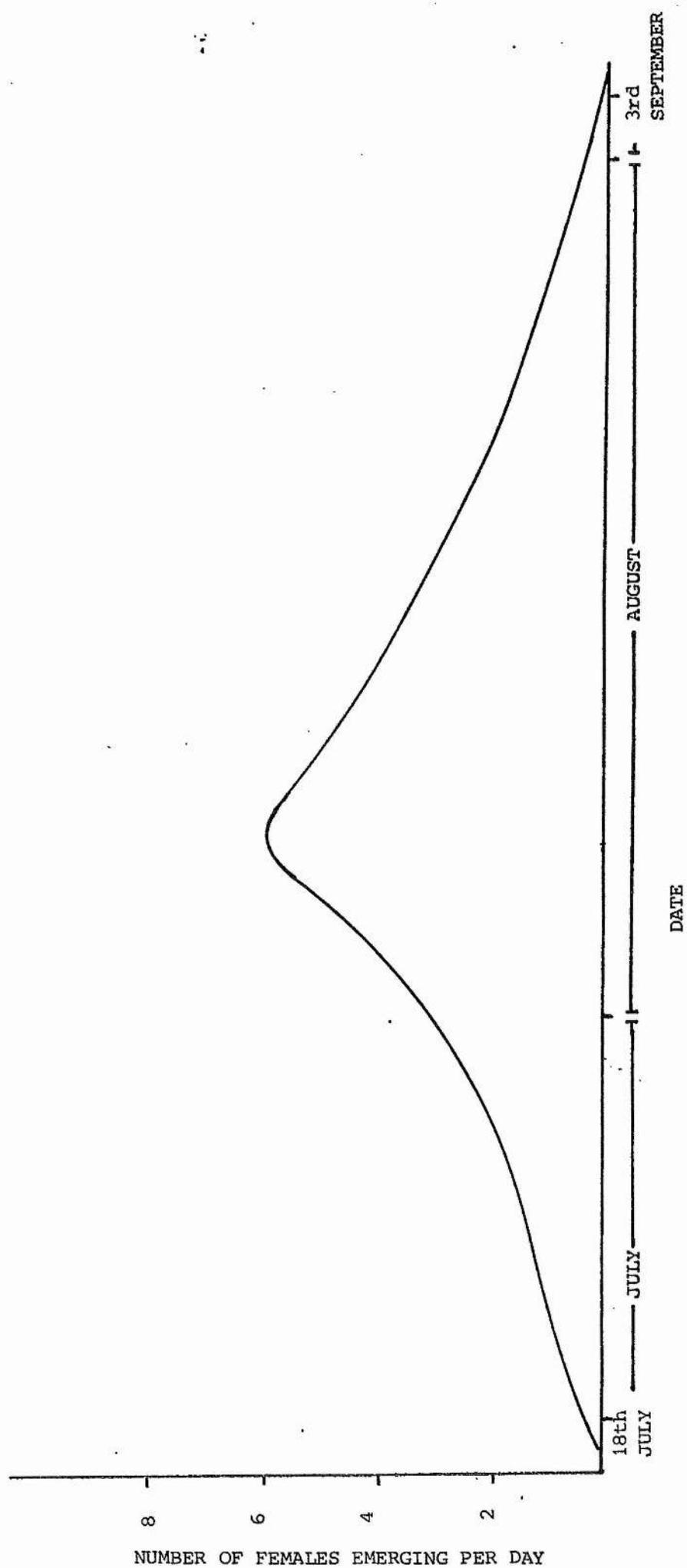


Fig. 5.10 The pattern of female *Mellinus arvensis* emergence at Street, 1983, (data from Paxton 1985).



Figures 5.11 and 5.12 The "usurper" and "searcher" models expressed as flow diagrams.

A positive symbol (+) indicates a positive correlation with the arrow pointing in the direction of the dependent factor.

A negative symbol (-) indicates a negative correlation with the arrow pointing in the direction of the dependent factor.

Solid lines indicate a direct influence, dotted lines indicate an indirect influence.

Fig. 5.11 A diagrammatic representation of the "Usurper" model.

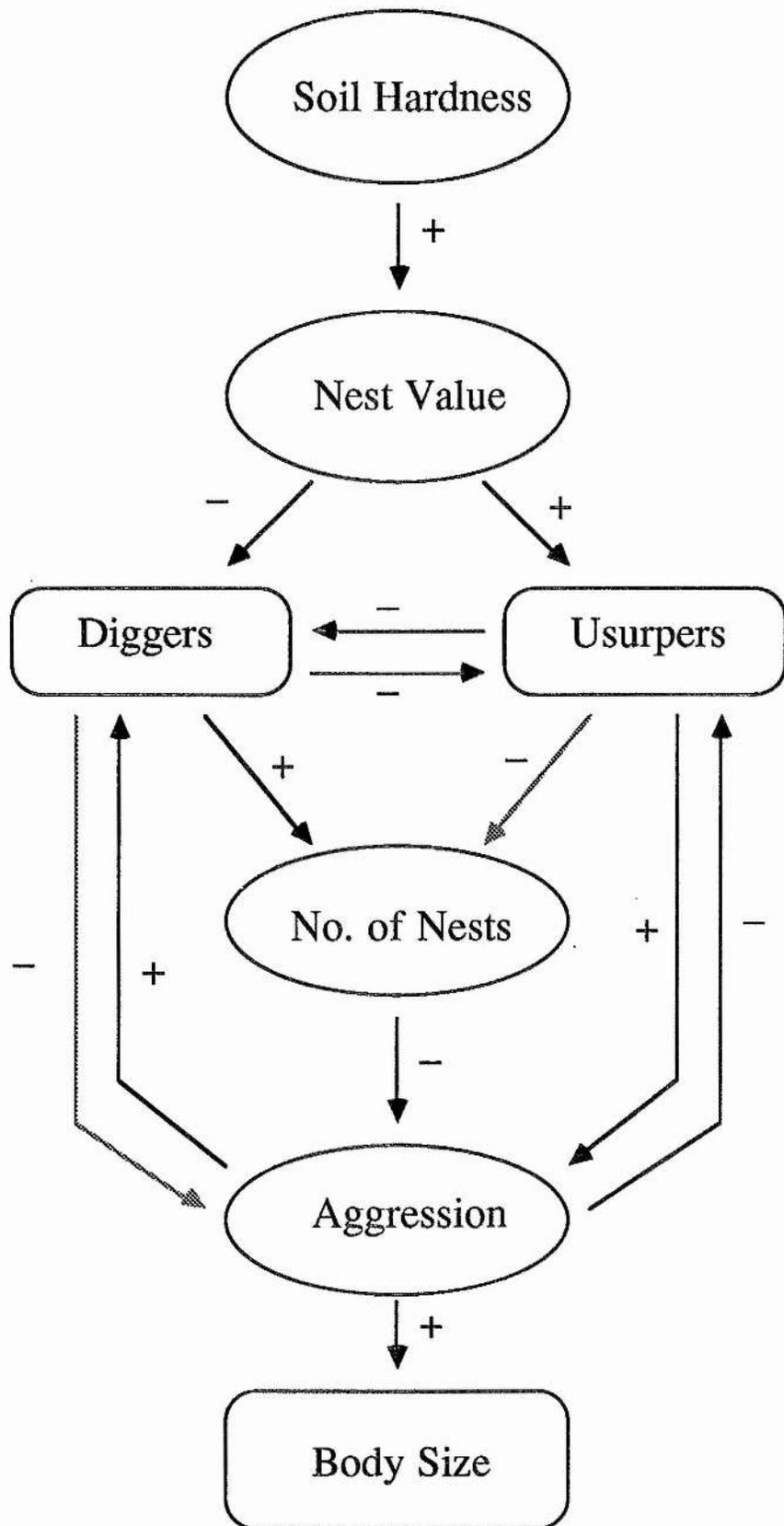
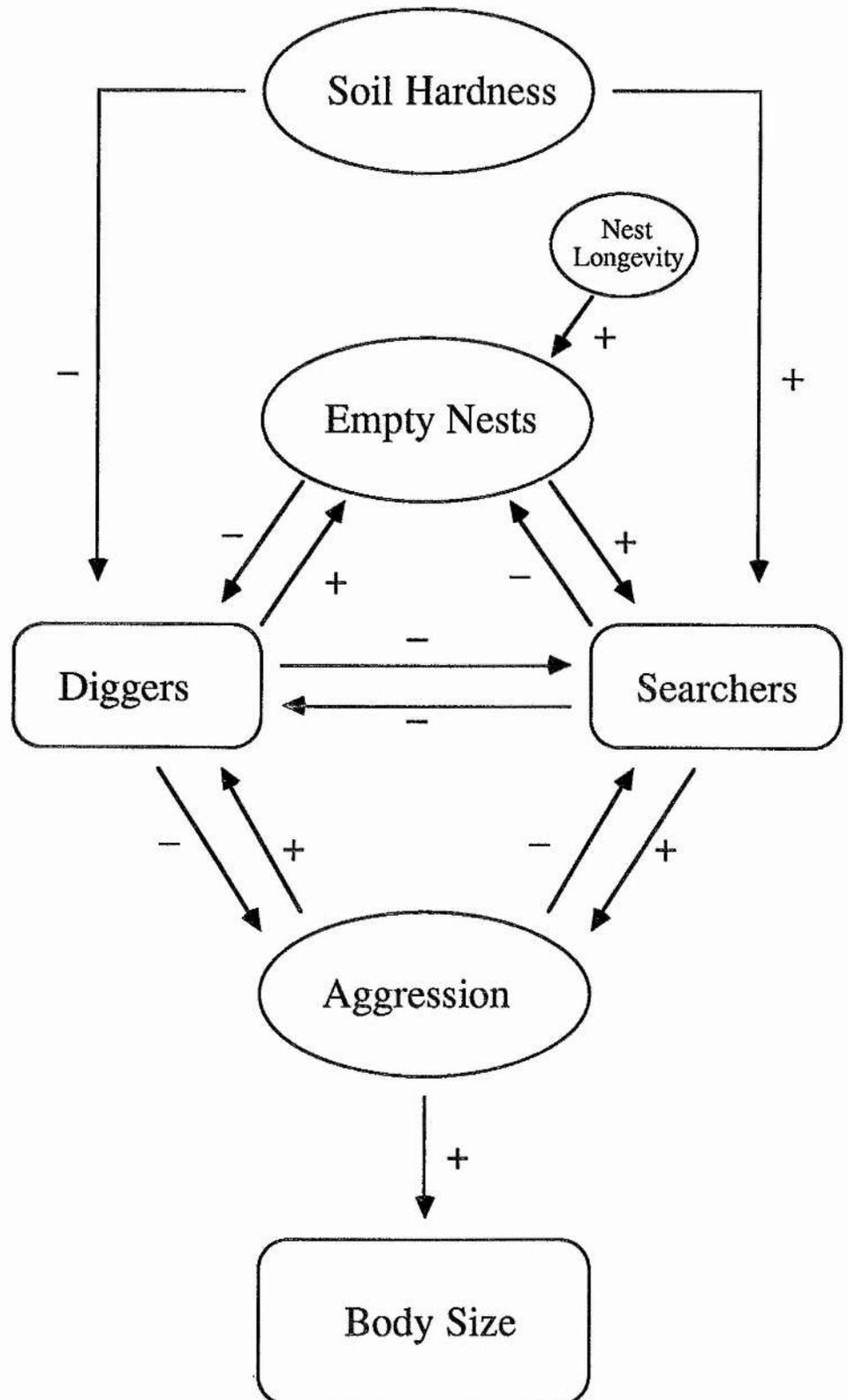


Fig. 5.12 A diagrammatic representation of the "Searcher" model, (see text for details).



Chapter 6 - Behavioural Thermoregulation and Endothermy in some Sphecid Wasps from Britain and Portugal

6.1 Introduction

The distribution and behaviour of insects are greatly influenced by their capacity for thermoregulation (Casey 1981; May 1985; O'Neill & Kemp 1990; O'Neill et al. 1990). Thermoregulatory capacity is important in foraging (Louw & Nicolson 1983; Willmer 1985a), mating behaviour (May 1977; Gilbert 1984; Larsson 1989a,b,c,d; review by Willmer 1991), predator avoidance (O'Neill et al. 1990; Srygley & Chai 1990), competitive interactions (W. J. Hamilton 1971; May 1977), optimizing physiological performance and increasing developmental rate (Whitman 1988). Many studies have been carried out on the behavioural aspects of thermoregulation in the Hymenoptera (eg, Heinrich 1979a; May & Casey 1983; Chappell 1984; Willmer 1988), but work on sphecid wasps has so far been limited to only a handful of studies (eg, Willmer 1985a,b; O'Neill & O'Neill 1988; Larsson 1989a,b,c; Larsson & Tengo 1989).

In addition to behavioural thermoregulation some insects have the ability to raise body temperatures by metabolic means using the flight musculature to generate heat (Adams & Heath 1964; Heinrich 1971a,b). Endothermy in the Apoidea is now well documented (eg, *Bombus spp.*, Heinrich 1972b,c,d, 1974, 1975, 1976; *Apis mellifera*, Heinrich 1980; and numerous solitary bee species, Stone & Willmer 1989a) but there have been no studies to date of endothermy in sphecid wasps. An endothermic insect is capable of remaining active over a wider thermal range and may have an advantage in competitive interactions (Heinrich 1977). Digger wasps have similar life styles and behavioural

interactions to many ground nesting bees and it might be predicted that endothermy would be advantageous for sphecids. The aim of this study was to determine the capacity for endothermy in some sphecid wasps from Britain and Portugal and to assess its relative importance in the daily activity of these wasps.

6.2 Sites, Materials and Methods

6.2.1 The Wasps Used in the Study and Their Nesting Behaviour

Three species in Britain, and two species in Portugal were studied (table 6.1). The three British species were relatively small in size compared to the two *Bembix* species from Portugal. *Ammophila sabulosa* differs from the other four species in having an elongate body shape, giving a large surface area to volume ratio. The five species can be said to be of varying degrees of "advancement" along the sphecid evolutionary tree, with *A. sabulosa* (Sphecinae) being the most primitive, *M. arvensis* (Nyssoninae) and *C. cribrarius* (Crabroninae) occupying the next level, with the most "advanced" being *B. zonata* and *B. rostrata* (Bembicinae) (Bohart & Menke 1976).

The nesting biology of *M. arvensis* has been described in Chapter 3.

Ammophila sabulosa (figure 6.1) digs shallow nests (1-4 cm deep) in sandy ground which end in a single cell. Cells are provisioned with one to five caterpillars which are carried to the nest on foot or in low short flights. Long lived females may provision many nests during the summer, depending on the weather. Usually, females are active only in direct sunlight.

Crabro cribrarius is a solitary ground nesting species which digs nests up to 50 cm deep containing several cells that are provisioned with a number of flies. These wasps are rarely found occurring in nesting aggregations.

Two species were selected for study at Portugal, *Bembix rostrata* (figure 6.2) and *B. zonata* (Bembecinae). The two species occurred sympatrically, hunting and feeding at similar plants. Nests of *B. rostrata* were aggregated while those of *B. zonata* were isolated. *Bembix rostrata* is one of the largest digger wasps in Europe. Its large size (and therefore small surface area to volume ratio) made it an obvious candidate for the possible existence of endothermy. It often nests in large aggregations in open sandy habitats, facilitating the observation of several nests simultaneously. Females construct nests in the ground each with a single cell (Larsson 1989a). During a period of about one week the cell is filled with flies (Larsson & Tengö 1989) upon which a larva will feed. The overwintering pupa develops into an imago and emerges the following summer during early May in Portugal, but may be considerably later in more northerly latitudes (Larsson 1989a). Males spend much of their time searching for females at the nesting site. Males often form 'mating clusters' (personal observations, Larsson 1989a) consisting of several individuals competing for access to a female at the centre of the cluster. Females mate only once, on the ground or on vegetation (Schöne & Tengö 1981).

