LEK AND SWARM BEHAVIOUR IN THE CALYPTERATE DIPTERA.

Thesis submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor in Philosophy by Ian Brendan Wooldridge.

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Frontispiece. Male *Gymnochaeta viridis*.

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Abstract.

Sexual selection is a potent force acting on male and female reproductive strategies. The effect of sexual selection on males by both inter-male competition and female choice is now recognised. The difference in the relative parental investment of the sexes results in the potential for differing sexual selection pressures on each sex. Usually because female parental investment is larger greater sexual selection pressure occurs on males' characteristics.

Leks exist in certain species where males defend a display site against rival males in order to mate with the females coming to the territory. Preadaptations for lekking of mobility, visual acuity and absence of male parental care are present in many insects and leks are found in many species. In the Diptera swarms aggregating at markers are the typical mating system in many families, leks and male terrioriality for mating purposes are known in some species.

Observations on seven species of calypterate Diptera show that territories, leks and swarms have similarities. The behaviour of *Gymnochaeta viridis*, *Calliphora erythrocephala*, *Lucilia caesar*, *Stomoxys calcitrans* and *Fannia canicularis* in the natural state and laboratory experimental observations on *Calliphora vomitoria* are described. *G. viridis*, *C. erythrocephala*, *C. vomitoria*, *L. caesar* and *S. calcitrans* show the same behaviour pattern of perching on look-out-posts which form the centre of the territory of the first four species when a conspicuous object is used as a perch by the males. Male *M. autumnalis* form swarms on conspicuous marker-objects. Male *F. canicularis* patrol territories beneath marker-objects by flying below them.

The perching territorial species have similar flight behaviour of inter-male circling flights used in inter-male competition and for epigamic recognition. The circling results from the males' need to stay within the area of the territory. With M. autumnalis the perching species share the performance of a display flight, derived from the swarm flight of Nematocera, advertising their presence to females and other males.

The influence of the marker-object on male behaviour is strong in all the species. It concentrates the males of M. autumnalis upon it and forms the centre of the territories of males of the other species. Its effect is the same as that of the swarm-markers of the Nematocera.

Swarming forms the basic dipteran mating pattern from which others are derived. The operational sex ratio in swarm and lek species is highly skewed towards males. Lek and swarm flight activity reduces male survival due to wing damage. Pheromones are not proven to exist in calypterates and are likely to be unimportant in their mating systems.

Lek and swarm mating systems have evolved when males which display achieve higher reproductive success than other males and also aggregate as a result of the density of males in an area and later sometimes as a result of the greater attractiveness of groups to females because of the enhanced stimulus effect of the display of a group of males. Although other interpretations of the available information are possible the predictions of a model based on this concept of lek evolution agree with observations of the behaviour of many lekking and swarming species.

Preface.

The importance of an understanding of lek behaviour to the study of mating systems and sexual selection is largely due to the need to comprehend the causes and action of mate choice in animals. It is now generally accepted by evolutionary biologists that female choice of certain males is the ultimate cause of lek behaviour, if lekking is to be interpreted according to modern Darwinian theory.

The problem with lek mating systems is to determine what males and females gain from lekking. Since females are more likely to determine the type of mating system in a species than are the males the main questions concerning lek systems are those related to female choice of mates. They can be formulated as follows:

What are females actually choosing?

Why are lekking males preferred to non-lekkers?

Why are certain of the lekking males sometimes preferred above others?

In these questions the implicit question is that of how females benefit from lek mating systems.

Understanding the cause and and operation of female choice in lek systems is important for evolutionary theory since much debate has recently taken place on the question of benefits to males and females of various mating systems. Some authors have put forward the concept of genetic choice mating systems. Females in such systems are supposed to choose males which have the best genes for the maximisation of the females' reproductive success. This seems to be part of a dominant trend in contemporary biological thought of looking for easily appreciated genetic payoffs for many pieces of animal behaviour. In many cases this has led to valid explanations, but in the case of lek behaviour it seems to have led to ever more complex theories (see for instance Borgia (1979) for his solution to the "Lek Paradox").

The explanation of lek systems by a genetic choice model has perhaps largely resulted from the historical fact that vertebrate leks were the first to be described. On these leks the usual pattern is for only a few of the males present to mate. This then easily led to the idea that females choose from among the lekking males the "best" one and that such a male has the "best" genes for the females' requirements, or that males by competing among themselves sort out the "best" male for the females.

Insect mating swarms, especially those of the nematoceran Diptera, often share many of the characteristics of leks and may be regarded as primitive leks or at least as their precursors. No female choice of particular males is usually found in these mating swarms and this indicates that females must be choosing the male behaviour pattern of swarming (lekking) rather than the lekking males for genetic benefits. Consideration of the possible sequence of evolution of leks should help in understanding their significance.

A complete theory of lek mating systems requires coherence and plausibility at both genotypic and phenotypic levels for all lek species. I think the answer to the problem of the evolution and maintainance of lek behaviour is not "good genes" but is rather to be found in a consideration of each lekking species evolutionary ecology..

In this thesis the model of evolution of lek behaviour proposed is one of choice for convenient and effective conspecific matings by females and inter-male competition for access to females, both of these factors resulting in sexual selection pressures on males and females.

In Chapters 2 to 8 the behaviour of seven species of calypterate Diptera at their mating sites is described from original observations. In Chapter 9 the flight behaviour of the species studied is discussed with reference to other authors work. In Chapter 10 certain features associated with dipteran swarms and leks are discussed with reference to other published work. In Chapter 11 the evolution of lek and swarm behaviour is considered using information and theories drawn from many sources.

Lengths of adult flies are those given in Emden (1954) and Assis Fonseca (1968), unless otherwise stated.

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PART ONE - INTRODUCTION.

Chapter 1. Introduction.

1:1. Sexual Selection.

Although Darwin proposed the theory of sexual selection in 1871 relatively little further thought or investigation of its effects took place until fairly recently. Darwin's main point in his argument for the existence of sexual selection was that it is necessary to account for morphological and behavioural differences between the sexes which appear unnecessary for survival and thus cannot be attributed to natural selection. Sexual selection "depends on the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction (Darwin 1871, p.209).

Darwin believed that the operation of sexual selection required 1) a "surplus" of males; 2) "struggle" among males for females; 3) female choice of males. He noted that it operates on females as well as on males and that the effects of sexual selection may oppose those of natural selection on either sex.

1:2. The effect of parental investment on sexual selection.

The forces of sexual selection operate differently upon the sexes due to the disparity in the amount of parental investment (PI) between them (Bateman 1948, Trivers 1972). Trivers defined PI as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring". The sex with the greater PI is a limiting resource for the other and individuals of the sex investing less will compete for access to those of the sex investing more. Usually females invest more, so in general males will compete for females.

In experiments upon Drosophila Bateman (1948) confirmed the theoretical prediction that male reproductive success (RS) will vary more than female RS, in terms of number of offspring, due to the disparity in the relative PI of the sexes. Trivers (1972) elaborated this argument into a comprehensive theory for predicting the action of sexual selection. Trivers noted that the greater variance in male RS compared to female RS, due to the disparity in PI, occurs because males have a higher optimal number of offspring than females, but the total number for both sexes must be the same. Thus there is the chance of great variance in males' RS due to differences in males' ability to mate females. Variance in male RS is effectively due to differences in the number of females mated by each male. The variance is a measure of the actual intensity of sexual selection in a species, as Bateman (1948) demonstrated with Drosophila. Trivers proposed that the difference in the number of offspring each sex optimally produces is a measure of the potential for sexual selection in a species. For the potential for sexual selection to become operative as actual selection pressure other factors must affect the mating system. For example spaced breeding allows males time to compete for females and/or for females to discriminate and choose between many potential mates (Emlen and Oring 1977).

1:3. Territories and leks.

A territory may be defined as any defended area (Noble 1939), but when considering lek territoriality it is essential to distinguish between resource based and non-resource based territories (Alexander 1975, Parker 1978). The non-resource based territories are quite distinct from those based upon a resource such as a feeding area or a nesting site. In a non-resource based territory the gain for the occupant does not come from something taken from the territory, such as food or a brood of offspring produced, or the chance to mate with a female attracted to a resource in the territory. The occupant of a non-resource based territory benefits from the possession of the defended site itself, the act of territorial defence being the requirement for gaining benefits.

Males may defend resource based territories in order to gain access to females for mating when females must use the resource defended. Such resources must be defensible by an individual male who benefits from this defence. Also it must be difficult or impossible for a male to control females directly and prevent them from mating other males, otherwise selection would favour this strategy. Defence of resources such as feeding sites is a strategy occurring in certain species of the Hymenoptera where males guard the flowers visited by females for pollen and nectar in order to mate with the females attracted to these resources. For instance this behaviour occurs in Protoxaea gloriosa (Andrenidae) (Cazier and Linsley 1963) and Anthidium banningense (Megachilidae) (Jaycox 1967). Oviposition sites may be guarded, this strategy is found in many species of anisopteran Odonata, for example Plathemis lydia (Campanella and Wolf 1974), and also in the yellow dung fly (Scatophaga stercoraria) (Borgia 1980) where, at least at low density of individuals, a female has to mate with a territorial male if she is to oviposit in fresh dung most suitable for larval development. In this species females choose to approach and mate with territorial males (Borgia 1981).

Male non-resource based territoriality may be expected to occur in certain of those species where males cannot effectively guard a resource needed by females or directly control females and where male parental care is absent. Non-resource based territoriality is lek territoriality as the term is usually understood. The word lek was originally used as the designation for the mating behaviour and mating grounds of various game birds. It is now used much more widely. Among birds leks have been described in grouse (Tetraonidae), for example Wiley (1973), and manakins (Pipridae) (Lill 1974). Leks have been described in the Uganda kob antelope (*Adenota kob thomasi*), for example Buechner and Roth (1974) and a bat (Bradbury 1977). In the insects leks have been found in Hawaiian *Drosophila* species (Spieth 1968), in the otitid fly *Physiphora demandata* (Alcock and Pyle 1979), in dragonflies, for example *Plathemis lydia* (Campanella and Wolf 1974) and in orchid bees (Apidae) (Kimsey 1980).

1:4. Definition of a lek.

Numerous factors combine to result in the evolution and maintainance of lek behaviour, this is discussed in Chapter 11. Here a set of criteria is listed which can be used to define and recognise a lek in a species.

1) The species does not have male parental care.

2) A mating arena exists where males gather solely for the purpose of mating. Its location is fixed for at least one breeding season.

3) Males establish and defend territories within the arena.

4) The males' territories contain no resources useful to females.

5) The behaviour of males is primarily directed towards one another and is usually highly ritualised for its use in inter-male competition.

6) Females come to the lek to mate and all mating occurs on the lek arena.

7) The area of the lek arena is significantly smaller than the home ranges of both sexes when they are not on the arena.

8) Females have an opportunity to select their mates.

9) Lekking aggregations are always of a single species.

1;5. Preadaptations for lekking in insects.

Very many species of insects are preadapted for lekking, especially those of the Diptera. These preadaptations are:

1) Mobility. Both sexes of a lekking species must travel to the lek arenas. Those insect species capable of sustained flight have this preadaptation.

2) Visual acuity. Recognition of and orientation to both the lek arenas and other active individuals is primarily by vision. Pheromone release seems to play a part in relatively few species, but occurs in Hawaiian *Drosophila* (Spieth 1968) and philanthine wasps (Alcock 1975), however even in such species visual stimuli must have a central role.

3) Absence of male parental care. Lack of care by either parent is the situation in most insect species, often correlated with the different requirements of adults and young or lack of overlap of the various stages in the life cycle.

1:6. Dipteran mating patterns.

There is a variety of mating systems in the Diptera ranging from large swarms flying over swarm-markers found in many nematoceran species (Downes 1958) to the resource based territory of the dung fly *Scatophaga stercoraria* (Borgia 1980, 1981). The intricacies of dipteran mating behaviour have only recently begun to be investigated, many years after the taxonomy of the group has been thoroughly analysed. No doubt many more complex aspects of dipteran behaviour await discovery anddescription.

The diversity of the mating systems can be illustrated by a selection of examples.

Swarming is characteristic of many nematoceran species. Downes (1958) described how swarms originate when a visually recognised swarm-marker interupts the forward flight of individual males and elicits dancing flight. The kind of marker depends on the particular species. Thus swarms of *Culicoides nubeculosus* occur over cow dung and those of *Aedes hexodontus* developed over a white cloth. Downes stated that swarms are always of a single species and that this depends upon a species-specific response to the swarm-marker. He noted that the behaviour is typical of species of the families Culicidae, Ceratopogonidae and Chironomidae.

Syrjämäki (1965) noted that females of swarming species make short "offering flights" over the swarm-markers. Charlwood and Jones (1980), working on the *Anopheles gambiae* complex, stated that anopheline mosquitoes orientate first to the swarm arena, places such as clearings in swamps, and then to the swarm-marker over which the males swarm and the females fly until they are mated.

Thornhill (1980) analysed a nematoceran swarm in detail. He found that the swarms of Plecia nearctica (Bibionidae) are vertically stratified, the larger males being at the bottom. Males interact in the swarm by bumping each other and so space themselves out a few centimetres apart. Since females fly into the swarm from below the result of the males' behaviour is that large males are more successful at capturing females for mating. Swarms occur over the emergence site.

Rather little seems to be known of the mating habits of the members of the Brachycera. Bailey (1948) noted that males of Tabanus nigrovittatus (Tabanidae) hovered in swarms and chased passing flies. Downes (1969) recorded other tabanid males hovering either in swarms, in smaller groups or alone depending on the particular species. Colyer and Hammond (1968) noted that males of Bombilius major (Bombilidae) hover. The males of many species of Empidae hover in swarms, often holding prey items as nuptial gifts for the females. These gifts are sometimes wrapped in a secretion and the secretion alone forms the gift in some species (Eibl-Eibesfeldt 1970, p.121).

In the sub-order Cyclorrhapha mating patterns vary from hovering species to perching lekking species and to resource based territorial species. The hovering habit of males of many syrphid species of the genera Chilosia, Volucella and Eristalis is well known, leading to their popular name of "hover flies", and is referred to by Colyer and Hammond (1968). Alcock and Pyle (1979) described the lek behaviour of Physiphora demandata (Otitidae) whose territorial males perform lengthy courtship sequences in displaying to the females. In species in various other families the males perch in certain places and wait for females. For example Catts, Garcia and Poorbaugh (1965) described the behaviour of Hypoderma lineatum (Oestridae). The males of this species perch in a "waiting attitude" and several males chase each passing insect. Males aggregate and remain at the same site for their life span of about one week. Males of Cochliomyia hominivorax (Calliphoridae) have "waiting stations" from which they chase passing insects (Guillot, Brown and Broce 1978). Interactions between males of Cephenemyia (Oestridae) limit the number at each "waiting station" (Catts 1964). Males of Cuterebra latifrons (Cuterebridae) each possess a "waiting station" and the surrounding flight area as their territories (Catts 1967).

The yellow dung fly (Scatophaga stercoraria: Scatophagidae) as mentioned above mates on and around cow pats. The males' behaviour consists basically of searching for females on and near the pats and then copulating with one and guarding her, mounted on her back, as she oviposits on the pat (Parker 1970). Recently it has been found that the males are territorial at low density. Large males were always found to control pats with the smaller ones being around the edges (Borgia 1980).

Hammer (1941) noted that many species associated with cattle and cattle dung meet at conspicuous objects in a field, among others Musca autumnalis, Mesembrina meridiana and Lyperosia irritans (Muscidae).

Downes (1969), in his excellent review of dipteran swarming and mating behaviour, concluded that in dipteran mating systems in many families throughout the order "mating takes place in flight at a visually determined assembly station. The station is occupied by both sexes, but usually the males fly there for long periods while the females remain only long enough to mate.

At the assembly station the female is recognized by movement vision, the eyes of the male often being highly specialized...". Richards (1927) similarly noted the greater development of the eyes of male insects being correlated with "marriage by capture". Downes continued later "In many Brachycera the assembled males rest on the landmark rather than fly above it, but nevertheless they capture the females visually, and in flight. Specificity of mating results primarily from specificity of the assembly station; neither the visual nor the auditory response to the female is adequately specific, and it is uncertain whether any specific recognition usually takes place on contact."

Thus the essential feature characteristic of many dipteran mating systems is the response of both sexes of a species to a species-specific marker object which results in the meeting of the sexes at the marker. The importance of this and its consequences for the evolution of mating behaviour are discussed later in Chapter 11.

1:7. Look-out-post and "alert posture".

The term look-out-post (abbreviated to LOP) is equivalent to the "waiting station" of various authors. The term "alert posture" is equivalent to the "waiting attitude" of the same authors.

1:8. The species studied.

The species studied and described in this thesis were all easily found and readily identified in the field. This made observation of their behaviour more practicable than trying to observe species difficult to identify in the field. When a particular insect was under observation it was certain that the behaviour would be attributed to the correct species.

Each species habits are briefly described in the chapter dealing with its mating behaviour.

PART TWO - OBSERVATIONS ON THE BEHAVIOUR OF SPECIES OF CALYPTERATE DIPTERA.

Chapter 2.

THE LEK BEHAVIOUR OF *GYMNOCHAETA VIRIDIS* FALL. (TACHINIDAE).

2:1. Introduction.

In wooded areas *Gymnochaeta viridis* is common in spring, when the males are frequently found basking on tree trunks and the females on flowers. The eggs are laid in places which are likely to be inhabited by the hosts of the parasitic larvae. Eggs give rise almost immediately to migratory larvae which actively seek hosts (Colyer and Hammond 1968). The hosts which are known for this species are the Small Dotted Buff (*Petilampsia minima*, Agrotidae), the Shaded Broad Bar (*Ortholitha chenopodiata*, Geometridae), the Pale Tussock (*Dasychira pudibunda*, Lymantridae), and the Black Arches (*Lymantria monacha*, Lymantridae).

Newly emerged adults are a brilliant green metallic colour which acquires a reddish-copper hue as the flies age. 20 males measured at Leahurst on the Wirral in 1976 ranged from 8.0 to 11.0mm. in length.

2:2. The observation sites.

During May 1975 and 1976 *G. viridis* was observed at a site about 15m in length along the side of a track known as Cuckoo Lane running through Wood Park Farm near Liverpool University Veterinary Field Station at Leahurst on the Wirral. This area contained a nettle bed with other plants and grasses. One edge was formed by the track, the other by a hedgerow of elder and hawthorn with trees behind. There were three wooden fence posts about one metre high spaced along the hedgerow. At the north end there was an oak tree, beyond this the ground was shaded by overhanging trees, and at the south end there was a piece of corrugated iron fencing, the area is shown in Fig. 2:1. The track ran in a south-westerly direction, so the part of it forming the major part of the lek arena faced roughly south-east and caught the morning sun. The iron fencing faced roughly south and was sunlit when other parts of the area were shaded.

Lekking males were found only on sunny days, always in sunlit parts of the site. In the morning they were found on the nettle bed area and the fence posts, gradually moving towards the oak tree as the nettle area became shaded. In the afternoon, when the rest of the site was shaded, they were found on the fencing.

In 1977 another site at Dungeon Lane close to Hale Cliff near Speke, Liverpool was used for observations. The site consisted of a wooden fence, about two metres high and ten metres long, with low plants at its base, running along the edge of Dungeon Lane and a flat grassy area with scattered trees next to the lane. Lekking males were found on the fence and on the trees on suitable sunny days.

2:3. Perching and territories.

Males perched on objects which gave a clear view of the surrounding area, using them as look-out-posts (LOPs). Males flew out from their LOPs and chased passing insects. When the LOP was on some conspicuous marker object, such as a tree trunk or fence post, the male perched on it returned to the same LOP after each flight, as long as he remained in that area. The males defended an area of up to one metre around the LOP against intrusion by other conspecific males, so that the area containing the LOP formed a territory. On tree and fence posts the LOPs were from about 20cm.

to 1.5m. above ground level.

Where LOPs were on low plants or fences males returned to roughly the same spot after each flight, but since there were no conspicuous marker objects for them to orientate by the site chosen for perching varied. Here the territories had less clearly defined boundaries, but still it was seen that males perched in mutually exclusive areas and maintained territorial behaviour.

The time a male spent in occupation of a particular territory was very variable. On the Leahurst site males moved as the sunlit area changed. They spent from 25min. to 3hr. 30min. in a territory, the mean time was 1hr. 23min., S.E. = 10min., N = 24. The variation in the time a territory was occupied resulted largely from differences between territories in the amount of time that they were sunlit. On the Hale Cliff site a male occupied an isolated tree, part of which was sunlit all day, for all of its active lekking time during one day, moving around the trunk in order to be in a sunlit spot.

While perched on LOPs males adopted an "alert posture" giving the impression of watching the surroundings and being ready for flight (see Fig. 2:2). Males sometimes walked distances of up to 2cm. at intervals, often later walking in another direction. They also turned from side to side occasionally, sometimes to face in the opposite direction, either before or after walking or while remaining in the same spot. Bouts of preening took place between flights.

2:4. Flight activity of lekking males.

a) Chases. All flying insects of roughly the same size and

Fig. 2:1. The area of the Leahurst lek arena.

Fig. 2:2. Lekking male G. viridis in "alert posture".

speed of flight as G. viridis passing within about 60cm. of a male were chased. Small stones thrown close to a male were also chased. The most persistent chasing was shown in response to green flies, such as Lucilia and Orthelia, which closely resemble G. viridis and to conspecific individuals. The species to which an individual being chased belonged was often impossible to determine due to the rapidity of the interaction.

A chase consisted of a male flying in pursuit of an insect, then briefly investigating it while flying close behind or alongside it and then returning to its LOP if the insect was not another G. viridis. When a conspecific male was chased either it was chased away from the chaser's LOP or a circling flight was performed by the males (see below). Conspecific males were often seen to be chased for distances of over 3m., but very often the pair were lost from view as they flew into surrounding vegetation.

Males were seen to mount and mate with conspecific females after having chased and caught them in flight. The mating pairs landed on nearby vegetation in order to complete mating (see 2:10) and were easily lost from view.

Following a chase males returned to their LOPs, unless a circling flight or mating took place, and perched again. The duration of chases from take-off to return and perching ranged from 0.5 to 12.0s., the mean being 2.0s., S.E. = 0.3s., N = 65.

b) Circling flight. Chases of conspecific males did not always result in the males being immediately chased away from a male's LOP. Sometimes the pair of males performed a rapid circling flight chasing each other round in a circle about 8cm. in diameter.

Occasionally in this type of flight the males faced each other and circled about 2cm. apart. There was usually some sideways movement in these flights and often the males rose and fell together (see Fig. 2:3). The distances flown by males in these interactions were up to 5m. from their LOPs, in such long flights the circling part of the flights would be interrupted as one male chased the other for a short time. If two males were perched on LOPs close together their interactions often consisted only of circling flights.

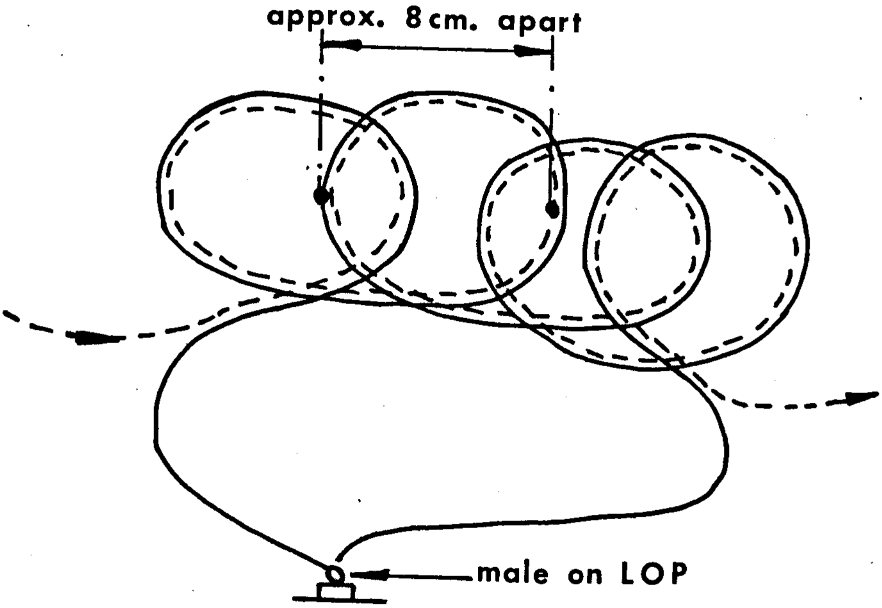
Both chases and circling flights occasionally ended in tussles between the males in flight. When this happened they often fell to the ground and continued to roll around locked together by their legs.

The duration of circling flights from take-off to landing ranged from 1.0 to 14.2s., the mean was 4.0s., S.E. = 0.5s., N = 50.

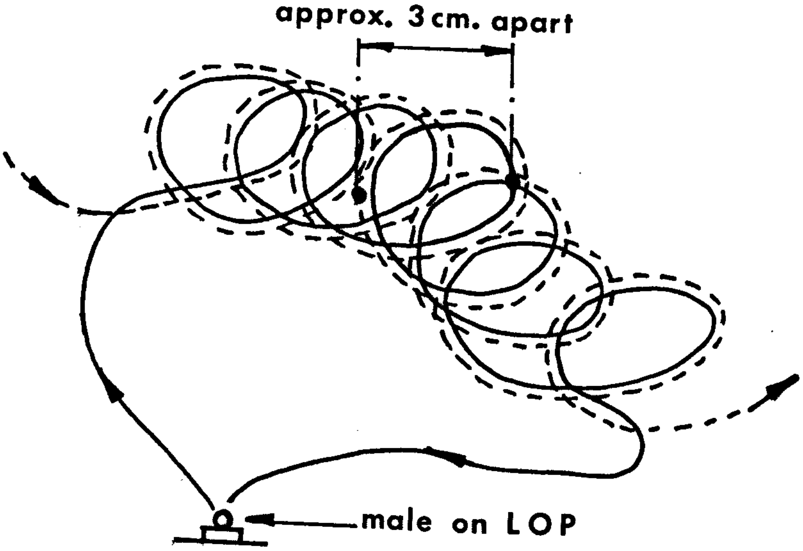
c) Display flights. These flights generally appeared to lack an external stimulus. A male flew around its LOP up to a distance of half a metre on each side, flying in a horizontal plane with little vertical movement, and then returned to it LOP. Sometimes the display flight appeared to be performed in response to a passing insect. When two males were perched close together a display flight by one often resulted in the other male chasing it and the pair interacted in flight.

The duration of display flights from take-off to landing ranged from 0.5 to 2.3s., the mean was 1.0s., S.E. = 0.05s., N = 60.

d) Flights from one LOP to another were seen, these lacked an



(a) Pursuit type of circling flight.



(b) Facing type of circling flight.

Fig.2:3. Forms of circling flight.
(view from above)

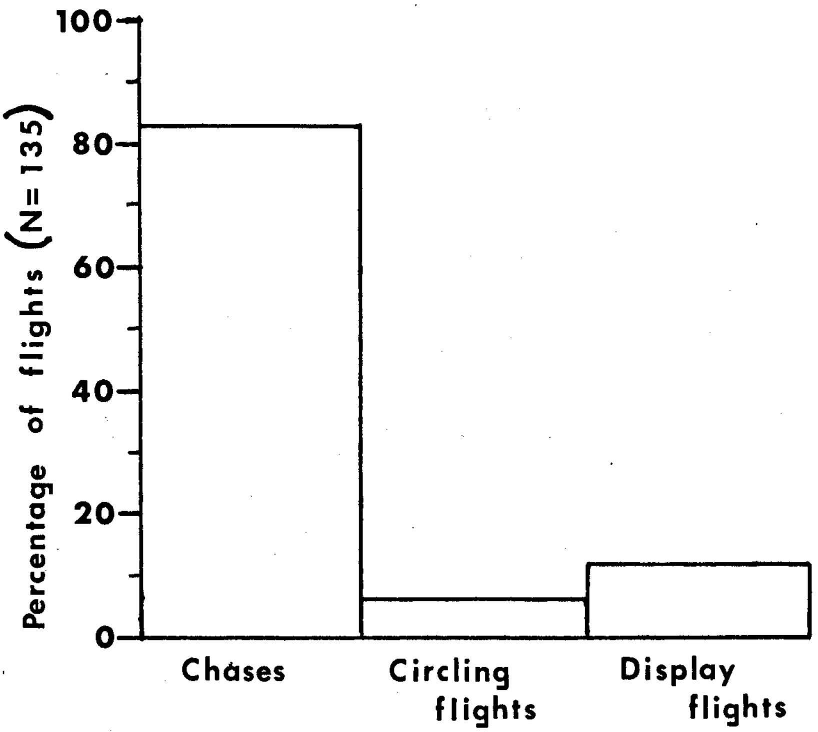
external stimulus except for the alteration in the position of the sun since a male had perched on a LOP. As the sunlit area of the lek arena gradually changed the flies moved their LOPs further into the sunlit area so as to be in a sunlit spot. A number of perche~~d~~ might be tried out before a male appeared to be satisfied with his new LOP.

The percentages of each type of flight performed by a male depended on the distance between males on the lek arena. Fig. 2:4 shows the percentages in the two cases where males were at least 2m. apart and where males were perched within 30cm. of each other. Most flights in the first situation were chases with fewer display flights and very few circling flights. In the second situation almost all flights ended up as circling flights by the adjacent males and are classified as such. When males were perched close together take-off by one resulted in immediate take-off and pursuit by the other.

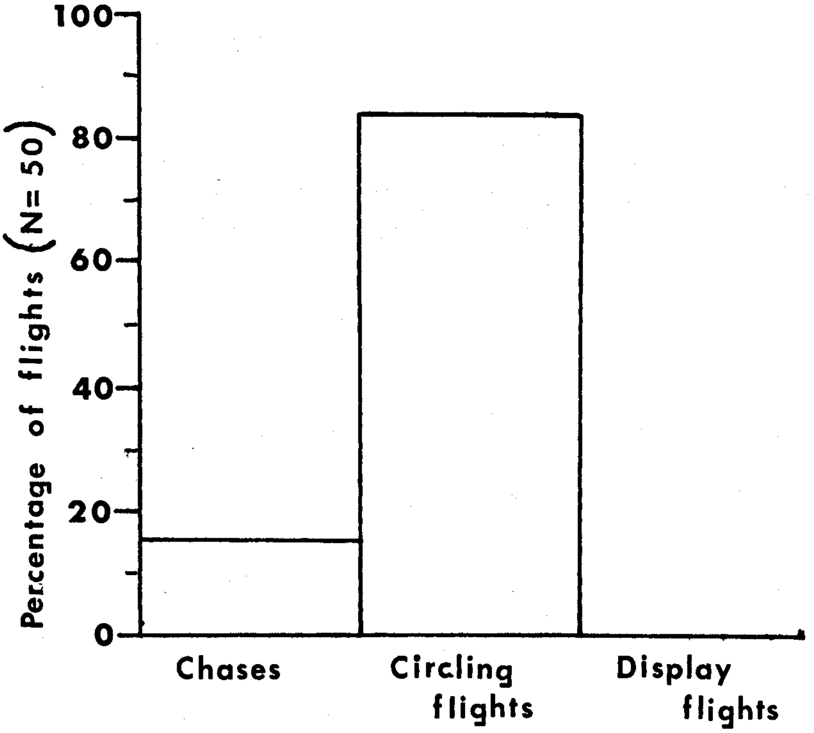
2:5. Identification of individuals.

