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DOCTOR OF PHILOSOPHY

Genetic and environmental factors in the migration of the African armyworm moth, *Spodoptera exempta* (Walker) (Lepidoptera :Noctuidae).

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Award date:
1987

Awarding institution:
Bangor University

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GENETIC AND ENVIRONMENTAL FACTORS
IN THE MIGRATION OF THE AFRICAN ARMYWORM MOTH,
SPODOPTERA EXEMPTA (WALKER) (LEPIDOPTERA : NOCTUIDAE).

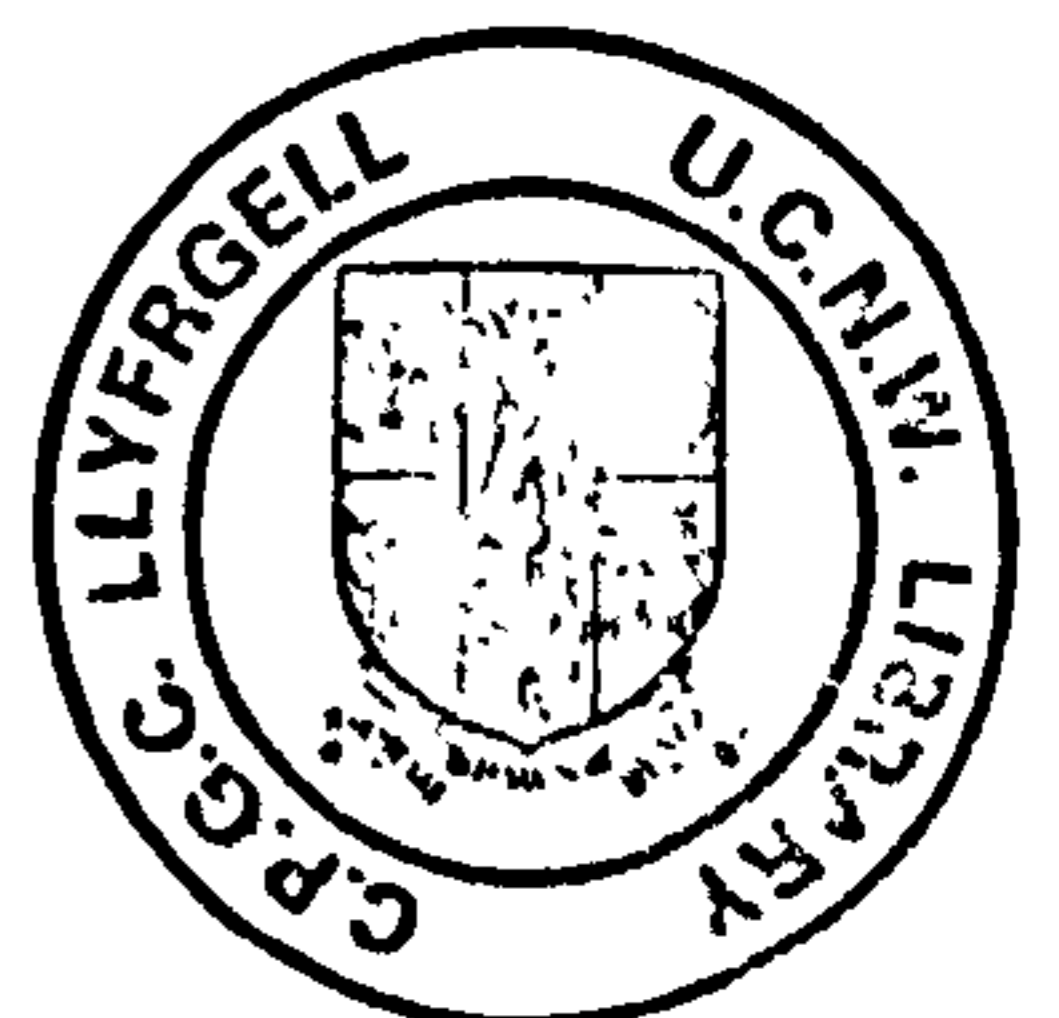
A thesis submitted for the degree of
Doctor of Philosophy

by

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September, 1987.



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SUMMARY

The tethered-flight technique used previously for studies of the factors regulating the flight performance of Spodoptera exempta moths was improved and developed to increase reliability and incorporate computerised datalogging permitting faster and more extensive analysis.

Larvae of S. exempta show a density-dependent phase polyphenism and the effect of larval phase on adult flight was examined. A consistently greater flight performance was observed in female moths reared as gregaria larvae compared with those reared as solitaria, but no significant effect was found in males.

The distribution of flight durations was examined and found to be log-normal. Using normalised data the heritability of flight duration was estimated in a number of strains. Significant heritabilities were obtained for flights beginning before, but generally not after, midnight when radar observations in the field have shown flights achieving substantial displacements to occur. It is suggested that prolonged flights in the laboratory which start before midnight and whose durations are under genetic regulation represent migratory flights in the field. Shorter flights, particularly those starting after midnight, achieve local redistribution of moths, some of them possibly representing the "pluming" behaviour observed using radar.