Bembix zonata is a smaller wasp (table 6.1) and, due to difficulty in locating its isolated and often hidden nests, little is known about its nesting biology. However this wasp was also observed to hunt flies.

6.2.2 The Study Site in Portugal

The study was carried out between May 18th and May 27th 1992, at Fonta de Telha, in the Costa Caparica, Portugal (figure 6.3). This is a coastal area of sandy soils, scrub vegetation and scattered clumps of pine trees. There are many paths through the vegetation providing open sandy habitats suitable for a wide variety of ground nesting sphecids. The particular nesting aggregation under study was located on such a sandy path and was directly insolated throughout daylight hours. The aggregation covered an area 20 metres long by 3 metres wide (60 square metres) and there were about 30 active nests in the area. *Bembix rostrata* was nesting elsewhere along the sandy path but this was the only distinct aggregation found.

6.2.3 Behavioural Observations of *Bembix rostrata* in the Field

The behaviour of a total of 11 marked females at the nesting site was recorded on two days. The time taken to perform a number of activities was recorded.

The activities are defined as follows:

In Nest - actual time spent inside the nest, ie. period between entering and emerging.

Closing - the time spent covering the nest entrance with sand.

Basking - any time on the sand surface where no activity could be seen to occur other than abdominal telescoping movements and occasional grooming.

Prey foraging - the time between the moment of leaving the nest site to returning to land in front of the nest entrance. This time may include some or all of outward flight time, basking, feeding at flowers, searching and catching prey, and returning (with or without the prey) to the nest.

Entering - the time between landing at nest entrance after returning from a trip to the moment of entering the burrow. This period includes the activity of scraping sand away from the closed burrow to gain access to the nest, and is the time that the wasps were most vulnerable to attacks from parasitic flies (personal observation).

Overall male and female activity was recorded on three days by counting the number of individuals seen at the nesting site during a one minute period at intervals of ten minutes. Ambient temperature (T_a) and ground temperature (T_g) were recorded at ten minute intervals using a shaded 25 gauge copper-constantan thermocouple and a Type T P9005 thermocouple thermometer (Portec Instruments, UK). Mating attempts by males were also noted.

Males and females were often seen foraging and flying around thyme plants (*Thymus vulgaris*). The behaviour of marked males and females on one *T. vulgaris* patch was observed on two days. The number of flowers visited by any one individual was determined indirectly by measuring foraging time on the patch. The mean number of flowers visited per minute had been obtained by prior observation, and from this value the total number of flowers visited could be estimated. Nectar volume and concentration were recorded at intervals throughout the day using 1 μ l microcapillaries (Drummond Scientific Company, Broomall, PA, USA) and a hand-held refractometer modified to allow measurement with very small volumes (Bellingham & Stanley, UK).

The method of marking wasps was different between the nesting and the foraging sites. At the nesting site females were marked by placing a small dot of enamel paint (Humbrol, UK) on the back of the thorax using a fine grass stem. They were not caught but rather marked in the time it took for them to

clear sand away from the nest entrance. During this time the wasps were relatively stationary apart from the front legs which were raking sand away from the nest entrance. This method of marking was easy, fast, and minimised handling. All eleven wasps marked in this manner were seen returning with prey or digging at the nest site within 24 hours of marking.

Seven wasps at the foraging sites were marked with coloured and numbered discs (E. Thorne [Beehives] Ltd.) to avoid confusion with wasps marked at the nesting site. Wasps were first caught and lightly anaesthetized with carbon dioxide before a disc was glued (Loctite Super Glue 3, Loctite, UK) onto the back of the thorax. Six of these individuals were seen again within twenty four hours.

6.2.4 Field Analyses of Thoracic and Abdominal Temperatures.

Body temperatures of wasps in the field were measured using the 'grab & stab' technique as described in Chapter 2 (section 2.9). The sex and size of each wasp were determined later in the laboratory. Head width was measured to the nearest 0.01 mm using a hand held digital micrometer (Mitutoyo Corporation, Japan) and fresh weight measured to the nearest milligram using a home made field microbalance (Unwin 1980).

Lethal thoracic temperatures of wasps were recorded by shallowly inserting a thermocouple into the thorax dorsally and then placing the wasp onto the hot sand surface. The lethal body temperature was defined as that temperature at which all movement ceased.

6.2.5 Laboratory Investigations of Warm-Up Rates

The methods used for obtaining warm-up rates of *Bembix* wasps has been described in Chapter 2 (section 2.10).

6.3 Results

6.3.1 Endothermic Warm-Up in Sphecid Wasps

Endothermic warm-up was recorded in *Bembix rostrata* and *B. zonata* from Portugal, but not in the three British species, *A. sabulosa* (N = 6), *M. arvensis* (N = 22) or *C. cribrarius* (N = 14). In the British wasp species, warm-up of the live wasp was similar to that of a control, whereas *B. rostrata* and *B. zonata* continued to warm-up beyond the maximum ambient temperature, and maintained an elevated thoracic temperature several degrees above ambient (figures 6.4 - 6.6b).

Ammophila sabulosa is an unlikely candidate for endothermy due to its high surface area to volume ratio, a consequence of its long and thin body shape. Loss of excess heat from this animal is likely to be very rapid and maintenance of a high body temperature by endothermy will require considerably more energy than a wasp of similar weight but with a more rounded shape (Bartholemew 1981). Being active only during periods of sunshine (Field 1989a) is another indication that this species is incapable of endothermy. The nests of *A. sabulosa* are not deeper than 4 cm (Field 1989a) and so the wasp is never far from the hot sand surface when digging the nest or provisioning a cell. When foraging the wasps always fly close to the ground and usually at a height of less than 20 cm landing frequently on the ground for several seconds before resuming flight (personal observation,

Findhorn). This flight pattern results in wasps being permanently near to, or within, a thermally favourable microclimate, the hot sand surface. Time spent on the sand surface between flights could be periods of ectothermic warm-up, heat being gained from solar radiation and through conduction from the hot sand. Because of the elongate body shape, loss of heat by convection during flight is likely to be rapid, perhaps necessitating frequent stops.

The small size of *M. arvensis* and *C. cribrarius* is not sufficient to explain the absence of endothermy in these wasps: endothermy has been recorded in bees of similar and smaller size (eg, *Megachile centuncularis*, *Osmia leaiana*, *Colletes daviesanus*, *Lasioglossum smeathmanellum*, Stone & Willmer 1989a). Evidence for the existence of endothermy in *C. cribrarius* and *M. arvensis* arises from observations of their behaviour when attempting to carry a particularly large prey item into the nest. Individuals from both species were often observed to emit a high pitched "buzzing" sound that was accompanied by rapid abdominal telescoping but without wing movement (personal observation, Findhorn, St Cyrus, Alderly Edge). Immediately after this, wasps would attempt to move towards the nest with the prey, using a combination of walking and flying. The production of a high pitched buzz is a frequent observation in flies that are in the process of endothermic warming (eg, *Syrphus* sp., Heinrich & Pantle 1975; *Gasterophilus intestinalis*, Humphrey & Reynolds 1980; *Criorhina nigriventris*, *Sercomyia chrysotoxoides*, Morgan & Heinrich 1987). The only other occasion on which *M. arvensis* was heard to make a sound was during a fight with a conspecific. Abdominal telescoping movements are also typical of an insect warming up endothermically (Weis-Fogh 1967; Bartholemew & Barnhart 1984; Stone 1989), and serve to increase the air flow within the tracheal system thereby supplying the muscles with a greater amount of oxygen. These observations suggest the existence of an endothermic ability in these small species.

While, of course, it is possible that endothermy in *M. arvensis* and *C. cribrarius* does not exist, it is also possible that the wasps are capable of endothermic warming but are not doing so under experimental conditions, perhaps due to the methods used, stress to the animals, or the absence of the correct stimulus. For example, to record endothermy in these wasps it might be necessary to increase their wing load by attaching small weights to their feet to represent a large prey item. In response to the increase in wing load wasps might initiate endothermy to achieve flight. Alternatively, the use of finer thermocouples, or better still, non-invasive methods of body temperature measurements, such as infra red thermal imaging (Stabentheiner & Schmaranzer 1988), may give more accurate results with minimal stress to the animals.

Endothermy in *Bembix rostrata* was observed and recorded in both sexes (figures 6.6a & 6.6b, and table 6.2). Wasps often underwent several bouts of pre-flight warm-up each bout raising body temperature by about 14 °C above ambient. Upon reaching the maximum temperature (usually between 33 - 38 °C) flight was generally initiated, at which point thoracic temperature was observed to drop rapidly. Wasps would cease flying when temperature dropped to about 25 °C and often underwent a second or third period of endothermic warm-up.

The following terms have been used in the analysis of the results and are defined as in Stone & Willmer (1989b). Mean warm-up rate (MWR) is the mean of all the warm-ups for all individuals over a temperature range of 3°C or more. Peak warm-up rate (PWR) is the highest rate maintained over a 5°C temperature interval for the species. Mean flight temperature (MFT) is the mean temperature at which flight was initiated.

The MWR of female *B. rostrata* was 3.42 ± 0.40 °C per minute, which is lower but comparable with data obtained at the same ambient temperature from bees of similar size (eg, *Psithyrus vestalis* 6.3 °C min^{-1} ; *Euglossa imperialis* 7.0 °C min^{-1} ; *Anthophora plumipes* 12.3 °C min^{-1} ; *Chalicodoma sicula* 4.2 °C min^{-1} ; all data from Stone & Willmer 1989a). Pubescence on the body of *B. rostrata* is present in far greater density than occurs on either *M. arvensis* or *C. cribrarius*, and no doubt acts to some degree as an insulator. The density of this pubescence is, however, considerably less than that found in many bee species. Therefore, greater rates of heat loss, rather than lower rates of heat generation, may account for the low rates of endothermic warm-up observed in *B. rostrata*, compared to bee species. Improved experimental procedure, such as the use of finer thermocouples and reduced handling times of the wasps, are likely to give higher values for MWR of *B. rostrata*.

The results for the endothermic abilities of *B. zonata* are from a single individual (female, wet weight 124 mg). The MWR was 0.83 °C/min, VFT was 30 °C and the maximum temperature reached by endothermic pre-flight warm-up was 32 °C. This is considerably lower than the results obtained for *B. rostrata*, but with results from only one individual, comparisons are of little value. Nevertheless, endothermy has been demonstrated in a second species of *Bembix* and in a second sphecid wasp.

Figure 6.7 shows the relationship between warm-up rates and body weights of *B. rostrata*. There is much variation within individuals and no significant correlation between size and warm-up rates. These data should be considered carefully as, due to a sample size of five wasps, up to three readings are taken from a single wasp resulting in non-independent data. Minimum ambient temperature for activity is about 22 °C, although this value is obtained from observations in the field rather than from direct empirical evidence.

Voluntary flight temperature (VFT) is also not correlated with weight (figure 6.8), although again the sample size is small and the data are non-independent.

6.3.2 Thoracic and Abdominal Temperatures in the Field

Wasps of the species *M. arvensis*, *C. cribrarius* and *B. rostrata* had thoracic temperatures several degrees above ambient while active (figures 6.9 - 6.11). The mean thoracic temperature excess ($T_{th} - T_a$) was similar for *M. arvensis* (4.5 ± 0.2 °C; figure 6.9) and *C. cribrarius* (5.2 ± 0.3 °C; figure 6.10) and was considerably higher for the larger, endothermic, *B. rostrata* (11.8 ± 0.7 °C; figure 6.11). Thoracic temperatures of *B. rostrata* reached much higher levels (mean 35.0 ± 0.8 °C for females) than the British species (*M. arvensis* mean 24.0 ± 0.4 °C; *C. cribrarius* mean 22.6 ± 0.7 °C). The large temperature excess observed in *B. rostrata* (figure 6.11) is probably due to relatively low rates of heat loss as a result of large body size and high ambient temperatures (21 - 28 °C), and high rates of heat production from the larger flight muscles of this species. *M. arvensis* and *C. cribrarius*, being small and occurring in a habitat where ambient temperatures are low, have relatively high rates of heat loss and correspondingly low thoracic temperature excesses. The two British species are therefore likely to be limited in their activity periods by low ambient temperatures, whereas *B. rostrata* may be limited by high ambient temperatures which could lead to heat stress. These thermal constraints should be reflected in the periods of activity of these wasps, with *M. arvensis* and *C. cribrarius* being active during the hottest part of the day, with activity decreasing during the cooler periods, while *B. rostrata* are expected to be active during the cooler mornings and late afternoons, and avoiding activity during the middle of the day.

All thoracic temperature measurements were taken from wasps caught in flight. However, some of the *M. arvensis* females were laden with prey, and the effect of increased wing loading on thoracic temperature is now investigated. Figure 6.12 plots ambient temperature against thoracic temperature for laden and unladen wasps. There is no difference in the thoracic temperature between the two groups ($p = 0.9$, $z = 0.073$, d.f. = 56), indicating, for this species at least, that an increased burden due to prey does not affect the thoracic temperature. Neither is there a correlation between prey weight and the thoracic temperature excess (figure 6.13). Thus there is no evidence to support the idea, suggested earlier (section 6.3.1), that increased wing loading requires an increased body temperature for flight in *M. arvensis*, as has been shown for *B. rostrata* (Larsson 1989a).

There is no correlation between body size and thoracic temperature excess in either *M. arvensis*, or *B. rostrata* (figures 6.14 & 6.15). The lack of correlation between these two parameters is a possible indication of the existence of endothermy which would enable individuals to raise body temperatures regardless of environmental conditions or body size. No evidence for the existence of endothermy was found for *M. arvensis* or *C. cribrarius*. Therefore, the lack of correlation between size and thoracic temperature excess suggests that either body size variation within the populations is not sufficient to cause variation in temperature excess, or that by regulating body temperature behaviourally, for example by microhabitat selection in a thermally heterogeneous environment, variation in temperature excess between individuals of different sizes can be reduced.

The highest recorded thoracic temperature of *B. rostrata* was 44.0 °C at an ambient temperature of 28.2 °C. Unfortunately, no wasps were caught at ambient temperatures beyond this, though wasps remained active at ambient

temperatures of up to 36.2 °C. At this ambient temperature, extrapolation from figure 6.11 gives a thoracic temperature of 49.5 °C. The lethal body temperature for *B. rostrata* from this site was 47.9 ± 0.8 °C ($N = 3$), which corresponds to an ambient temperature of 34.6 °C. The fact that some wasps were seen to be active at temperatures in excess of 34.6 °C suggests that they have some degree of temperature regulation, either behavioural or physiological, by which they can keep thoracic temperatures below the lethal limit. Ambient temperatures in excess of 34 °C are not unusual for this site in Portugal, and a physiological mechanism by which body temperatures at high ambient temperatures can be regulated to avoid overheating is likely to be of great adaptive value (eg, Heinrich 1972c; Heinrich & Casey 1978; Heinrich 1980a,b; Cooper et al. 1985).

The lethal thoracic temperature of *M. arvensis* was 44.9 ± 1.0 °C, which corresponds to an ambient temperature of 39.5 °C. The highest recorded thoracic temperature of *M. arvensis* was 30.2 °C at the relatively low ambient temperature of 19.5 °C. The highest temperature at which a thoracic temperature measurement was taken was 23.0 °C, at which the thoracic temperature was only 29.0 °C. In Britain it would be very rare for ambient temperatures to reach levels that would be close to the critical upper temperature. It is therefore unlikely that a physiological mechanism regulating body temperature in order to avoid heat stress would have evolved, as such a mechanism is not needed.

The situation is very similar for *C. cribrarius*, which had a maximum recorded temperature of 30.9 °C at an ambient temperature of 22.0 °C. If an upper lethal temperature of 45 °C is assumed for this wasp, ambient temperature would have to rise to 35.3 °C before this state is reached.