In 1975 and 1977 males were identified by means of naturally occurring damage to the wings, taking the form of notches and tears. Each male had a unique pattern of wing damage and so could be readily distinguished from the others. Figs. 2:5 and 2:6 show two males and illustrate the differences between individuals in the pattern of damage to the wings.

In 1976 all males were marked. The marking procedure consisted of capturing the flies by means of a net, etherisation and then marking them with metallic aluminium paint by putting one or more



(a) Males at least 2 metres apart.



(b) Males less than 30cm. apart

Fig.2:4. Difference in percentage of flight types due to spacing of males.

Fig. 2:5. Male G. viridis showing wing damage.

Fig. 2:6. Male G. viridis showing wing damage.

dots or lines on the thorax or abdomen. Following this the flies were allowed to recover in specimen bottles and then released. No adverse reaction to this procedure was ever seen, usually the flies resumed activity as soon as they were released.

2:6. Inter-male competition for LOPs.

a) Perching by intruder males in occupied territories. When a male perched in an area which formed the territory of another male the newcomer was almost invariable driven away. Of 36 cases of intruders perching in an occupied area they were driven away by the occupier in 34 instances, in the other two cases both males shared the territory. The number of interactions in flights between males before an intruder was driven away ranged from one to ten, the mean was 2.14, S.E. = 0.32, N = 29, (see Fig. 2:7).

There must have been relatively few occasions when a male could perch in an occupied territory without being intercepted by the resident male. Therefore most of the competition for territories would take place before an intruder had the chance to perch in another male's territory. Thus an estimate of successful territorial defence based on the number of times perched intruders were driven away will be lower than that actually occurring. Intruders which did perch in occupied territories possibly had been involved in interactions with the resident male before they perched, but since they could not be identified until they perched it is not possible to be certain on this point.

b) Removal of males. On May 10th 1976 all males arriving at the Leahurst lek arena were captured, etherised and marked (this was part of an experiment during May 1976 to investigate the

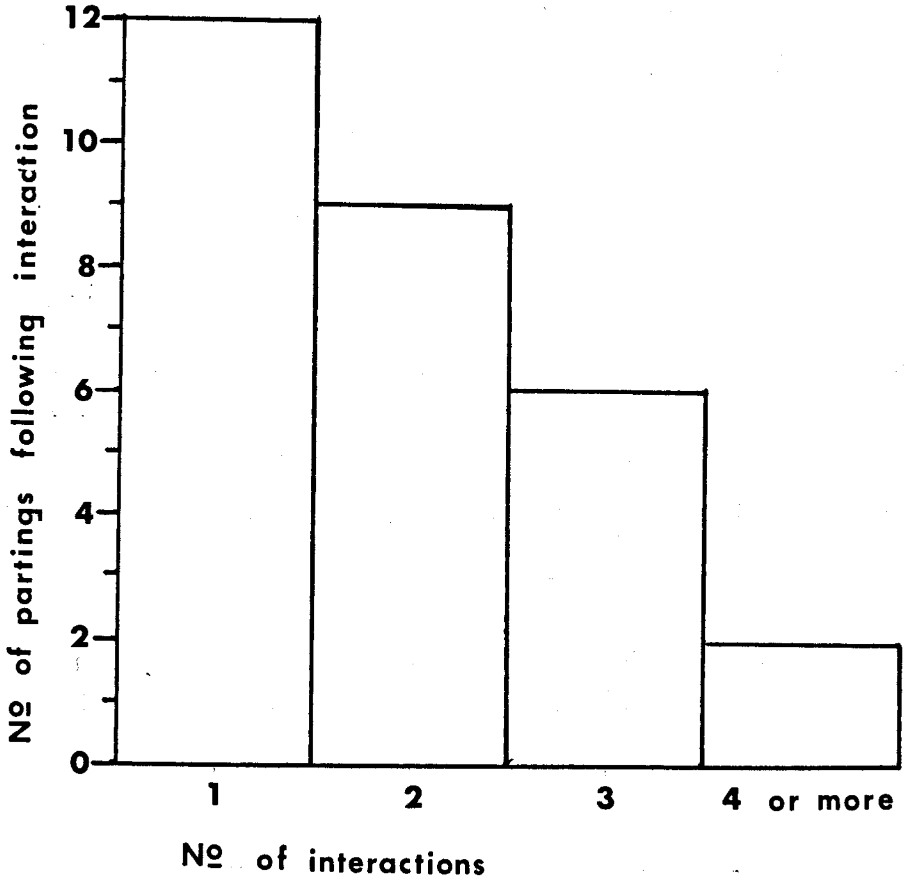


Fig.2:7. Number of interactions before males parted.
(29 series of interactions observed)

return of individuals to the lek arena through the month). In general the LOPs from which the males were removed were soon reoccupied by newly arrived males. A total of eleven males was captured during the day. One particular fence post was occupied twice by a new male, after removal of its previous occupants, within one hour in the morning. Eight other males were taken from the nettle bed area. Although here LOPs were not in a fixed position, unlike the fence post LOP, new males were found in roughly the same places as the captured males had been taken from. Thus removal of a lekking male from its LOP or territory allowed an incoming male to occupy the same site.

It appears that the size of the lek arena limited the number of males on it. The number of available territories in the morning determined the number of males there for the rest of the day. Later in the day the same males which had perched on the lek arena in the morning were found there, but sometimes they were found closer together than earlier due to the reduction in the sunlit area. Often they were found perched on the fence, frequently interacting in flight. However the males did not disperse, perhaps because by this time of day it was more advantageous to remain in the same lek arena than to leave and search for LOPs elsewhere. Since lekking males filled all the spaces in lek arenas in the morning the chances of finding vacant sites in the afternoon were probably low.

c) Size differences between males. Large differences in size between the largest and smallest males were found. A small male, about 8mm. in length, appeared to be only half the size of a large male, about 11mm. in length, because large males had proportionally thicker bodies than small males. These differences must have been due to larval conditions. If, as stated in the literature, eggs are laid more or less randomly in areas where host larvae are likely to be present and upon hatching G. viridis larvae take the first suitable host available the size differences between adults can be accounted for by differences in the size of larvae of the host species. The smallest known host species, the Small Dotted Buff (Petilampsia minima), is much smaller than the largest, the Pale Tussock (Dasychira pudibunda).

The larger males were always successful in aggressive interactions with the smallest males. Very small males rarely appeared to have territories, but flew around the lek arena from one area to another. Where there were no fixed territories the smallest males were always driven away by larger males. This did not appear to be a conditional strategy dependant on size resulting in a different behaviour pattern in small males. The small males appeared to be searching for a territory in the lek arena but were constantly thwarted by the presence of larger males.

2:7. The diurnal pattern of male lekking behaviour.

a) The Leahurst site. Flies were never seen on the lek arena before 9a.m., the usual time of arrival was between 9.30 and 10.00a.m. each day. The flies remained in the area until between 3.30 and 4.00p.m., unless it became cloudy, in which case activity ceased and the flies disappeared. On days which were sunny all through the number of males in the lek arena increased until about noon, after midday very few or no more males arrived. For example in May 1975, on two sunny days, the last male to arrive and obtain a territory arrived at 11.18a.m. on one day and at about 11.30a.m.

on the other. Males arriving later were unable to find territories.

On May 10th 1976, when all males coming to the lek arena were captured if possible, nine males were caught in the morning and only two after midday. This indicates that the number of males searching for territories declined after noon, probably because by then the chances of finding an unoccupied territory will be low, and males would already have had to perch close to other males in order to obtain places on the lek arenas.

The number of males found on the lek arena during one day is shown in Fig. 2:8 from data collected on May 31st 1975, a day which was sunny from morning until afternoon and so the flies were not affected by adverse weather. Data from separate days is not pooled because the changeable weather at this time of year did not allow this.

b) The Hale Cliff site. Males arrived in the morning at about the same time as at Leahurst, but they remained active until about 7p.m., unlike at Leahurst. The reasons for the difference are unknown, otherwise the behaviour of the males was the same.

On both sites males which had obtained territories stayed in the lek arena for as long as lekking continued that day. Sometimes a male could not be found for up to half an hour. This was occasionally due to it being in part of the area not being watched at the time, but often it was probably due to males leaving the lek arenas to feed and also to matings taking place unobserved in the surrounding undergrowth.

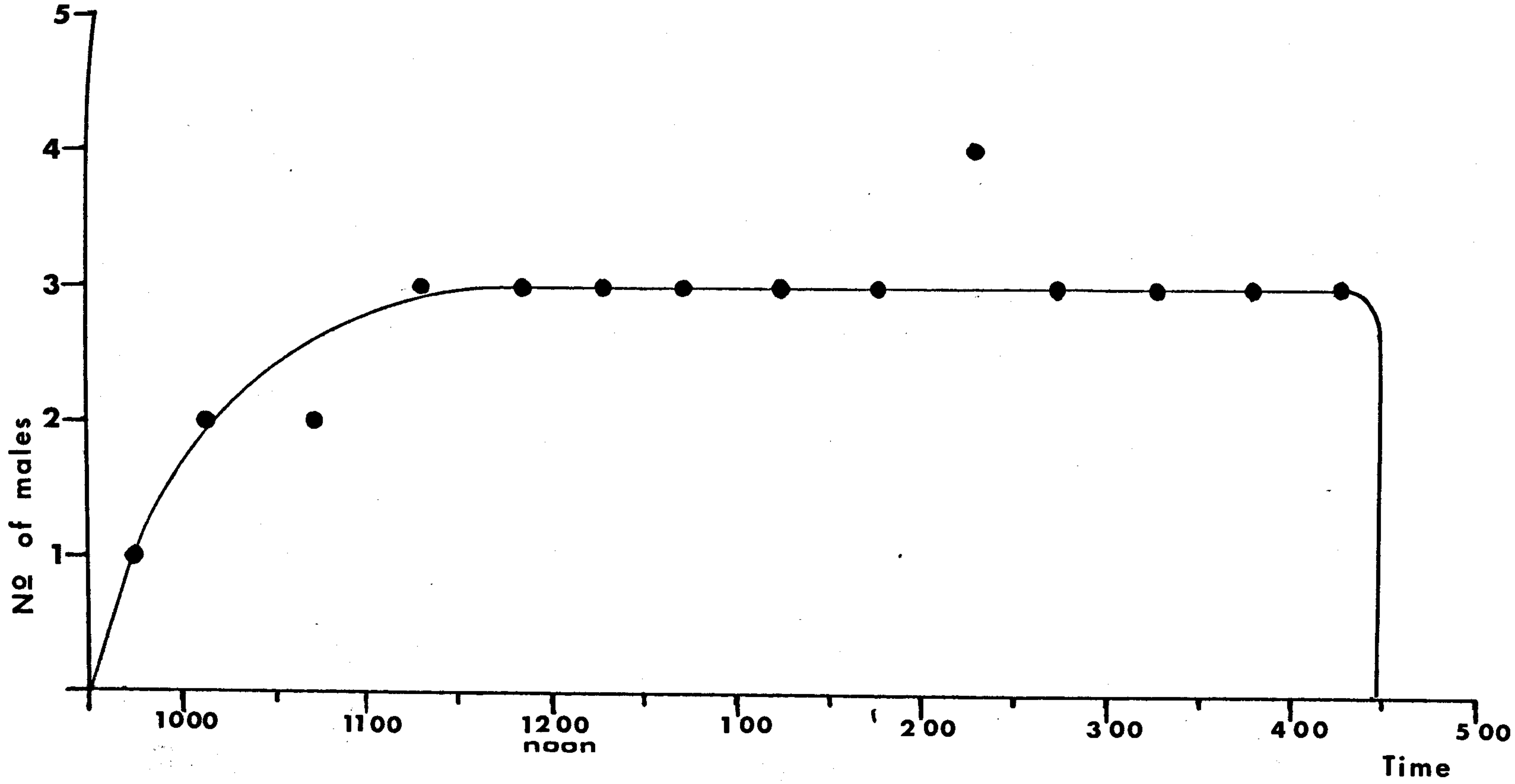


Fig.2:8. Nº of males through one day on lek arena. (May 31st. 1975)

2:8. Female behaviour and copulation.

Females were not seen in the lek arena except in instances of copulation observed. Only two copulations were definitely seen. In both cases the female was caught in flight by the male after a brief chase and the pair flew in tandem down to perch. In one instance the pair disappeared into vegetation and could not be found, the other copulation was observed until the pair separated.

The mating pair sat on the top of a nettle leaf at first, the copulatory position being the "male vertical pose" of Lamb (1922). Copulation lasted for 27min., during which time there were two attempts at take-over of the females by other males. A male attempting take-over of a female tried to push itself between the mating male and female by standing on the female's back and inserting its abdomen between the mating pair. During the first take-over attempt, which lasted for 4 to 5min., the female remained motionless, but during the second, which lasted from 7 to 8min., she walked beneath the nettle leaf on which the pair were perched. The copulating male vigorously defended the female from take-over on both attempts by pushing the attacking male with his pro- and mesothoracic legs, also vibrating his wings and producing an audible buzz.

2:9. Return to the Leahurst lek arena over the flight season.

In 1976 a total of 24 males were seen in this area. Of these 16 were seen for one day only, the other eight returned for a varying number of days. Since flies were found in the area only on days when the weather was suitable a few days often elasped between sightings of individuals. Fig. 2:9 shows the occurrence

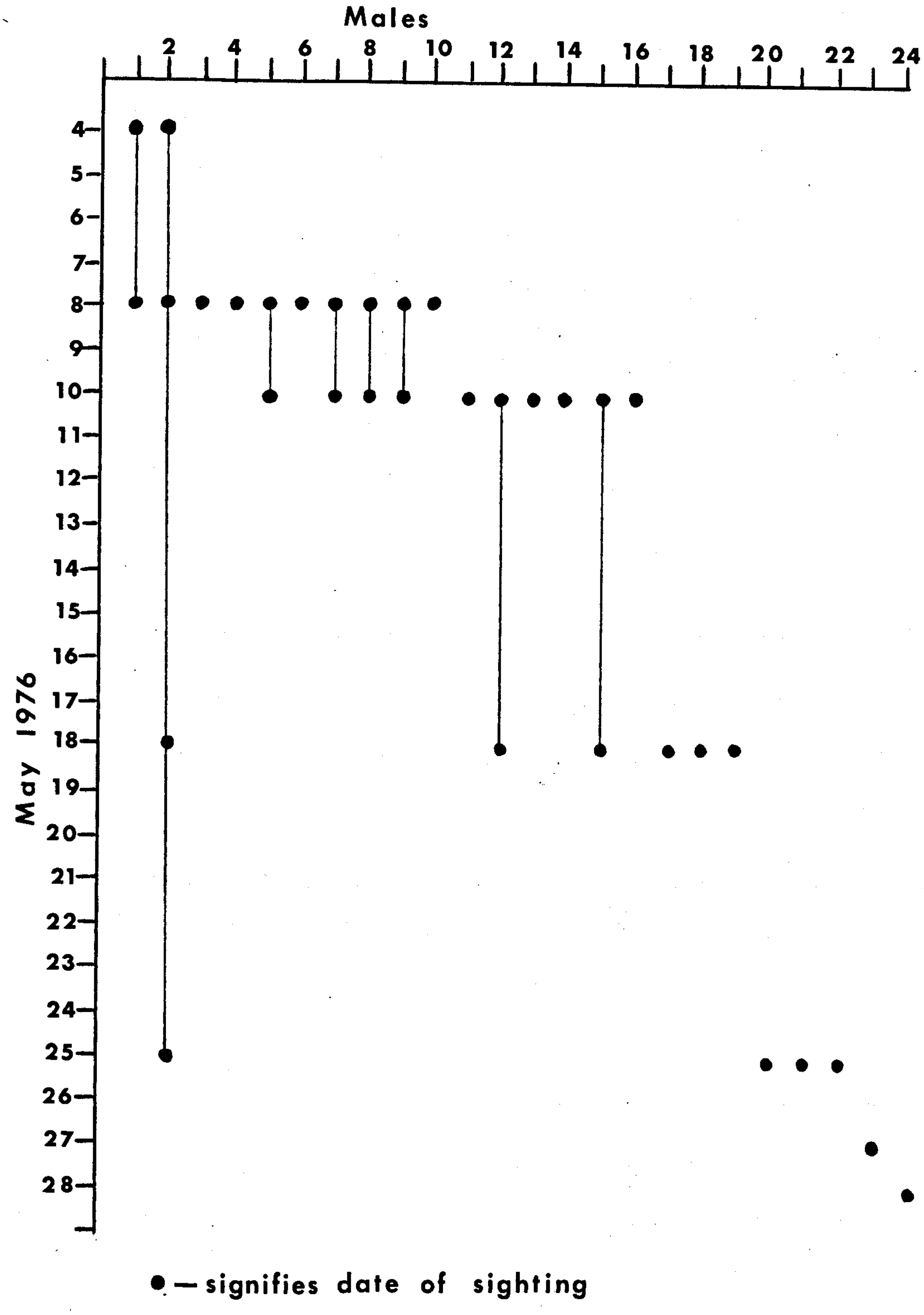


Fig.2:9. Dates of sighting of individuals in lek arena during May 1976.

of all males seen in the area during May 1976. Similarly in 1975 five males were seen to return to the lek arena over a period of some days. Males were not collected and marked in 1975, so only those males which established themselves in territories in the area were recorded. Neither was the identification of males carried out over the whole flight season, unlike 1976. The dates on sighting of identified males in 1975 is shown in Fig. 2:10.

The data indicates that if a male obtained and held a position in the lek arena it was likely to return on subsequent days, if the weather was suitable. Those males seen on only one day when all males found were captured and marked (May 10th 1976) which arrived when other males had already established themselves on the lek arena must have had difficulty in finding a place on the lek. Capture of the male did not prove that it had a territory.

2:10. The flight season of *G. viridis*.

In 1976 the species was found at the Leahurst site from May 4th to May 28th, although an individual male was found at another site as late as June 4th. Over the month of May 24 males were seen, the maximum number being on May 10th when eleven males were found. Fig. 2.11 shows the number of new captures, returning males and number of males for each day of the month when the flies were active on the lek arena.

Clearly the flight season of the Leahurst population of *G. viridis* was limited to May. During May the number of days on which lek behaviour could occur was limited by the need for sunny weather. Thus in May 1976 there were only seven days in May when lek activity could take place, so the amount of time available for lekking was short in comparison to a male's likely life span

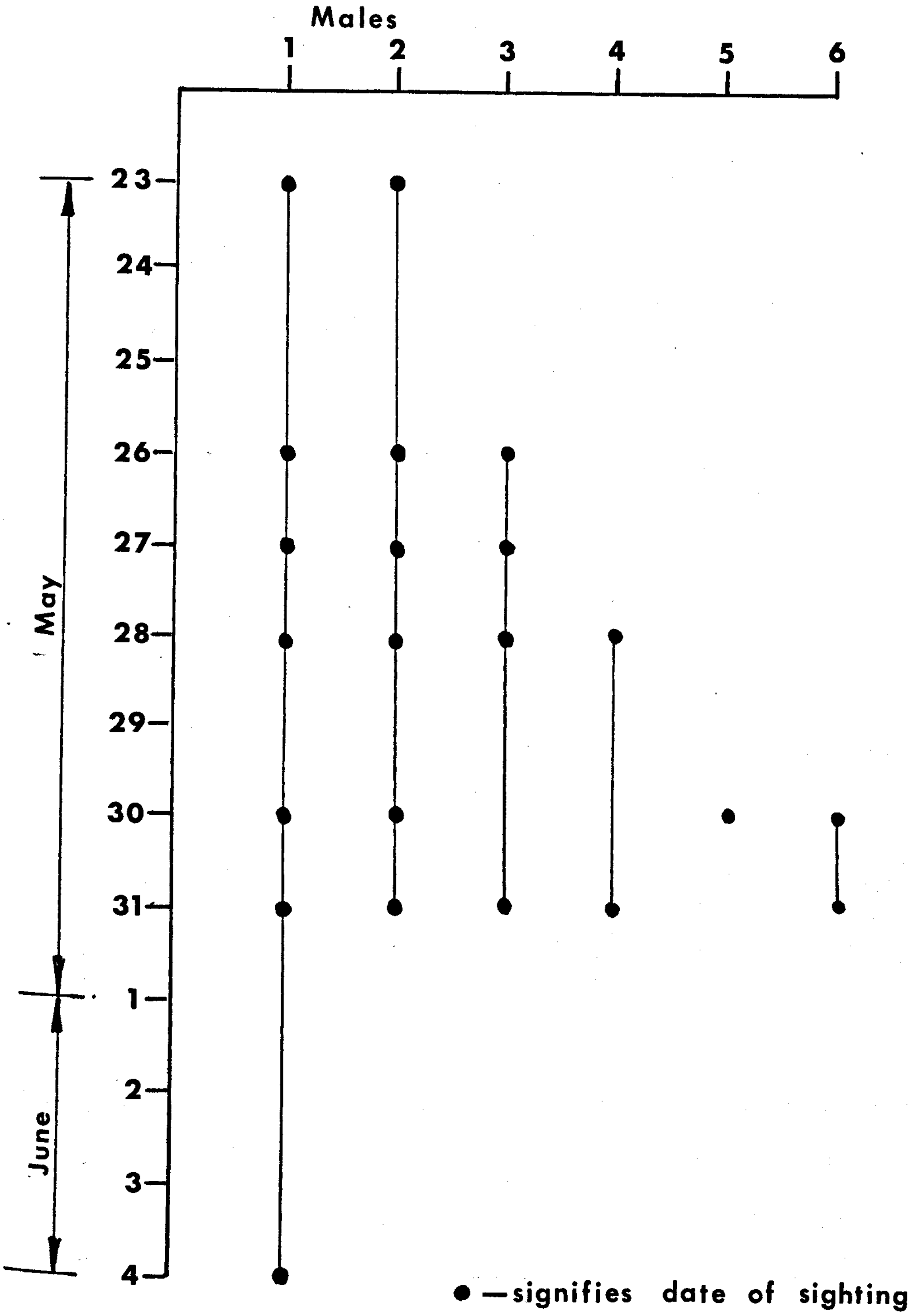


Fig.2:10. Dates of sighting of individuals in lek arena during May and June 1975.

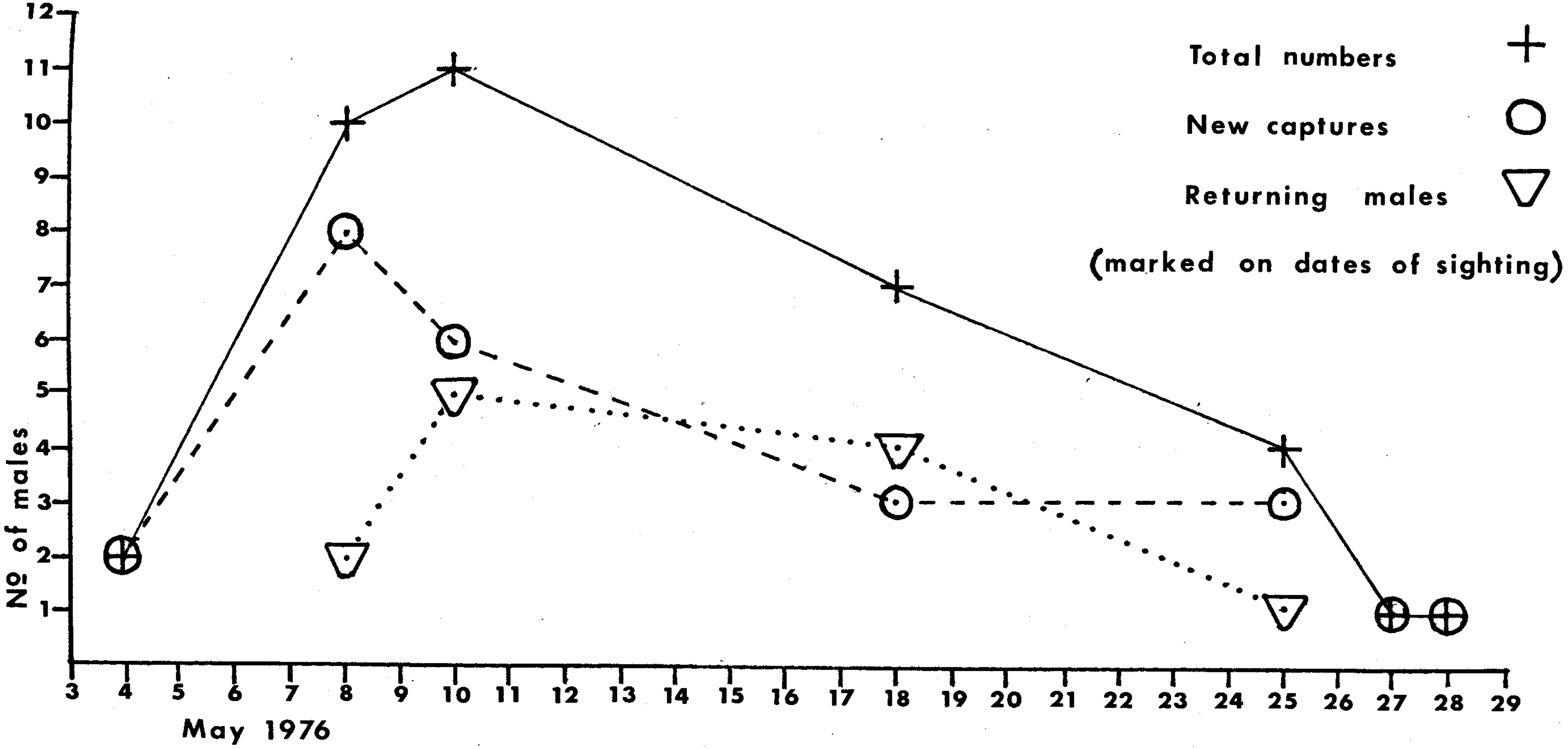


Fig.2:11. Nº of males in lek arena during flight season each day.

of two or three weeks. Also on the days when peak numbers of males were present there was a large number of males entering the area of the lek arena searching for LOPs. These factors must have intensified competition between males in this area.

2.11. Thermoregulation by lekking males.

Males on the lek arena adjusted their body temperature by altering the angle of their bodies to the sun. Occasionally when a male first appeared on the lek arena in the morning it would not chase passing insects for a few minutes. Instead it sat in the sunshine with its dorsal surface at 90° to the incident sunlight, thus exposing as much of its body surface as possible for heating. Once it had warmed up it did not assume this posture as often. On warm days with a shade temperature of about 17°C males were sometimes seen to incline their bodies at an angle to incident sunlight so as to decrease the area exposed to heating. On sunny days with a cold wind when a cloud passed in front of the sun the males crouched in crevices in fence posts and tree trunks or hid in the grass and other low plants to shelter. They restarted lek activity only when it was sunny again.

G. viridis is a conspicuously bristly fly, as is shown in Fig. 2:2, and this may be an adaptation for heat retention. Its flight season is during May and early June in the north-west of England and at this time air temperatures are often quite low and cold winds are frequent. Adaptations of morphology and behaviour for heat conservation are likely to occur together with ones to prevent overheating given the unpredictable nature of the weather.

2.12. Conclusions.

The behaviour of G. viridis fulfils the criteria necessary to establish that its mating system is of the lek type.

1) There is no male parental care.

2) There were mating arenas where the males gathered solely for mating. The locations of the arenas were fixed for at least one breeding season.

3) Males usually established territories based upon conspicuous marker objects which were used as LOPs. Where no marker object was present the boundaries of a male's territory were less clearly defined.

4) The males' territories contained no resources useful to females.

5) The behaviour of the males was primarily directed towards one another for the purpose of territorial defence. Chasing flights were used in territorial defence and for capturing females for mating. Circling flights were highly ritualised flights performed by males as part of inter-male competition. Display flights were ritualised advertisement of a male's presence in an area to other males, there is no evidence that they attracted females.

6) Females came to the lek arena to mate and mating was never seen to take place elsewhere.

7) The area of the lek arena was significantly smaller than the home ranges of both sexes when they were not on the arena.

8) Females probably had the opportunity to select their mates, however no evidence that they did so was obtained.

9) The aggregations were of G. viridis with no other species present on the same lek arenas.

Chapter 3.

THE LEK BEHAVIOUR OF CALLIPHORA ERYTHROCEPHALA MG. (CALLIPHORIDAE).

3:1. Introduction.

C. erythrocephala is the more common of the two familiar bluebottles, the other species being C. vomitoria L. (see Chapter 4). Both species occur from March to October and their habits are similar. Females oviposit on any exposed flesh food as well as on mammal carcases. The males are found basking in the sun on leaves, bare ground, paths and walls. Both sexes feed on carrion and nectar, but males are less frequently found on carrion than females (Colyer and Hammond 1968). C. erythrocephala ranges in length from 6 to 12mm., the males are holoptic and in general are slightly smaller than the dichoptic females. It differs from C. vomitoria in having red jowls with black hairs while those of C. vomitoria are black with red hairs.

C. erythrocephala was studied during 1976 and 1977 around Liverpool where it is apparently much commoner than C. vomitoria.

3:2. Perching and territories.

On sunny days males gathered on sunlit ground, paths and walls. Their perches functioned as look-out-posts (LOPs) from which they chased passing flying insects. The areas where they aggregated formed the lek arenas. Lekking males adopted an "alert posture" when perched, appearing to be watching the surroundings and to be ready for flight. Fig. 3:1 shows a lekking male. In a lek arena each male maintained a minimum separation of about one metre from other males. When a conspicuous marker object formed the LOP, such as a tree, stone, window ledge or post, the male

Fig. 3:1. Male <u>C. erythrocephala</u> in "alert posture".

defended the surrounding area as his territory. After each flight the male returned to the same LOP until he left the territory. When there were no marker objects to use as LOPs males moved around the lek arena changing their perch after each flight.

Where there were large amounts of refuse with many females present very many males were often found. The high density of males in these areas resulted in them perching in any unoccupied spot and not maintaining a minimum separation or having territories. Males moved around the areas continually, often chasing each other in a swarm. Males did not perch on the food or oviposition materials in the refuse which attracted the females but perched close to the refuse.

Males arrived in the lek arenas at between 8 and 9a.m. in May and June. They initially basked in the sun with their bodies tilted so as to expose the maximum area for heating. After warming up flight activity began. Lekking ceased at about 7p.m. in May and June.

When perched on their LOPs males generally remained stationary between flights. Occasionally they turned or walked short distances. Preening took place between flights..