Thoracic temperature of *M. arvensis*, *C. cribrarius* and *B. rostrata* increased at the same rate as T_a , causing T_{ex} to remain constant regardless of T_a (figures 6.9 - 6.11). Abdominal temperatures of *B. rostrata* also increased at the same rate as thoracic and ambient temperatures (figure 6.11). The difference in temperature between the thorax and abdomen of *B. rostrata* varied between individuals (1.9 - 10.9 °C) but was independent of T_a (figure 6.16). These data provide no evidence of an active physiological mechanism for temperature regulation (eg, by controlling haemolymph flow between the thorax to the abdomen), as has been shown to occur in other insect species (eg, *Manduca sexta*, Heinrich 1971a,b; Heinrich & Bartholemew 1971; Casey 1976; *Bombus vagans*, Heinrich 1972b; *B. vosnesenskii*, Heinrich 1972c). Indeed, there is a sharp drop in the number of *B. rostrata* males and females seen at the nesting site when ambient temperature exceeds 32 °C (figures 6.17a and 6.17b) suggesting, in contrast to the evidence presented above, an inability to maintain low body temperatures independently of ambient.

6.3.3 Overall Activity Patterns of *Bembix rostrata*

On most days wasp activity at the nesting site started at about 0930 local time and wasps remained active until 1700. Temperature seemed to limit the period of activity at both the lower and upper temperature limits. A minimum temperature of 22 °C, comparable to the value of 20°C for a population of *B. rostrata* in southern Sweden (Larsson 1989), was required for male and female activity. When T_a ^{subscript} exceeded 32°C (often around 1100-1200) there was a sharp drop in the activity of both males and females (figures 6.17a & 6.17b). On cooler days activity was considerably delayed, and activity remained low when temperatures were cool (figures 6.18a & 6.18b). Unfortunately, temperature remained unusually cool for the time of year, and temperatures exceeding 30 °C rarely occurred during the period of study.

Because of this it is difficult to determine the importance of the thermal environment to the overall activity of this wasp.

It is unusual that *B. rostrata*, being an endothermic insect, should be so constrained by low temperatures. *M. arvensis* at British sites started activity at the much cooler temperature of 14 °C (Chapter 3), and a large number of wasps and bees were active in Britain at temperatures below 20 °C. *B. rostrata* is a large wasp (fresh weight of about 200 mg compared with 60 mg for *M. arvensis*) and because of this large size, a long period of ectothermic warm-up might be necessary. It has already been ascertained that these wasps use endothermic pre-flight warm-up in the laboratory, and therefore have the ability to raise thoracic temperatures independently of ambient conditions. This ability does not seem to be used to initiate or maintain activity at low temperatures.

Flight leads to cooling of the body (figure 6.6a & 6.6b) by convective air currents created by the movement of the insect through the air, and the flow of air caused by wing flapping (May 1978). Cooling of the body would be expected to occur more rapidly at lower temperatures, and under such conditions cooling of the body upon the initiation of flight may lower the thoracic temperature below the minimum temperature required for flight. If wasps were to use endothermic pre-flight warm-up under conditions of low ambient temperatures, the subsequent loss of heat upon the initiation of flight might require wasps to undergo repeated bouts of warm-up to maintain activity (figures 6.6a & 6.6b). Such a routine is energetically costly, and results in periods of time when the wasp is exposed to predators while warming up. Possibly for this reason, wasps were not observed to be active at temperatures below 22 °C despite their capacity for endothermy.

Endothermic warm-up might be used only when additional heat is required for a particular purpose. Wasps may therefore rely largely on energetically cheap ectothermic warm-up to raise body temperatures for flight (much basking behaviour on the relatively hot sand surface was observed), and use energetically costly endothermic warm-up during brief cool spells, when loaded with heavy items such as prey or a mate, or during periods of scramble competition between males for mates.

6.3.4 The Foraging and Provisioning Biology of *Bembix rostrata*

All the prey items caught by *B. rostrata* were Diptera (N = 63) from a diverse range of families. Flies from the families Bombyliidae (11.1 %), Syrphidae (12.7 %), Muscidae (15.9 %), Calliphoridae (23.8 %), and Sarcophagidae (28.6 %), were most frequently caught. The dry weight of the flies ranged between 3.42 mg to 19.06 mg with a mean value of 11.36 ± 0.91 mg (N = 21).

The time taken for provisioning females to find a prey item and return to the nest with it (foraging time) varied from a minimum of 2 minutes to a maximum of 170 minutes (N = 51). There was no pattern to this variation with time of day or with temperature (figure 6.19, $p > 0.05$, $t = 1.792$, d.f. = 61) although the temperature range was small during the period of data collection (21 - 26 °C).

The mean duration of a successful foraging trip was 31.7 ± 5.0 minutes (N = 57) while an unsuccessful foraging trip lasted 49.4 ± 6.8 minutes (N = 6). There is no significant difference between these two values ($p > 0.2$, $t = 1.116$, d.f. = 61) although this might be due to the small data set on unsuccessful foraging trips.

Differences in the mean duration of foraging trips are revealed when foraging times are grouped according to prey size classes (small, medium, and large, as with *M. arvensis*, Chapter 3) (table 6.3). There is a significant difference in prey foraging time between the medium and large prey size categories ($p = 0.010$, $t = 2.69$, d.f. = 40), but no significant differences between the small and medium categories ($p = 0.097$, $t = 1.70$, d.f. = 42) or small and large categories ($p = 0.403$, $t = 0.86$, d.f. = 14). Small data sets for two of the prey size categories (small prey, $N = 9$; large prey, $N = 7$) make the results difficult to interpret.

Wasps may select prey items according to size depending on the ambient temperature. Large prey items are expected to be of greater value to a wasp as they represent a larger packet of food, and so fewer foraging trips, and overall less time, are needed to stock each cell. More cells can therefore be stocked during the wasps' lifetime resulting in a greater number of offspring and hence greater fitness. Fewer foraging trips per cell reduces opportunities to parasites, and increases the percentage of surviving offspring. However there will only be fewer foraging trips per cell if the length of time taken to forage for a large prey item is the same as that for a small prey item. Prey foraging time is, to an extent, dependent on flight efficiency and the ability and ease with which a wasp can return with the prey to the nest. A heavy prey item incurs greater wing loading on a wasp and a higher body temperature may be necessary for efficient flight (Bartholemew & Heinrich 1973; Larsson 1989a). It is energetically costly to raise body temperature through endothermy and more energy is required to sustain a large temperature excess between T_{th} and T_a as opposed to a low one. It might therefore be expected that wasps will only select large prey when T_a is high, thus reducing the energetic costs of maintaining a high thoracic temperature needed for efficient flight. A balance must be reached between the advantages of foraging for large prey

items and the energy costs incurred in maintaining high T_{th} . The cost of maintaining a high T_{th} decreases with increasing T_a and vice versa so it is expected that wasps will forage for large prey only when T_a is high and forage for small prey when T_a is low. Due to the small temperature range (21.3 - 25.4 °C) over which data were collected it is difficult to establish whether there are any differences in prey selection by females at different temperatures (table 6.4). There are no significant differences in mean temperature between the different prey size categories. Medium sized prey comprised 67% of the total prey caught, however, and this may reflect selection for this prey size at this temperature range. More data need to be collected at higher ambient temperatures for this question to be resolved.

6.4 Discussion

6.4.1 The Endothermic Ability of Sphecid Wasps

Recent research has shown that endothermy in insects is much more widespread than previously thought (Kammer 1970; Heinrich & Pantle 1975; Bartholemew & Casey 1977; Heinrich & Bartholemew 1980; Humphreys & Reynolds 1980; Gilbert 1984; Bartholemew & Lighton 1986; Joos 1987; Casey 1988; Martin 1988; Stone & Willmer 1989a). From the results presented in this study it is clear that at least one sphecid species, *Bembix rostrata*, is also capable of endothermy. This is the first recorded case of endothermy in a sphecid, although it is probably not unusual in other large sphecid species. *Bembix rostrata* is active only during sunny periods (Larsson 1989a; personal observation) and thermoregulates behaviourally through conduction and convection by sitting on the hot sand surface in the sun. Basking is often accompanied by rapid abdominal movements which are typical of an insect undergoing physiological warm-up. Although no measurements of

endothermic ability were made in the field it is likely that the insects use a combination of both endothermy and behavioural thermoregulation to raise body temperatures, particularly on cooler days.

Wasps with greater wing load (defined as the ratio between body weight and wing area) require higher temperatures for efficient flight (Larsson 1989a) and thus endothermy would be important in raising body temperature to that which is optimal for flight, especially when carrying a load such as prey, or in the case of males, a female wasp. The sphecid wasps *Mellinus arvensis* and *Crabro cribrarius*, when returning with a particularly large prey item, often perform rapid telescoping movements of the abdomen and 'buzzing' of the thorax, both behaviours indicating the possibility of physiological warm-up (personal observation), although there was no difference of temperature excess between *M. arvensis* that were laden with prey and *M. arvensis* that were not (figure 6.12). Abdominal telescoping movements could serve the same purpose in *Bembix rostrata*. Males would be able to resume mate searching activities more quickly after a period of low temperature, and may have greater success in the intense competition for females at the nesting site. A male that is able to maintain an optimal temperature for flight with minimal time spent basking would have more time to search and chase females. Furthermore a male that can regulate body temperature physiologically may be more successful in chasing and catching females, defending himself from attacks by other males and interfering competitively with other pairs. The purpose of digging behaviour observed in males is probably to secure virgin females emerging from the ground (behaviour also observed in *Bembecinus quinquespinosus*, O'Neill & Evans 1983; and *Centris pallida*, Alcock et al. 1976, 1977b). No male was seen to locate and dig out a female successfully, but several mating clusters, consisting of up to five males and one female, were observed. After locating a female, males quickly carry

her away from the nesting site to avoid the attentions of other males. The speed at which this occurs may be dependent on body temperature and hence efficiency of flight.

It is unusual that *Bembix rostrata* does not forage on overcast days despite being capable of endothermy. Activity rapidly decreases and females enter the nest and seal the entrance from the inside as soon as the sun is ~~hidden~~ behind clouds. One explanation for this behaviour is that the prey species cease to be active in these cooler conditions. Another explanation is that it is energetically too costly to maintain a high body temperature at low ambient temperatures. As ambient temperature decreases there is a corresponding decrease of both thoracic and abdominal temperature indicating that wasps do not actively regulate their body temperature around a fixed optimal point but rather maintain a constant temperature excess above ambient. The energetic cost of maintaining constant high body temperature during cool weather may be prohibitive.

B. rostrata were observed to be active at ambient temperatures in excess of 34.0 °C which, based on measured lethal body temperatures and extrapolation from figure 6.11, is the theoretical upper tolerance limit. To be active at these temperatures wasps must have some way of regulating their thoracic temperatures to avoid overheating. This might be achieved by behavioural or physiological thermoregulation. Physiological regulation of body temperature by shunting hot blood from the thorax to the abdomen has been demonstrated in moths, honeybees and bumblebees (Heinrich 1970, 1979b, 1976). There was no evidence for this kind of temperature regulation in *B. rostrata*, as thoracic and abdominal temperatures increased linearly with ambient temperature, although this might have been due to the narrow temperature range in which body temperatures were measured. Evidence of

temperature regulation at higher temperatures has been observed in *B. rostrata* (Larsson 1989a), indicated by the levelling off of T_{th} at T_a , although no indication was given as to whether this was physiological or behavioural thermoregulation.

6.5 Conclusion

A study of endothermy was carried out for five species of sphecid wasp. Two species, *Bembix rostrata* and *B. zonata*, were capable of endothermic warm-up, although data for the latter species were based upon a single individual. Endothermy does not seem to be as important in shaping the behaviour of *B. rostrata* as might be expected from similar work on bees (Stone 1989). Rather, this energetically costly process is perhaps used periodically, for example when loaded with prey or a mate.

The body temperatures of three species were recorded in the field. *M. arvensis* and *C. cribrarius* maintained a mean thoracic temperature excess of 4.5 and 5.2 °C, while the much larger *B. rostrata* had a mean thoracic excess of 11.8 °C. There was no evidence of temperature regulation, as thoracic temperature increased at the same rate as ambient temperature. This was also true for the abdominal temperatures of *B. rostrata* indicating that no physiological regulatory mechanism, based on the control of blood flow between the thorax and abdomen, was being used.

The existence of endothermy has now been shown in two sphecid species. Further work on this subject with other large sphecid species will undoubtedly prove that this capacity is widespread throughout the aculeates, and is not restricted to the Apoidea and Vespoidea.

Table 6.1 The size and distribution of the sphecid species considered in laboratory studies of endothermy.

| <u>Species</u> | <u>Subfamily</u> | <u>Location</u> | <u>Weight (mg)</u> |
|--------------------|------------------|-----------------|--------------------|
| Ammophila sabulosa | Sphecinae | Britain | 40 - 90 |
| Crabro cribrarius | Crabroninae | Britain | 35 - 70 |
| Mellinus arvensis | Nyssoninae | Britain | 15 - 40 |
| Bembix zonata | Bembicinae | Portugal | 80 - 170 |
| Bembix rostrata | Bembicinae | Portugal | 160 - 240 |

Table 6.2 The combined results of endothermy experiments on *Bembix rostrata*.

| | <u>Mean Mass</u> (mg) | <u>MWR</u> (°C/min ⁻¹) | <u>PWR</u> (°C/min ⁻¹) | <u>MFT</u> (°C) | <u>N</u> |
|---------|--------------------------|---------------------------------------|---------------------------------------|--------------------|----------|
| Males | 222 (± se) | 2.03 (se) | 2.42 (se) | 30.1 (se) | 2 |
| Females | 198 " | 3.42 " | 5.37 " | 35.7 " | 10 |

Table 6.3 The influence of prey size on female *Bembix rostrata* hunting and provisioning behaviour. Results are expressed as means \pm SE (N).

| | <u>Small Prey</u> | <u>Medium Prey</u> | <u>Large Prey</u> |
|---------------------|---------------------|---------------------|---------------------|
| Prey Foraging (min) | 43.4 \pm 11.7 (9) | 23.8 \pm 5.0 (35) | 64.3 \pm 23.3 (7) |
| Opening (sec) | 35.9 \pm 8.2 (10) | 28.7 \pm 5.7 (32) | 18.5 \pm 1.8 (4) |
| In Nest (sec) | 52.7 \pm 7.8 (9) | 52.1 \pm 4.3 (32) | 57.5 \pm 12.0 (6) |
| Closing (sec) | 37.1 \pm 10.9 (8) | 38.8 \pm 8.3 (30) | 40.6 \pm 11.7 (7) |

Table 6.4 Temperature at which prey of different sizes are taken by *Bembix rostrata*. Prey are divided into three categories, small, medium and large, according to size. Mean temperature (in $^{\circ}$ C) at which the prey were taken is calculated together with standard error).

| <u>Prey size</u> | <u>Mean Ta</u> | <u>N</u> |
|------------------|-------------------|----------|
| Small | 23.3 (\pm 0.4) | 10 |
| Medium | 23.2 (\pm 0.2) | 35 |
| Large | 23.8 (\pm 0.2) | 7 |

t-test between the three categories:

| <u>Comparison between</u> | <u>p</u> | <u>df</u> |
|---------------------------|----------|-----------|
| S-M | 0.76 | 43 |
| M-L | 0.15 | 40 |
| L-S | 0.34 | 15 |

Fig. 6.1 The sphecid wasp *Ammophila sabulosa*.



Fig. 6.2 The sphecid wasp *Bembix rostrata*.



Fig. 6.3 The site of the nesting aggregation of *B. rostrata* in Portugal.



Fig. 6.4 Endothermy in *Bembix zonata* (Female, Weight 124 mg). Thoracic temperatures were recorded every 15 seconds and are here plotted at 1 minute intervals. Ambient temperature was 22 °C. This wasp did not attempt to fly while attached to the thermocouple.

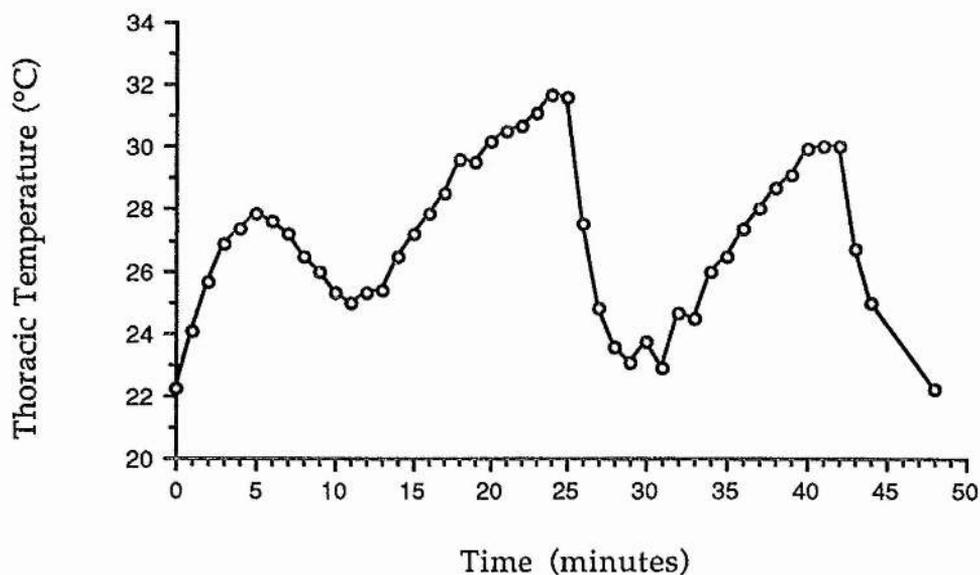


Fig. 6.5 Endothermy in *Bembix rostrata* (Male, Weight 210 mg). Thoracic temperatures were recorded every 15 seconds and are here plotted at 1 minute intervals. Ambient temperature was 22 °C. This wasp did not attempt to fly while attached to the thermocouple.

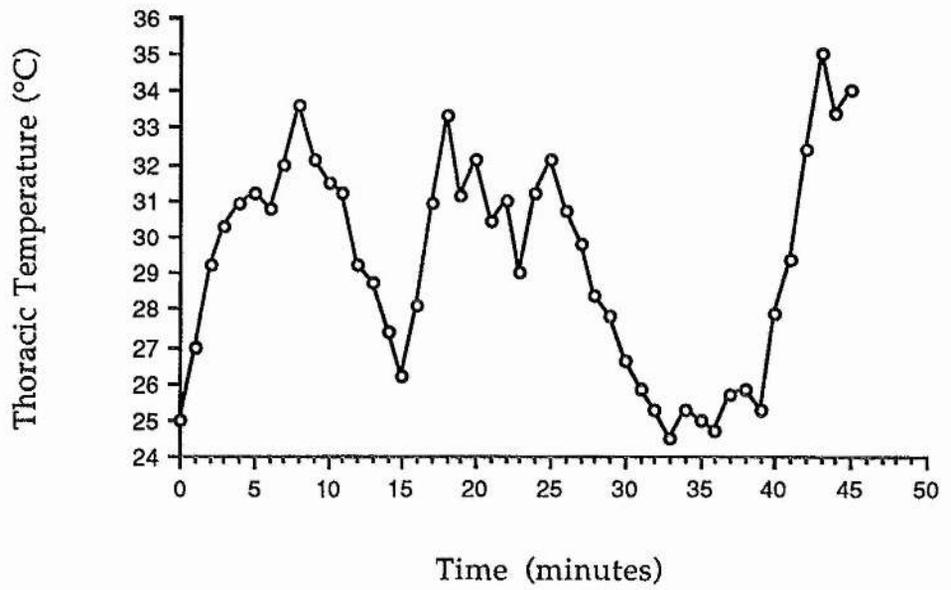


Fig. 6.6a Endothermy in *Bembix rostrata* (Female, Weight 190mg). Thoracic temperatures were recorded every 15 seconds and are here plotted at 1 minute intervals. Ambient temperature was 22 °C. Initiation of flight is indicated by the letter 'F', and the point at which flight stopped is indicated by the letter 'S'.

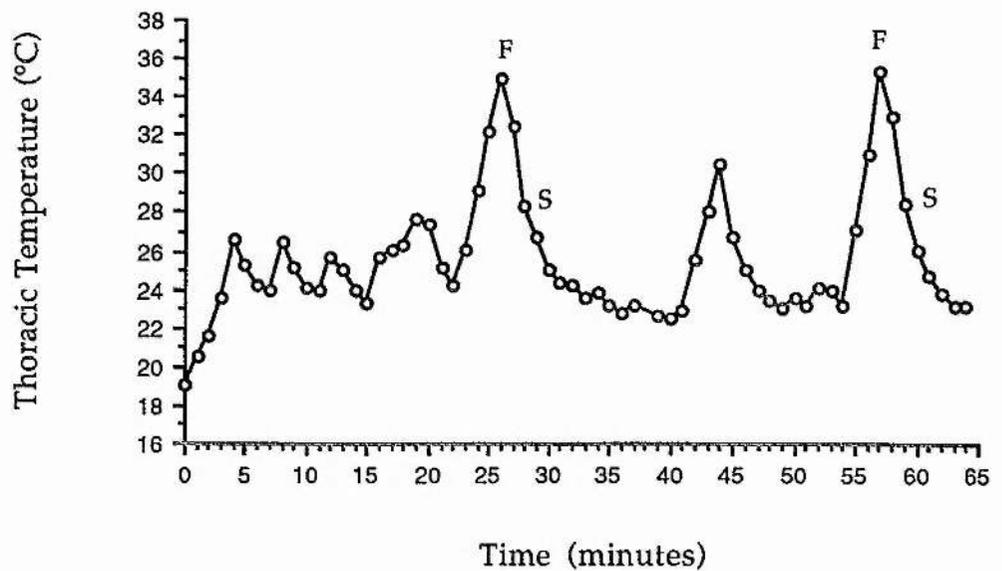


Fig. 6.6b Endothermy in *Bembix rostrata* (Female, Weight 186mg). Thoracic temperatures were recorded every 15 seconds and are here plotted at 1 minute intervals. Ambient temperature was 22 °C. Initiation of flight is indicated by the letter 'F', and the point at which flight stopped is indicated by the letter 'S'.

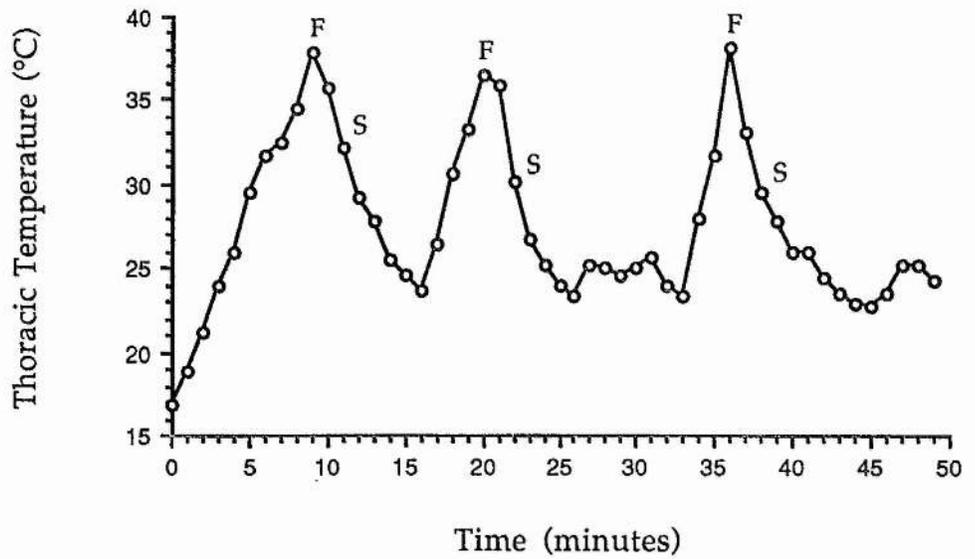


Figure 6.7 The affect of body size on warm-up rates of female *Bembix rostrata*. Data from five wasps are used for the analysis, and up to three readings are taken from a single wasp. The regression equation is: $y = -3.64 + 0.036x$, $R^2 = 0.206$; $p > 0.1$, $t = 1.441$, d.f. = 8.

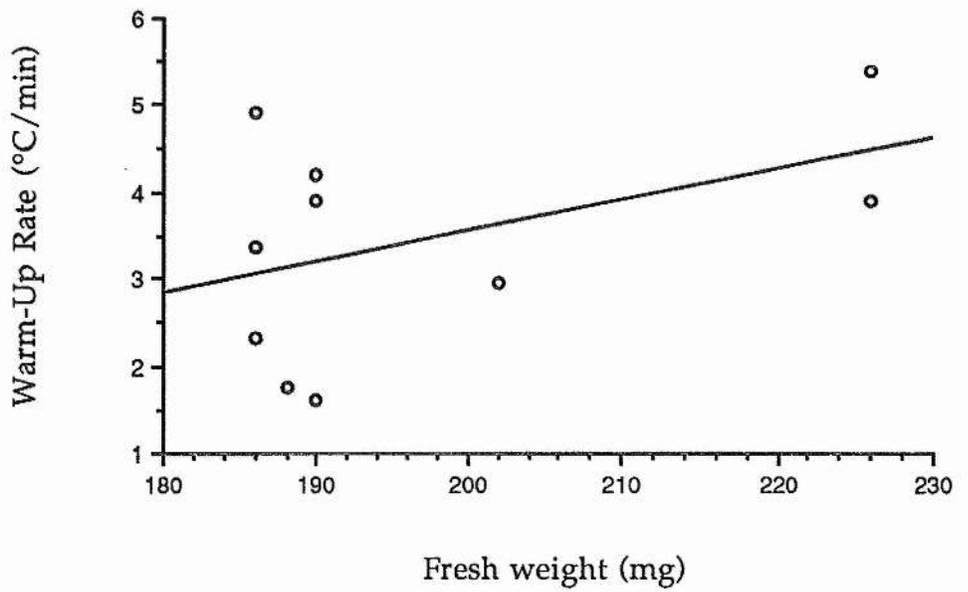


Fig. 6.8 The affect of body size on the voluntary flight temperature of female *Bembix rostrata*. Data from five wasps are used for the analysis, and up to three readings are taken from a single wasp. The regression equation is: $y = 46.59 - 0.055x$, $R^2 = 0.070$; $p > 0.4$, $t = 0.776$, d.f. = 8.

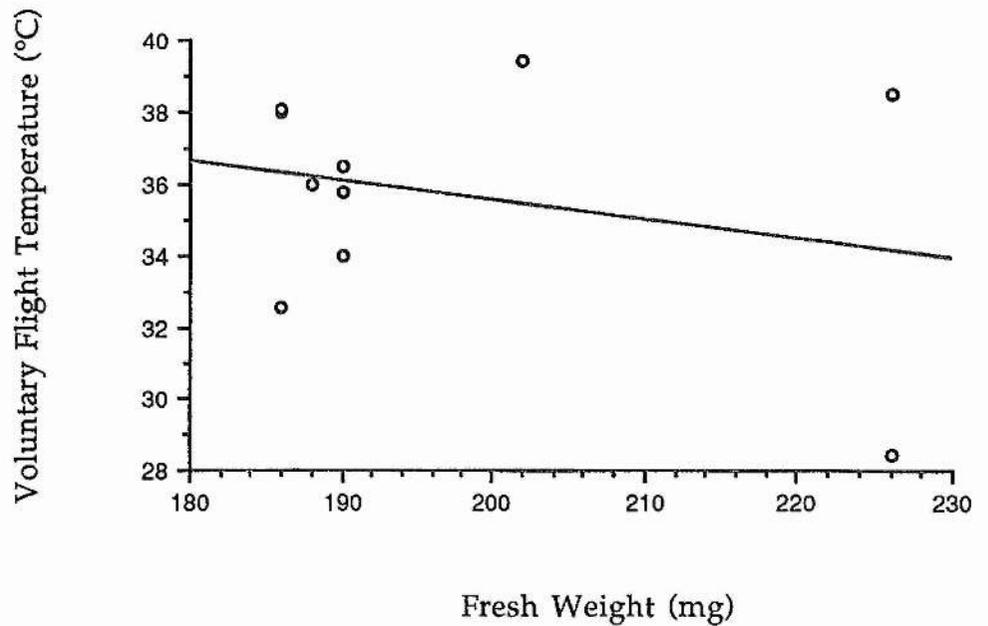


Fig. 6.9 Thoracic temperatures of *Mellinus arvensis* (females only) caught in flight in the field. The dashed line is where $T_a = T_b$. Regression equation for $T_{th} = 3.88 + 1.04x$, $R^2 = 0.547$; $p < 0.001$, $t = 8.000$, d.f. = 53.

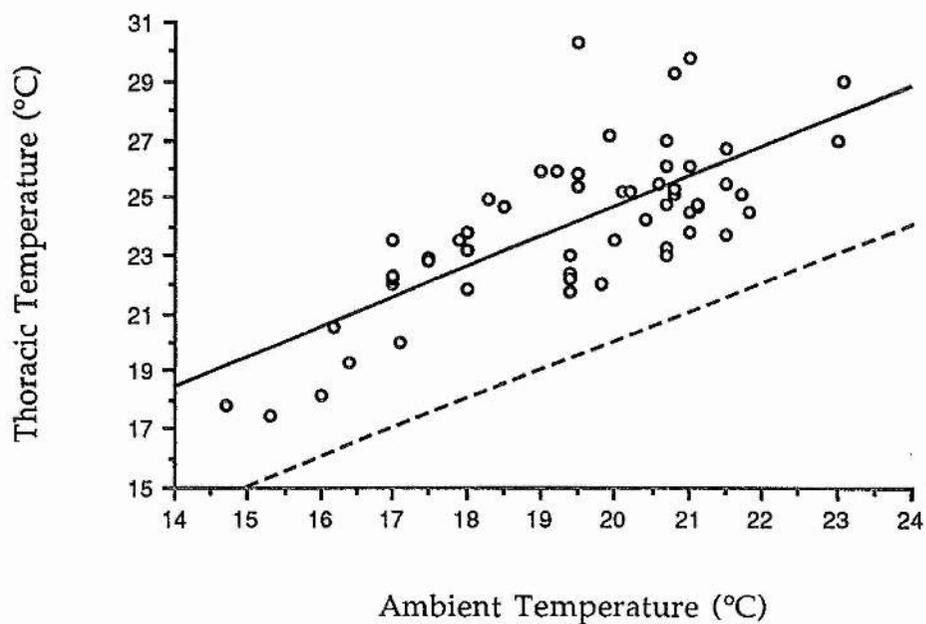


Fig. 6.10 Thoracic temperatures of *Crabro cribrarius* (females only) caught in flight in the field. The dashed line is where $T_a = T_b$. Regression equation for $T_{th} = 2.39 + 1.16x$, $R^2 = 0.863$; $p < 0.001$, $t = 11.224$, d.f. = 20.