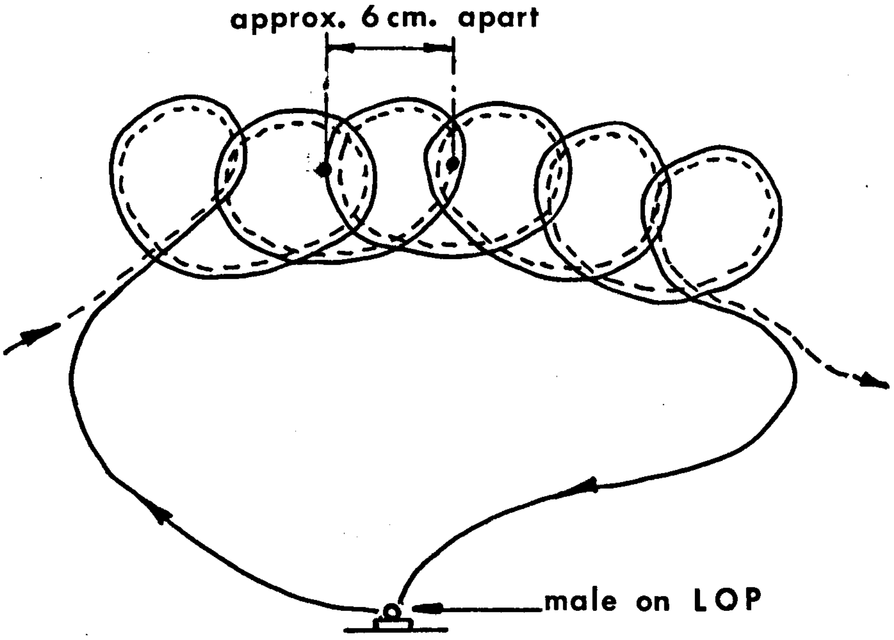
3:3. Flight activity of lekking males.

a) Chases. Flying insects passing within about 60cm. of a male were chased if they were of roughly the same size and speed of flight as *C. erythrocephala*. Such insects were usually muscids and other calliphorids occurring in waste places and gardens as well as conspecific individuals. Small stones thrown past a male were also chased. In a chase a male flew up to and briefly investigated the insect, flying close to it. Insects were chased for distances of up to 4m. from the LOP. Males chased and mounted females in flight in mating attempts. When conspecific males were chased a circling flight by the pair sometimes occurred (see below). The duration of chases from take-off to landing ranged from 0.6 to 4.2s., the mean was 1.54s., S.E. = 0.10s., N = 60.

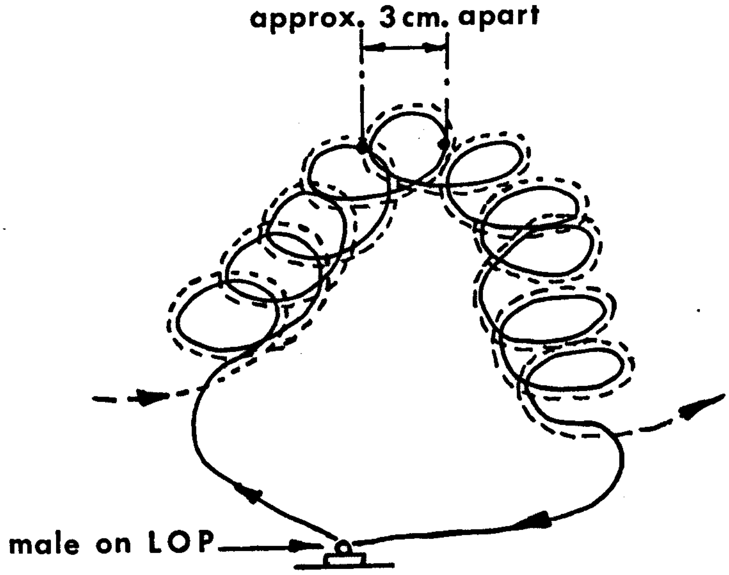
b) Circling flights. These interactions took place only between males when one chased another. The males chased each other in a circular course about 5 to 8cm. apart moving sideways and sometimes up and down or circled facing each other about 3cm. apart, rising and falling in flight. When males circled facing each other they often butted their heads together in flight. Fig. 3:2 shows the forms of circling flight. During a circling flight males occasionally grappled and then fell to the ground locked together by their legs.

In the longer of these interactions the circling parts of the flight were interspersed with chases of one male by the other. Very rarely circling flights took place with males of other species, such interactions did not last very long. Males flew up to 4m. from their LOPs in circling flights. The duration of these interactions from take-off to landing ranged from 1.0 to 25.0s., the mean was 4.44s., S.E. = 0.55s., N = 50.

c) Display flights. These flights usually took place with no apparent external stimulus, but sometimes appeared to be in response to a passing insect. A male flew up from his LOP to a height of about 30cm. and then descended in a spiral back to the LOP (see Fig. 3:3). Display flights by one male sometimes



(a) Pursuit type of circling flight.



(b) Facing type of circling flight.

Fig. 3:2. Forms of circling flight.
(view from above)

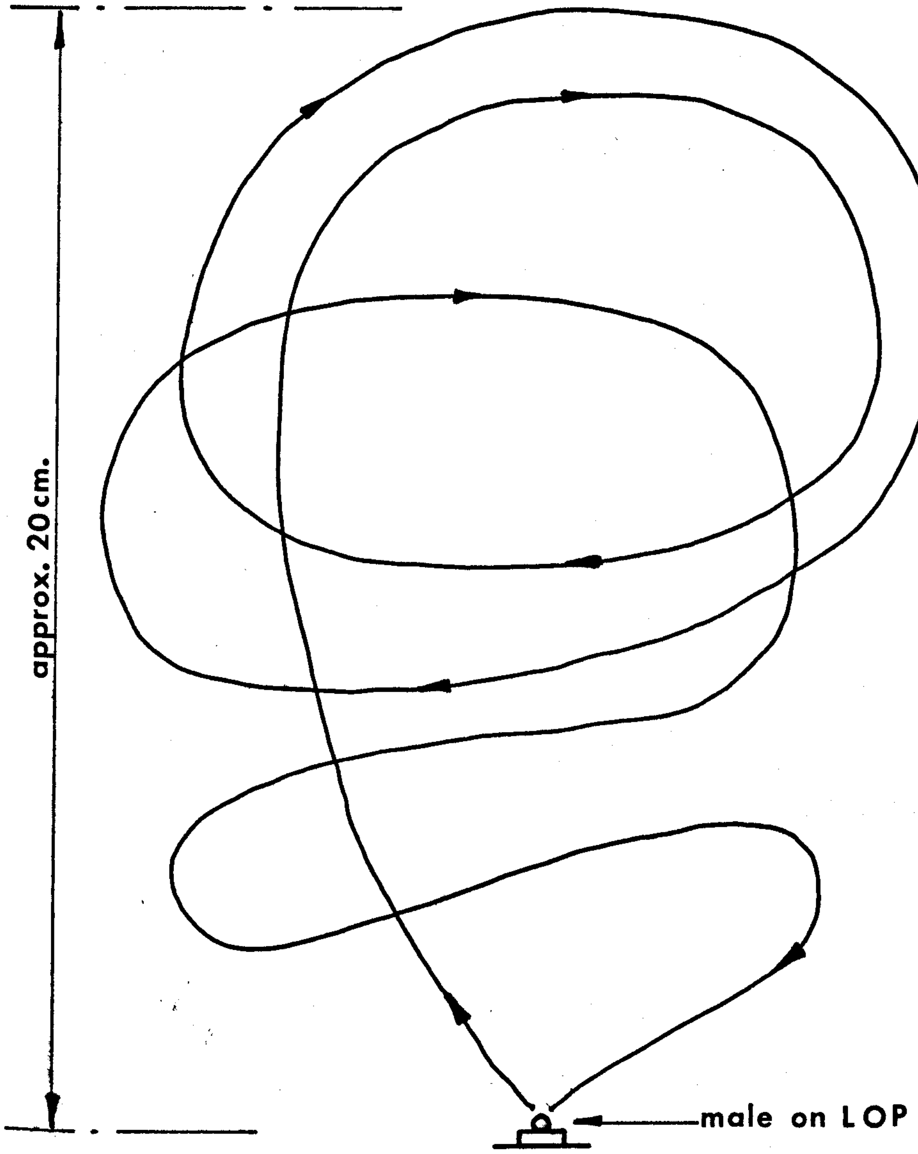


Fig.3:3. Form of typical display flight.
(side view)

resulted in a nearby male chasing the displayer. The duration of display flights from take-off to landing ranged from 0.5 to 3.9s., the mean was 0.96s., S.E. = 0.08s., N = 60.

3:4. Identification of individuals.

Males were identified by means of the naturally occurring wing damage many of them showed. Each male's pattern of notches and tears was unique and readily separated him from others. By identifying individuals it was possible to determine how long a male stayed in a territory and the outcome of males intruding in occupied territories.

3:5. Territorial defence.

Where territories were present males were never seen to share them. Territorial males were always at least one metre apart. If a male perched in the territory of another interactions between the pair occurred in flight and they separated. In most cases (20 out of 24 observed) the original male remained in the territory and the intruder left, in the other four cases the intruder stayed and the original male left. Usually separation took place after one interaction, the mean number of interactions before separation was 1.38, S.E. = 0.16, N = 24 (see Fig. 3:4).

Most potential intruders would be intercepted before they could perch in an occupied territory so the estimate of successful territorial defence above is probably low. Intruders may have had interactions with territorial males before they perched in occupied territories also, this would lower the estimate of successful defence.

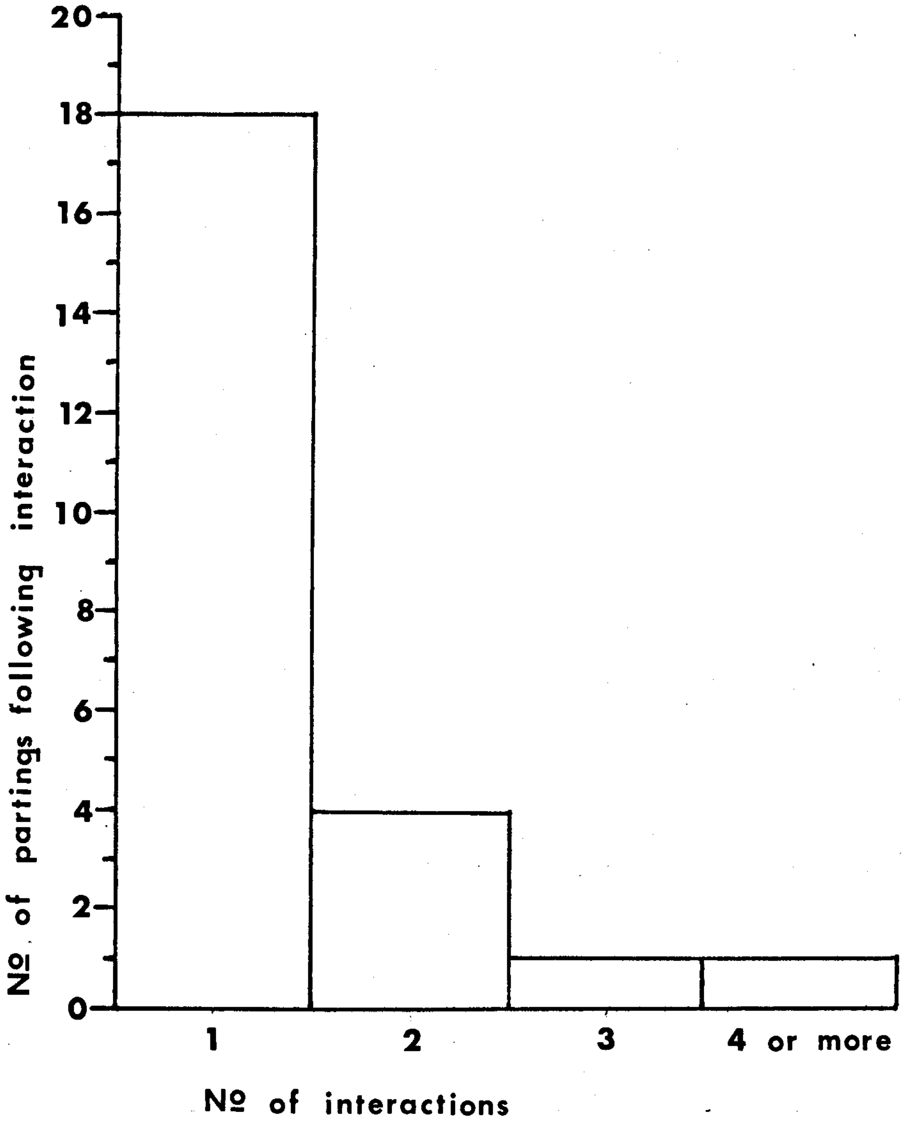


Fig.3:4. Number of interactions before males parted.
(24 series of interactions observed)

3:6. Female behaviour and copulation.

Females were found feeding on flowers, carrion and dung and around rubbish piles and ovipositing on carrion and exposed flesh foods. Females were seen to perch in lek arenas.

Males chased females flying in lek arenas and caught and mounted them in flight. Females often rejected mating attempts by males and flew away after being briefly mounted. When males were successful the pair flew down onto a convenient object to complete copulation. The copulatory position was the "male vertical pose" (Lamb 1922). Other males were never seen to interfere with copulating pairs.

3:7. Conclusions.

C. erythrocephala fulfils the criteria necessary to establish that its mating system is of the lek type.

1) There is no male parental care.

2) There were mating arenas where males gathered solely for mating. These locations were used for at least one breeding season.

3) Males established territories based upon LOPs on marker objects where such objects were present. Where no markers were present males maintained their separation by a minimum distance. Only under conditions of very high density of males in a small area did this system break down due to the impossibility of territorial defence and maintaining separation.

4) The males' territories and lek arenas contained no resources useful to females.

5) Most of the males' behaviour was directed towards other males. The circling flight is a highly ritualised flight used

in inter-male competition and the display flight is a ritualised advertisement of a male's presence in an area to other males, there is no evidence that they attracted females.

6) Females came to the lek arenas to mate and all mating takes place on the lek arenas as far as is known.

7) The area of the lek arenas is significantly smaller than the home ranges of both sexes when they are not on the arenas.

8) Females probably had the opportunity to select their mates, however no evidence that they did so was obtained.

9) The lekking aggregations of C. erythrocephala contained no other species mixed with them.

Chapter 4.

LABORATORY OBSERVATIONS ON CALLIPHORA VOMITORIA L. (CALLIPHORIDAE).

4:1. Introduction.

C. vomitoria is one of the two common species of blue-bottles, the other being *C. erythrocephala* Mg. the behaviour of which in the wild state is described in Chapter 3. *C. vomitoria* was used for the laboratory studies because it was easily available in large numbers by raising maggots sold for fish bait. The adults are quite large (8.5 to 14mm.) allowing them to be easily marked with aluminium paint for identification purposes. Both species of *Calliphora* show similar lekking behaviour in the natural state making the use of *C. vomitoria* for laboratory study appropriate.

It was soon found that under certain conditions lekking behaviour was shown in the laboratory. In the laboratory it was easier to observe some aspects of lek behaviour than in the field.

4:2. Materials and methods.

Larvae were allowed to pupate and then were sexed on emergence and the sexes housed in separate cages. The flies were fed on marmite, sugar and water soaked into cotton wool supplied *ad lib.* in separate petri dishes. Under laboratory conditions the flies became sexually mature in about five days. Mature flies were transferred to the observation cage as needed.

Each male in the group in the observation cage was marked with aluminium paint so as to be individually identifiable. The marking was done during transfer between cages after etherising the fly. A pattern of dots and dashes enabling individual identification was painted on a male's thorax and then the fly was allowed to recover in the observation cage. No adverse reaction to the marking procedure was ever seen.

The dimensions of the observation cage were 1.2m. by 0.6m. by 0.6m., it was covered with netting on the top and on three sides and with transparent cellulose acetate on the front, the floor was of hardboard. Food and water was supplied ad lib. as in the maturation cages. Fig. 4:1 shows the observation cage. A raised look-out-post (LOP) was often placed in the cage. The males used this LOP as a perch as they used conspicuous objects in the wild. The LOP was made by placing a white polystyrene tile about 8cm. by 8cm. on top of a 500ml. beaker about 12cm. high.

At any time twelve marked males were in the observation cage. Males aged between one and four weeks were used for the observations because older males often had considerable damage to their wings and had some difficulty in flying. For observations on male-female behaviour ten mature females were put into the cage.

Observations were carried out on sunny days between October and May because the flies were usually inactive unless sunlit. Occasionally they were active on dull days.

Observations on the males' behaviour were made following an artificial sunrise produced by removing a black plastic sheet with which the cage had been covered overnight.

4:3. General features of lek behaviour.

Males perched on the floor of the cage, on the side netting and on the raised LOP when it was present. Males were almost always at least 15cm. apart, except when more than one was perched on the raised LOP. From their perches the males chased other

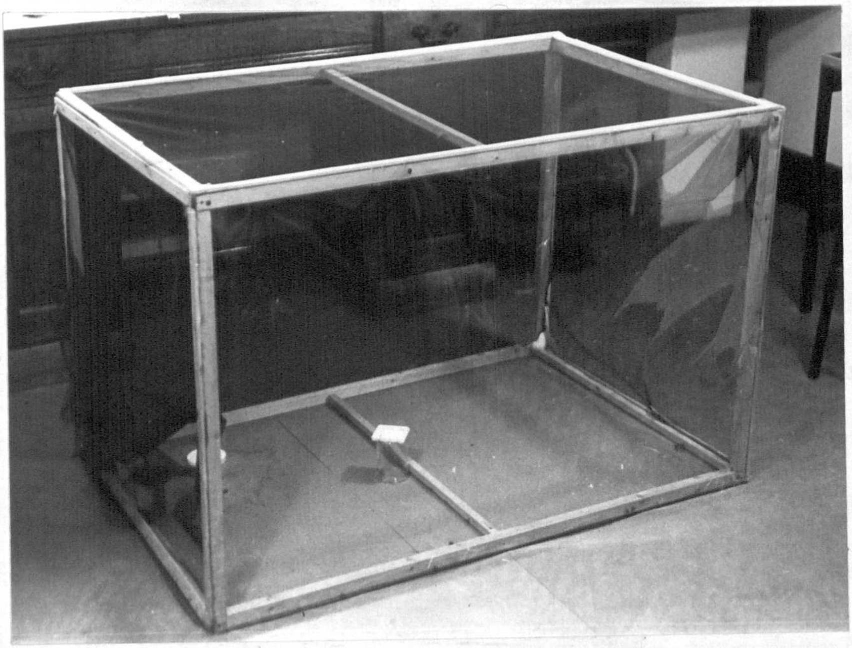


Fig. 4:1. The laboratory observation cage for C. vomitoria.

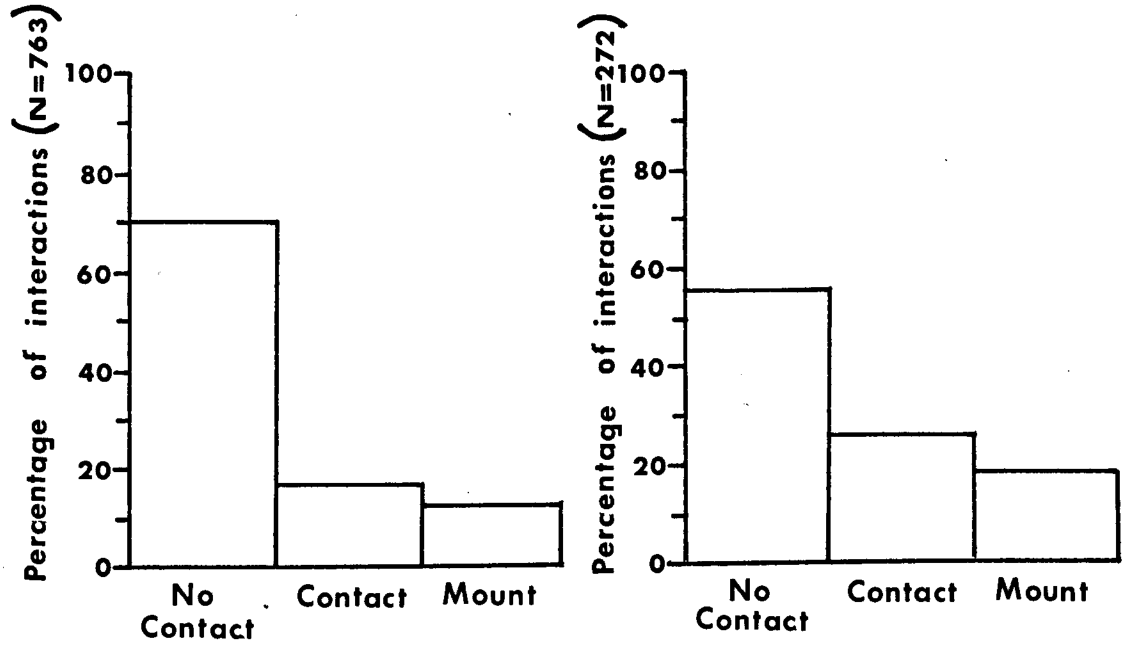
males flying by and females flying by when they were in the cage. Males actively maintained their separation by interacting mainly during flight. The presence of an object higher than the cage floor acting as a marker resulted in the males competing to perch on it. Active males perched in an "alert posture".

4:4. Flight activity of lekking males.

a) Chases. Males chased other males and females around the cage. The male flew from its LOP to pursue the insect flying past, the insect was then briefly investigated and sometimes mounted or merely touched by the male. After a chase the male returned to its LOP. Chases took from 0.5 to 5.0s., the mean was 1.9s., S.E. = 0.21s., N = 85.

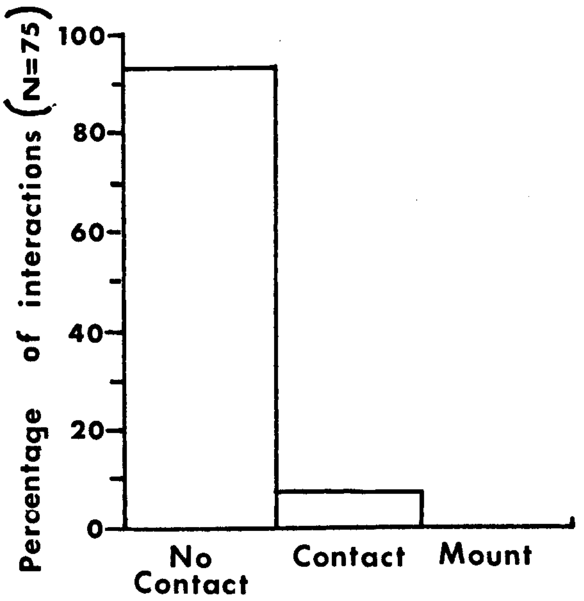
The outcome of male-male chases was significantly different from that of male-female chases. Males chasing females were much more likely to make contact with them by touching them or by mounting them. Contact between the chaser and chased always took place during flight. Fig. 4:2 shows the outcome of chases of males and females. The differences between male-male and male-female chases was significant, chi-squared = 20.79, P less than 0.1%, df = 2. These differences probably are due to females being generally bigger than males and so slower in flight rather than rapid sexual recognition of females by males. Males would cease to chase females before making any contact although the females were virgin and there seemed to be no reason why the males should not catch them.

b) Circling flights. These flights were performed only by



Male-male chases

Male-female chases



Male-male circling flights

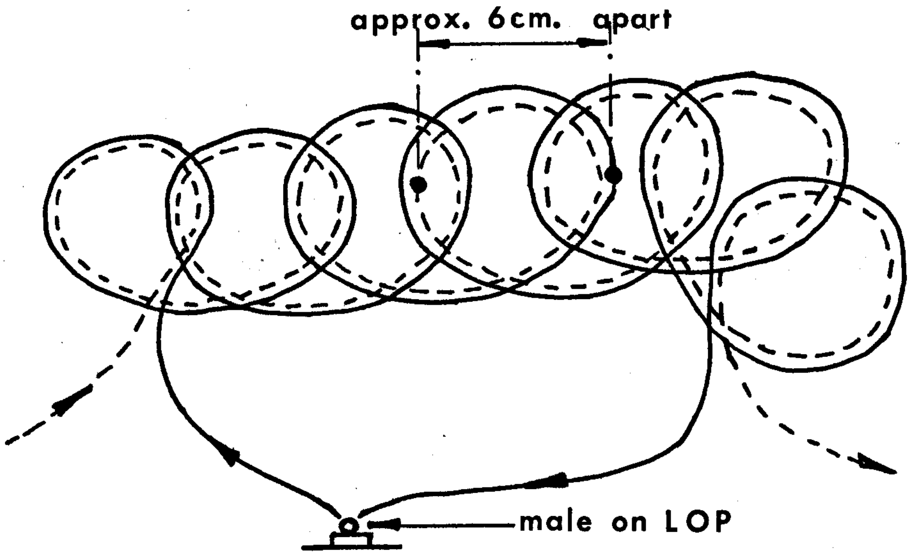
Fig.4:2. Outcome of male-male and male-female interactions.

males. The interactions began as a chase of one male by another then the males circled either in pursuit of each other 5 to 8cm. apart or facing each other about 3cm. apart. During circling flights the males often ascended or descended as they flew around the cage (see Fig. 4:3). Circling flights took from 0.9 to 8.0s., the mean was 2.55s., S.E. = 0.36s., N = 51.

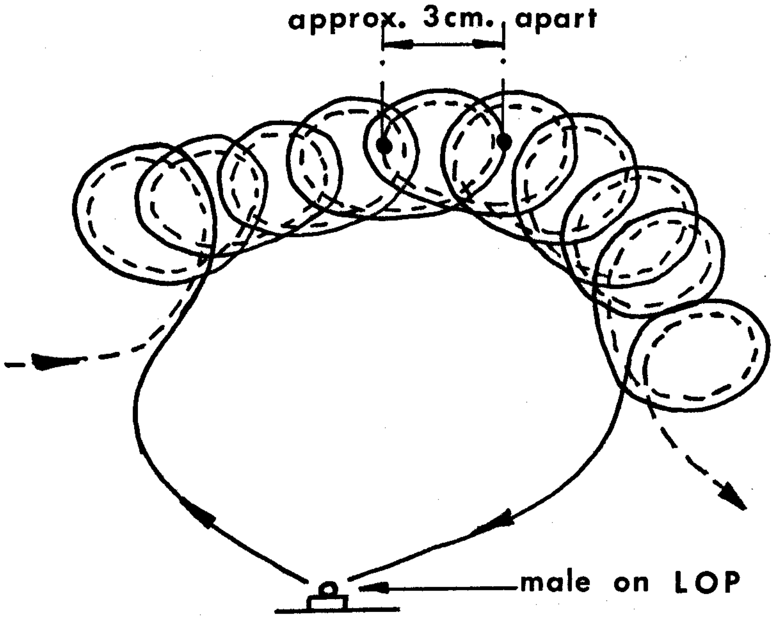
Circling flights usually ended with the males separating and perching individually. Occasionally the males made contact in flight but did not mount each other. Very rarely following contact the males fell to the floor in a tussle, grappling with their legs before separating. The difference between male-male chases and circling flights in the number of times contact or mounting took place was found to be significant, chi-squared = 18.2, P less than 0.1%, df = 1 (see Fig. 4:2).

c) Display flights. Most flights of this type were performed in the absence of any external stimulus for flight. A male on its LOP took off and flew upwards and then descended in a spiral back to its LOP. The form of a typical display flight is shown in Fig. 4:4. The duration of display flights with no external stimulus ranged from 0.5 to 9.5s., the mean was 3.0s., S.E. = 0.37s., N = 66. 23.8% of display flights with no external stimulus resulted in the displaying male being chased by another male (N = 155).

Display flights were also performed in response to a passing male or female. The male flew up but did not chase the flying insect. These flights differed from the display flights performed with no external stimulus in varying from a very short flight up



(a) Pursuit type of circling flight.



(b) Facing type of circling flight.

Fig.4:3. , Forms of circling flight.
(view from above)

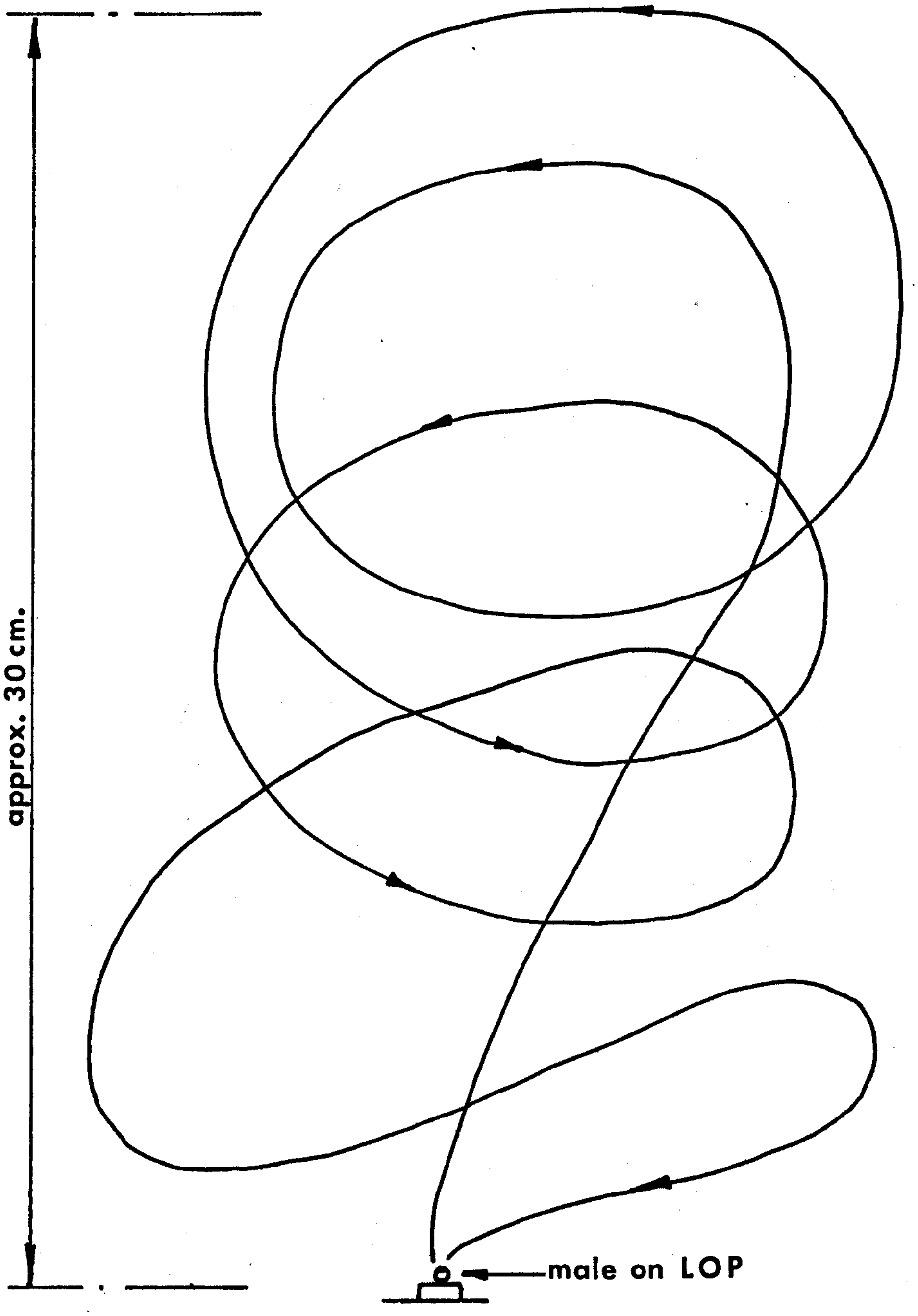


Fig.4:4. Form of typical display flight.
(side view)

from and down to the LOP to the longer display flights described above. The duration of these flights ranged from 0.3 to 7.8s., the mean was 1.7s., S.E. = 0.22s., N = 62.

There was a significant difference between the duration of display flights performed in the absence of an external stimulus and those performed in response to a passing fly, P less than 0.1%, t = 3.92, df = 127. This difference must result from the different circumstances in which the flights were performed and indicates that in the absence of other flies flying past males may advertise their presence by longer display flights than when males see other flies nearby.

4:5. The influence of a marker object on male behaviour.