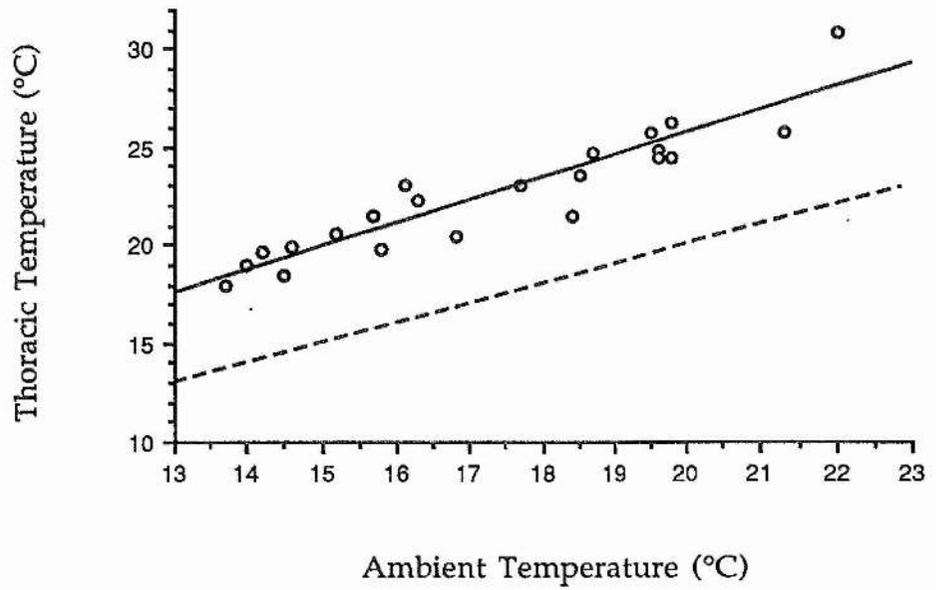


Fig. 6.11 Thoracic and abdominal temperatures of *Bembix rostrata* (both sexes) caught in flight in the field. Thoracic temperatures are represented by the open circles, abdominal temperatures by the closed circles. The dashed line is where $T_a = T_b$. Regression equation for $T_{th} = 7.38 + 1.17x$, $R^2 = 0.297$; $p < 0.01$, $t = 3.117$, d.f. = 23. Regression equation for $T_{ab} = 9.12 + 0.86x$, $R^2 = 0.387$; $p < 0.01$, $t = 3.641$, d.f. = 22.

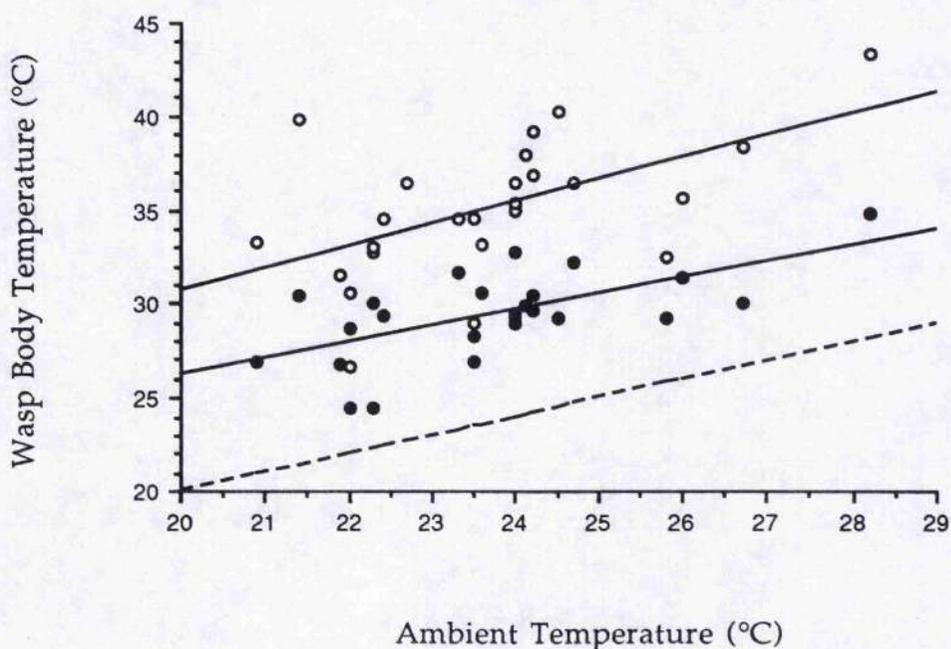


Fig. 6.12 The thoracic temperatures of *M. arvensis* wasps laden with prey (open circles) and unladen with prey (closed circles) caught while in flight. Regression equation of T_{th} of wasps with prey = $6.50 + 0.899x$, $R^2 = 0.639$; $p < 0.001$, $t = 5.645$, d.f. = 18; and without prey = $3.66 + 1.051x$, $R^2 = 0.804$; $p < 0.001$, $t = 13.281$, d.f. = 43.

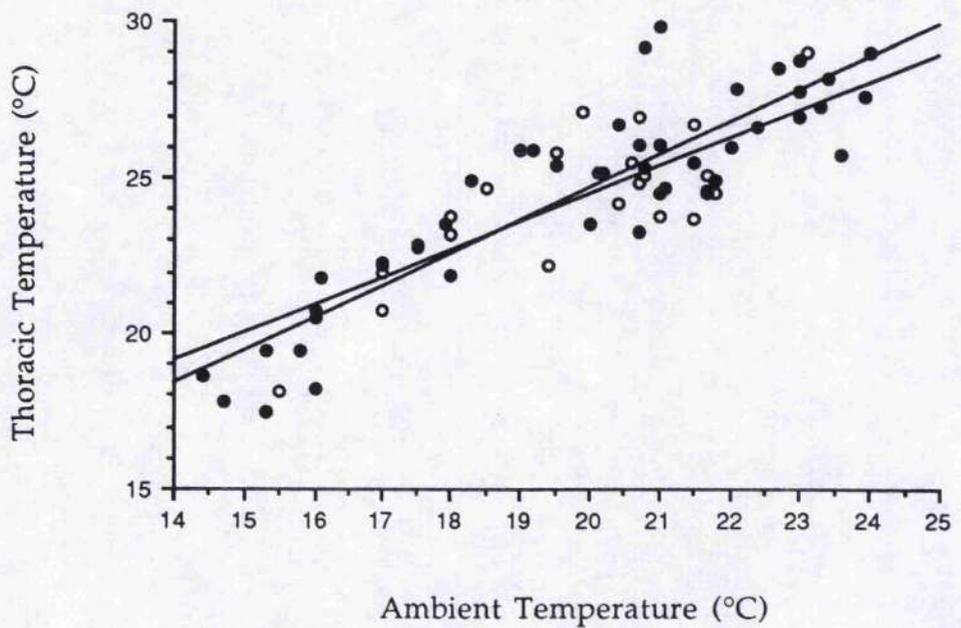


Fig. 6.13 The affect of prey weight on the thoracic temperature excess (T_{ex}) of *M. arvensis*. Regression equation of $T_{ex} = 4.10 + 0.031x$, $R^2 = 0.010$; $p > 0.5$, $t = 0.461$, d.f. = 21.

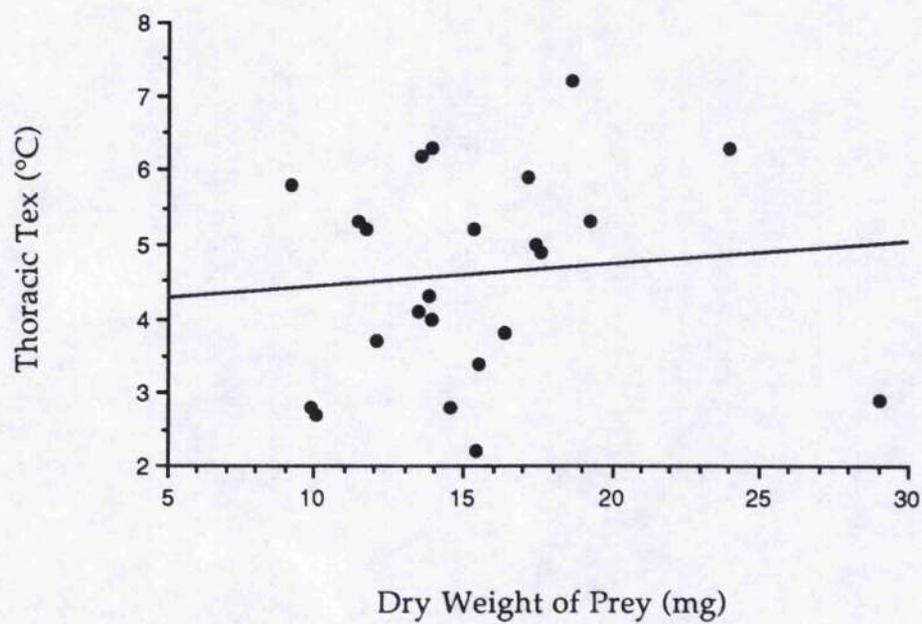


Fig. 6.14 Thoracic temperature excess (T_{ex}) of *M. arvensis* females of varying body size. Regression equation is $T_{ex} = 5.88 - 0.439x$, $R^2 = 0.004$; $p > 0.5$, $t = 0.563$, d.f. = 79.

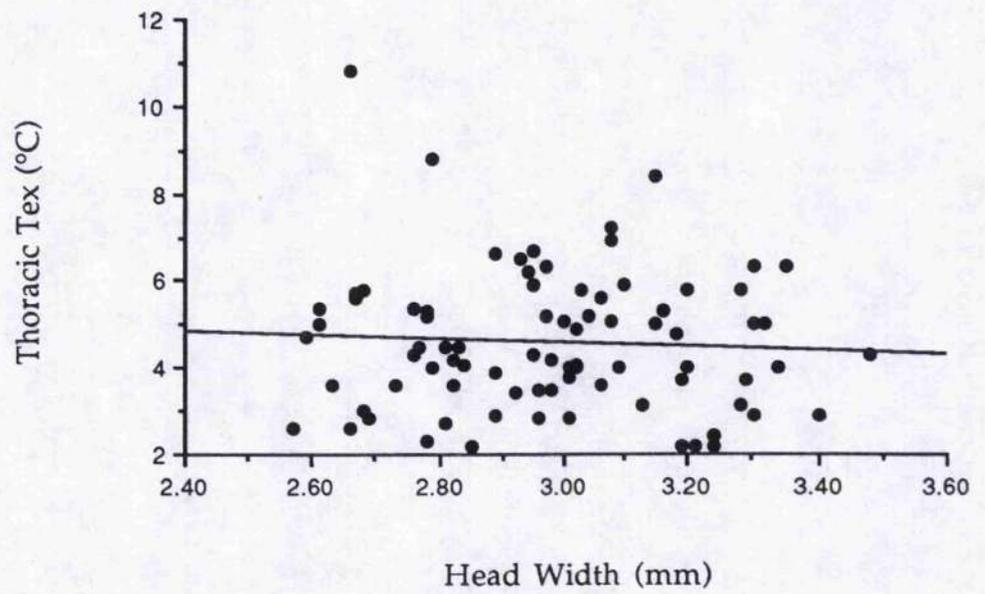


Fig. 6.15 Thoracic temperature excess (T_{ex}) of *B. rostrata* (both sexes) of varying body size. Regression equation is $T_{ex} = 17.67 - 1.191x$, $R^2 = 0.008$; $p > 0.5$, $t = 0.431$, d.f. = 23.

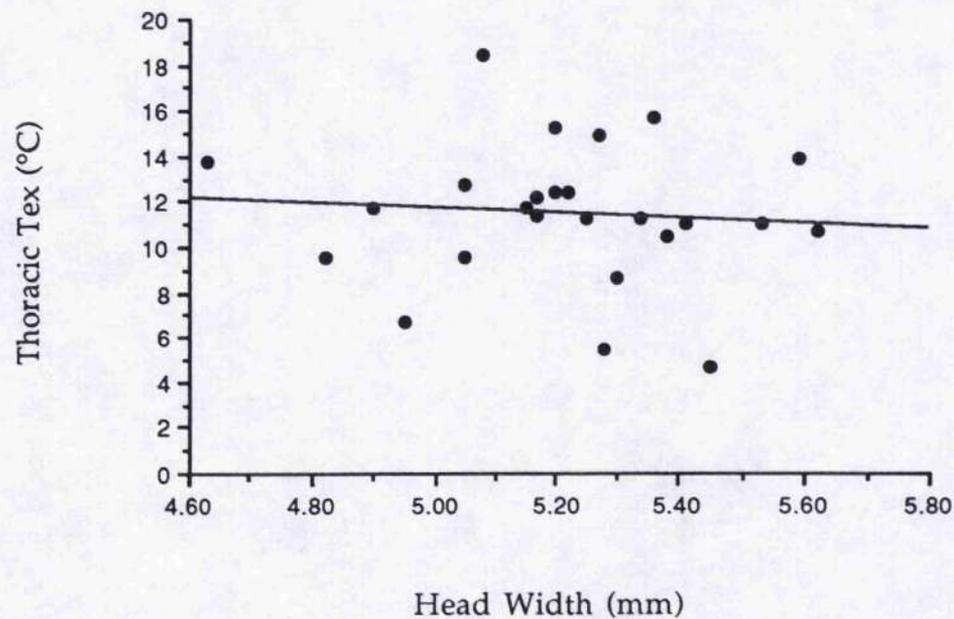


Fig. 6.16 The temperature difference between thorax (T_{th}) and abdomen (T_{ab}) of *B. rostrata* at a range of ambient temperatures. Regression equation of $T_{th} - T_{ab} = -1.33 + 0.294x$, $R^2 = 0.038$; $p > 0.2$, $t = 0.994$, d.f. = 25.

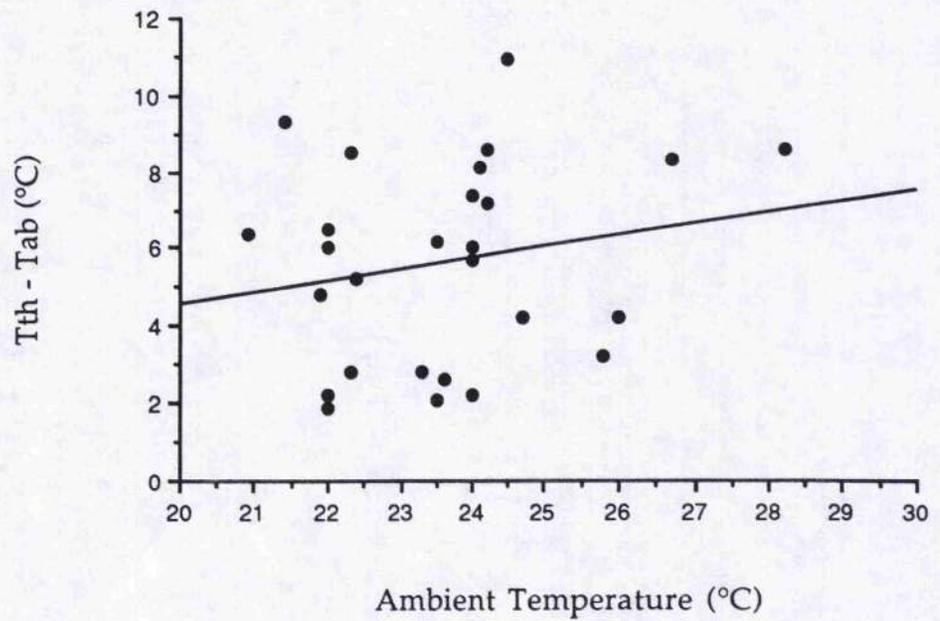


Fig. 6.17a The number of males seen at the nesting site during 30 second periods at intervals of 10 minutes on 20th May 1992. Male activity is represented by open circles; ambient temperature is represented by the dotted line.

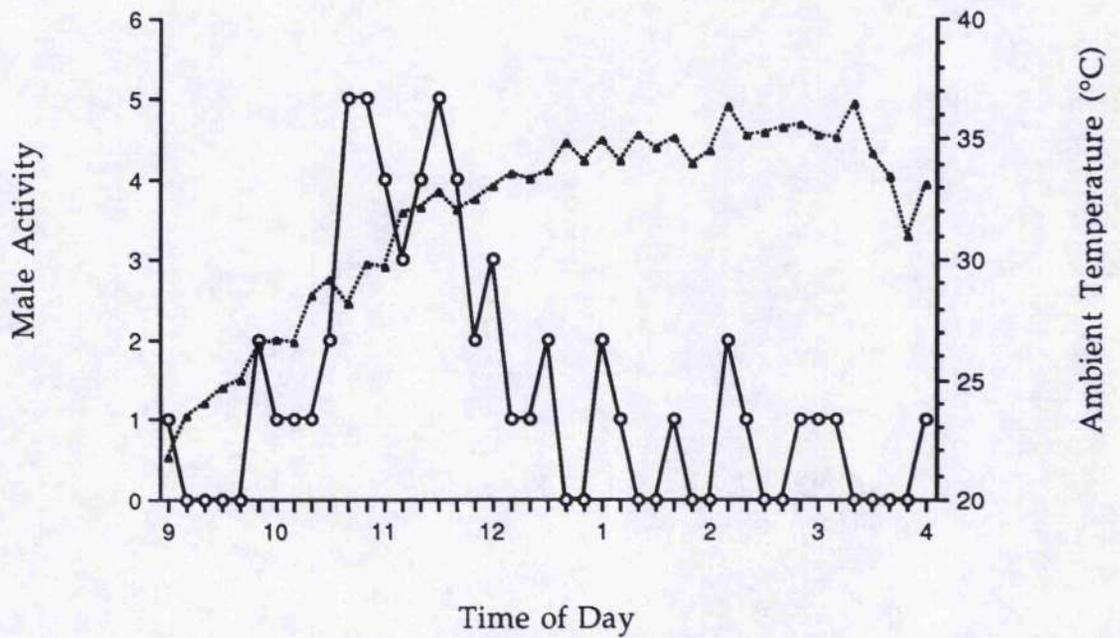


Fig. 6.17b The number of females seen at the nesting site during 30 second periods at intervals of 10 minutes on 20th May 1992. Female activity is represented by closed circles; ambient temperature is represented by the dotted line.

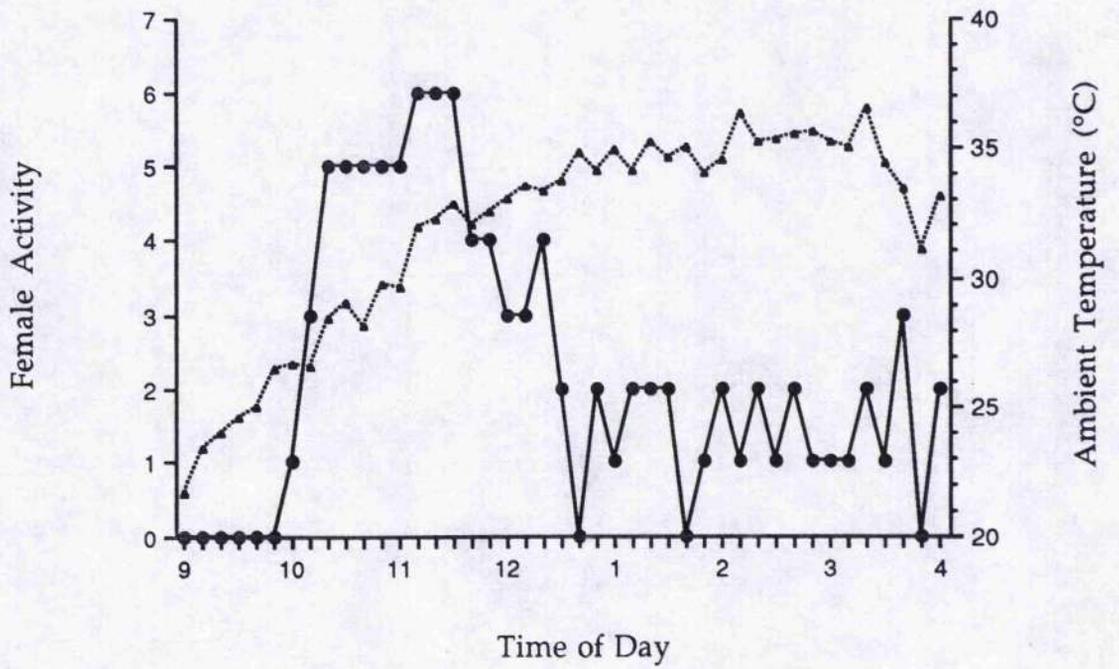


Fig. 6.18a The number of males seen at the nesting site during 30 second periods at intervals of 10 minutes on 23rd May 1992. Male activity is represented by open circles; ambient temperature is represented by the dotted line.

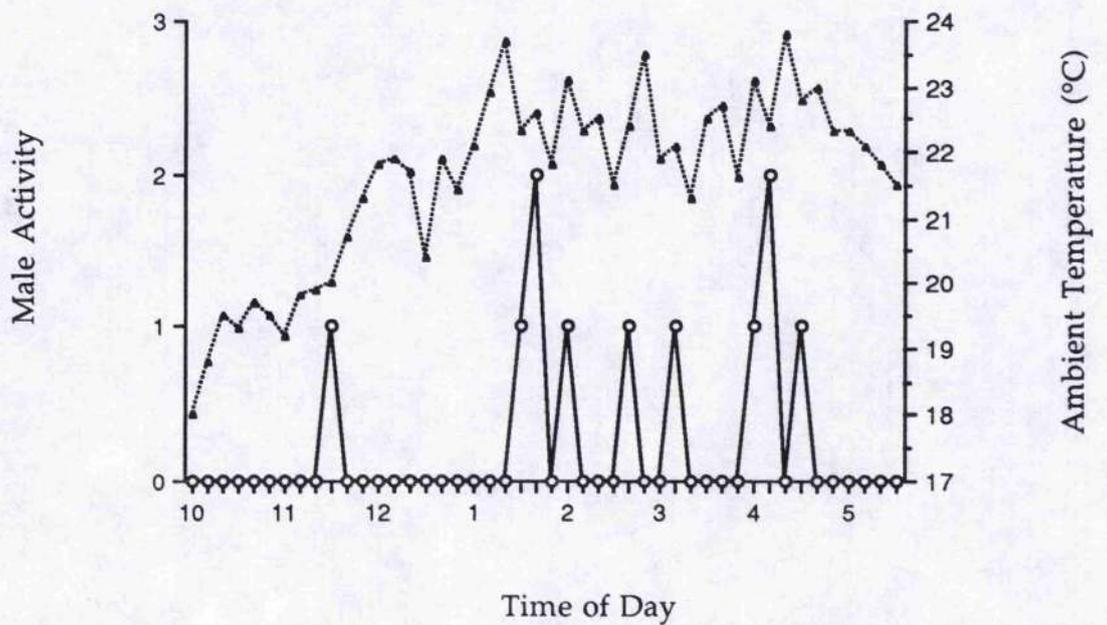


Fig. 6.18b The number of females seen at the nesting site during 30 second periods at intervals of 10 minutes on 21st May 1992. Female activity is represented by closed circles; ambient temperature is represented by the dotted line.

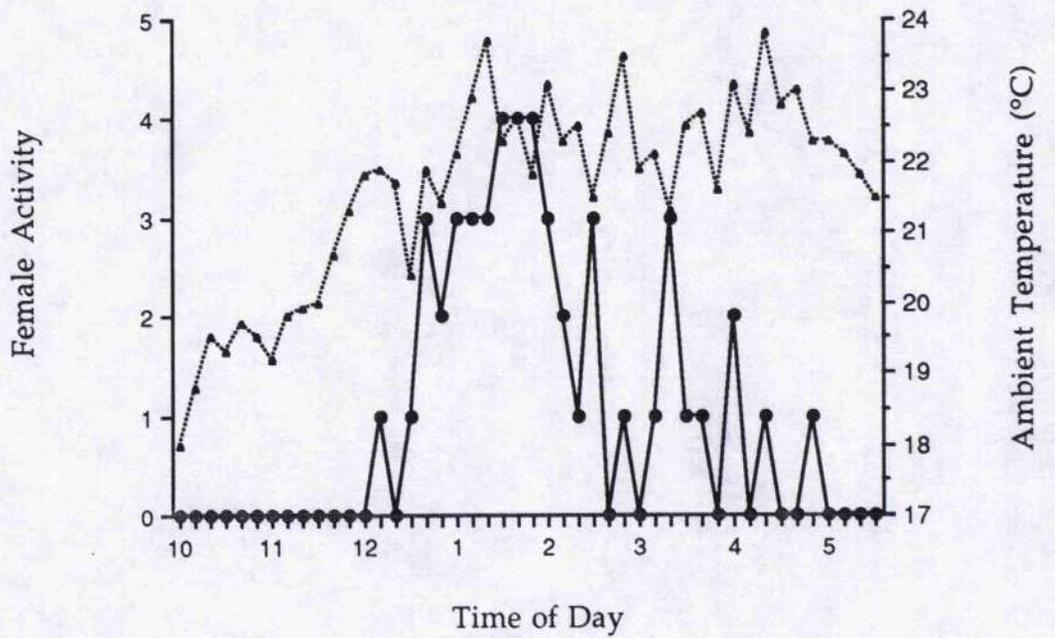
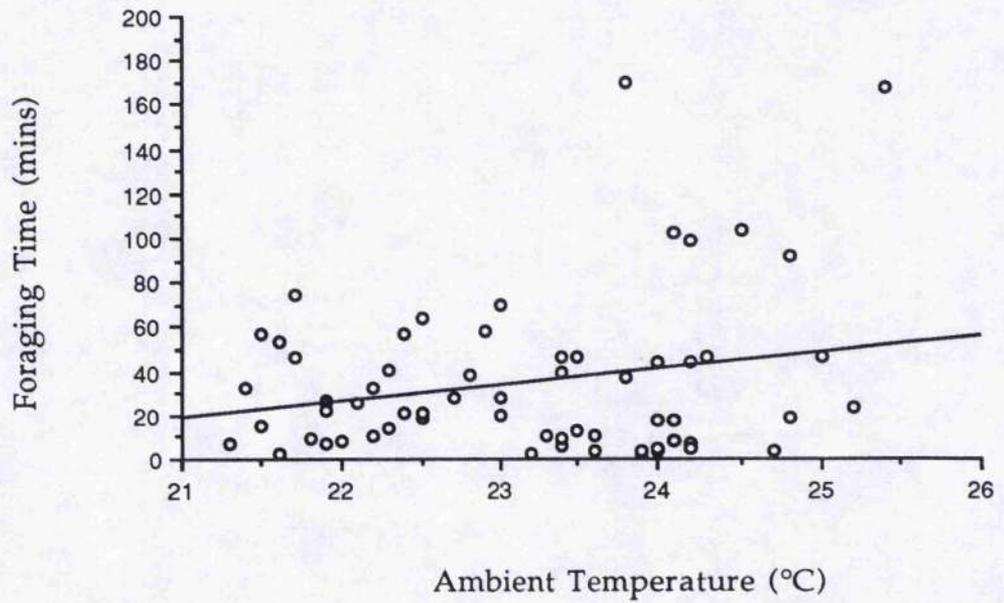


Fig. 6.19 Foraging trip length of *B. rostrata* and ambient temperature. $y = -135.5 + 7.33x$, $R^2 = 0.050$; $p < 0.1$, $t = 1.792$, $d.f. = 61$.



Chapter 7 Discussions and Conclusion

7.1 Introduction

This chapter brings together all the conclusions that have been reached on the causes of geographic variation in *Mellinus arvensis*, and discusses the relative importance of the various environmental and biological factors in shaping inter-population differences in behaviour and morphology. The theme of Chapter 5, that of the mixed evolutionarily stable strategy, is discussed with reference to other sphecid species in which multiple nesting strategies exist, and also with regard to the evolution of sociality in the Hymenoptera. Finally, several ideas are developed that would constitute interesting avenues for further research in geographic variation of size and behaviour, insect endothermy, and the study of the evolutionary origins of diverse nesting patterns.

7.2 A Summary of the Findings of this Thesis

Variation in the behaviour and morphology between populations of *M. arvensis* have been reported, and possible factors causing such variation were investigated and discussed. Chapter 3 described the variation in the nesting and foraging behaviour of *M. arvensis* between populations. Significant differences in nest depths and the time taken to dig nests by wasps at different sites were observed. Temperature could not explain these differences and it was proposed that soil characteristics might be the cause of the variation. Evidence in support of this idea was obtained from soil hardness measurements (Chapter 5). Further differences were apparent in the time spent at the nest entrance before leaving the nest for the first time each

day. These differences were highly correlated with temperature of the ground surface.

Differences in the duration of foraging trips were ascribed to wasp size and the size of prey the wasp was carrying. The larger the prey relative to the wasp, the longer the duration of the foraging trip. Some of the variation could also be explained by temperature, with increased ambient temperatures leading to decreased foraging times.

There was a highly significant difference between two sites in the length of time spent at the nest entrance which was neither correlated with ambient nor ground temperatures. It was speculated that wasps might spend more time at the nest entrance in areas where there was much intra-specific activity. This idea was developed in Chapter 5.

Chapter 4 investigated the large variation in body size between sites, to which there was a latitudinal component. Much, but not the majority, of the variation could be explained by climate, with small wasps being generally found in the north where the climate was cooler. This result is in contradiction to Bergmann's rule, but could be explained if the length of favourable activity periods were considered, small wasps being at an advantage when there are many, but brief, warm periods.

Several non-thermal explanations of body size variation were suggested, and it was confirmed that wasps tend to take prey from similar relative size categories to themselves. ^(see also - - 19 -) While this provides a mechanism for the persistence of size differences between individuals and populations it ~~could~~ cannot, by itself, explain how these differences arose. Analysis of the Diptera population

by random sampling did not reveal differences between sites in the distribution and abundance of prey of particular size classes.

Chapter 5 introduced intra-specific aggression as the mechanism explaining body size variation. There is some evidence for the hypothesis that increased "usurpation" pressure in areas where nest value is high, due to soil hardness, leads to the evolution of large body size in response to aggression. There was however, much contradictory evidence against this hypothesis, such as the very low incidence of nest usurpations at all sites, and a modified hypothesis has been proposed, introducing the idea of the mixed evolutionarily stable strategy.

This "searcher" hypothesis states that there are two alternative nesting strategies, digging a new nest or searching for an empty nest. The strategies are frequency dependent but the stable state is subject to variation according to environmental conditions that affect the costs and benefits of each strategy. Pressure from searchers for a limited number of nests leads to an increase in body size, which gives an advantage in aggressive encounters that arise when two females meet at, or inside, a nest. Nest "usurpations" are thus an unintentional result of a searcher entering an active nest which is subsequently abandoned by the resident female. Much of the evidence in support of the usurpation hypothesis could be equally applied to the searcher hypothesis. Additional evidence in support of the latter model was also presented.

In Chapter 6 the existence of endothermy in two large sphecid wasps from Portugal (*Bembix rostrata* and *B. zonata*) has been demonstrated for the first time. Although no evidence for this ability was found in three smaller British sphecids, further work using non-invasive techniques might prove otherwise.

B. rostrata and two British species, *M. arvensis* and *Crabro cribrarius*, were shown to maintain a constant elevated thoracic temperatures during activity in the field, although there was no indication of physiological temperature regulation. Variation in thoracic temperature excess between individuals could not be explained by wasp body size (*B. rostrata* and *M. arvensis*) or by whether they were carrying prey (*M. arvensis*).

7.3 The Relative Importance of Environmental and Biological Factors in the Evolution of Body Size

This thesis has shown that there are two major factors ^{can cause} that ~~are the causes of~~ body size variation in *M. arvensis*. The first is climate, an environmental variable with a latitudinal cline. The second is intraspecific aggression which varies in response to environmental and biological factors such as soil hardness and nesting density. Soil hardness is not correlated with latitude and is the cause of the "noise" observed in the correlation between latitude and body size. The relative importance of these two factors can be assessed by referring to the amount of variance explained by each factor, with 36.0% of the variance explained by latitude (Chapter 4) and 40.9% explained by soil hardness (Chapter 5). A multiple regression of head width against latitude and soil hardness explains 69.4% of the variance, leaving 30.6% to be explained by other factors, such as prey size and abundance, and possibly different rates of development due to genetic variation.

7.4 Latitude as a Factor Affecting Geographic Variation Within Species

By far the majority of studies of variation along latitudinal and climatic clines come from vertebrates, and, most commonly, from endotherms (eg, James 1970; McNab 1971). In addition to endotherms, the positive correlation

between latitude and body size, known as Bergmann's Rule, has been documented in vertebrate ectotherms (Ray 1960; Lindsey 1966). As yet there have been very few studies documenting intraspecific latitudinal variation in the insects, and in the Hymenoptera in particular.