By placing a beaker with a piece of polystyrene tile on top of it on the floor of the cage it was possible to simulate the presence of a conspicuous marker object. Such markers are often used as LOPs in the natural state by male *Calliphora* which perch on stones, tree trunks and posts. The presence of the object had a distinct effect on the males' behaviour.

a) Behaviour with no marker object in the cage. Males perched around the floor of the cage and on the netting and showed no preference for any particular site. After a flight a male perched in a spot unoccupied by other males rather than at the same place it had taken off from. This resulted in the males being more or less evenly spaced around the cage when a number of them were active. Usually males were no closer than 15cm. to each other. If two males were closer than this then following 76.5% of interactions in flight between them the males perched further apart (see Fig. 4:5). The number of interactions between males before they separated ranged from one to four, the mean was 1.33, S.E. = 0.08, N = 60 (see Fig. 4:6).

With no marker object in the cage there was no indication that males defended specific parts of the cage as territories.

b) Behaviour with the marker object in the cage. Males perched on the marker object in preference to elsewhere in the cage. They also perched on the floor and netting but only when the marker object was occupied by another male. Males competed to occupy the object and once a male was perched on it he remained there for some time. The mean duration of occupation was 21.0min., the range being from 6 to 62min., S.E. = 2.0min., N = 55. Males left the object to feed or mate and sometimes were unable to return to it because another male had occupied it in their absence.

As a result of the inter-male competition for occupation of the object the presence of more than one male on it did not usually result in the males interacting and separating almost at once, unlike when two males were close together in the absence of the marker object. In the majority of interactions in flight between two males occupying the object no separation resulted (62.8% of interactions, see Fig. 4:5). The number of interactions between males before one left the object, if one did go, ranged from one to eight, the mean was 1.74, S.E. = 0.14, N = 68 (see Fig. 4:6).

When a male on the marker object was joined on it by a second male then usually the second male left after interacting in flight with the occupying male, this occurred in 65% of observations.

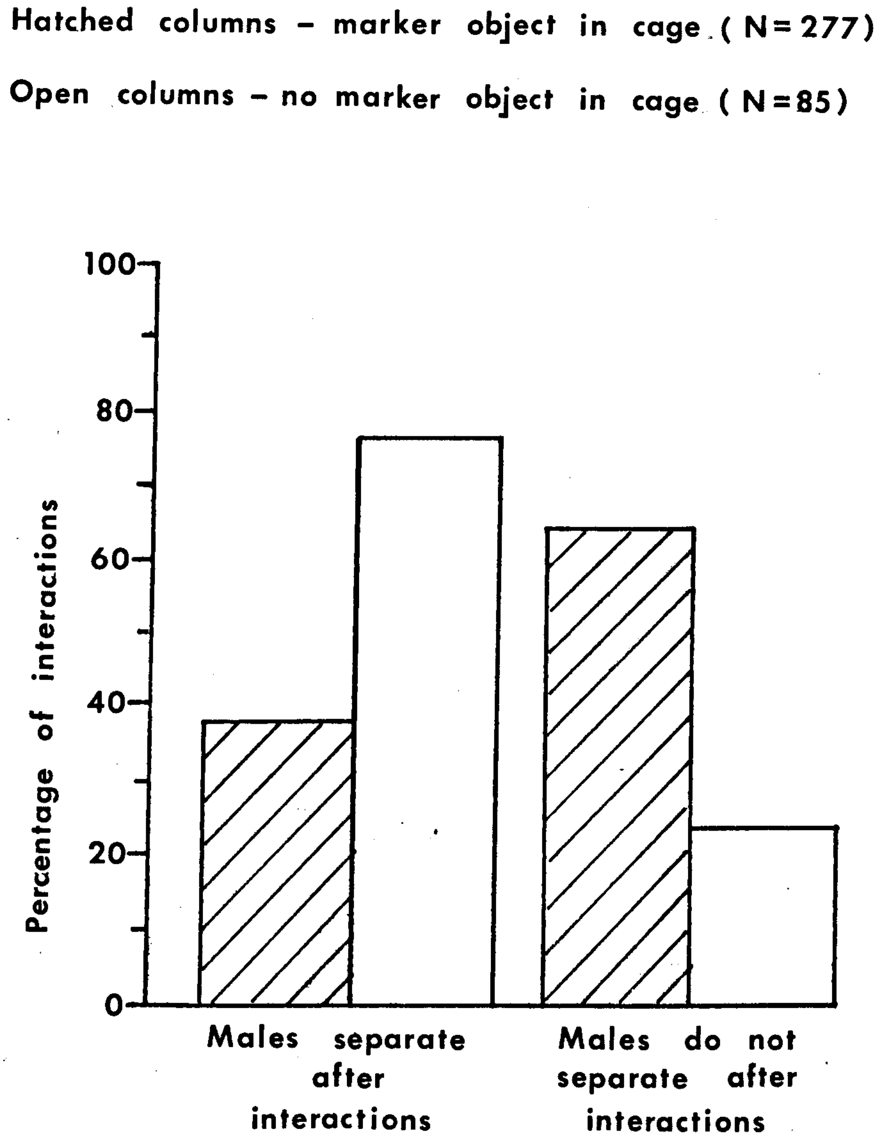


Fig.4:5. Influence of a marker object on male behaviour a) separation by males.

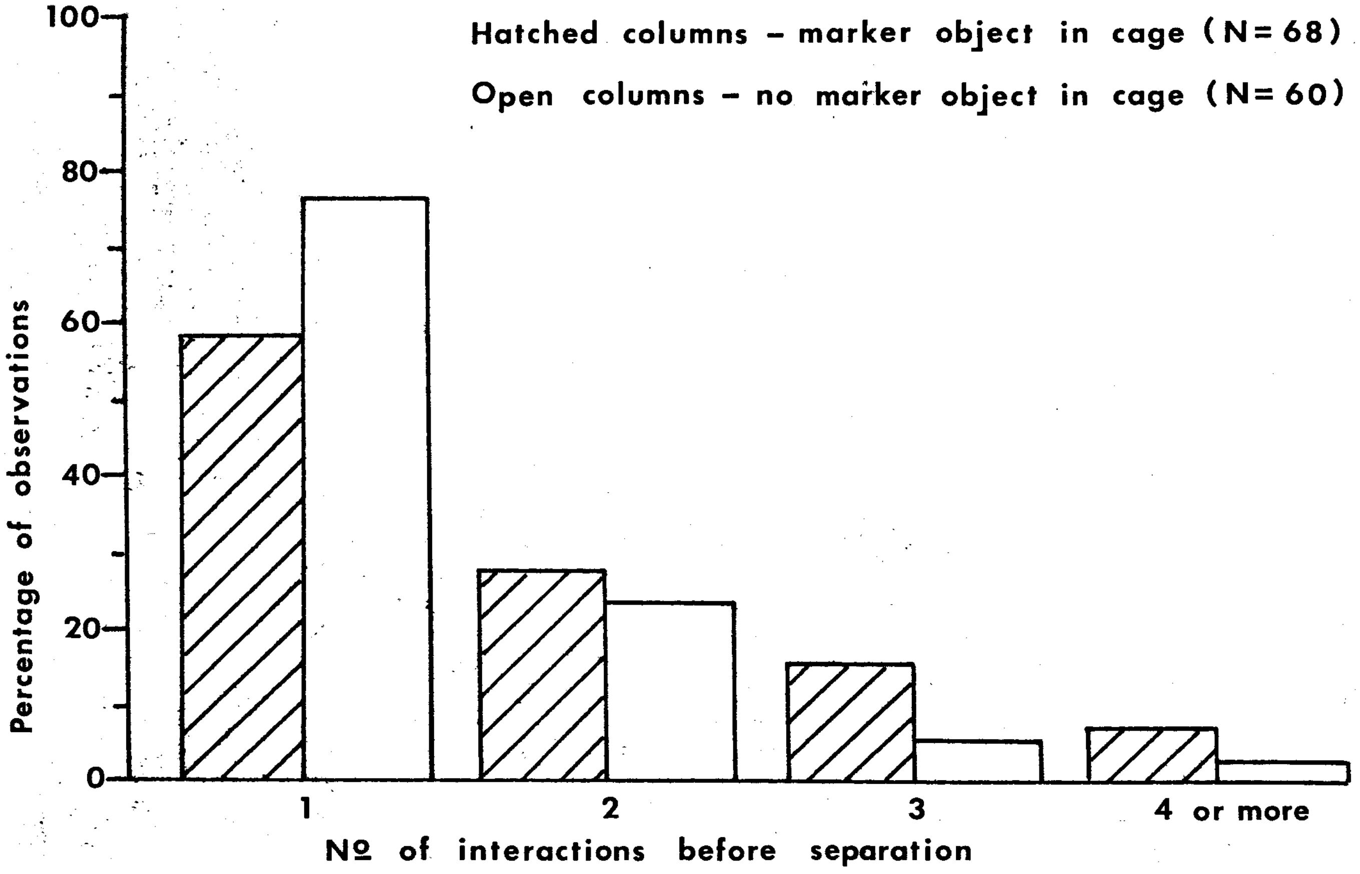


Fig.4:6. Influence of a marker object on male behaviour b) interactions before separation.

The chances of the occupying male leaving or of both males staying were roughly the same (see Fig. 4:7). The bias towards the male occupying the object staying indicates the effect of the marker object in producing territorial defence of it by males. This effect of the object is further shown by comparing the number of times males separated following an interaction in flight and the number of interactions before they separated, when they did, in the two cases of the presence and absence of the marker object. Fig. 4:5 shows the percentage of interactions resulting in separation and shows that males perched on the marker object were much less likely to separate than males perched close together elsewhere in the cage. The mean number of interactions in the two cases were significantly different, t = 2.42, df = 126, P between 2% and 1%. 1.74 interactions before separation was the mean when two males were on the object, 1.33 was the mean for males elsewhere. Fig. 4:6 shows the number of interactions before separation in the two situations.

4:6. Differences between males in lekking activity.

As stated in the materials and methods section it was possible to produce by sudden illumination an artificial rapid sunrise. This technique resulted in many of the males becoming active soon after illumination and starting to perform lek behaviour.

The flies were then observed continuously for the next two hours. After this time only one or two males were still active and these individuals remained alone in their lekking for the rest of the day. During the two hours the number of active males was counted every five minutes and individual males were scored

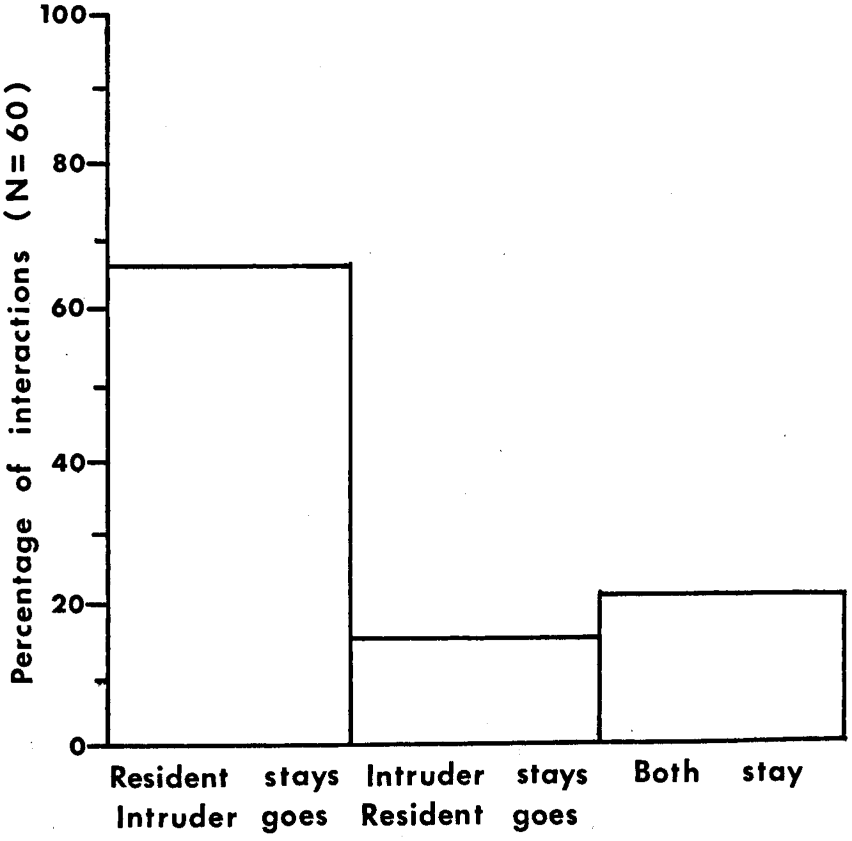


Fig.4:7. Results of an intruder male joining a resident male on the marker object.

as active or inactive for each half hour period of the two hours. The number of active males was greatest in the first five minutes after illumination and then gradually declined as is shown in Fig. 4:8. On 15 of 19 days of these observations the last male or males still lekking after two hours remained active for the rest of the day. On the other four days two of the last three lekking males had been active all through the period since illumination. Males rarely joined the group of lekking males after the first half hour of activity.

Males varied greatly in the amount of time they were active and lekking, as measured by the number of half hour intervals in which they were recorded as active. The male most frequently recorded as lekking appeared five times as often as the male recorded least (see Fig. 4:9). The males which appeared most active on the basis of the number of half hour periods in which they were recorded also were those most often still active after two hours activity following illumination, this measure of the males' relative activity is shown in Fig. 4:10. Taken together this data indicates considerable differences in the behaviour of individual males in lekking, some males were much more persistent lekkers than others.

Competition between males must have caused the observed differences in the number of times individuals were recorded as active. Males which ceased to be active did so because other males had outcompeted them, perhaps by showing more persistence or aggression in inter-male interactions. It was noticeable that a small amount of wing damage in the form of tears and notches did not affect the activity of the males, although such damage must have

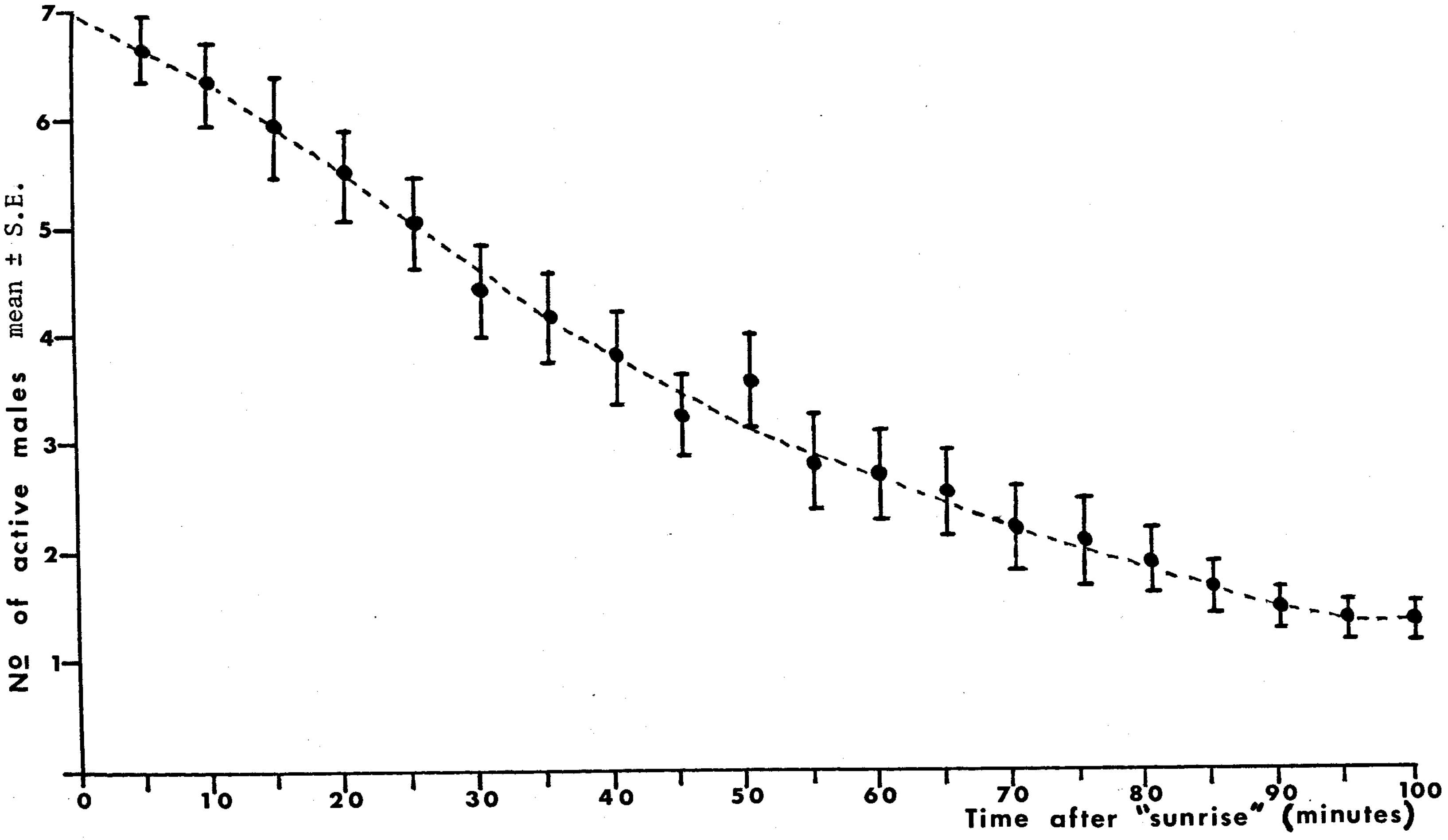


Fig.4:8. Decrease in number of active males with time. (20 days observations)

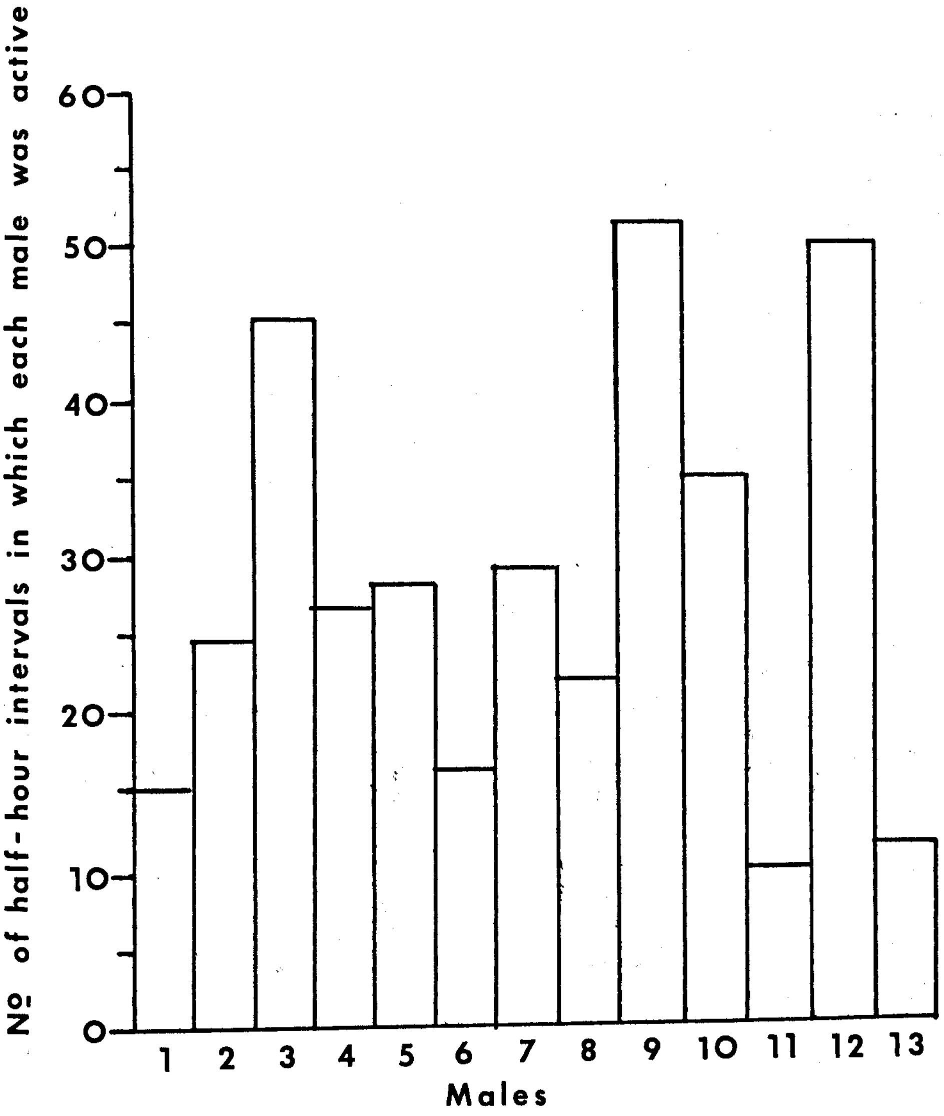


Fig.4:9. Lekking by individual males in a group of 13 during the first 2 hours observations.

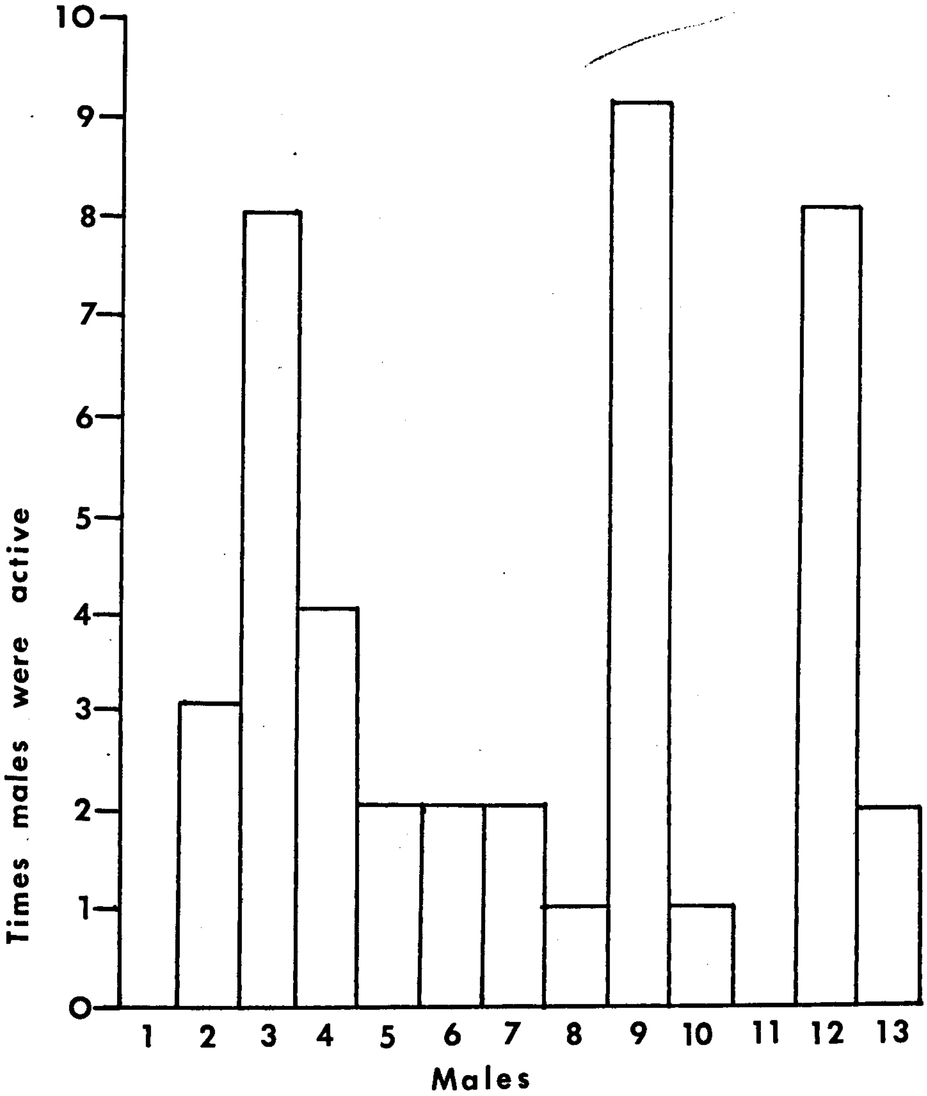


Fig.4:10. Number of times when each male was still active after 2 hours.

had some slight effect on a male's manoeuverability. This indicates that small differences in manoeuverability between males did not decide the outcome of interactions in flight between them.

Removal of those males which were most persistent at lekking and therefore the dominant males resulted in some of those males which usually ceased activity early continuing to lek and taking the places of the removed males. Thus some males refrained from lekking until there was less competition.

The intense competition between the males resulted from the size of the cage which was smaller than the area usually defended by one male Calliphora as a territory in the wild state.

4:7. Female behaviour and copulation.

Females flying around the cage were chased by lekking males. Capture by a male and mounting preceding mating always took place in flight. The pair then flew in tandem and perched, if the female was receptive genital contact followed. Non-receptive females prevented genital contact by bending the tip of their abdomen downwards and at the same time vibrating the wings.

Copulation lasted about half an hour, the copulatory posture was the "male vertical pose" (Lamb 1922).

No attempts were made by males to mate feeding females or resting females. Only flying females were approached for mating purposes. Since females were confined in a relatively small cage with sexually active males the males could easily have searched for females in order to mate with them. That this did not happen indicates that males do not use this method of mate acquisition even when it would be relatively easy to find and attempt mating with a number of females quickly. It also is evidence that females obtain mates by flying past lekking males and do not wait to be found by males.

4:8. Conclusions.

Males of *C. vomitoria* showed lek behaviour under suitable laboratory conditions as they and males of *C. erythrocephala* did in the natural state.

1) When the marker object was in the cage males established a territory centred on it as they did on marker objects in the wild.

2) The males did not base their territories on the food present in the cage, thus they exhibited non-resource based territoriality.

3) As in the wild most male activity was directed at other males. Circling and display flights were performed as highly ritualised parts of lek behaviour. Inter-male circling flights provided males with rapid sexual recognition as shown by the observation that males never mounted one another after these flights. Males did mount other males after chasing them. Males chased other males performing display flights indicating that display flights advertise the presence of an active lekking male in an area to other active males.

4) Females probably had the opportunity to select their mates, however no evidence that they did so was obtained.

5) All mating took place between lekking males and females they had chased and caught in flight. The meeting of the sexes occurred as it did in the wild showing that this must be the only

mating system in these species of *Calliphora*.

6) Sexual identification of other individuals by chasing males apparently occurred only when they were very close to or in contact with them, except in the case of inter-male circling flights. Both males and females were chased and mounted. There is therefore no evidence for any sex attractant pheromone emitted by females in order to obtain mates. The response of chasing a flying insect, basic to the mating system of *Calliphora*, is caused by the movement of the insect and not by a pheromone produced by it.

Chapter 5.

THE LEK BEHAVIOUR OF LUCILIA CAESAR L. (CALLIPHORIDAE).

5:1. Introduction.

L. caesar is a very common green bottle found from May until October in woods, waste ground and gardens. The larvae feed in animal droppings and carrion. Adults are bright metallic green in colour, ranging from 5.5 to 10mm. in length. They feed on flowers, sucking the nectar, animal droppings and carrion. The males are holoptic and the females dichoptic.

During July and August 1976 L. caesar was observed on various pieces of waste ground in Liverpool.

5:2. Perching and territories.

Lek activity took place only on sunny days. Males began activity early in the morning and continued until an hour or so before sunset. The maximum number of males was active between 9a.m. and 7p.m., but others were active before and after these times.

Lekking males perched in sunlit areas on waste ground. The lek arenas were usually in places where there was vegetation consisting of various wild flowers such as willow herb (Epilobium spp.) and ragwort (Senecio spp.) on which the flies fed. Males adopted look-out-posts (LOPs) on various objects such as stones, walls and leaves from which they chased passing insects. LOPs were never on flowers visited by feeding females. LOPs occurred from a few centimetres above the ground on stones to about one metre high on walls. They were always in places giving a male a good view of his surroundings.

The area around an LOP was defended against intrusion by conspecific males by its occupier and formed the occupant's territory. Frequently territories were shared by two males and rarely by three. Fig. 5:1 shows a low wall among vegetation that was frequently used as a LOP. The time spent in a territory was very variable, ranging from 2 to 63min., the mean being 14.7min., S.E. = 2.7min., N = 31.

When perched on LOPs males adopted an "alert posture", giving the impression of watching the surroundings and being ready for flight. Fig. 5:2 shows a male perched on a LOP. Between flights males generally reained stationary, occasionally they turned or walked short distances. They also preened while perched.

5:3. Flight activity of lekking males.

a) Chases. Insects of roughly the same size and speed of flight as L. caesar were chased if they passed within about 60cm. of a male. In areas of waste ground most flies were L. caesar and various calliphorids, muscids and sarcophagids. All of these flies were chased. Small stones thrown past lekking males were chased. In a chase a male flew up to and briefly investigated the insect flying close to it. Chases of conspecific males often resulted in circling flights by the pair (see below). Chases of females were sometimes seen to result in the male capturing and mounting the female in flight and subsequently mating with her.

Males chased insects for distances of up to 2m. from their LOPs. Following a chase males returned to their LOPs. The duration of chases from take-off to landing ranged from 0.5 to 3.6s., the

Fig. 5:1. Wall used as LOP by L. caesar.

Fig. 5:2. Male L. caesar in "alert posture".

mean was 1.3s., S.E. = 0.1s., N = 50.

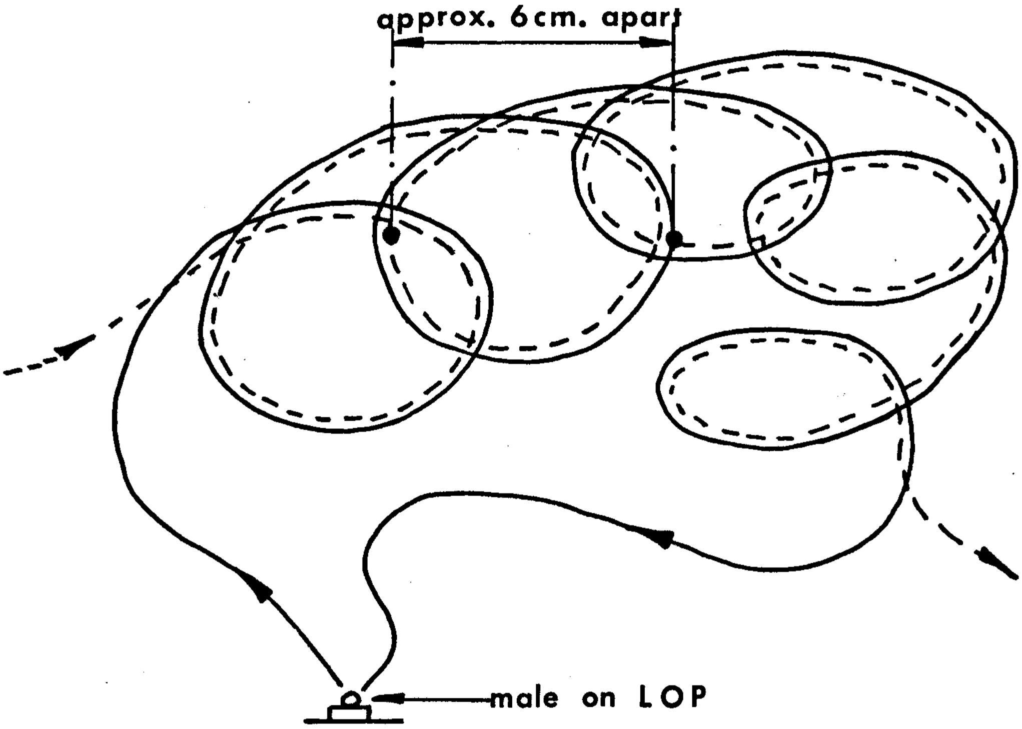
b) Circling flights. In these interactions a pair of males either circled around facing each other 1 to 2cm. apart, usually rising and falling in flight, or pursued each other in a circular course about 6cm. apart as they flew from side to side. These forms of flight are shown in Fig. 5:3. When males flew facing each other they often butted their heads together during flight.