The observed decrease of body size with increasing latitude observed in *M. arvensis* in Britain is the opposite of what might be expected from Bergmann's Rule. The thermal limitations imposed upon ectotherms may be quite different to those of obligate endotherms, and the small size of *M. arvensis* at high latitudes has been suggested to be in response to rapidly fluctuating climatic conditions. A recent study of geographic variation in *Apis mellifera* revealed the opposite trend with an overall increase in body size from low to high latitudes that corresponds to Bergmann's Rule (Daly et al. 1991). This adds to earlier studies on *Apis mellifera* of Alpatov (1929) and Ruttner (1988) that also show a trend towards smaller size at lower latitudes, although no explanations were proposed for these results. However there has been much debate over the relevance of this rule, and whether it is actually valid (Mayr 1956; Scholander 1956; McNab 1971; Maurer et al. 1992) and the adaptive significance of this and other biogeographical trends remains obscure, although geographically variable phenotypic traits frequently respond to temperature.

Results such as ^{those} ~~that~~ obtained for *M. arvensis* might also be explained by temperature, although in ways that are not immediately obvious. Wasps might be adapted to make the best use of brief periods of favourable temperature, or temperature might impose small size on wasps by reducing foraging time and hence reducing the number of prey caught. Where large size is not an advantage, selection would act to maximise the number of offspring at the expense of reducing the number of prey in each cell, and

hence the wasp size. A more detailed analysis of the thermal ecology of *M. arvensis*, together with comparative information on the nest contents and reproductive output of wasps from a variety of latitudinal locations, are needed for the elucidation of the unexpected latitudinal size cline that is found in this wasp.

7.5 Soil Hardness as a Factor Influencing the Frequencies of Behavioural Strategies

There are often marked differences in the frequencies of behaviour patterns between different populations (eg, Evans & O'Neill 1978; Alcock 1979b; Brockmann 1980a). A similar situation has been shown to occur in the behaviour of *M. arvensis* from different sites. In this thesis it is suggested that the two behaviours, digging and searching, are frequency dependent, and that the success of one strategy relative to the other is different in different locations, being dependent on the relative costs and benefits of each strategy. Hence the populations are likely to be at different evolutionarily stable states. While this has been shown to be true for *M. arvensis*, the influence of soil hardness on the frequency of nesting strategies (which can also be measured in terms of the amount of aggression, the proportion of nest usurpation or the amount of communal nesting) in other sphecid species has yet to be investigated. Several studies have hinted that a link between soil hardness and behaviour does occur, but as yet (excepting this study) the relationship between soil hardness and behaviour has not been directly studied.

Soil hardness as a factor influencing costs of nest construction, and therefore the frequency of nest sharing, has been shown for *Cerceris antipodes* (Alcock 1980; McCorquodale 1989a), *C. australis* (Evans & Hook 1982a,b) and *C. simplex* (Alcock 1975a), as well as the bee *Andrena erythronii* (Michener and

Rettenmeyer 1956; Michener 1958). In each of these cases it was postulated that hard soils increase the proportion of wasps searching for completed burrows, thus promoting nest sharing. Nest initiation could be induced in *C. simplex*, *C. intricata graphica* (Alcock 1975a) and *C. antipodes* (McCorquodale 1989a) by adding water to the soil which softened the crust, suggesting that such treatment reduces the costs of nest digging. Furthermore, Alcock (1980) noted that the communal nesters *Cerceris rubida* and *C. rufimana* both nested in hard packed firm soil, and Evans (1973) speculated that burrow sharing among *Philanthus gibbosus* might be more frequent in heavier soils.

Communal nesting of two or three individuals in a single nest has been observed for the wasp *Euphilis longinodus* (Janvier 1928) which nests in dry, clay soils. In contrast, no nest sharing was observed in six species of *Bembix* which nest in friable sandy soils (Evans et al. 1982). The costs of nest construction for these wasps are likely to be low due to the friable substrate, but also reduced due to the fact that, unlike *M. arvensis* and *Cerceris* spp., these wasps are powerful and efficient diggers (Evans 1966a). Willmer (1985a,b) reported no nest usurpation in an aggregation of over 1000 nests of *Cerceris arenaria*, which was nesting in loose sand where, presumably, nests were relatively easy to dig.

Usurpation of nests and nest switching is often observed in *Crabro monticola* (Alcock 1981) and *Sphex ichneumoneus* (Brockmann & Dawkins 1979) but joint occupation in either of these species did not occur because wasps were quick to abandon nests if they found them occupied. Both these species nest in open sandy areas where nest construction might not be costly.

Elliott and Elliott (1987) found that interactions between females of *Cerceris cribrosa* were more aggressive than those described for other *Cerceris* species, and correlated this with the difficulty of nesting in the hard rocky clay

substrate. Females of *C. cribrosa* that had lost their nest to a usurper attempted to re-usurp the nest for several days afterwards. In contrast, females of *C. halone* nesting in more favourable soil conditions abandoned nests blocked with plaster of Paris within the hour (Byers 1978).

Usurpation of empty nests by *Ammophila sabulosa* was rarely observed (3.6% of intraspecific parasitism events; Field 1989a). Far more common was brood parasitism (31.3%), and prey theft (18.1%), and 90% of the nests that were discovered by parasites to be empty were closed and abandoned (data from Field 1989a). This suggests that nest construction in these wasps is not costly and there is little to gain from the usurpation of an empty nest. In these wasps the cost of foraging for prey might be far greater than nest construction, and it might be of greater benefit to steal cell provisions. As the nests of *A. sabulosa* are unicellular and reach a maximum depth of only 4 cm (Field 1989a), the time and energy invested in the nest structure by a wasp is likely to be small. Indeed *A. braunsi* is unique amongst the *Ammophila* in its habit of nesting in hard clay soils and in its use of abandoned burrows of other wasps, particularly of the eumenid *Parachilus insignis* (Weaving 1989). Curiously, this species seems to be confined to nesting only in areas of clay soil even when sandy friable sand is available nearby (Weaving 1989).

The fact that nest sharing in *M. arvensis* is extremely rare, if indeed it occurs at all, suggests either the costs of nest joining are very high to both the joiner and the original occupier, or that the costs of nest construction are not so high that they preclude the excavation of new nests. Should a population of *M. arvensis* be discovered at a site where the soil is of similar hardness to that encountered by the species mentioned above, then co-occupation of nests might also be observed. In such a situation, pressure from searchers will reach a point where it might become more costly for residents, in terms of injury or

loss of the nest, to continue responding aggressively to females attempting to enter the nest, rather than tolerating a second female provisioning the same nest. If each female proceeds to provision the nest at a similar rate as a single female, there may be no cost to either individual. Indeed there may be much to gain from such an association as two females occupying a single nest are better able to defend the nest against parasites and foreign conspecifics due to the increase in activity at the nest (Lin & Michener 1972; Evans 1977; Evans & Hook 1982a; Elliott & Shlotzhauer 1979; McCorquodale 1989c).

7.6 Multiple Nesting Strategies in the Sphecidae and the Evolution of Sociality

The Sphecidae are often considered to be a solitary nesting group in that each female constructs and provisions her own nest without help from others. In recent years observations of marked individuals have revealed that there are many species that show varying degrees of nest sharing, and cooperation, among individuals. Joint nesting in the Sphecidae might be a short lived rare occurrence arising from an individual entering the wrong nest by mistake (*Sphex ichneumoneus*, Brockmann & Dawkins 1979), or might be the result of fully social behaviour (*Microstigma comes*, Matthews 1968). There is a continuous series of intermediate positions in between these two extremes, each of which must be successful in order to persist. The multiple nesting strategy described for *M. arvensis* in this thesis could possibly represent the first step towards the evolution of sociality, by a "semisocial" route, in the Hymenoptera.

The obvious route to eusociality is through cooperation between related individuals, to which the haplodiploid Hymenoptera seem to be particularly well preadapted (Eberhard 1972; W. D. Hamilton 1972; Alexander 1974; West-

Eberhard 1975; Trivers & Hare 1976; Crozier 1977; Bull 1981). This is the "subsocial" route which involves altruistic cooperation among family members (eg, *Polistes metricus*, Metcalf & Whitt 1977; *Myrmecocystus mimicus*, Bartz & Holldobler 1982; *Cerceris antipodes*, McCorquodale 1988, 1990). Another possible route, proposed by Michener (1958) and Lin and Michener (1972), is through communal nesting by females, not necessarily related, from the same generation. If the fitness of each communally nesting female exceeds that of a solitary nester, then this mutualistic behaviour might begin to evolve towards eusociality. Before this can occur simple joint nesting has to evolve, and I believe that observations of the nesting behaviour of *M. arvensis* provide the clues as to how this came about.

The habit of searching for and entering empty burrows may be a pre-adaptation to the evolution of joint nesting. The initial pre-adaptation is likely to be the aggregating of solitary nests (Bock 1959) due to limited suitable nesting sites (Michener 1974), or parasite pressure (Wcislo 1984; Larsson 1986; Rosenheim 1990). Joint nesting might have arisen from mistakes made by females on their return from foraging trips. Wasps may become confused and disorientated by unfamiliar landmarks (Brockmann & Dawkins 1979) or may enter other nests if their own nest entrance is destroyed (*M. arvensis*, personal observation). Such mistakes are however rare and are usually quickly corrected. For joint nesting to persist there has to be a more common and lasting pre-adaptation for selection to act upon. The strategy of searching for and entering nests is such a pre-adaptation that could result in nest sharing, and does result in nest usurpation. Furthermore, this is a durable pre-adaptation as it is part of a mixed evolutionarily stable strategy rather than an occasional freak event brought about by unusual changes in the environment. The strategy is maintained due to the strong selective pressures resulting from the advantages of entering truly abandoned burrows. In *M. arvensis*

joint nesting does not seem to be advantageous, and no instance of nest sharing in this wasp was observed in this study, or that of Paxton (1985; and personal communication). Joint provisioning of a single nest by two individuals of *M. arvensis* has been recorded by Bristowe (1948), Olberg (1959), Huber (1961) and ^{W.D.}Hamilton (1971), although in each case the interactions between the two wasps were aggressive. Because this pre-adaptation is part of an evolutionarily stable strategy, it is likely to persist through evolutionary time, allowing the rapid evolution of social behaviour should joint nesting become advantageous.

A central theme of the model applied to *M. arvensis* is that digging and entering are equally successful and are maintained at equilibrium frequencies by natural selection. Aggression and incidental usurpation are unfortunate byproducts of the entering habit. Should selection pressures shift so that communal nesting was favoured there would be a greater advantage to those wasps that enter already occupied nests. This would not need to involve a separate "decision" to join an active nest, but rather the benefits to the search and enter strategy would increase as entering an active nest ceased to be a disadvantage and became an advantage. Consequently, the frequency of searchers would increase and the number of empty nests decrease (as fewer diggers existed to dig new nests) leading to an acceleration in the evolution of joint nesting. Thus selection for joining an active nest is superfluous, as a strategy for entering is sufficient. Therefore evolutionary progression from solitary nesting to nest co-occupancy can be postulated without inferring large scale changes in wasp behaviour.

A shift in selection pressures favouring nest sharing could be brought about simply by increasing the costs of aggressive encounters to the nest owners. Such a situation might arise as the proportion of searchers increases, and thus

the frequency of encounters for nest residents increases (see section 7.5 above). Another idea that has been proposed in several studies of communal nesters is that of nest defense. Females that co-habit a nest gain through increased nest defense against parasites and conspecifics. In nests shared by two or more individuals of *Cerceris australis*, nest entrances are occupied throughout the day by one or more non-provisioning females which deter the entry of ants and mutillids (Evans & Hook 1982a). McCorquodale (1989c) demonstrated that the frequency of nest guarding by *Cerceris antipodes* against conspecifics and mutillids is higher when more than one female is resident in the nest. Other examples of improved nest defense as a result of nest sharing are to be found in *Cerceris goddardi* (Evans & Hook 1982b), *C. californica* (Linsley & MacSwain 1956), *C. antipodes* (Alcock 1980), *C. simplex* (Alcock 1975a) and *Lindenius columbianus errans* (Miller & Kurczewski 1973).

Thermal constraints may favour joint occupation of a nest by two females of differing sizes (Willmer 1985a). Large wasps are favoured during cool temperature periods, whereas small wasps can remain active at high temperatures that deter large individuals. A nest that is jointly occupied by a small and large female will be continuously provisioned through a much wider temperature range than a nest containing a single individual. Both females will profit from the others activities at times when they themselves are unable to forage due to thermal constraints.

The model developed for *M. arvensis* could be applied, at least in a modified form, to other species of sphecoid wasp. Similar observations of behaviour have been noted by Brockmann and Dawkins (1979) for the wasp *Sphex ichneumoneus*. In this study it was concluded that joint nesting was a consequence of inadvertently entering an occupied nest, and such an outcome benefitted neither the joiner nor the joined. Individuals of this species also did

not seem to be able to distinguish between occupied and empty nests, a key feature of this model. There are several other species that have similar nesting patterns to *M. arvensis* and that may also fit the model. *Philanthus gibbosus* (Evans 1973), *Lindenius columbianus errans*, *L. armaticeps*, and *L. buccadentis* (Miller & Kurczewski 1973), *Cerceris hortivaga* (Tsuneki 1965) and *Trypoxylon politum* (Brockmann 1980a), *Bembix spinola* (Lin & Michener 1972), *Tachytes distinctus* (Lin & Michener 1972), *Parischnogaster* spp. (Sakagami & Hayashida 1968) all search and enter empty nests, usurp the nests of others and nest jointly, but it is not known whether they are discriminating between empty and occupied burrows. Females of *Crossocerus maculiclupeus*, *Entomagnathus memorialis* and *Crabro rufibasis* commonly aggregate and search for pre-existing burrows and crevices in which to start new nests (Miller & Kurczewski 1972) although no information was given as to whether there is any nest usurpation or sharing.

Some loose parallels may be drawn between this proposed evolution of sociality in the Hymenoptera and the theory of punctuated equilibrium (Gould & Eldredge 1977) which describes evolution as occurring very rapidly after long periods of little change. Wasp populations are, for much of the time, in periods of stasis at the evolutionarily stable state. These populations containing solitary nesters will evolve into social ones when the pressures opposing communal nesting are reversed, and will do so quickly due to the high degree of pre-adaptation. As has been shown for the "dig or search" model developed for *M. arvensis*, the evolution of joint nesting need not involve large changes in behaviour, but could be accomplished simply by altering the success of one strategy relative to the other.

7.7 Possible Directions for Further Studies

The incredible diversity of aculeate nesting behaviour provides a great number of opportunities for the study of the effects of biological and environmental factors on the range of behaviour patterns. With such variability in nesting and reproductive tactics observed in closely related species, or even within a single species (eg, *Trypoxylon politum*, Brockmann 1980a) it is not difficult to imagine how such great diversity could have evolved. What is probably more difficult to comprehend is how such diversity is maintained within a population.

A relatively simple evolutionarily stable system, as has been described for *M. arvensis*, may allow us to interpret more complex interactions between other sphecid wasps or species from parallel groups such as the Pompilidae and Apoidea. Further comparative studies of nesting, foraging and reproductive strategies between populations of single species from widely separated geographical locations will undoubtedly reveal the source of many evolutionary developments that make the Hymenoptera so behaviourally, and morphologically, diverse.

Comparative studies between closely related species should lead to an improved understanding of the costs and benefits of solitary and communal nesting. The genus *Cerceris* would have many advantages for such a study. It is a very large group with over 900 species worldwide. Recent research has shown that a wide range of nesting behaviours and conspecific interactions occur within this genus, providing a good opportunity to study the evolutionary progression from solitary species to those that are close to eusociality.

Interesting comparisons could be made between tropical and temperate species which are subject to very different climatic and time constraints. Usurpation of nests and communal nesting might be more likely to occur in temperate regions where time constraints are more severe (Brockmann 1993). On the other hand, increased threat from a greater diversity and number of predators and parasites might increase the selective pressure for communal nesting in tropical species.