In circling flights with intruder males resident males flew up to 50cm. from their LOPs. If two males were perched close together they usually moved less than 30cm. from their LOPs. Circling flights were performed only with other conspecific males.

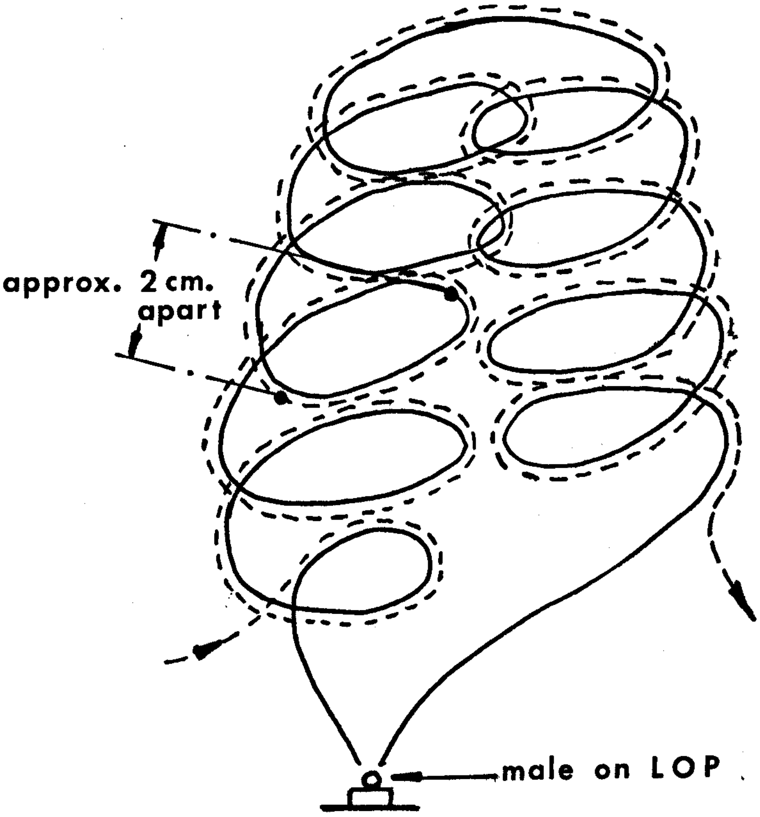
The duration of circling flights from take-off to landing ranged from 1.0 to 9.8s., the mean was 3.7s., S.E. = 0.3s., N = 50.

c) Display flights. These flights were generally performed in the absence of any apparent external stimulus. Males flew up to about 30cm. above their LOPs and then descended in a spiral back to the LOPs (see Fig. 5:4). Display flights also appeared to be performed occasionally in response to passing insects. When two males were perched close together a display flight by one resulted in the other chasing it almost always. The duration of display flights from take-off to landing ranged from 0.2 to 1.0s., the mean was 0.5s., S.E. = 0.03s., N = 50.

The percentage of each type of flight performed by a male depended on whether he was alone in a territory or shared it with another male. A lone male performed mostly chases with a smaller



(a) Pursuit type of circling flight.



(b) Facing type of circling flight.

Fig. 5:3. Forms of circling flight.
(view from above)

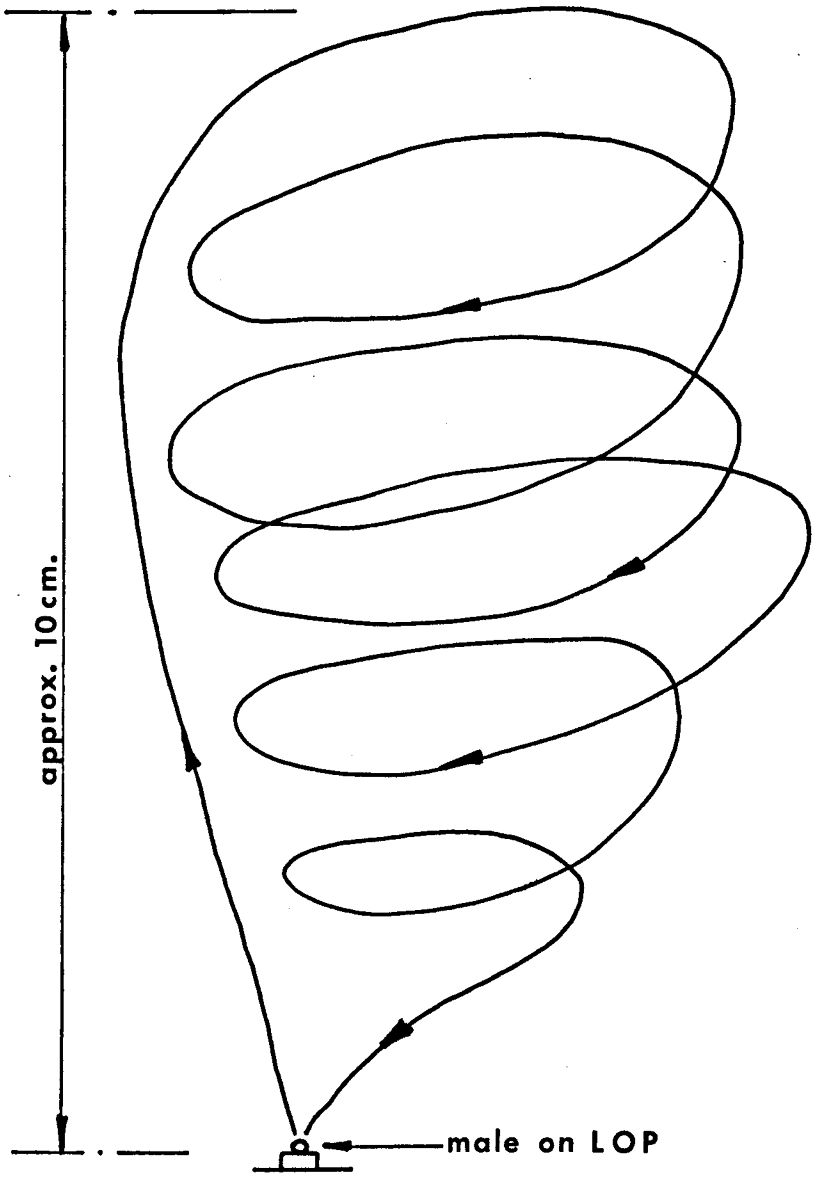


Fig.5:4. Form of typical display flight.
(side view)

number of display flights and far fewer circling flights. When two or more males were together almost all flights resulted in circling flights by the males. Fig. 5:5 shows the percentages of each type of flight performed by males in the two situations.

5:4. Identification of individuals.

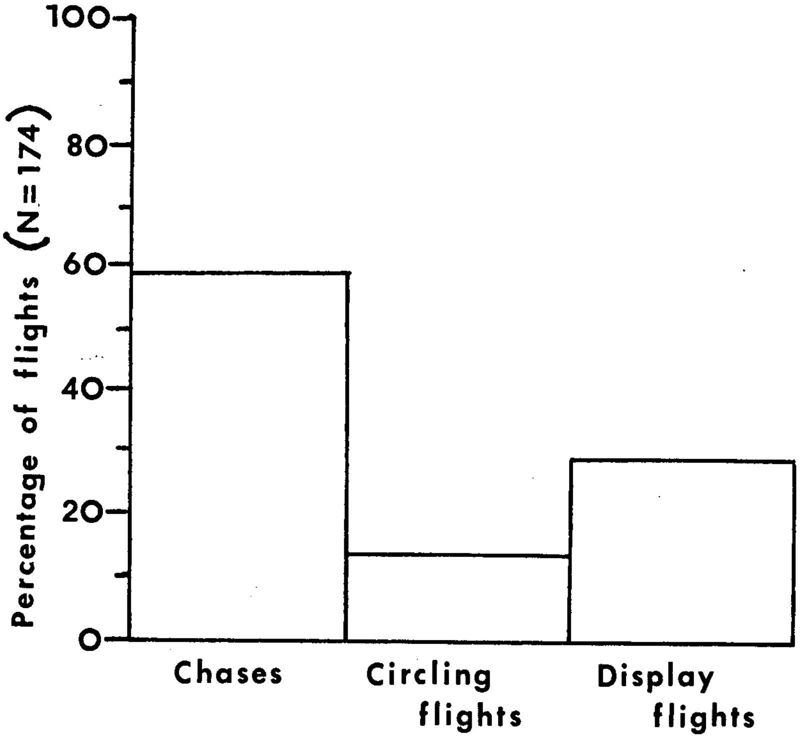
Identification by means of marking males was attempted. The marking procedure consisted of capturing males with a net, then etherising them and marking with aluminium paint on the thorax. The flies were then allowed to recover in specimen bottles before release.

About twelve males were marked in this way but none was ever seen again. This was possibly due to an adverse reaction to the marking procedure causing the flies to leave the area where they were caught. Also the large population of L. caesar during the summer made the chances of finding a few marked individuals low. Marking large numbers of individuals would not have been appropriate because many would have had to be given the same mark and so they would not have been individually identifiable.

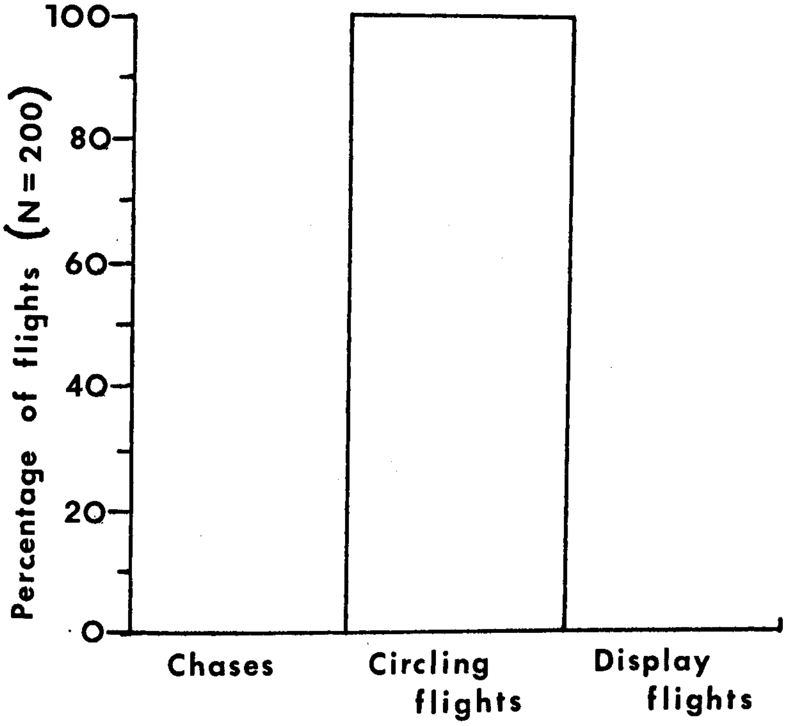
However it was possible to identify some individuals by means of the naturally occurring wing damage in the form of notches and tears. A male's pattern of wing damage was unique and could be used to identify individuals.

5:5. Territorial defence.

The result of interactions between a resident male and an intruder into a territory was generally that the intruder was driven away by the resident, a resident was never seen to be driven away by an intruder. 37 series of interactions were



(a) Males well separated (LOPs > 60 cm. apart)



(b) 2 males on same LOP

Fig. 5:5. Difference in percentage of flight types due to spacing of males.

observed of intruders perching in occupied territories. In 32 of these the intruder left, in the other five the intruder and the resident male both remained together in the territory.

Intruders usually left after no more than three interactions with the resident male. The number of interactions which occurred before an intruder left ranged from one to seven, the mean was 2.30, S.E. = 0.28, N = 30, see Fig. 5:6. It appears that if an intruder stayed in an occupied territory after having had three or more interactions with the resident male he would share the territory with the first male.

It is very probable that most potential intruders were intercepted before they had a chance to perch in an occupied territory and so the number of times perched intruders were seen to leave does not give a true measure of territorial defence. Intruders which perched in occupied territories may have already have interacted with the resident male before they perched.

All interactions took place in flight and when two or more males shared a territory every flight by either of them resulted in an interaction between them, usually a circling flight.

Sharing of territories probably resulted from the high population of L. caesar during the summer. Since the number of LOPs and therefore territories would be expected to be a limiting factor for males it is probable that after a certain amount of time spent searching for an unoccupied territory a male should be more and more likely to perch in an already occupied one and share it. When a male left his territory it was usually reoccupied by another within a few minutes. This indicates that there was a large number of males searching for territories ready to

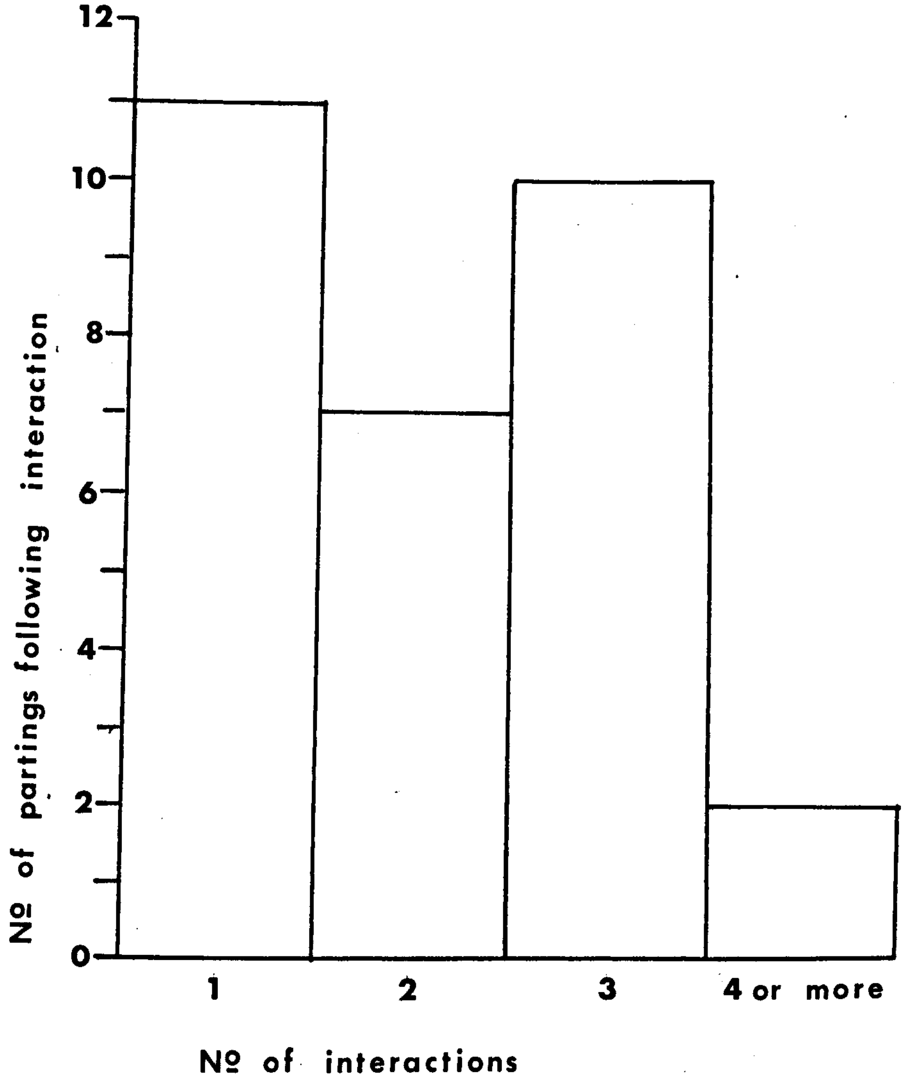


Fig.5:6. Number of interactions before males parted. (30 series of interactions observed)

perch in unoccupied areas.

Whether an individual was alone or shared a territory did not appear to influence the time it stayed in the territory. However it was not possible to be certain of this because instances where both of the males sharing a territory could be individually identified were insufficient.

5:6. Female behaviour and copulation.

Many females were present in the areas where males were active. The females were found feeding on flowers, carrion and animal excrement. At feeding sites relatively few males were seen. Fig. 5:7 shows a group of L. caesar, almost all females, feeding on a dead nestling. Females were found on vegetation near males' LOPs and on the LOPs themselves. Males never attempted to mate with females at feeding sites or to approach perched females elsewhere, unless the males had previously chased the females in flight.

Males chased females flying near to their LOPs. Whenever a male was seen to chase another fly and then to perch by it when it perched the chased fly was always found to be a female L. caesar. This indicates that males rapidly recognised females by some means. When a male perched near a female he had chased he repeatedly approached her and attempted to mount her. If the female flew away the male pursued her, usually this resulted in the pair flying out of sight into surrounding vegetation.

Copulations were seen to take place on vegetation and in other places around the males' territories. The copulatory position was the "male vertical pose" (Lamb 1922). A mating pair were

Fig. 5:7. A group of L. caesar feeding on a dead nestling.

stationary unless disturbed. During copulation females were seen to stroke the tip of the male's abdomen with their metathoracic legs. No interference by other males with copulating pairs was seen.

Males were never seen to gather at feeding sites where large numbers of females occurred or to attempt to mate feeding females.

5:7. Conclusions.

L. caesar fulfils the criteria necessary to establish that its mating system is of the lek type.

1) There is no male parental care.

2) There were mating arenas where males gathered solely for mating. These locations were used for at least one breeding season.

3) Males established territories based upon LOPs which they defended against other males.

4) The males' territories contained no resources useful to females.

5) Most of the males' behaviour was directed towards other males. The circling flight is a highly ritualised flight used in inter-male competition and the display flight is a ritualised advetisement of a male's presence in an area to other males, there is no evidence that they attracted females.

6) Females came to the males' territories to mate and all mating takes place on lek arenas as far as is known.

7) The area of the lek arenas is significantly smaller than the home ranges of both sexes when they are not on the arenas.

8) Females probably had the opportunity to select their mates, however no evidence that they did so was obtained.

9) The lekking aggregations of *L. caesar* contained no other species mixed with them.

Chapter 6.

THE SWARMING BEHAVIOUR OF MUSCA AUTUMNALIS DEG. (MUSCIDAE).

6:1. Introduction.

M. autumnalis is the very common fly found in areas where cattle are pastured from May to October. The adults feed on the eye secretions of cattle, on liquid dung and on wounds caused by biting flies such as *Tabanus* spp. and the biting muscids *Lyperosia irritans* L., *Haematobia stimulans* Mg. and *Stomoxys calcitrans* L. on cattle. The eggs are laid on the surface of cattle droppings and then pushed into the dropping by the female. The larvae feed inside the dropping.

Adults range from 6.25 to 7.75mm. in length and are markedly sexually dimorphic. Males have holoptic eyes, a black thorax and an orange-brown abdomen with a black central stripe. Females are dichoptic and a dull grey colour with numerous black dots on both thorax and abdomen. Fig. 6:1 shows a male and Fig. 6:2 shows a female.

During June, July and August 1976 *M. autumnalis* was observed in the area of the cattle pastures on Wood Park Farm, near Liverpool University Veterinary Field Station at Leahurst on the Wirral.

Hammer (1941) noted that males and females of *M. autumnalis* met to mate on objects standing out in fields such as water carts and stiles.

6:2. Perching behaviour of males.

Males were found to perch on gates and posts around the cattle

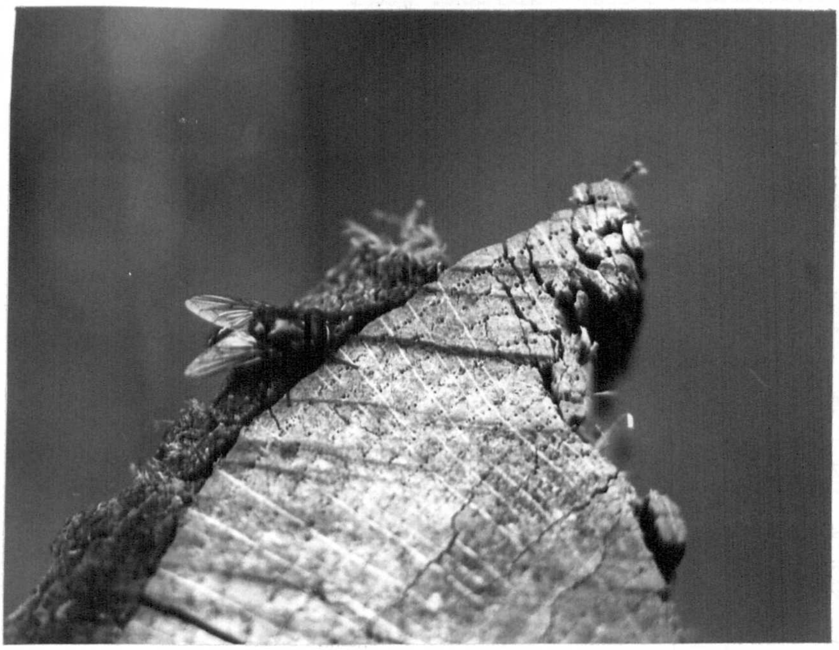


Fig. 6:1. Male M. autumnalis.

Fig. 6:2. Female M. autumnalis.

fields. When perched on these objects, which were the look-out-posts of the males of this species, males adopted an "alert posture" appearing to be watching the surroundings and to be ready for flight. Flying insects of about the same size and speed of flight as M. autumnalis were chased. Between flights males occasionally turned or walked a short distance on the LOP.

The number of males on any particular object was very variable. Fence and gate posts often had a densely packed group of up to 20 males on them (see Fig. 6:3), while on gate bars a number of males were often found spaced out evenly along the top bar (see Fig. 6:4). These were the typical grouping patterns for the two locations. Males were also found perched alone on objects such as fence posts away from groups.

Swarming activity took place on most days except very dull or wet ones. However flight activity was much lower when there was no sunshine, although hazy cloud cover did not affect the flies very much. Heavy clouding resulted in almost total cessation of flying by the males.

During June and July males appeared on the swarm-markers at about 7.30a.m. and were active until about 7.00p.m. in the evening,

6:3. Flight activity of swarming males.

a) Chases. When a flying insect passed within about 40cm. of a male or group of males it was chased. In the chase the insect was briefly investigated as the male or males flew close to it. Males were seen to chase and mount females in flight and then to mate with them, although such chases of females were often not successful for the male and the pair separated before mating.

Often when males were gathered in a dense group of ten or more

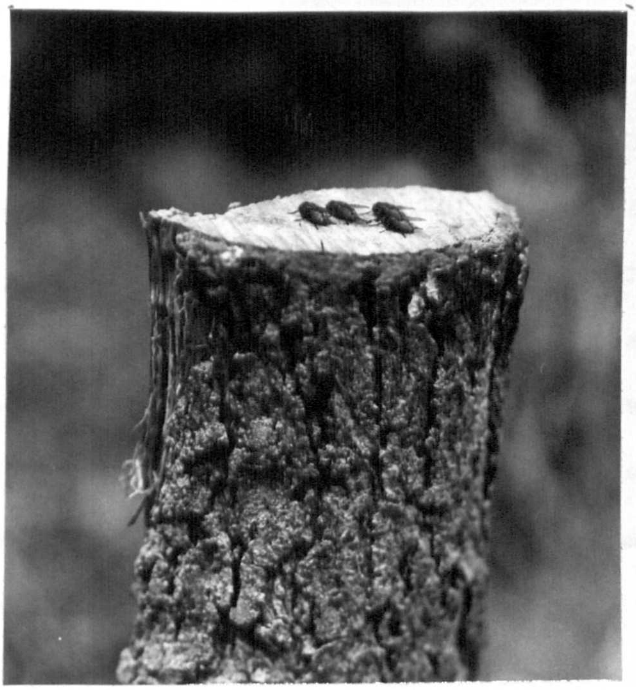


Fig. 6:3. Group of male M. autumnalis on a post.

Fig. 6:4. Group of male M. autumnalis on a gate bar.

on a post half to all of the group flew almost simultaneously in pursuit of passing insects. This resulted in the males flying as a swarm chasing each other. Similarly when smaller groups of two to ten males were perched in the same area chases of passing insects frequently resulted in them chasing each other. Sometimes with groups of ten or more males and occasionally with smaller groups before the last individual flying in a swarm had returned to the LOP another had taken off and the group would be in flight again. Although the groups often took off together the males returned individually to perch. First the majority of a group perched and then the remaining males circled around the LOP to find a perch. A male searching for a perch usually flew around until it found an unoccupied spot, if it tried to perch where there was another male it was either pushed away by that male and then flew away or sometimes both males flew away to different perches.

The duration of chases by single males ranged from 0.4 to 4.3s., the mean was 1.46s., S.E. = 0.13s., N = 50. It was not possible to time chases by males in groups perched close together because of the difficulty of following an individual in a swarm by eye.

b) Display flights. These flights were usually performed in the absence of any apparent external stimulus. A male flew up to about 25cm. above its LOP and then descended in a spiral to its LOP as shown in Fig. 6:5. In densely packed male groups display flights by individuals always resulted in other males chasing them. Some display flights appeared to result from the stimulus of insects flying past the perched males but which

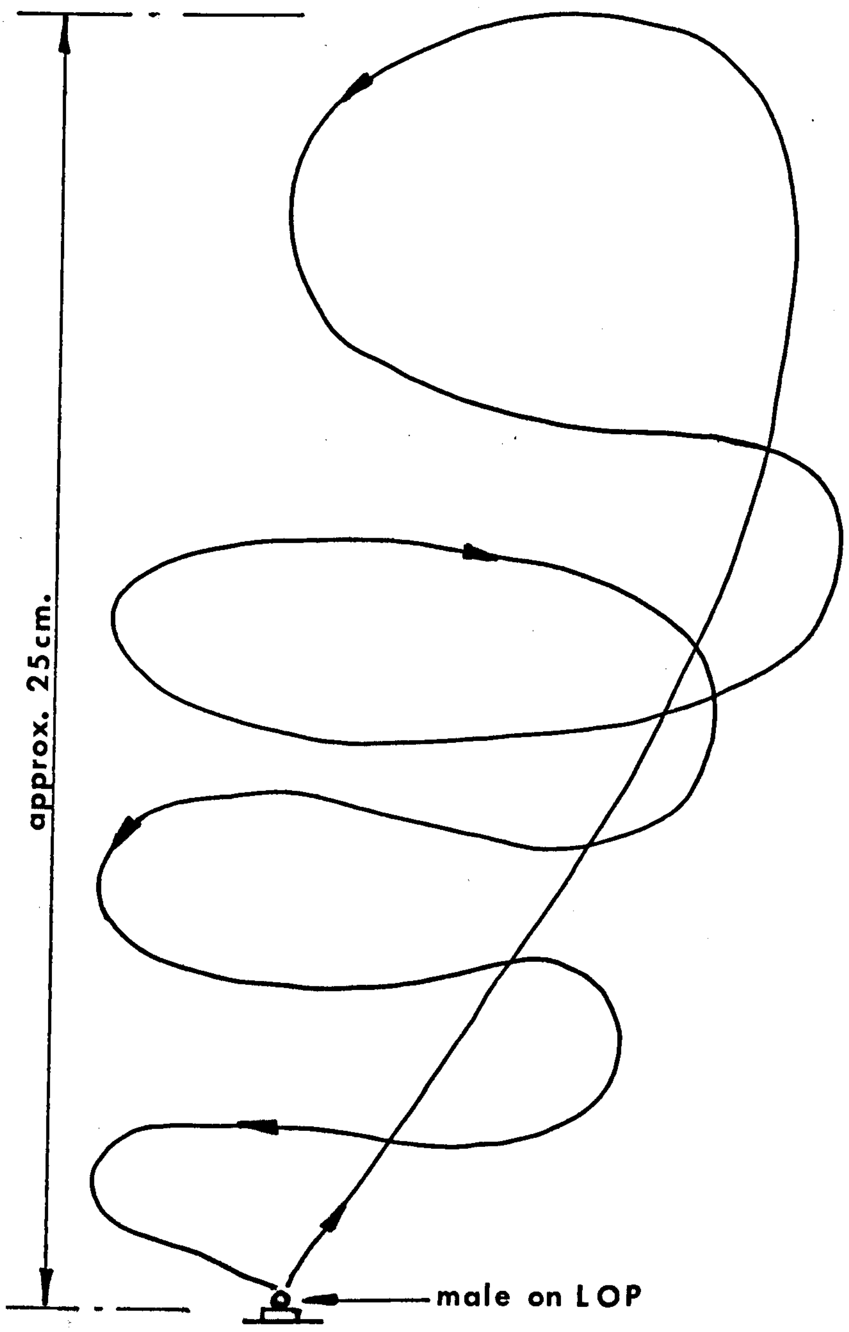


Fig.6:5. Form of typical display flight.
(side view)

were not intercepted.

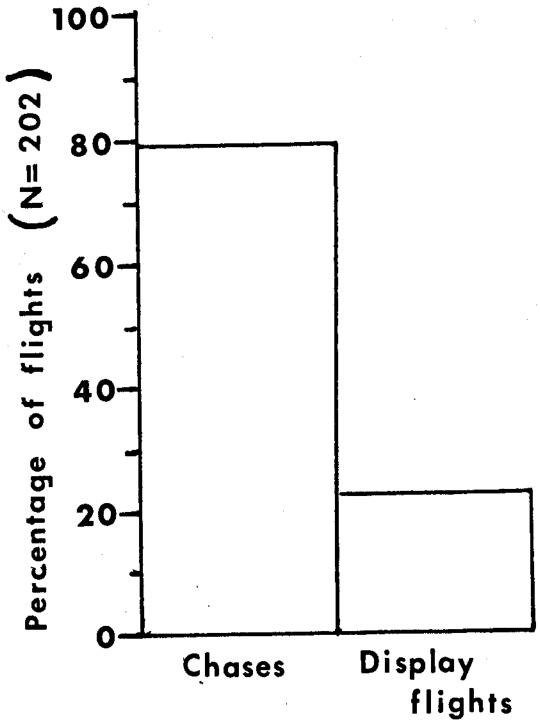
The duration of display flights from take-off to landing ranged from 0.3 to 0.7s., the mean was 0.5s., S.E. = 0.02s., N = 50.

The percentage of each type of flight performed by a male depended on whether it was in a dense group of males or in a more widely spaced group. In the first case if a male flew up in a display flight it was almost immediately chased by other males and it then chased them in turn. In this way most display flights became chases and males in effect performed very few actual display flights. In a more widely spaced group males performed many more display flights. The difference between the two situations is shown in Fig. 6:6.

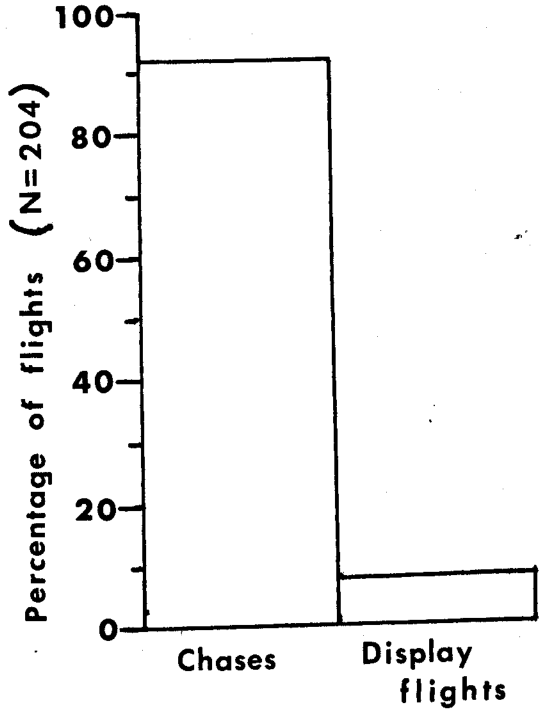
Chases between males perched along gate bars and fences maintained the spacing of these groups. This occurred because after an interaction between a pair of males they perched further apart or at least no closer together. Males were usually at least 15cm. apart in the spaced groups.

6:4. Examples of swarm-markers used by males.

Males gathered on a wide variety of objects, almost any object raised slightly above the surroundings being used at some time. As well as the usual places such as gate posts and fences males were seen to perch on small stones only two or three centimetres above ground level, on fallen trees and even on fallen leaves on the ground on one occasion when there were very large numbers of males present in the area. The range of objects is illustrated in the figures described below. The reasons for the use of any particular site were not clear because some gate and fence posts



(a) Male in spaced group.



(b) Male in dense group.

Fig.6:6. Difference in percentage of flight types due to spacing of males.

were not used while others nearby were. Swarm-markers were always in sunlit places but other factors such as wind direction or the location of cattle must have affected the use of some sites because they were sometimes found to have males on them and at others times no males were present. The objects most frequently used were those such a posts which gave males a good view of the surroundings. Fence posts surrounded by vegetation were not used by the males.

Fig. 6:7 shows a fence post frequently used by groups of up to twenty males, the post being the one nearest to the camera. It was 1.8m. high and was the highest object in the immediate area. Fig. 6:8 shows a post 1.0m. high on the edge of a wood opposite the cow pastures which was often used by one to five males when it was sunlit. Other fence posts on the edge of the wood were never used owing to the presence of tall grasses next to them which blocked the view from them. Fig. 6:9 shows a group of four males on the post shown in Fig. 6:8. Fig. 6:10 shows two posts used as swarm-markers. The gate post was 1.5m. high and groups of twenty or more males were often found on it as shown in Fig. 6:3. The higher of the two posts to the left of the gate post shown in Fig. 6:10 was also used by smaller groups of males. Fig. 6:4 shows four males perched along the top bar of a gate in the characteristic spacing pattern found in this situation. When males were present in very large numbers they perched spaced out on the ground in the same way that they perched on gate bars. They also gathered on stones and leaves as shown in Fig. 6:11.

The location of these groups of males indicates that the male

Fig. 6:7. Fence post used as swarm-marker by M. autumnalis.

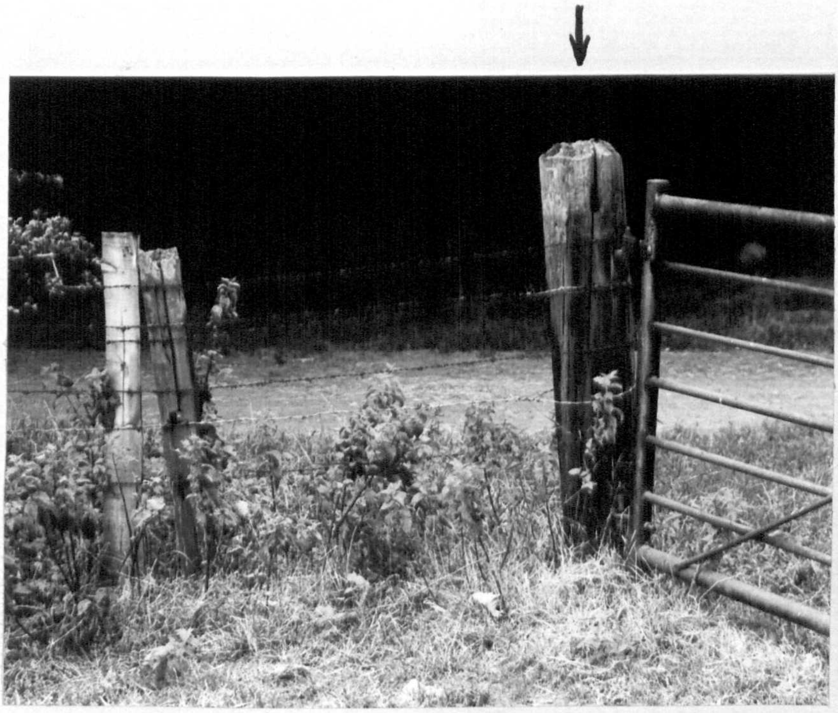


Fig. 6:8. Post used as swarm-marker by M. autumnalis.

Fig. 6:9. Group of male M. autumnalis on post shown in Fig. 6:8.

Fig. 6:10. Two posts used as swarm-markers by M. autumnalis.

Fig. 6:11. Male <u>M. autumnalis</u> perched on a leaf.

aggregation pattern is to cluster in dense groups on prominent objects and to perch spaced out in the immediate area around such objects. Males were seen to move between groups on posts and to perch with the males spaced out on the gate bar next to the post. Males were seen to leave and join both kinds of group on many occasions.

6:5. Predation of swarming males.

Males in large groups on posts were seen to be attacked by workers of *Vespula* spp. which repeatedly dived at them while flying around the post. Although these attacks appeared to be usually unsuccessful there seemed to be a risk of predation for active males. *Vespula* workers also dived at the flies, mainly *M. autumnalis*, clustered around the eyes of cattle.

6:6. Feeding behaviour of adults.

Dense clusters of feeding flies, mostly females, were found gathered around the eyes of cattle and on wounds caused by other species of flies. Both sexes were also found feeding on fresh cattle droppings, usually there were more females than males. No attempts at mounting females by males were seen in these feeding groups.

6:7. Female behaviour and copulation.

Females were commonly seen in the vicinity of swarm-markers perched on gates and other nearby objects. Males were occasionally seen to approach and touch females with their pro-thoracic legs when both sexes were perched on swarm-markers but these approaches were never observed to lead to mating. Males sometimes pounced on perched females as they came in to land on swarm-markers but again no matings were seen to result from this.

Copulations were always preceded by males chasing and mounting females in flight. The pair then flew in tandem and perched on the ground, nearby vegetation or a gate to complete mating. The copulatory position was the "male vertical pose" (Lamb 1922). Copulations lasted about 15min. during which time the male stroked the top and sides of the female's thorax with one or both of his pro-thoracic legs in bouts of one to ten strokes four to eight times a minute. After copulation the pair parted rapidly, the male flew off and was seen in some cases to return to a swarm-marker and the female remained perched near the mating site and repeatedly extruded and withdrew her ovipositor for a few minutes..

During copulations no interference by other males was ever seen although the mating pairs were sometimes in the middle of a group of perched males. Males walked past mating pairs, even stepping on them when the insects were crowded together, but never gave them any attention.

6:8. Pheromones in M. autumnalis.

Chaudhury and Ball (1974) found a midday mating peak in a laboratory population of M. autumnalis and suggested that this might correspond with a peak in a male-attracting pheromone release by females. However no evidence to show that females produce such a pheromone has been found in any field studies and all field data indicates that females go to swarming males for mating. If a pheromone does exist in M. autumnalis then males should possess and release it in order to attract the females to the swarm-markers rather than females using a pheromone to attract males.

6:9. Conclusions.

The mating system of M. autumnalis has many of the characteristics of lek systems, however it is a swarming rather than a lekking species. The main features of the mating system are listed below.

1) There is no male parental care.

2) There were mating arenas where males gathered solely for mating. The locations of the main arenas were fixed for at least one breeding season although other arenas were used at times of very high population.

3) The males did not establish territories and males in large groups did not maintain a spacing between themselves. Thus there did not appear to be the inter-male competition in this species which is characteristic of lek systems. Probably the high population density which is usual for this species makes a system based on territorial defence or maintenance of inter-male spacing too costly for the males. A male which spent its time defending a territory by chasing away other males might be expected to have little time left to capture females for mating. The spaced groups of males found on gate bars probably resulted from there being fewer males on these places so the males spaced out in order to reduce the competition between themselves for females.

4) The swarm arenas contained no resources useful to females.

5) The behaviour of the males on the swarm-markers was mainly

directed towards attracting females to the swarm arenas for mating. The display flight was a ritualised behaviour pattern advertising the presence of a male in an area to other males, there is no evidence that they attracted females.

6) Females came to the swarm arenas to mate and as far as is known all mating takes place on swarm arenas under natural conditions.

7) The area of the swarm arenas is significantly smaller than the home ranges of both sexes when they are not on the arenas.

8) Females probably had the opportunity to select their mates, however no evidence that they did so was obtained.

9) The swarming aggregations were always of M. autumnalis alone with no individuals of other species mixed in the groups.

10) The pronounced sexual dimorphism in this species may result from the need of the female for cryptic colouration for protection from predators and the need of displaying males to be as conspicuous as possible.

11) There is no fundamental difference between males in dense groups and males in spaced groups or between the types of group. The spaced groups occurred around those swarm-markers which attracted many males. Sometimes males perched in dense groups and sometimes in spaced ones, freely and frequently moving between the two. The taller posts formed a focus for the males that the flat gate bars and fences did not and so posts concentrated the males into a smaller area. Thus the spacing pattern of the males resulted from the physical features of their perches. Generally the more conspicuous the swarm-marker the more males perched on it.

Chapter 7.

THE LEK BEHAVIOUR OF STOMOXYS CALCITRANS L. (MUSCIDAE).

7:1. Introduction.

S. calcitrans is one of the three British species of biting muscids. It is greyish with dark brown spots on the abdomen and dark brown stripes on the thorax. Both males and females are dichoptic, but males' eyes are slightly larger than those of females. The piercing proboscis, which is very conspicuous (see Fig. 7:1), is used to suck the blood of mammals and the fly is often numerous near cattle pastures and stables. Adults range from 5.5 to 7.5mm. in length. The larvae develop in debris impregnated with animal excretions such as stable litter and in cattle dung. Adult flies occur from June to October. Their habit of mating at conspicuous objects in fields was mentioned by Hammer (1941).

S. calcitrans was observed in the area of the cattle pastures on Wood Park Farm, near Liverpool University Veterinary Field Station at Leahurst on the Wirral, during the summers of 1975 and 1977.

7:2. Perching behaviour of males.

Acivity took place on days when there was some sunshine and conditions were warm with no rain and little wind. Scattered clouds or hazy sunshine did not prevent activity. During July males were present in the lek arenas from about 8a.m. to about 7p.m. in the evening.

Males perched on a variety of objects, alone or in groups, from which they flew in pursuit of flying insects. Objects used as LOPs included fences, gates and prominent standing stones in fields. When a gate was occupied by a large group of males each bar and cross strut had individuals perched on it, so that flies were perched all over the gate, usually no closer than 15cm. to each other. Objects used as LOPs were sometimes in sunlit areas and sometimes in shaded ones, the insects did not appear to favour one situation over the other.

When perched on its LOP a male adopted an "alert posture", this is shown in Fig. 7:2, appearing to be watching the surroundings and to be ready for flight.

Males in groups on gates and males perched alone were often seen to return to almost the same spot after a flight, but the length of time a male spent on a particular LOP could not be determined because individual males could not be identified. Males were seen to change their LOP, whether or not conspecific males were nearby. Males in groups were sometimes seen to move their LOP by up to one metre after a flight. The perch used by a male in a large group probably changed by a short distance after many flights because on return from flights males perched in unoccupied places and they must often have had their previous LOP occupied by another male during their absence. Also a gate bar or fence presents a large area of relatively uniform appearance to a fly, unlike a fence post for example, so in many instances it would be difficult for a male to orientate so as to relocate its previous LOP.

Males maintained their separation by means of chases and circling flights described below. When males which were closer together than about 15cm. interacted in flight separation to a

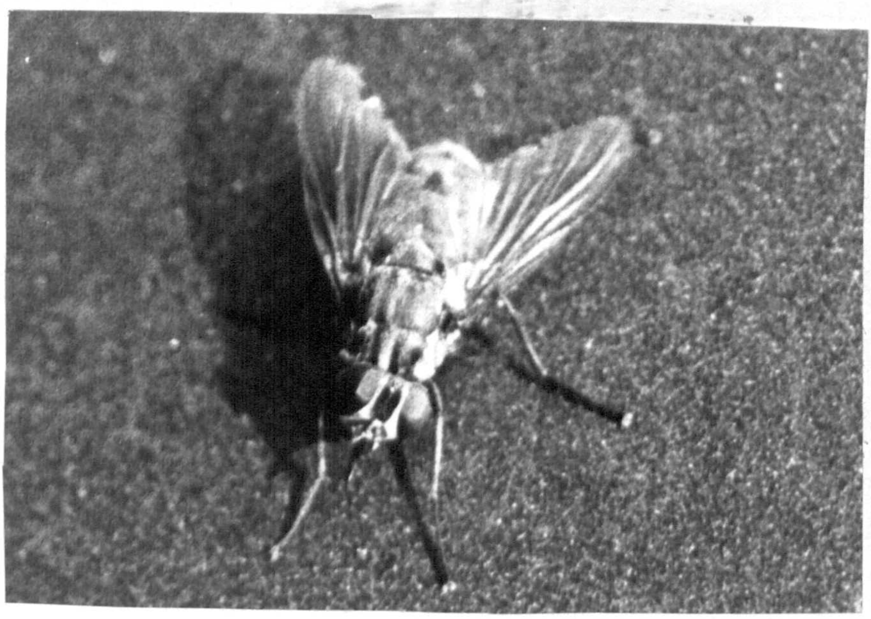


Fig. 7:1. S. calcitrans.

Fig. 7:2. Male S. calcitrans in "alert posture".

greater distance resulted.

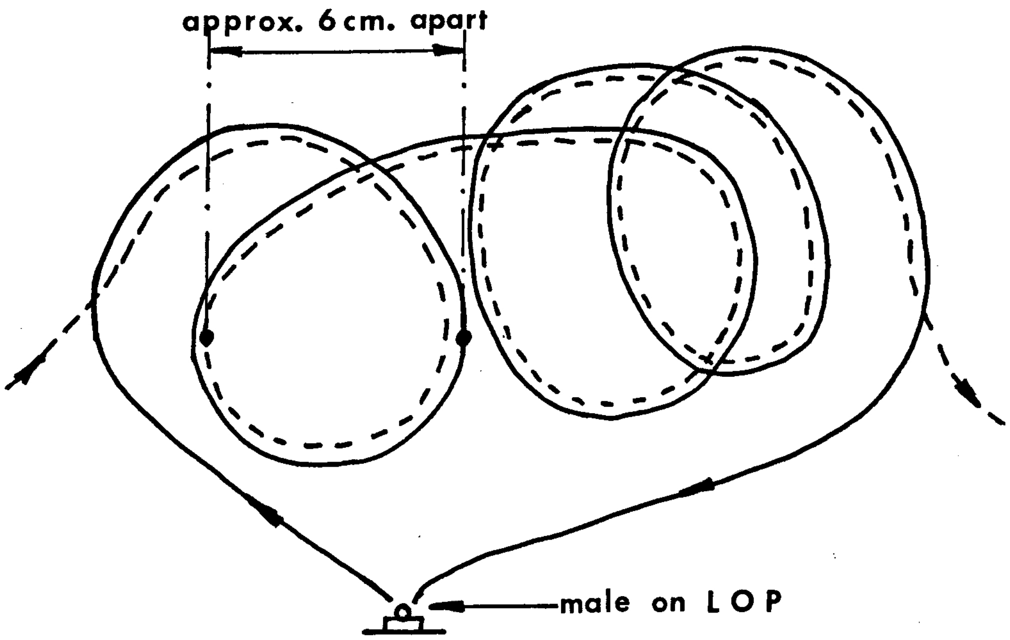
Groups of S. calcitrans males were never mixed with males of the other species present in the area which have a similar perching behaviour pattern such as Haematobia stimulans Mg. or Musca autumnalis Deg., both of which occurred on the cattle pastures. The odd individual of these species sometimes seen in a group of S. calcitrans soon moved away.

7:3. Flight activity of lekking males.

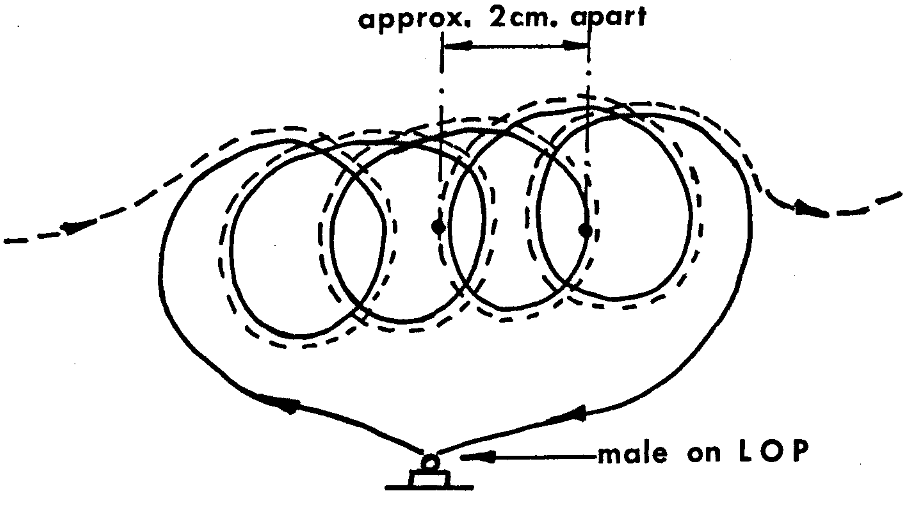
a) Chases. Flying insects of roughly the same size and speed of flight as S. calcitrans which passed within about 40cm. of a male were chased. In a chase a male flew up to and briefly investigated the insect flying close to it. Chases of conspecific males sometimes resulted in circling flights (see below). Males were seen to capture and mount females after chasing them in flight. Insects were chased for distances of up to one metre from the chasing male's LOP.

The duration of chases from take-off to landing ranged from 0.6 to 3.4s., the mean was 1.31s., S.E. = 0.09s., N = 50.

b) Circling flights. These interactions took place between conspecific males after one had chased another. In circling flights the males pursued each other in a circular path about 6cm. apart moving sideways at the same time. Occasionally males faced each other while circling, in this case they were about 2cm. apart. The forms of circling flight are shown in Fig. 7:3. In the longer flights of this type the males flew back and forth around the lek arena one metre or more from their LOPs.



(a) Pursuit type of circling flight.



(b) Facing type of circling flight.

Fig.7:3. Forms of circling flight.
(view from above)

The duration of circling flights from take-off to landing ranged from 1.0 to 5.5s., the mean was 2.33s., S.E. = 0.14s., N = 50.

c) Display flights. These flights generally took place with no apparent external stimulus. A male flew upwards about 10cm. and then spiralled downwards and perched again (see Fig. 7:4). Some display flights appeared to be performed in response to passing insects. Display flights by one male often resulted in nearby males chasing the displayer.

The duration of display flights from take-off to landing ranged from 0.4 to 1.6s., the mean was 0.79s., S.E. = 0.05s., N = 50.

The percentage of each type of flight performed by a male depended on whether it was alone or in a group. When alone a male performed mostly chases and display flights, but when in a group a male performed mostly chases and circling flights because take-off by one male resulted in another male or males chasing the first male, which would respond by chasing the other male or males in turn. Fig. 7:5 shows the percentage of each type of flight in the two situations.

7:4. Female behaviour and copulation.

Females were seen in lek arenas only when copulating with males. Males caught females for mating by chasing and mounting them in flight. The pair then flew in tandem downwards and landed on vegetation or other objects near ground level where copulation took place. The copulatory position was the "male vertical pose"

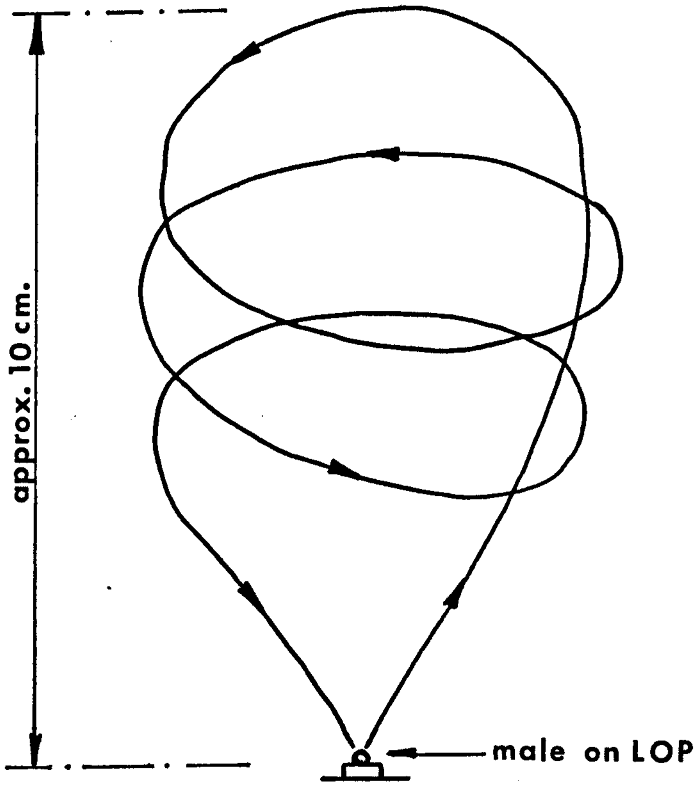
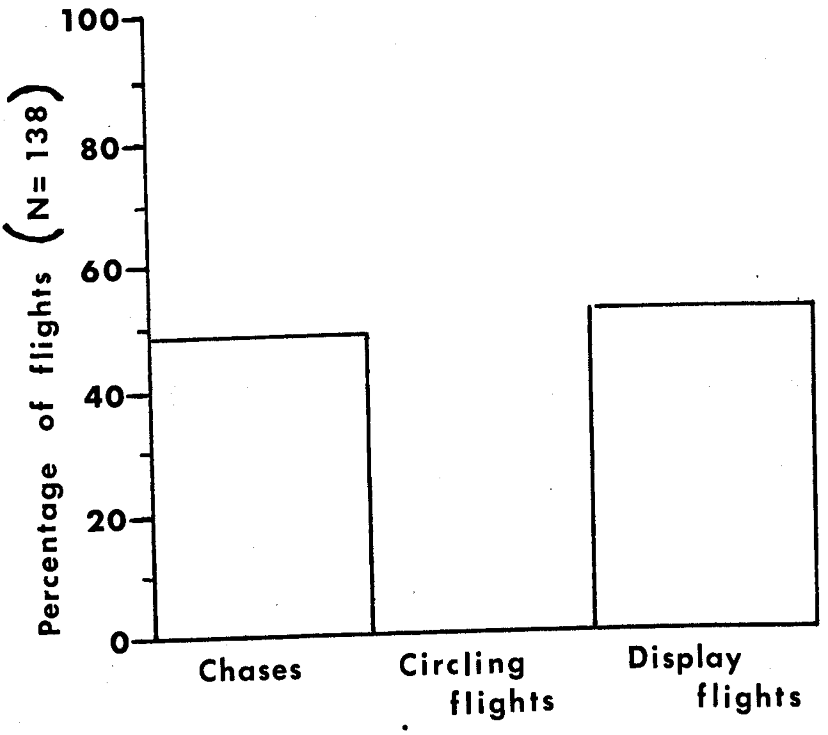
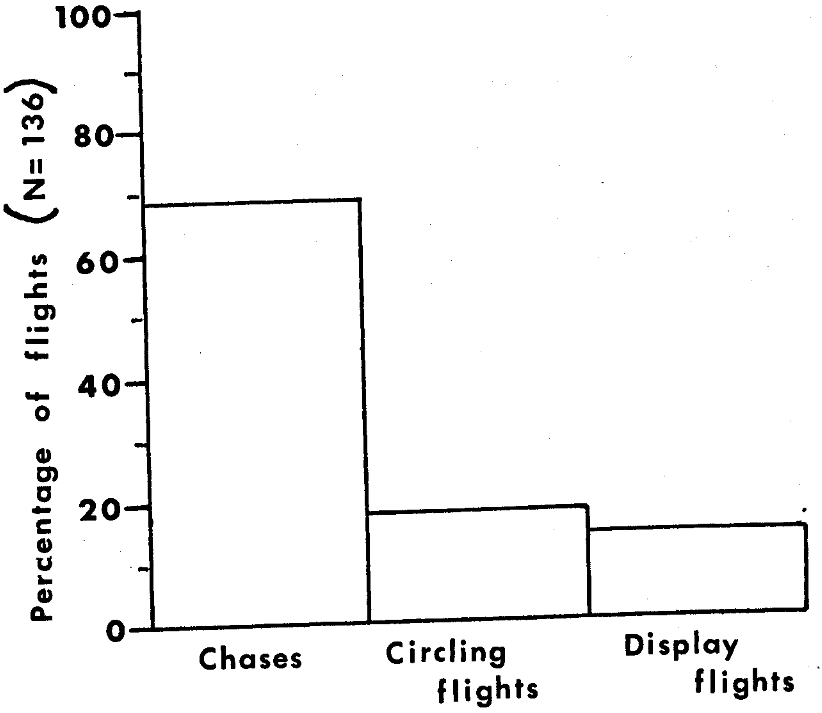


Fig. 7:4. Form of typical display flight. (side view)



(a) Lone male.



(b) Male in group.

Fig.7:5. Difference in percentage of flight types due to spacing of males.

(Lamb 1922). Following copulation, which lasted for only a few minutes in the instances observed, the male returned to a LOP and the female flew away.

7:5. Conclusions.

S. calcitrans fulfils the criteria necessary to establish that its mating system is of the lek type.

1) There is no male parental care.

2) Mating arenas exist where males gather solely for mating. The location is fixed for at least one breeding season.

3) Males established themselves on LOPs on the lek arenas, although no territories were seen to occur the males maintained a spacing between themselves which probably reduced inter-male competition for females.

4) The lek arenas contained no resources useful to females.

5) The behaviour of males was primarily directed towards one another. Most chases were of other males, circling flights were highly ritualised flights performed by males as a means of sexual recognition in order to maintain their spacing. Display flights were ritualised flights performed as advertisement of a male's presence in an area and resulted in interactions with nearby males, there is no evidence that they attracted females.

6) Females came to the lek arenas to mate and as far as is known all mating takes place around the lek arenas.

7) The area of the lek arenas is significantly smaller than the home ranges of both males and females when they were not on the arenas.

8) Females probably had the opportunity to select their mates, however no evidence that they did so was obtained.

9) The aggregation on the lek arenas were always on S. calcitrans alone with no other species present.

Thus the mating behaviour of S. calcitrans has all the characteristics of other lek species except that males do not occupy territories. However in other lek species systems male territoriality is basically a means of reducing inter-male competition for females. In S. calcitrans the same function is served by the spacing out of males on their LOPs which is a characteristic feature of this species.

Chapter 8.

THE LEK BEHAVIOUR OF FANNIA CANICULARIS L. (MUSCIDAE).

8:1. Introduction.

F. canicularis is the very common lesser house fly found around human habitations during the summer months. The larvae are associated with decaying matter or excrement and are of an unusual form for muscids. The segments are equipped with protuberences bearing cilia serving for progression or floating in semi-liquid matter. The eggs also have float-like modifications (Colyer and Hammond 1968). Adults range from 4.75 to 6.5mm. long.

8:2. Male lekking behaviour.

Colyer and Hammond (1968) refer to the habit of males flying continuously beneath pendant objects in rooms in "a series of irregular triangular or quadrilateral courses, an almost imperceptible hovering taking place at the corners and the sides being covered in a rapid dart. When undisturbed and alone, these flies maintain a more or less constant height and regular course, but when more than one decides to patrol the same "beat", it usually happens that one darts towards the other, a sharp flurry and prompt dispersal ensues and eventually one of them recommences the patrolling." (pp. 296-297).

Land and Collett (1974) analysed the behaviour of males by filming. They found that the speed of patrolling flight was about 65cm./s., half that of the speed in chases. They noted that the sides of the area patrolled were about 20cm. long and that individual males patrolled with their planes of flight 10 to 30cm. apart. When males approached each other within 10cm.

chasing always resulted.

Additional personal observations on the males' behaviour follow which expand the descriptions above.

Inter-male chases often resulted in brief contacts between a pair followed by separation and a return to patrolling. However most chases between males consisted only of males approaching others and a rapid pursuit flight. Males also chased other insects such as other small flies and clothes moths (Tineidae).

Large numbers of males flying beneath an object resulted in the patrols of individual males becoming much closer together. This caused many more reciprocated chases by the males. When about ten males were present in a group patrolling could not take place because chasing between the males was continuous. In these conditions there were always males flying in patrolling flights a short distance away from the large male group. These peripheral males flew alone, usually a few centimetres below the ceiling from which the marker object of the large group hung. Thus the result of large numbers of males was a group flying beneath the marker object constantly interacting with each other and a smaller number of males patrolling singly in the area around the marker.

When conspicuous marker objects such as hanging light bulbs or lamp shades were absent males patrolled singly beneath ceilings in the same way they did beneath marker objects when few males were present.

Males often perched for some time upon the object that they flew beneath. However there is no evidence that they used the object as a look-out-post, unlike the other species of flies described in Chapters 2 to 7. It seems that they needed to rest from time to time and used the nearest object for this purpose, this inevitably being the one that they were flying beneath. In the same way males flying beneath a ceiling rested on it from time to time. Thus the marker object of this species is a species-specific marker for leks having the same function as the swarm-markers in nematoceran matings systems as described by Downes (1958).

8:3. Female behaviour and copulation.

Females were frequently found perched in rooms where males were active. Females flew into male groups and were pursued and caught by a male, copulation then took place upon a convenient surface where the pair perched. The copulatory position was the "male vertical pose" (Lamb 1922).

8:4. Sexual dimorphism.

This species shows sexual dimorphism in size and colour. Males are somewhat darker than the females, both sexes having the same colour pattern of a greyish-black thorax with darker stripes and a creamy-white abdomen with a greyish-black median stripe and tip. Presumably males are selected to be conspicuous for display purposes while females need to be more cryptically coloured. Females have larger abdomens than males and this must correlate with females need for maximum production of viable eggs and so result in their larger size compared to the males. Males require the ability to maintain sustained flight in order to obtain matings and reduced weight would be expected to assist them in achieving this.

In common with other muscid species males are holoptic and females are dichoptic, this correlates with "marriage by capture" (Richards 1927).

8:5. Conclusions.

The behaviour of F. canicularis fulfils the criteria necessary to establish that its mating system is of the lek type.

1) There is no male parental care.

2) A mating arena exists where males gather solely for mating. The location is fixed for at least one breeding season, unless the marker object is removed.

3) Males establish and constantly patrol temporary aerial territories beneath marker objects, unless the number of males present prevents territorial defence. Territories occur beneath ceilings if no markers are present. Males defend their territories by chasing away intruder males.

4) The males' territories contain no resources useful to females.

5) The behaviour of the males is primarily directed towards one another being mostly inter-male chases for territorial defence.

6) Females come to the lek to mate and mating always takes place after females have been caught by lekking males, as far as is known.

7) The area of the lek arena is significantly smaller than the home ranges of both sexes when they are not on the lek arena.

8) Females probably had the opportunity to select their mates, however no evidence that they did so was obtained.

9) The aggregations of F. canicularis never contain individuals of other species.