Studies of genetic variation, using gel-electrophoretic techniques (Easteal & Boussy 1987), between populations of single species would complement studies of behavioural and morphological variation. Much of the variation might be attributed to real genetic differences rather than to phenotypic plasticity, possibly indicating the first steps to the formation of separate races, and ultimately speciation.

It has become clear that many insects, far from being passive ectotherms, are dynamic heterotherms, capable of modifying and adjusting body temperature by behavioural and physiological means. The capacity for endothermy and/or thermoregulation complicates the relationship between size, temperature and behaviour and many studies of insect thermal physiology fail to take into account possible endothermic abilities of insects. Because most field studies provide only a partial view of body temperatures under a particular set of conditions, the roles of endothermy and thermoregulation within a broader ecological context are wide open for rigorous analysis. The Sphecidae provide an ideal study group for such an analysis. Large variations in size and colour, both within and between species, give rise to a variety of possible thermal strategies. Sphecids also cover the range of insect body shapes, some being long and thin while others have stout bodies. Many species nest in hot dry sands and are therefore subject to a variety of

microclimates where thermal and hydric stress will be of considerable importance.

Further studies should aim to discover how widespread endothermy is in the Sphecidae, and establish the thermal causes of variation in behaviour and morphology within and between species. Thus, new behavioural strategies to cope with local environmental conditions might in this way be discovered, and we can then begin to integrate physiology, ecology and behaviour into a proper environmental framework.

Appendix 1 - A Test for Equality For Two Regression Lines

Where two regression lines are obtained from similar data collected under different conditions, (e.g. from two populations), the functional relationships described by the two regression equations must be tested for differences, before the data can be assumed to come from the same population, and therefore pooled. The method used to test for differences between two regression lines is that described by Elton & Greenwood (1987). Briefly, the test considers the difference between the two parameter estimates, scaled by the standard error.

Thus, $z = (b_1 - b_2) / \sqrt{(s_1^2 + s_2^2)}$, where s_1 is the standard error of the estimate b_1 .

'z' is tested against Student's t, with degrees of freedom calculated using the formula :

$$(n_1 - 2) (n_2 - 2) (s_1^2 + s_2^2)^2 / \{(n_1 - 2) s_2^4 + (n_2 - 2) s_1^4\}$$

If the null hypothesis is rejected, then the two data sets cannot be assumed to come from similar populations, and therefore the data cannot be pooled.

Appendix 2 - Some Notes on the Behavioural Ecology of *Bembix rostrata*

A 2.1 Introduction

In addition to investigating the thermal ecology of *Bembix rostrata*, observations on the behavioural ecology of this species were made. Comments on the behaviour of *B. rostrata* at the flower foraging site, male mating behaviour, and female nesting behaviour are included in this section.

A 2.2 The Behaviour of *Bembix rostrata* at the Flower Foraging Site

Very few females were observed feeding at flowers. However *B. rostrata* wasps were frequently observed to fly over the plant, pausing briefly in flight and sometimes "zig-zagging" as if searching. This behaviour lasted for no more than 2 - 3 seconds and it was impossible to determine the sex of the wasp in this time.

Males were most commonly observed at patches of *T. vulgaris* (figure A 2.1a) and were seen foraging as well as pursuing and attempting to mate with females that were visiting the patch or flying past. There were frequent interactions with conspecific males encountered on the plant. It was difficult to tell whether male-male interactions were simply due to mistaken identity (males and females are difficult to distinguish at a distance, at least to the human observer) or whether they were aggressive interactions between competing males. However, no territorial behaviour by males was observed at the plants, indeed at times four males were feeding at a plant at the same time.

Male wasps were capable of sampling a very large number of the small flowers of *T. vulgaris* in a short space of time, the mean value being 94.3 ± 4.8 flowers per minute ($N = 6$). The mean number of flowers visited per foraging trip was 164 ± 20.0 ($N = 91$), with a minimum of 5 and maximum of 1286 flowers per trip during the period of observation. Two marked males were monitored throughout the day and the total number of flowers visited by each was 2288 and 2681 flowers respectively.

Male interactions on *T. vulgaris* peaked at about 1430 (figure A 2.2) and this coincided with an increase in the number of visits to the patch by males. There was also an increase in the number of nectar foraging trips and the number of flowers visited during each trip, later in the day (figure A 2.3).

The huge number of *T. vulgaris* flowers visited by these wasps corresponds with the very low volumes of nectar provided by the plant. Out of a total of 174 flowers sampled only eleven contained any detectable trace of nectar. The mean volume and sugar concentration of the nectar in these eleven flowers were $0.08 \mu\text{l}$ and 41 % respectively.

There were several other plants flowering nearby. *Carpobrotus edulis* is a low lying composite with fleshy leaves and large yellow flowers. No wasps were seen at this plant despite several hours observation. Other insects were attracted to it, notably large solitary bees, bumblebees, butterflies, chafers and small beetles. *Pastinaca sativa* (figure A 2.1b), a tall standing umbellifer, attracted many insects including several species of solitary wasp most notably *Cerceris* sp. Male *Bembix rostrata* were seen at this plant but in very much lower numbers and frequency than at *T. vulgaris*.

Male behaviour on *T. vulgaris* is characterised by a huge number of flower visits for seemingly little reward, interspersed with interactions with other males. These interactions are always brief chases and are not in any way similar to territorial behaviour reported in other sphecids. After a chase both males would often return to the plant to continue feeding. Attempted mating was observed on a number of occasions and it could be that the male-male interactions are cases of misdirected copulation attempts. Such futile mating attempts have been reported for other species, for example *Bembecinus nanus strenuus* (Evans & O'Neill 1986). Male *B. rostrata* may play an important role in the pollination of *T. vulgaris* due to the very large number of flower visits effected by each individual.

A 2.3 Some Notes on the Male Mating Behaviour of *Bembix rostrata*

Male activity is also greater in the morning (see Chapter 6) and this is easier to explain as it coincides with peak emergence of virgin females (Larsson 1989a). Males of *Bembecinus quinquespinosus* and *Bembecinus nanus strenuus* are also predominantly active in the morning in response to peak female emergence (O'Neill & Evans 1983; Evans & O'Neill 1986). Males spent most of their time flying in low and elliptical sweeps 2 - 5 cm above the nesting area. Between flights males would land on the sand surface where they would bask or dig. Digging typically lasted from a few seconds to a few minutes after which they moved to a new location and repeated the digging behaviour. Upon location of a female, the male would pounce on her and attempt to fly off with her to the relative safety of the surrounding vegetation. A mating cluster of competing males is often formed around a newly emerged female, but only one male eventually succeeds in mating with her (personal observation; Larsson 1989a). The switch to flower clumps by males later in the day may serve not only the need to feed, but may also result in encounters

with virgin females that were not detected on emergence. Males were often seen pursuing and attempting to mate with females at flower patches. As females mate only once (Larsson 1989a) these attempted copulations would be of no reproductive importance unless virgin females were encountered.

The male mating system of *Bembix rostrata* shows many similarities with those of the sphecid *Bembecinus quinquespinosus* (O'Neill & Evans 1983), the anthophorid bee *Centris pallida* (Alcock et al. 1976, 1979b) and the colletid bee *Colletes cunicularius* (Larsson 1989b). In all four species the males emerge before the females, they are able to locate and dig out newly emerging females, they form mating clusters that involve intense male competition, and males carry mates away from the nesting area. Males of *B. rostrata* have 'rake spines' on their foretarsi that aid in digging, a typically female character, and a feature also found in *B. quinquespinosus* males. There is also discontinuous colour polymorphism in males, small males having predominantly dark tergites and yellow sternites and large males having the opposite pattern of colouration. This too is similar to *B. quinquespinosus* and *C. pallida* males although there is a continuous variation in these two species. Larger sample sizes may reveal continuous colour variation in *B. rostrata*. The significance of colour polymorphism, if any, is not known.

A 2.4 Some Notes on the Female Behaviour of *Bembix rostrata*

It is not clear why female activity at the nesting site is lower in the afternoon than morning (see Chapter 6). It may be that females spend more time feeding on nectar in the afternoon to coincide with the period of maximum nectar availability from plants. However the volume of nectar at *T. vulgaris* flowers is very low and the period of highest nectar availability is at 1200. No data were obtained on nectar production of *Pastinaca sativa*.

The relative independence from environmental conditions is reflected in the lack of correlation between temperature or prey size with time taken for each step involved in provisioning the nest. *B. rostrata* females are likely to provision the nest in the fastest time possible to maximise reproductive output. Selection may have speeded up the process of opening the temporary closure at the burrow entrance and entering the nest with the prey in the presence of parasitic flies (Miltogramminae) as this is the period that wasps are most vulnerable to attacks from these parasites. Indeed these wasps do not need to put down their prey to open the nest entrance, as is illustrated in figure A 2.4.

On one occasion a female was observed to remove and discard dried flies from a burrow. It is not known if the burrow was excavated by the female or whether it belonged to another wasp. This behaviour has been reported in a few other sphecid species (Field 1992) but remains enigmatic (see Chapter 5). The wasp did not feed on the removed provisions nor did she take them away to be stored inside another nest. The prey may have been removed from the cell by the provisioner if they had dried up or become rotten thereby reducing the risk of disease or fungal attack to the larva. Alternatively if the wasp had usurped the burrow from another, the removal and discarding of provisions might be a way of ensuring that the cell was free of eggs oviposited by parasites onto the prey.

A 2.5 Size of *Bembix rostrata*

Bembix rostrata is slightly sexually dimorphic, males having smaller head widths and fresh weights than females (table A 2.1a). There is no difference in

size between the *B. rostrata* population in Portugal and that of Larsson's study (1989a) in southern Sweden (table A 2.1b).

Unlike most aculeate Hymenoptera, there is no obvious sexual size dimorphism, males and females being of similar size. In many species which have intense competition between males for mates, as in the cluster mating systems, large males have an advantage over small males and consequently there is a loss of the sexual size dimorphism as males become large and approach the size of females (eg, Borgia 1980; O'Neill 1983; O'Neill & Evans 1983). No evidence of a large size advantage among males of *B. rostrata* has been found, and the maintenance of size variation among males of this species might be due to alternative thermal strategies (Larsson 1989a).

Table A 2.1 Sexual size dimorphism of *Bembix rostrata* from Fonta de Telha, 1992.

| Sex | Head Width mm (mean \pm SD) | Wet Weight mg (mean \pm SD) | N |
|---------|----------------------------------|----------------------------------|----|
| Males | 5.07 \pm 0.35 | 179.2 \pm 50.48 | 14 |
| Females | 5.25 \pm 0.23 | 195.0 \pm 33.42 | 27 |

Table A 2.2 Size (head width, mm \pm SD) of *Bembix rostrata* from two populations; Portugal and Sweden.

| Sex | Portugal | Sweden |
|---------|-----------------|-----------------|
| Males | 5.07 \pm 0.35 | 5.07 \pm 0.22 |
| Females | 5.25 \pm 0.23 | 5.20 \pm 0.16 |

Fig. A 2.1a A patch of *Thymus vulgaris*, where male *B. rostrata* were often seen.



Fig. A 2.1b *Pastinaca sativa*, a tall standing umbellifer to which many insects were attracted.



Fig. A 2.2 The number of interactions between male *B. rostrata* on *Thymus vulgaris* (O), and the number of male visits to patch (•).

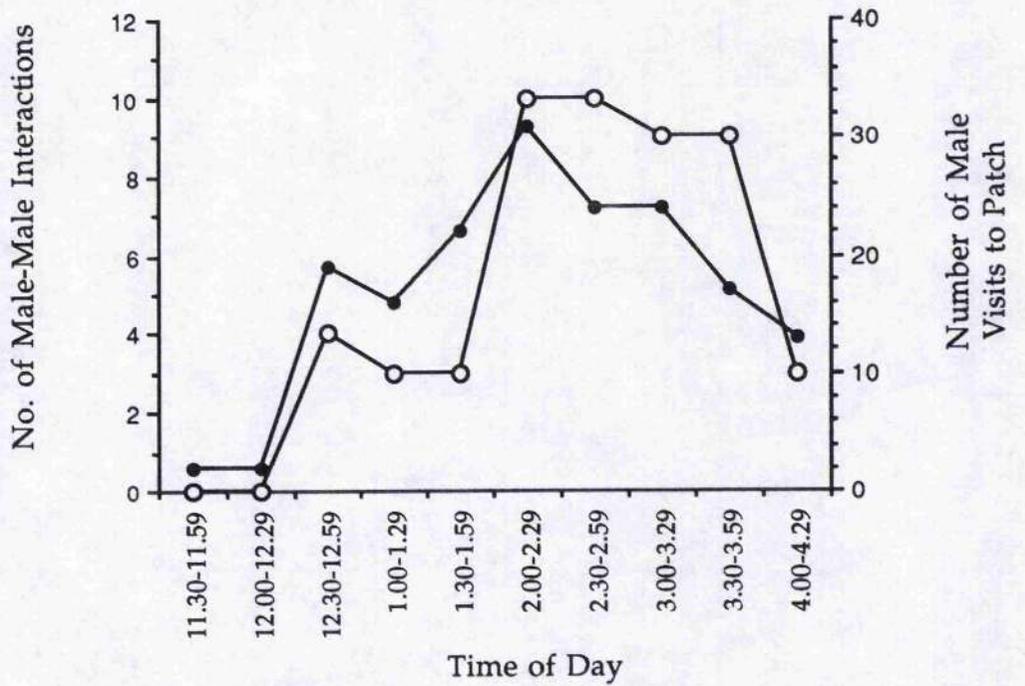


Fig. A 2.3 The number of foraging trips (O) to *Thymus vulgaris*, and the number of flowers visited by *B. rostrata* per foraging trip (•).

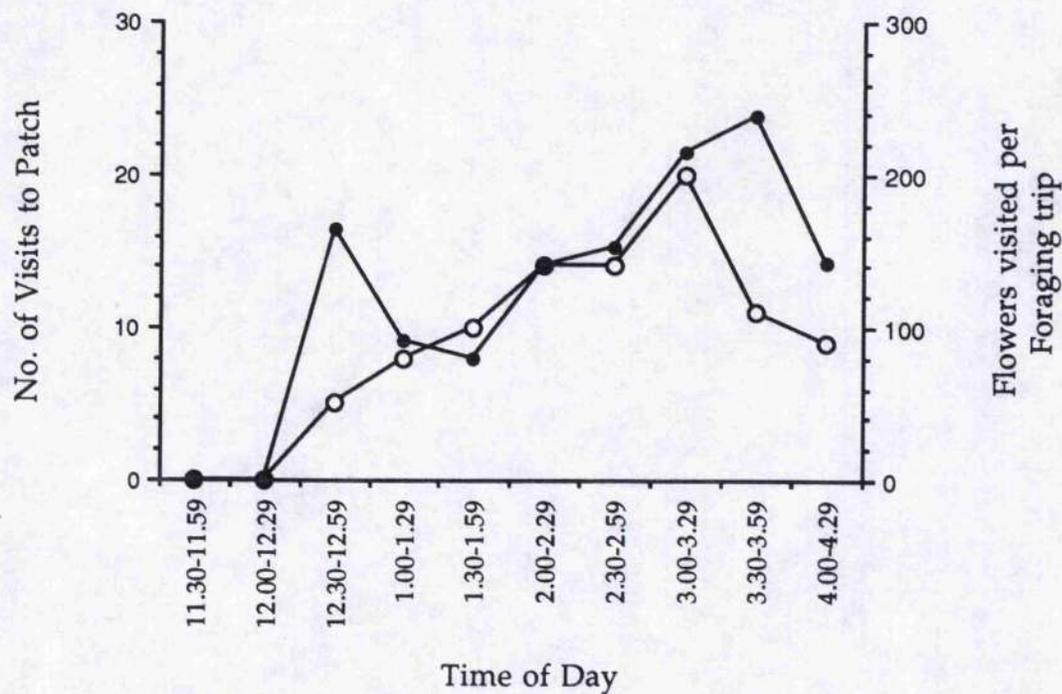


Fig. A 2.4 A female *Bembix rostrata* opening the nest entrance on return from a foraging trip with a prey item.



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