F. canicularis and other related species having a similar mating system represent an important and interesting evolutionary stage in the development of dipteran mating patterns. Males fly in a swarm-like manner, rather than perch, as do males of many species of the Nematocera. Also the marker object where males aggregate is not used as a perch, but as the focus for sexually active individuals as are swarm-markers in the mating systems of many species of the Nematocera. *F. canicularis* can be considered as an evolutionary link in the development of mating systems from the nematoceran swarm to those found in the species described in Chapters 2 to 7.

PART THREE - DISCUSSION.

Chapter 9.

THE DISPLAY AND CIRCLING FLIGHTS.

9:1. Introduction.

The display and circling flights are highly ritualised flights performed by males of certain species of calypterate Diptera as part of their mating behaviour pattern. Only males perform these flights and their occurrence in a species correlates with the presence of swarming or lekking behaviour.

9:2. The display flight.

The display flight is found in the lekking species, Calliphora vomitoria, C. erythrocephala, Lucilia caesar, Stomoxys calcitrans and Gymnochaeta viridis and in the swarming species Musca autumnalis. It has probably evolved directly from and in evolutionary terms is homologous with the swarm flight above the swarm marker seen in many nematoceran species (see Downes 1958). The main difference between the display flight and the swarm flight is the much shorter duration of the display flight compared to the continuous swarm flight. Fannia canicularis performs an almost continuous flight beneath its markers essentially similar to the nematoceran swarm flight.

The existence of two categories of display flights was demonstrated in laboratory observations on C. vomitoria (see 4:4). One category of display flights was performed in the absence of a flying conspecific individual as a stimulus and the other category was performed in response to a flying individual. This supports the interpretation of field observation of display flights as sometimes being performed as display to passing insects and otherwise being performed to attract unseen conspecific males near to the displaying male.

The importance of "movement vision" in the Diptera by which females are recognised at the meeting place of the sexes (Downes 1969) is often correlated with the use of flight as display by male Diptera. A display flight above the marker object used as the meeting place of the sexes, probably evolved by reduction from a continuous swarm flight above the marker, in those flies which perch on the marker is a very effective advertisement of a male's presence in insects specialised for the perception of movement. Receptive females as well as males may be expected to respond to a displaying male or males as an added stimulus to that presented by the marker and to approach the marker for mating. Males may respond by joining the male in a swarm or lek or by interacting with him if he has perched in their territory or is otherwise too close to them. Thus the display flight functions as advertisement of the presence of a male or males on the species-specific marker objects to conspecific individuals of both sexes.

Apparently display flights occur in various other species of territorial insects. The flights are usually described as short flights from and return to a perch. In the Odonata *Leucorrhinia caudalis* and *L. rubicunda* males perform such flights (Pajunen 1964, 1966a). Among other hymenopterans *Eucercis arenaria* and *Clypeadon taurulus* males perform short flights (Alcock 1975). The need for a male in a swarming. lekking or other territorial species to advertise his presence must have led to the convergent evolution of these behaviour patterns in these different orders.

9:3. The circling flight.

The circling flight is seen in C. erythrocephala, C. vomitoria, L. caesar, G. viridis and S. calcitrans. It is not found in the swarming species M. autumnalis or F. canicularis which patrols its aerial lek. It is also found in territorial species in other orders, for example Calopteryx virgo (Odonata) (Pajunen 1966b), Aglais urticae and Inachis io (Lepidoptera) (Baker 1972) and various species of the genus Philanthus (Hymenoptera) (Alcock 1975, Evans 1975). These authors sometimes refer to it as a spiralling or swirling flight but the main features of the flight of two conspecific males flying around each other in a tight circling flight are present in all the species.

The circling flight was suggested to be a "manoeuverability contest" by Baker (1972) in the species A. urticae and I. io. Baker proposed that in the "spiralling flight" one male demonstrated his superior manoeuverability to the other by being able to maintain a position slightly above and behind the other. Baker thought that the more manoeuverable winning male would be more likely to catch a female if in competition with the losing male and therefore the losing male would do better to wait for females elsewhere. However he found that these interactions did not necessarily lead to the contestants separating and that males of A. urticae tended to share territories as the day went on, with up to six males in one territory. Baker found that the length of the first and second interactions influenced whether or not an intruding male returned to an occupied territory in I. io. The longer the interactions the less likely was the intruder to return. After three interactions both males were equally likely to return. This applied only to intruders which had perched in an occupied territory. When an intruder was intercepted before it had perched the length of the interaction did not affect whether or not the intruder left the territory.

Male C. erythrocephala observed in the field usually left an occupied territory after one interaction, almost always a circling flight, with the resident male (see 3:5). Observations on C. vomitoria in the laboratory showed that a second male perching on the marker object usually left after one interaction, usually a circling flight, with the resident male, the cramped conditions of the cage compared to the natural situation may have resulted in males tending to remain together on the marker more often than they would in the wild (see 4:5). Intruding male L. caesar usually left an occupied territory after one to three interactions, almost always circling flights, with the resident male. Following more than three interactions both males often shared the territory (see 5:5). Male G. viridis intruding into an occupied territory usually left after one to three interactions, usually circling flights, with the resident male (see 2:6).

Circling flights occurred with very few exceptions only between conspecific males of the lekking species. They formed a major part of inter-male competition resulting in spacing out of males in these species, producing this in Stomoxys calcitrans and territoriality in the other four lekking species when males used conspicuous markers as perches.

The "manoeuverability contest" theory of Baker (1972) does not appear to apply with the species of flies mentioned above since there was no indication that a pair of males engaged in a circling flight were attempting to outmanoeuver each other, but the very rapid flight of these species may have obscured this.

Observations on other species of insects having a similar type of flight do not seem to fit in with the "manoeuverability contest" theory. Shields (1967) reported that male Papilio zelicaon (Lepidoptera) flew in tight circles and climbed high into the air and sometimes locked legs and beat their wings together. Although this type of flight appears identical to that of A. urticae and I. io as described by Baker (1972) such behaviour is not simply a manoeuverability contest. Baker observed that a male "outmanoeuvered" on two occasions always left the territory in dispute. This observation could be interpreted instead as a signal by a defeated male to the winning male that he will leave the territory or is likely to leave the territory. The signal being that the loser allows the winner to fly above and behind him at the end of the circling flight, the contest being decided in another way.

If manoeuverability decided the contests for territories in A. urticae and I. io then intruders should win about half of these contests because there is no reason to expect them to be less manoeuverable than the resident males. Each male should be displaced by the next more moanoeuverable male coming along and territoriality would not exist to any extent. This contradicts Baker's (1972) finding that the butterflies were territorial. The usual pattern in territorial and lekking species is that of residents winning interactions with intruders and the intruders then leaving the territory. This occurred in the flies C. erythrocephala, C. vomitoria, L. caesar and G. viridis. Davies (1978) observed circling flights by male speckled wood butterflies (Pararge aegeria) taking place between intruders and residents and found that the resident male always won the territorial dispute and was never displaced.

An alternative explanation for the circling flight is that it is part of a motivation assessment contest for the territory. A difference in motivation and therefore in persistence in a territorial dispute would be expected due to the difference in the amount of time spent in a territory by the resident and the intruder. Such a territorial contest is an asymmetric contest which should be settled by an asymmetric cue (Maynard Smith and Parker 1976). The asymmetric cue of time of arrival can be used to decide the contest as Davies (1978) suggested. The asymmetry in time of arrival should lead to the resident being more persistent than the intruder due to its higher motivation to remain in the territory resulting from the greater value to the resident from having learned the features of the area of the territory. A male can show his level of motivation to the other male by his persistence in the territorial dispute in the circling flight and by physically attacking the other male as Shields (1967) observed to occur and which also occurred in G. viridis, C. erythrocephala and L. caesar (see 2:4, 3:3 and 5:3 respectively). An intruder will often be easily able to find another unoccupied territory and would do better to search for one than to waste time in disputes with resident males.

While motivation assessment and the use of an asymmetric cue explain the usual outcome of territorial contests involving circling flights the reason for the circling as opposed to flight in straight paths is not so explained. If the males are not trying to outmanoeuver each other there must be another reason for the circling. Circling probably results from the need of both the resident and intruder males to stay in the area around the territory in order to prevent yet another male perching there in their absence and also to ensure that they do not get lost somewhere away from the territory. The existence of what is apparently the same type of flight in odonates, lepidopterans, hymenopterans and dipterans suggests that this is correct since it seems unlikely that differences in manoeuverability in all these orders, especially the more strongly flying Odonata, Hymenoptera and Diptera, would be sufficient to settle the territorial contests. However individuals of territorial and lekking species can perform longer interactions in flight in a small area if a circling type of flight is performed. Pajunen (1966b) suggested that male C. virgo kept within a limited area by means of the circling type of flight during their interactions over territories. The same need to stay in a limited area for individuals defending a territory in flight has led by convergent evolution to the circling flight in territorial species in these diverse orders of insects.

The circling flight also results in instant epigamic recognition between males because females never perform it. In the laboratory observations on C. vomitoria it was found that males which had circled with each other never mounted one another following the interaction, unlike when they had only chased each other (see 2:4).

The absence of the circling flight from the behaviour of M. autumnalis correlates with the lack of inter-male competition for places on the swarm marker, where males are often closely crowded together.

9:4. Summary.

The display flight was found in the lekking and swarming species studied. It is derived from the continuous swarm flight performed by many species of the Nemarocera. F. canicularis performs an almost continuous display flight similar to that of the Nematocera. The display flight advertises the presence of a male or males on the swarm or lek marker. Similar flight behaviour occurs in the territorial behaviour of males of insect species in other orders.

Circling flights occurred in the behaviour of the lekking species studied. Similar flights by territorial males of other insect species occur. It has been suggested that the circling type of flight is a manoeuverability contest between the males, but it seems more likely that circling has evolved so that the interacting males can remain in the area of the territory. The circling flight forms part of a motivation assessment contest decided mainly by the time of arrival in the territory which almost always is won by the resident male when interacting with an intruder.

Chapter 10.

FEATURES ASSOCIATED WITH SWARMS AND LEKS IN THE DIPTERA.

10:1. Swarms and leks.

Swarms of members of species of the Nematocera have certain characteristics (Downes 1958):

1) The response to the swarm-marker is purely visual and depends only on size, colour and contrast.

2) Individual males may perform the swarm flight over a marker, thus no gregarious process is needed to initiate a swarm flight.

3) Swarms are always of one species only, mixed species swarms are never found.

Downes (1958) considered swarms occur because all members of a population are thereby gathered into a small area and concentrated for mating and that females are ensured of a conspecific mating.

Usually in descriptions of swarming behaviour no consideration is given to the possibility of competition within the swarm between the males forming it. However recent research by Thornhill (1980) has shown a high degree of competition in a nematoceran swarm. Thornhill found that males of the bibionid *Plecia nearctica* competed for positions at the base of the swarm where females tended to enter it. Larger males obtained the best positions.

The feature common to many dipteran mating systems is the use of a visually determined assembly station for the meeting place of the sexes. Matings are initiated in flight in all species having this behaviour, even in those members of the Brachycera whose males perch on the landmark used as the assembly point (Downes 1969).

The swarming behaviour of many species of the Diptera has the basic features of a lek. There is a gathering of males at a species-specific location where they display in order to attract the females which come to the swarm for mating. When inter-male competition results in each male defending a territory within the swarm the stage of a lek system has been reached, as long as the location of the assembly site is not based upon the presence of a resource useful to the females there.

Thus the lek arena of the lekking species is derived from the swarm arena of swarming species and the look-out-post marker object used by perching territorial males is derived from the swarm-marker of swarming species. The change from swarm-marker to LOP occurs when males perch on and defend the marker object instead of flying above it in the swarm flight. The males of the lekking species studied and described in Chapters 2 to 6 performed display flights around their LOPs acting as advertisement of their presence in the way that the males of nematoceran species advertise their presence by the swarm flight. Competition between males for places in the swarm arena may have resulted in perching on the swarm marker becoming adaptive when a continuous display flight was no longer necessary. By perching on the marker object a male is ensured of his place in the arena, which he may defend against other males.

Charlwood and Jones (1980) describe how response and orienttation first to the swarm arena and then to the swarm marker occur in anopheline mosquitoes, species-specific responses result in monospecific swarms. A similar process must take place in the lekking species which also gather in monospecific groups.

The influence of the marker object was noticeable in all the species studied. In the lekking species *G. viridis*, *C. erythrocephala*, *C. vomitoria*, *L. caesar* and *S. calcitrans* males competed for places on the markers to use as their LOPs. In *M. autumnalis* males were much more densely concentrated upon the markers and were present in large numbers around them. In *F. canicularis* males flew beneath the markers in preference to other patrols and competition between the males occurred for patrols beneath the markers. In common with many other dipteran species these species show the influence of the marker on the behaviour of the males and also on the females which come to the markers to mate.

10:2. The operational sex ratio in lekking and swarming insects.

A common problem with the analysis of the mating systems of swarming, lekking and territorial insects is that matings may be seldom seen in nature. Thus there may be little evidence to support the contention that male swarms are part of the mating system. This problem can be partly resolved by a consideration of the probable operational sex ratio in these insects. Using a method of calculation based on that of Charlwood and Jones (1980) for anopheline mosquitoes it is possible to arrive at a value for the operational sex ratio (OSR) for the lekking and swarming flies described in this thesis.

The assumptions for the calculation are as follows: an equal sex ratio, an average sexually active life for a male of ten days, that a male can mate as often as he finds receptive females, that females mate only once and that lek activity lasts on average for ten hours a day. The equal sex ratio follows from basic evolutionary theory. The sexually active life span appears reasonable given the observations on the life span of *G. viridis* described in 2:9. Male flies are generally seen to mate as often as they find receptive mates. It seems likely that females of the closely related families Tachinidae, Calliphoridae and Muscidae mate only once following the observation that female *Musca domestica* mated at maturity by mature males were unlikely to remate (Riemann and Thorson 1969).

If it is further assumed that a female flies into a lek and is captured by a male for copulation in approximately 15s. the relative amount of time spent in the lek arena by the females compared to the males is 15s. compared to 60s. x 60min. x 10hr., this is 1:2400. Since males are active for ten days one new virgin female appears every day for each ten males. This results in an OSR of 24,000 males per female. The loss of one male from a lekking group for the duration of his copulation with a female is assumed to have no significant effect on the OSR.

Although this is probably an overestimate of the OSR in natural conditions given such factors as the influence of the weather on lek activity it demonstrates the potential for sexual selection by inter-male competition and female choice in these flies. It also shows why matings are relatively rarely observed in the field.

10:3. The effect of lekking and swarming on male survival.

Males of the species described in this thesis must reduce their lifespan by taking part in lek behaviour. Inter-male chases and circling flights sometimes resulted in clashes between the participants. This would certainly cause damage to the wings of the males on occasion. Wing damage was used as a means of identifying individual males in observations on *G. viridis*, *C. erythrocephala* and *L. caesar* in the field. Such damage to the wings probably eventually results in the males being unable to fly and therefore extremely vulnerable to predators. This will probably happen when the flies are otherwise still capable of living for some time judging from the life span of *C. vomitoria* kept in the laboratory which lived long after their wings were totally useless for flight. Thus in order to increase their mating success males reduce their life expectancy by swarming or lekking. Males of *S. calcitrans* and *M. autumnalis* were also seen with damaged wings indicating that they too suffer from this problem.

10:4. Sexual dimorphism.

a) Eye dimorphism. *L. caesar*, *C. erythrocephala*, *C. vomitoria*, *M. autumnalis* and *F. canicularis* have strongly sexually dimorphic eyes. Males of these species are holoptic while the females are dichoptic with much smaller eyes than the males. The eyes of male *G. viridis* and *S. calcitrans* are larger than those of their females but they are not holoptic. Richards (1927) noted the correlation between holoptic eyes in males and "marriage by capture" in the Diptera. The males' eyes are enlarged to enhance the perception of movement in order to assist in catching females in flight for mating and also for interactions with other males as part of inter-male competition in lekking species and display flight behaviour in the case of *M. autumnalis*.

b) *Colour dimorphism*. The two muscid species, *M. autumnalis* and *F. canicularis*, show a degree of sexual dimorphism in colour. Male *F. canicularis* are slightly darker than their females while male *M. autumnalis* are very differently marked from their females. Female *M. autumnalis* are cryptically coloured, but the males have a shiny black thorax and an orange abdomen with a black median stripe. These differences are most likely to be due to selection for cryptically coloured females for protection from predators while males are require more conspicuous colours for display purposes to attract females. Males of both species perform conspicuous display flights at their mating arenas and dark markings might enhance the effect of their display.

10:5. *Interference with matings.*

Only in *G. viridis* were males seen to attempt to disrupt the matings of other males. Since only two attempted disruptions were seen the rate of successful disruption and possible take-over of females is unknown. The other species studied did not show this behaviour even when males commonly encountered mating pairs. A possible cause of this difference is the smaller population of *G. viridis* and its shorter flight season which may result in an increase in inter-male competition for females compared to the other species. This may lead to the evolution of a male strategy of disrupting matings with the chance of taking over females and to some extent reducing a competiting male's reproductive success.

10:6. Thermoregulation by males.

Males of G. viridis and C. erythrocephala adjusted their body temperature by altering the angle of their bodies to incident sunlight (see 2:11 and 3:2).

Alteration in body posture by insects in order to thermoregulate has been recorded in libellulid dragonflies by May (1976) and Heinrich and Casey (1978) and in Colias butterflies by Watt (1978). These species expose the maximum area to the sun to warm themselves and if overheated orientate so as to expose the minimum area to the sun. Heinrich and Pantle (1975) reported thermoregulation by Syrphus species (Diptera). The males bask in the sun at their hovering places and also "shiver" by vibrating their indirect flight muscles and wings.

Digby (1955) found that Calliphora, Lucilia and Sarcophaga species in a 50cm./s. wind and heated at 1.5cal./cm./s. (equivalent to bright spring sunshine from above) had a temperature excess of about 8°C over air temperature. Digby suggested that the thorax in Diptera had evolved so as to enable the insects to obtain as high a temperature excess as possible, the thorax being attached to the head and abdomen by slender supports to minimise conduction. Conductivity is also reduced by pubescence which results in a stagnant layer of air between head and thorax and thorax and abdomen. At low wind speeds pubescence of the thorax would also serve to reduce convective heat loss by creating a stagnant layer of air all round the thorax according to Digby.

Because successful mating by males depends on flight activity to catch females or in competition with other males the flight muscles in the thorax need to be kept at their optimal temperature so as to function efficiently. Thus the morphological adaptation of pubescence found in *C. erythrocephala*, *C. vomitoria* and especially *G. viridis* and behaviour patterns of orientation to sunlight and also of sheltering from cold wind seen in *G. viridis* are probably selected for in males to increase their mating success. The habits of the other species *L. caesar* and *M. autumnalis* of perching in sunlit spots shared with those mentioned above all appear to be adaptations to gain heat so as to enable efficient muscle activity for rapid flight. As Heinrich and Pantle (1975) noted chasing males need to be rapid flyers in order to catch females and therefore high thoracic temperature favours mating success.

10;7. *Pheromones*.

The question of whether a volatile sex- and species-specific pheromone is present in any species of calypterate Diptera has been the subject of research for some years. Some authors have claimed to have demonstrated the presence of a volatile pheromone in female *Musca domestica* and *Lucilia cuprina*, see Roggoff, Beltz and Plapp (1964) and Bartell, Shorey and Browne (1969) respectively. Other researchers have found no evidence for a pheromone in *M. domestica* (Ilse and Mulherkar 1954, Murvosh, Fye and Labreque 1964, Mayer and Thaggard 1966) or in *Protophormia terraenovae* (Parker 1968).

In these studies little weight has been given to the behaviour of the species under natural conditions. When present "scent glands must show ecological adaptiveness" (Thiessen, Blum and

Wallace 1971). All the researchers claiming to have demonstrated the presence of pheromones in calypterates have used experiments on laboratory populations for evidence with no research on the behaviour of the species in the wild state. Without a knowledge of the normal behaviour of wild populations speculations on the possible existence of pheromones lack a proper basis.

Ilse and Mulherkar (1954) and Chaudhury and Ball (1974) tested *M. autumnalis* for a sex attractant released by the female. The description of the behaviour of wild populations of this species in Chapter 5 of this thesis shows that a pheromone produced by females to attract males would not fit into its mating system. Rather it might be expected that males would emit a pheromone to attract females.

Bartell, Shorey and Browne (1969) did not demonstrate the existence of a pheromone in *L. cuprina*, only that males were attracted by the odour of females. The field observations described in 5:6 suggest that males respond rapidly to the female, perhaps as a result of female odour, but there is no evidence for a species-specific sex attractant produced by females of *L. caesar*. Thus in the genus *Lucilia* the available data suggests a response by males to the odour of females but not to a pheromone.

Supposed proofs of the existence of pheromones by laboratory experiments should be tested against the behaviour of wild populations. Evidence for the presence of a pheromone should preferably come from field observations rather than laboratory experiments.

The validity of the approach from field observations to laboratory experiments is proved by the examples of those moths in the females wait for males attracted by the pheromone they emit. Here the female produced pheromone provides the males with a reliable indication of the location of females ready for mating and is clearly adapted to the behaviour and ecology of the species. The stationary female attracts the mobile male. Similarly certain species of Hawaiian *Drosophila* which have leks have males which advertise their presence to females with a pheromone (Spieth 1968). The territorial males of various species of Hymenoptera in the genera *Centris*, *Eucercis* and *Philanthus* are known to produce pheromones which they deposit on their perches (Alcock 1975).

The general rule is that the stationary sex emits pheromones to attract the mobile one. In calypterate Diptera there is no reason to expect the female to be immobile and emit a pheromone any more than to expect the male. So far males of territorial and lekking species have been found to produce pheromones, not the females, so perhaps it would be best to look for them in males of the swarming and lekking species of Diptera rather than in the females.

Chapter 11.

THE EVOLUTION OF LEK BEHAVIOUR.

11:1. Characteristics of leks.

Emlen and Oring (1977) defined a lek as "a communal display area where males congregate for the sole purpose of attracting and courting females and to which females come for mating". Leks do not contain essential resources used by females. Since females on leks are free to choose their mate on the basis of characters shown by males sexual selection on males due to female choice can lead to elaborate male epigamic characteristics and behaviour.

Territories in a lek may be tiny as in frogs (Emlen 1976) or manakins (Lill 1974) where they are only a few centimetres across on the ground. At the most lek territories are only a few metres in diameter in such species as black grouse (Lyrurus tetrix) (Kruijt and Hogan 1967) and Uganda kob antelope (Adenota kob thomasi) (Buechner and Schloeth 1965). Males vigorously defend their territories against other males.

Usually the few males occupying the central territories on a lek perform almost all the matings. Apparently the occupation of these central territories is the essential factor for a male's mating success. Lill (1974) did not find any feature of male morphology or display or any feature of the territory a male occupied correlated with mating success except the location of the territory. Wiley (1973) did not find any correlation between display and mating success in sage grouse (Centrocercus urophasianus). Female sage grouse and Uganda kob choose the place at which they mate on a lek rather than a particular male occupying the territory (Wiley 1978; Buechner and Schloeth 1965). Wiley (1978) found that male sage grouse moved towards the mating centre favoured by females as vacancies appeared nearer to it than their own territories. Wittenburger (1978a) stressed that young males moved in to fill gaps left by the removal of older males in all species of grouse tested.

It is often suggested that females in lek systems let inter-male competition sort out the "best" males for them, for example see Emlen (1976). This assumes that the males preferred by females are chosen for those characters enabling them to obtain and occupy the central territories on a lek and that such characters are heritable. According to this view females choose to mate these males in order to gain genetic benefits for their offspring. An alternative view is that females choose to mate displaying males for more immediate benefits than genetic ones. The various theories put forward to explain lek behaviour are discussed later in 11:3.

11:2. Female choice.

The importance of female choice is often little appreciated because the factors resulting in selection upon females to discriminate between sexual partners are usually difficult to separate from the general action of sexual selection on males. Male sexual selection due to inter-male competition is usually very intense and all male sexual behaviour may easily be attributed to it. It is often impossible to separate the effects of female choice from those of inter-male competition. Also the cues used by females in their choice of mates are often difficult to determine. However female choice will be a powerful selective pressure upon those male attributes which form the basis of that choice, perhaps to the extent that many characters present in male morphology and behaviour are the result of that choice.

Darwin (1871) was convinced of the existence of female choice as part of sexual selection but only recently has the concept gained general acceptance. Adaptive female choice as part of sexual selection due to differences in the relative parental investment of the sexes (Trivers 1972) has been demonstrated in insects. Female *Drosophila* choosing outbred rather than inbred males produced four times the number of offspring of females choosing inbred males (Maynard Smith 1956). Thornhill (1976) found that female *Bittacus apicalis* (Mecoptera) chose males with large prey items as nuptial gifts for the female and that this increased the females' fecundity.

The principle of adaptive female choice has been established, the problem in many cases is to find out what females **do** actually choose when picking a mate.

The effect of female choice on territorial and lek behaviour was discussed by Trivers (1972). He pointed out that females tend to choose males which, by competition with other males, have already increased their chances of mating. Thus female choice augments the effects of inter-male competition. The reasons Trivers put forward to account for female choice of the dominant males are that by mating such males, that is those occupying a territory or a favoured place on a lek, a female can usually mate more quickly and a female also allies her genes with those of a male who by his dominance has demonstrated his reproductive ability and whose offspring may be expected to have the same ability.

O'Donald (1962) pointed out that if some females favour one type of male, determined by genotype, while other females mate at random, other things being equal, selection will rapidly favour the preferred male type and the females with the preference.

It is generally agreed that lek mating systems evolve due to female choice of the displaying males on leks. This follows from sexual selection theory that females will determine the mating system when males cannot either control them directly or those resources needed by them. Under these conditions the behaviour of the female will determine the mating strategy of the males, that is whether males search for females or display or use some other means to attract them. Females can choose when and where to mate and which males to mate and thus control the basic features of the mating system.

11:3. Theories of the evolution of leks.

There is an obvious disadvantage for a male in waiting near other males seeking females since he will have to compete with his neighbours for any females which come along. In lekking and swarming species males by their own behaviour aggregate and therefore produce this apparent disadvantage for themselves. It is generally found that lek species never mate away from the lek arenas and this must be highly disadvantageous for males because they are unable to take advantage of chance encounters with females away from the lek arenas and mate in the absence of competing males. In spite of these apparent disadvantages for lekking males they must have greater reproductive success than non-lekkers for the lekking trait to be favoured by selection. In order for lek systems to evolve both males and females having these mating behaviour patterns must have thereby gained higher reproductive success than those individuals not performing lek behaviour.

Five theories which attempt to explain the evolution of lek mating systems are discussed below and then a model of lek evolution is proposed which suggests that typical leks with a high degree of inter-male competition and mating swarms, such as are found in many species of Diptera, which appear to lack such intense competition have much in common and their evolution can be explained in similar ways.

1) Attraction of females by groups of displaying males.

Lack (1939), Snow (1963) and Hjorth (1970) suggested that leks evolve when the effect of a group of displaying males makes the display arena more conspicuous to females than the display of a lone male. Snow pointed out that if a group of n displaying males attracts more than n times as many females as a lone male then it is advantageous for a male to display in a group, unless other disadvantages such as predators outweigh this. Snow noted that group displays are more continuous and are therefore likely to be more effective than solitary displays and that mutual stimulation between the males enhances the displays that they produce.

Although this theory explains why males should display in groups it does not explain why females should be attracted to males which display and actively search for such males rather than waiting to be found by searching males. Also, at the start of a lek mating system, if intense inter-male competition on the lek results in very few of the males present getting most of the matings then there is no reason for those males which fail to mate to stay there and display. If they have a choice and can stay or go and can also recognise their lack of mating success they might do better to leave the lek and either to display elsewhere or to search for females.

2) Predation pressure.

Avoidance of predators has been suggested as the cause of lek behaviour by various authors, for example in birds by Lack (1968) and in insects by Spieth (1974). Enhanced detection of predators by groups of animals combined with the lessened risk to an individual in a group are postulated as the advantages of mating in leks. However it is difficult to see why predators should not take advantage of leks where their potential prey makes itself conspicuous by display behaviour. Wiley (1978) saw eagles attacking sage grouse at their lek site. Brown (1964) and Crook (1965) stressed that predator attraction by conspicuous displaying males is avoided by conspecific females and their young. Female grouse, ruff (Philomachus pugnax) and Uganda kob congregate on the central territories of leks (Hogan-Warburg 1966; Wiley 1973; Floody and Arnold 1975) possibly to reduce the danger of predation while on the lek arena.

Wittenburger (1979) pointed out that the leks of species living in dense forests where visual detection of predators could not take place over long distances, such as those of manakins (Snow 1963, Lill 1974) or hammer-headed bats (*Hypsignathus monstrosus*) (Bradbury 1977) do not seem likely to have evolved due to predation pressure.

If predation pressure were the cause of lek evolution then many more species already preadapted for the evolution of lekking would be expected to develop this mating system. Avoidance of predators seems unlikely to be able to explain lekking in all the diverse animal groups in which it is found.

3) *Genetic quality of males.*

Numerous authors have attempted to explain lek behaviour by postulating that females choose males in order to obtain genetic benefits from them for their offspring, see for example Williams (1966), Trivers (1972), Alcock (1975), Alcock and Pyle (1979) and Borgia (1979). Others have pointed out that if females choose males for their genetic qualities in highly polygynous mating systems, such as leks, then the genetic variance among males is rapidly used up and female choice for genetic benefits would no longer be adaptive (Williams 1975, Davis and O'Donald 1976). Lately Borgia (1979) has put forward a long argument in support of the genetic quality theory, suggesting that either females choose for heterozygosity in their offspring or that selective pressures change in each generation sufficiently for different males to offer advantages to females and also maintaining the required genetic variance. Borgia suggested that if heterozygous males are fitter than males with more homozygous loci and if females do not know their own genotype and so cannot choose a male to complement it then females should mate with the fitter and presumably dominant heterozygous males in order to produce offspring with the chance of having the maximum of heterozygosity. His alternative argument suggested that genetic variance is kept at an equilibrium value in a population by changing selective pressures in each generation so the predicted loss of genetic variance among males does not occur and since genetically different males are present in the population mate choice for genetic benefits by females is adaptive. Borgia proposed that females favour lek mating systems because they can compare many males which are and already have been tested by inter-male competition. Alexander (1975) similarly suggested females favoured leks because of the large number of potential mates to choose from at lek arenas.

The ways in which Borgia (1979) proposes genetic variance is maintained can be shown to be highly unlikely in both situations. In the case of heterozygous advantage if the female does not know her genetic constitution she may as well mate at random with males irrespective of the males' genetic constitution because on average one half of the offspring produced will be heterozygous when a heterozygous female, presumably favoured by selection, mates with a heterozygous male similarly favoured by selection. Only homozygous females benefit from mating with heterozygous males, but they would benefit more by mating with males homozygous for the alternative gene if they could detect the differences in their own and in males' genetic constitutions.

The genetic choice model cannot account for the maintenance of genetic variance by heterozygous advantage. The alternative explanation of changing selection pressures in each generation assumes that the relevant advantageous male genetic constitution is recognised by females in each generation. This would require females to possess a high degree of awareness of the prevailing selection pressures in the environment and of the male genotype best endowed to provide them with high quality offspring for a given environmental change. Such a situation seems inherently unlikely to occur.

There does not seem to be any means of sustaining the necessary genetic variance to maintain the adaptiveness of female choice based on this factor. The theory of genetic quality of offspring as explanation of female preference for lekking males cannot explain the evolution of lek behaviour.

4] Grouping of males' territories.

Bradbury (1979) proposed a process whereby leks resulted from the grouping of individual males' territories in certain favourable areas. Kimsey (1980), following this suggestion, asserted that the leks of orchid bees (Apidae) resulted from such a process. However it is difficult to see how either a male resource based territory or a solitary display territory could evolve into a lek territory with other territories close to it unless some advantage due to aggregation is present.
As a stage in the evolution of leks the facultative aggregation of individual display territories in favourable areas appears as a likely step in the process of development of the typical

small territories seen in leks. Although there is no obvious way in which resource based territories could change into non-resource based ones it seems likely that non-resource based display territories might occur in proximity to each other and that this could lead to the evolution of leks when a number of males displaying together enhances the effects of the males' display. When the effects of inter-male competition are reduced by those of aggregation leks may evolve.

5) Convenience for females.

Wrangham (1980) proposed that female choice has resulted in lek systems because for certain species this mating system has the least harmful effects on female reproductive success. Wrangham suggested that female choice of mate is adapted to maximising the females' reproductive success directly rather than to maximising the females' fitness by means of the genetic quality of offspring. He proposed that the evolution of female choice has depended upon how male behaviour affects female reproductive success. Males can help females by male parental care, they can harm females by interference with matings or with offspring or they can be supposedly neutral in their effects on females.

Wrangham (1980) noted that classical leks are often assumed to occur when males are apparently neutral in their effects on females and can provide only supposed genetic benefits. He proposed that males in lekking species are not neutral in their effects on female reproductive success and since males cannot offer positive benefits to females, disregarding hypothetical genetic ones, that the basis for female choice is avoidance of the costs imposed by males in their mating behaviour. Wrangham's argument is that males impose costs on females if females do not prevent matings except when at lek sites chosen by the females. Females are envisaged as choosing those males as mates which do not impose such costs but conform to the behaviour pattern desired by females. A female allowing a male to mate at a feeding site or elsewhere on her home range is rewarding the male for his presence and will attract other males, thereby increasing male harassment of females. Females will benefit by refusing to mate at these places as long as it is less costly for them to go and visit males at leks for mating. Males are thus viewed as potential hazards due to their persistent attempts at mating if they move freely on females' home ranges as well as potential competitors for food.

This explanation of the evolution of lek behaviour has implicit in it the idea that females either teach males to stay out of the females' home ranges by refusing to mate there and so restrict males' mating activities to the lek arenas or that males which do not molest females on females' home ranges have a higher reproductive success than males which attempt to mate with females found on their searches while searching is still the dominant male strategy for finding mates. It is difficult to see how females could teach or otherwise cause searching males not to attempt to mate them if this was the mating system dominant in the species at the time. There is no apparent advantage for the male in waiting to be found by a female rather than actively searching for females if all other males search for females and most females accept the searching males as mates. Similarly the consequence for a female of refusing to mate with searching males is almost certainly that she will not mate at all. Unless the change in male behaviour from searching to displaying and the change in female behaviour from waiting for a male to searching for displaying males occurred at the same time and individuals with this altered behaviour were more reproductively successful then the rest of the population lekking will not evolve by this process. It is difficult to see how these changes could all happen at the same time and therefore it is unlikely that leks evolved due to the causes suggested by Wrangham (1980).

11:4. Female choice of mate in lek systems.

The choice of dominant males, usually the older males present, so often seen to be part of female behaviour at leks, is probably due to females choosing males able to protect themselves from attacks by other males during mating, thereby also protecting the females that they are mating with. Females thus avoid injury during inter-male fights. Borgia (1981) found that females of the yellow dung fly (*Scatophaga stercoraria*) probably prefer to mate with larger males for the protection they provide against attacks by other males. It is not necessary to suppose that females are choosing older males because they have survived to a certain age, so demonstrating supposed genetic superiority, Rather that older males, being larger and more experienced than younger males in lekking species such as many grouse, are dominant on leks and would disrupt matings by younger males. Wittenburger (1978a) considered that large size in male grouse is selected for due to inter-male competition and Wiley (1974) found that female grouse choose older males because males become more experienced in courtship as they get older and females choose on the basis of courtship behaviour.

Trivers (1972) suggested that females choose dominant males in order to speed mating and thus minimise the time spent on leks. However, as Borgia (1979) pointed out, females may spend some time on leks watching and displaying to several males, see for example Lill (1976). Borgia took this to imply that females were assessing males for their genetic qualities exhibited in their display and courtship. An alternative interpretation is that females are assessing each male's status before risking mating, so that they can be sure of choosing a male which can protect them during copulation. Safe mating does not necessarily mean minimising the time spent on the lek by females.

Courtship displays between males and females on leks may be prolonged in order to reduce mutual fear and aggression in those species where males are large and aggressive, as are the males of lekking species of grouse. Females may need to appease a male before approaching him for mating so as to be sure that their potential mate will not attack them. In lek species where the sexes meet only for mating such a function of courtship seems especially likely to be important. Assessment of different males' genetic qualities does not need to be invoked to explain these aspects of female behaviour on leks.

11:5. A model for the evolution of lek and swarm behaviour.

The essential prerequisite for the evolution of leks and swarms, that is aggregations of displaying males, is that a displaying male gains more matings than a male employing any other strategy for mate acquisition. Unless male display is the means of gaining mates there is no way for aggregations of displaying males to develop because there will be no displaying males to form the groups. Therefore the first problem is to explain why males display rather than employing other strategies for obtaining mates.

a) Displaying males. When direct control of females or of essential female resources is not possible for individual males then males must either search for females or display to attract them. Displaying will be favoured when search costs involved in finding receptive females for fertilisation are high. High search costs for males will occur when females are unpredictable in occurrence and even when found are likely to be unreceptive or perhaps already mated. If females behave cryptically and are also cryptically coloured then a searching male faces the same problems as a predator, unless the female signals in a species-specific manner to attract him. During his searching a male also faces the risk of predation. Thus when males' search costs are high displaying males will have greater reproductive success than searching males if females are attracted by their display.

A female of a species with high male search costs for finding mates may experience a long delay before a male finds her and mates with her. Females should reduce their waiting time for mating if they can. Therefore in highly mobile species females which reduce their waiting time for mating by searching for and mating with displaying males will be favoured by selection and will have a higher reproductive success than females which wait to be found.

Thus male display to attract females should evolve when males' search costs for finding females are high and females are mobile and can reduce their waiting time for mating by going to males. When males display in certain conspicuous places where females are likely to see them as the females move around their home ranges the costs to females of finding mates are reduced even more. Thus males should display in conspicuous places to increase their chance of attracting females. Females will benefit by being able to find conspecific males capable of mating in certain places and therefore be able to rely on a suitable mating when in breeding condition rather than having to wait for a male and perhaps miss the chance of breeding because of the lack of a mating.

This system would be expected to result in males displaying in individual non-resource based display territories which they defended against other males so as to mate with all the females attracted by their display, unless other factors led to the aggregation of males.

b) Aggregations of displaying males. Both leks and male swarms can be considered as resulting from the same process of aggregation of males. The differences between them in the degree and nature of inter-male competition within the groups must develop after aggregation occurred.

When the number of males in an area is higher than the number of suitable display territories a time should come when a male will choose to share an already occupied territory following a certain time spent searching (Baker 1972). Similarly when a growing density of males occupying territories is encountered in an area by a male searching for a territory the advantage of sharing a territory with another male increases, until at a certain density of males in an area a male should join a male already occupying a territory rather than continue to search. If a male responds to the density of males in an area rather than the time spent searching he will not waste time on fruitless searching for an unoccupied territory when the density of males indicates that there a likely to be very few to be found. This argument is shown in Fig. 11:1 where, as the number of occupied territories (N) increases until at density of males D there are almost no unoccupied ones remaining, the advantage to a male of sharing a territory (Ad) increases until at density D it outweighs the disadvantages of sharing females because of the excessive search time needed to find a vacant territory.

Another effect dependant on the density of males in an area affecting the behaviour of males occupying territories will also result in sharing of territories. Following the argument presented by Otte and Joern (1975) the effect of increased male density on a occupying male will be an increase in his defence effort until all his time is spent on territorial defence and none on mating females. This argument is shown graphically in Fig. 11:2 where with defence effort DE1 rising to 100% a male's female quota FQ1 falls to zero. Therefore to maintain his reproductive success a male should reduce his defence effort above a certain density of males. This is shown by defence effort DE2 in Fig. 11:2 which falls off at high male density in order that the

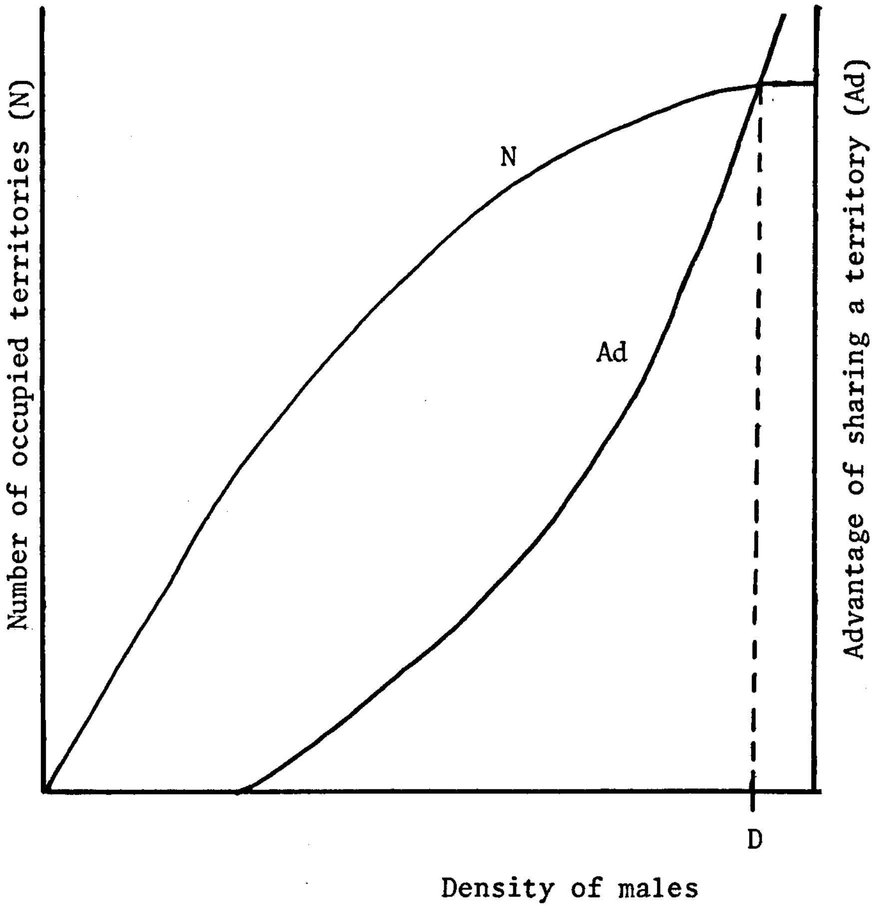


Fig. 11:1. The influence of the number of occupied territories on males' behaviour.

The advantage of sharing a territory (Ad) equals the difference in the time spent searching for a territory between a male searching for an unoccupied territory and a male prepared to share an already occupied territory. The greater the number of occupied territories the higher is the search time for a vacant one and the greater is the advantage of sharing a territory in order to reduce search time.

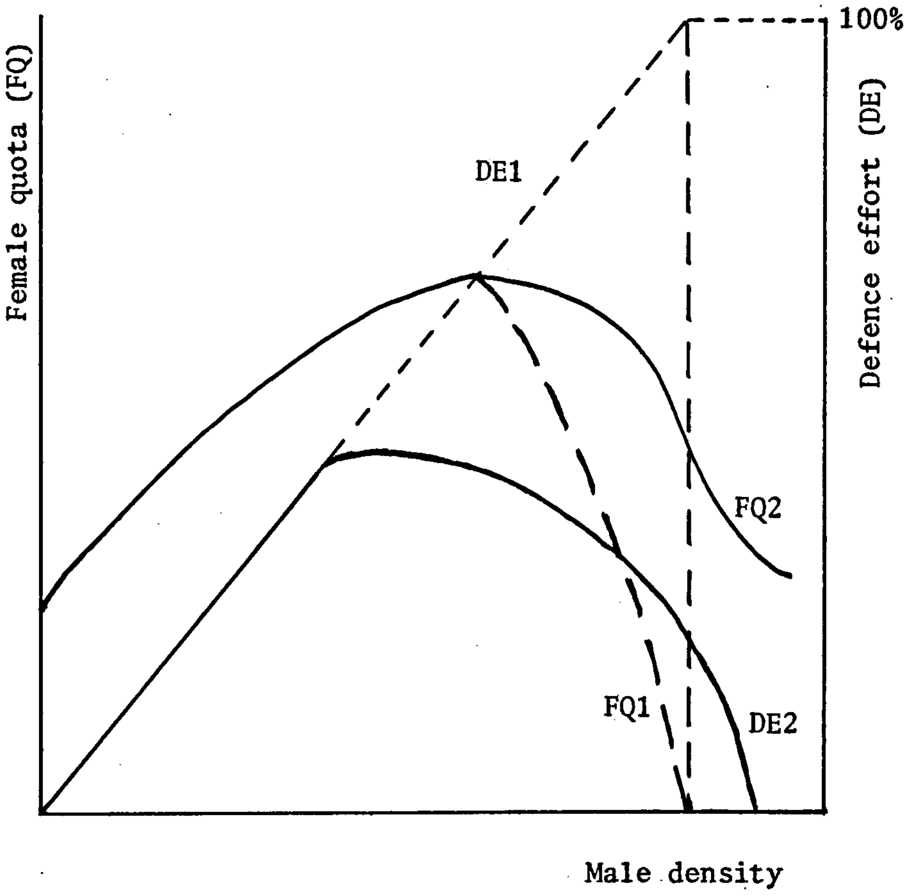


Fig. 11:2. The influence of territorial defence effort on the female quota of males (after Otte and Joern 1975).

female quota FQ2 does not drop to zero. The reduction in female quota in this case comes not from the male expending all his time on territorial defence but from the sharing of his territory with other males and the resulting sharing of the females which are attracted to the territory.

This effect of reduction in territorial defence by males assumes that all males in the population behave in the same way in maintaining the optimal female quota they obtain given the conditions of male density prevailing at the time. When the level of defence effort drops to zero the result will be a swarm of males in a display area waiting for females and approaching them for mating when they arrive.

In certain areas with many suitable sites for display territories males may become facultatively aggregated on nearby sites, not grouped as a result of sharing territories. This effect of facultative grouping was suggested by Bradbury (1979) as a step in the evolution of classical leks. Individual males may still defend their separate display arenas, but some effects resulting from the grouping of territories may occur.

When groups of displaying males, occurring for either reason of increased male density or grouping of suitable display sites, begin to attract more females than lone males due to the enhanced stimulus effect of large male groups further aggregation of males for display purposes will result. Snow (1963) suggested that leks evolve when a group of n displaying males has more than n times as great an attacting power on females than a lone male has. The attractiveness of a group of displaying males to females will depend upon the number of males in the group up to a certain limit beyond which its attractiveness will increase only by relatively small amounts when more males are present. The power of attraction of a group will also depend upon the conspicuousness of the display arena apart from the number of males in it. When both of these factors are combined so that attractiveness of a group (A) depends on the number of males displaying in it and a factor derived from the conspicuousness of the display site, the number of females attracted per displaying male, the average female quota for each male in the group (FQ), will reach a peak at a certain number of males (Nm) for any particular group. This is shown in Fig. 11:3 from which it can be seen that at Nm the males have their optimal attractiveness in terms of females attracted and matings obtained. Therefore if males are to gain the maximum number of matings as a result of females being attracted to displaying groups the number of males at a particular display arena should have an upper limit, which will depend in part on the inherent conspicuousness factor of the arena. Male display groups in different sites will be expected to have different optimal sizes. The optimal size of a group will depend on the number of males in any particular area from which the members of displaying groups in that area are drawn and males within the area should move from a group if it exceeds the optimal size for the conditions of male density occurring at the time. Clearly the larger the population the larger is the optimal size and the smaller the population the smaller the optimal size, due to there being a limited number of suitable display sites. At the optimal size a male in any particular group will have the same female quota as a male in any other group.

This effect will produce aggregations of males in displaying

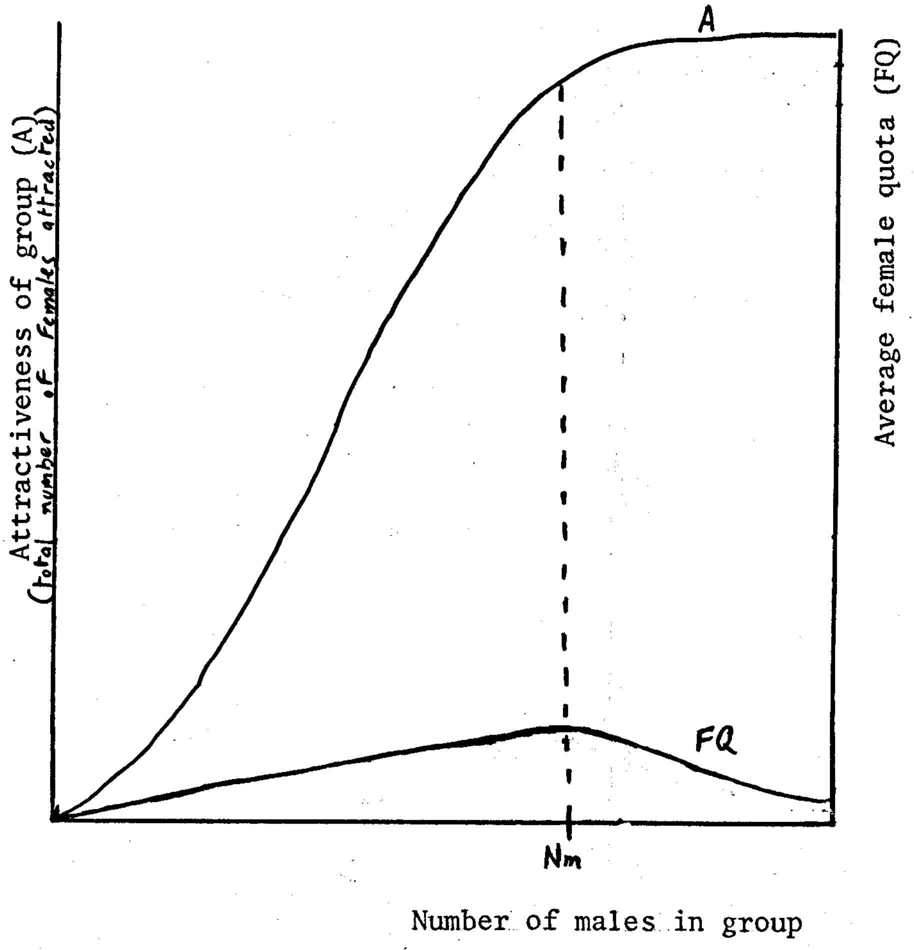


Fig. 11:3. The effect of a group's size on its attractiveness to females and on the female quota of the males in it.

groups the nature of which, that is whether they are leks or swarms, will depend on the presence or lack of inter-male competition for places in the groups, an effect dependant on the possibility for territorial defence by individual males as discussed above. Aggregations with no inter-male competition for places within them are usually described as swarms, although there may be competition within the swarm for the most advantageous positions and for females coming to the swarm to mate. Aggregations of males where there is inter-male competition for display sites within the display arena are usually classified as leks, here the size of the display arena puts an upper limit on the number of males which can display in it, because each male requires a certain amount of space which he defends as his display territory.

The interrelationships of solitary displaying males, swarms and leks as proposed by this model are shown in Fig. 11:4., a change in any of the factors involved, which mainly depend on the density of males forming the groups, will result in an appropriate change in the pattern of aggregation.

Leks are usually associated with complex ritual behaviour by males forming part of inter-male competition for display territories. These behaviour patterns must develop due to sexual selection acting on the males after the original formation of the display aggregations. Thus those features of male behaviour and morphology used in inter-male competition are expected to result from direct selection acting on males. However female choice of males for characteristics used in display which attract females will be selected for by sexual selection due to female

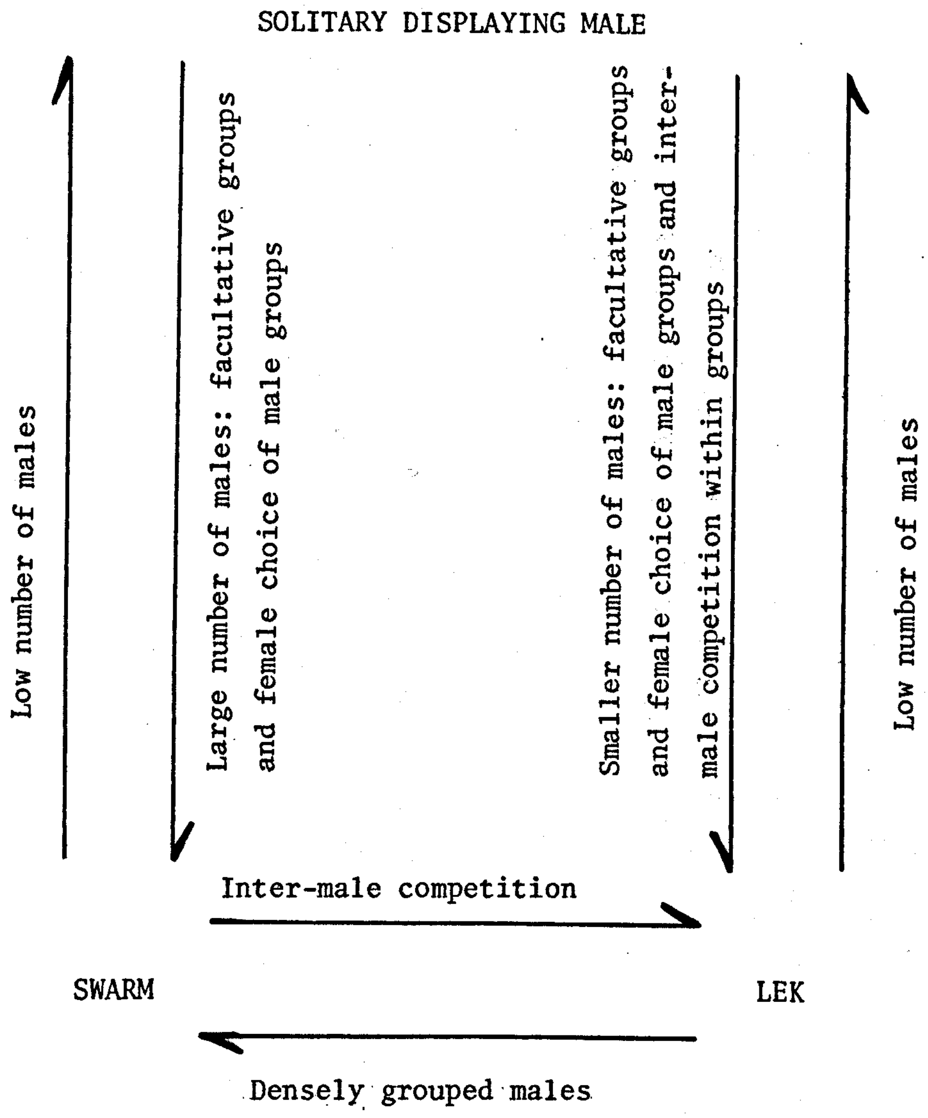


Fig. 11:4. Proposed relationships of solitary displaying males, swarms and leks.

choice. Those male characteristics involved in sex and species recognition seem most likely to be chosen by females as a means of ensuring conspecific mating. Female choice of such features of male morphology and behaviour will be expected to lead to exaggeration of these characteristics.

11:6. Evidence for the model.

Most displaying aggregations occur in open areas so as well as enhancing the conspicuousness of the males' display to increase the attractiveness of the group such groups should also help in the detection of predators (Lack 1968, Powell 1974). Even if aggregations attract predators the use of conspicuous sites, usually traditional ones, should offset any reduction in the males' life expectancy whenever the propensity of females is to mate at such sites (Wittenburger 1978a). This effect of increased predator detection is often taken to be the cause of lek behaviour. Wittenburger (1979) suggested that predation pressure may explain why leks occur in open country game birds which all display in groups while those in forests display alone (see for example Koivisto 1965; Hjorth 1970; Wiley 1974; Wittenburger 1978a). Wittenburger (1979) suggested that this correlated with increased ability to detect predators in open country by large groups and the lesser ability to detect predators in forests due to decreased visibility. However it might be argued to the contrary that if leks evolve to enhance predator detection then they would be as important, if not more important, in forests where predators would get closer to displaying males before being seen, Groups of males in forests should be able to provide the increase in predator detection to safeguard their members as they are supposed to do in open country.

An alternative view to explain why males display in groups in open country but singly in forests is that suitable display sites tend to be scattered in forests, resulting in solitary display, but grouped in open country allowing many males to gather on them. Also the effect of enhanced display by males in groups will not be so important in forests where visibility to females is lower compared to the effect of group display in open country.

Wittenburger (1979) took the observation that lek size did not correlate with average male copulatory success (Koivisto 1965; Hogan-Warburg 1966; Lill 1976) as evidence against the effect of enhanced attractive powers of male groups. However increased lek size will not be expected to result in increased male copulatory success on the basis of the model proposed in 11:5 because any lek attracting more females than another will be expected to increase further in size until the average female quota of males in both leks is the same. Males will be expected to move to a lek offering them a higher female quota than the one they are in. There is no reason why young game birds should not move between the leks in their home range and assess the average female to male ratio at each and then join the one having the highest ratio when they are ready to mate, in those species where males return to the same lek year after year. In other lekking animals males may be expected to move from lek to lek to assess the relative female quotas and to join those giving high female quotas.

The size of a lek in terms of the number of males does not determine the attractiveness of the lek to females by itself. Factors due to the conspicuousness of the site also will result in differences in attractiveness and therefore in average male copulatory success on any particular lek irrespective of the number of males there. Therefore the observation that lek size does not correlate with average male copulatory success is in keeping with the model of lek evolution proposed in 11:5.

The behaviour of M. autumnalis males when swarming on marker-objects is predictable on the basis of the model for the attractiveness of different sites. The densest groups of males were found on the most conspicuous marker objects, both factors would be expected to result in such males having the greatest power of attraction to females. On less conspicuous objects fewer males were found, such groups would be expected to attract fewer females. Around conspicuous marker-objects scattered males were found spaced out in groups, these males would be expected to have the least attractive power on females. Thus more males were generally found to be perched on the more conspicuous marker-objects and although the female quotas of the male groups is not known the aggregation pattern fits in with the concept that the average female quota for a male in each group being approximately the same. Also male groups on any marker-object rarely exceeded about twenty in number, the effect predicted by the model that male groups should not exceed a certain maximum number because when this number is exceeded the average female quota of the males in the group falls.

The model predicts that solitary males will display at the swarm or lek arenas when the population is low. This is seen in M. autumnalis where solitary males were sometimes found away from large male groups on isolated marker-objects. Also Downes (1958) noted that no gregarious factor is needed to initiate swarm formation in swarming nematoceran species, individuals perform the swarm flight when they encounter the swarm-marker. Similarly in the lekking species described in this thesis no gregarious factor initiates the formation of male aggregations. They occur when the number of males in an area is high enough to result in the occupation of suitable display territories which are close together.

M. autumnalis fits the prediction that males occurring in high numbers will form swarms to attract females with no inter-male competition for individual display territories due to the impossibility of territorial defence at high male density. Of all the species studied and described in this thesis M. autumnalis was the only one typically found in such large numbers at its mating sites that this effect would be likely to apply.

11:7. The leks and swarms of calypterate Diptera.

In all the species described in this thesis except M. autumnalis facultative grouping of males' display territories seems to be the cause of leks. Certain places or marker-objects provide display sites for more than one male and so males aggregate in such areas. Only in M. autumnalis does the effect of many males attracting more females than lone males when perched in a group on a conspicuous marker-object appear to affect the males' behaviour.

The swarm and lek arenas of the six species described in this thesis which mate out of doors, with the exception of S. calcitrans, are always in sunlit areas. Parker (1978) suggested that sunlit leks in the Diptera may have arisen because of the need of females to increase their body temperature in order to increase the rate of conversion of food into ova. Males would then be attracted to such sites because of the presence of females there. Parker suggested that this then resulted in harassment of the females by males and caused the females to stop going to sunlit sites except when ready for mating. However it would seem to follow that males should accordingly search for females elsewhere when the females were no longer to be found at sunlit places.

The use of sunlit areas as territories and swarming sites by male flies and also by male butterflies (Davies 1978) suggests that these sites are used by the males to increase their body temperature so as to be able to fly more rapidly in pursuit of females, as proposed by Heinrich and Pantle (1975) for syrphids.

11:8. Summary and conclusions.

Leks are areas where males aggregate and display in order to attract females for mating. In a lek each male defends his display territory against other males. Usually only a few of the males on a lek perform almost all of the matings due to the effect of inter-male competition.

Female choice is an important part of sexual selection and tends to augment the effects of inter-male competition in lek species.

Five theories of the evolution of lek mating systems are discussed. These are that groups of displaying males have a greater attractive power than lone displaying males; that predation pressure has resulted in the evolution of leks for enhanced detection of predators; that females prefer large groups of males to choose a mate from because they can compare many males and choose as mates those which have superior genetic qualities to aid females' reproductive success; that leks evolve by the facultative grouping of males' territories in favourable areas; that leks evolve because females refuse to mate elsewhere in order to avoid harassment by searching males.

The observed female choice of older dominant males often found to be characteristic of vertebrate lek systems is considered to result from the requirement of females for a safe mating uninterrupted by other males with the possible danger of injury during inter-male fights as a consequence on interruption. The dominant males should be able to provide protection against other males. Females display to a succession of males in some species to determine each male's status. Courtship displays between males and females also allow for the reduction of mutual fear and aggression.

A model for the evolution of swarms and leks is proposed. It is suggested that males display rather than search for mates in some species because of the high search costs involved in finding mates. Females choose to mate with displaying males in order to reduce the time they spend waiting for mating. When the defence effort to maintain an individual display territory is high and the search costs to find an unoccupied territory are also high due to a high male density males will share territories and so groups of males will occur. Also facultative grouping will occur when suitable display territories are found within a small area. When groups of males occur the enhanced stimulus of their combined display may attract more females for each male than a lone male will attract. This will lead to further aggregation by males until the effect of increased female quota is no longer effective due to the size of the group and the average female quota of the males begins to fall as more males join a group. Therefore there will be an optimum number of males in any group at a particular aggregation site because the attractiveness of the group will depend on factors affecting the conspicuousness of the display site to females as well as the number of males there. The interrelationships of solitary displaying males, swarms and leks are discussed.

Observations on lekking species of birds and the Uganda kob antelope are discussed in relation to the model. Observations on swarming and lekking species of flies are considered. Although other interpretations are possible the available information does not contradict the lek and swarm behaviour predictable from the model proposed.

The use of sunlit areas as display sites by certain species of calypterate flies is considered to have resulted from the males' need to raise their thoracic temperature so as to be able to flt rapidly in pursuit of females for mating.

Display sites will be chosen by males in order to maximise their female quota and hence their reproductive success.

In many species of Diptera males display to attract females because females are unpredicable in occurrence, receptivity and mating status. This has led to the evolution of swarms and lek territoriality. The mating systems of the seven species of calypterates described in this thesis have resulted from this evolutionary process.

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