Flight duration was shown to respond to selection for both short and long flight. The F1 generations of the lines of four strains selected for increased flight capacity revealed a bimodal distribution of flight durations indicating two types of moth. It is suggested that a major gene could account for this effect and that the longer fliers represent potential migrants while the shorter fliers are capable only of flights achieving local dispersal.

The effect of flight on the fecundity of females was examined. It was found that in moths subsequently fed water (necessary for oocyte development), a decrease in fecundity resulted which was related to the duration of flight. In moths fed sucrose fecundity was maintained at the level of unflown moths.

These results are discussed in relation to the behaviour and ecology of S. exempta in East Africa and the prospects for the success of a regional approach to its control.

CHAPTER ONE
General introduction.

The African armyworm, Spodoptera exempta, is an endopterygote insect of the order Lepidoptera and the family Noctuidae. The success of this order, which contains more than 100 000 species (Richards and Davies, 1977) appears to be associated with the evolution of higher plants, and especially angiosperms (Common, 1970). The characteristic haustellum (proboscis) of adults, found in no other order, allows the easy uptake of water and facilitates the use of the carbohydrate contained in nectar, which many species are able to convert to fat (Common, 1970). Larvae of the Lepidoptera are predominantly phytophagous and species from many families are economically important pests e.g. armyworms, bollworms and cutworms (Noctuidae), leaf-miners (Gracillariidae), leaf-rollers (Tortricidae) and webworms (Pyralidae) (Common, 1970).

The Noctuidae contains more described species than any other family of the Lepidoptera (Richards and Davies, 1977; Brotherton et al., 1983). Members of the family are remarkably uniform in structure and habits (Richards and Davies, 1977). The moths are largely nocturnal and are often avid feeders at flowers, being attracted also by "sugaring" by entomologists (Brotherton et al., 1983). Few species are pests in Britain (Brotherton et al., 1983) but, worldwide, members of the Noctuidae cause widespread and economically important damage to crops and pasture. For example, larvae of the bollworms, Heliothis armigera, H. punctigera, H. zea and H. virescens attack cotton, lucerne, linseed, maize and tomatoes (Common, 1970). Cutworms (Agrotis spp. - so called because their larvae often bite through the

stems of plants at the base and so fell them (Baker, 1983)) are well known, nocturnally active pests in Australia and North America (Common, 1970; Richards and Davies, 1977). The U.S.A. also suffers damage to cereals and grasses from the true armyworm Pseudaletia unipuncta, and Australia from the armyworms P. convecta, Spodoptera litura and S. mauritia (Common, 1970; Richards and Davies, 1977).

S. exempta, the African armyworm, has been recorded throughout Africa and the Pacific as far east as Hawaii. Haggis (1984; see also Haggis (1986)) has comprehensively reviewed its distribution and has compiled a worldwide distribution map showing the occurrence of larval infestations or moths recorded in one degree squares of latitude and longitude (c. 12 000km²). The map shows the widespread distribution of the species throughout Africa and southwestern Arabia south of the Saharan and Arabian deserts. Records of the insect's occurrence are not uniformly spread, however, with no records of the species from Benin, Equatorial Guinea, Chad or the Central African Republic and moths but no larvae have been identified in Togo, Ruanda and Djibouti.

To the west of Africa, the only record is of a single moth taken on the island of Sao Tome, west of Gabon and south of Nigeria. Off the east coast, larval infestations have been reported from Zanzibar and Mafia Island (close to the Tanzanian coast) with moths but no larval infestations reported from Madagascar. Larval infestations have been reported from somewhere in Africa in almost every year since 1919 although there has been a general increase in the number of reports since

1945, particularly from West Africa.

Reports from the countries abutting, and islands of the Indian and Pacific Oceans are generally more scattered in space and time, although again a marked increase in the reports of infestations and moths has occurred since 1965. In particular, increases and new records have been reported from Papua New Guinea, the Philippines, the Solomon Islands, New Caledonia, the Northern Territory of Australia, New Zealand, Japan and the Cocos-Keeling Islands in the Indian Ocean.

Although the increasing number of reports may be due in part to better communications and awareness of the pest, it has also been suggested that climatic change or more extensive deforestation and irrigation projects, with subsequently increased areas of grassland or crops, may be producing a real increase in the occurrence of infestations (Baker, 1978; Rainey, 1981; Haggis 1986).

Females appear to exercise little choice of oviposition site in the field and have been observed ovipositing on dry grass stems in the presence of lush grasses, on bushes and trees in the presence of grasses and on poles and fences. Some preference seems to be expressed for high vegetation, irrespective of type, perhaps to allow for greater larval dispersal (Hattingh, 1941; Page, 1985).

A single egg batch laid by a female S. exempta moth will hatch within a few hours, at least in the laboratory. If undisturbed, the larvae will remain on their egg shells which they will begin to eat within a few minutes of hatching

(Hattingh, 1941). After about six hours they will begin to walk away from the oviposition site in a looping gait and with no observable gregarious behaviour, so that they disperse in all directions (Hattingh, 1941). Whellan (1954) easily located hatched egg masses in the field but seldom found larvae near them, indicating rapid dispersal of the larvae. If, at any time while the egg shells are being eaten or afterwards, the larvae are disturbed by vibration of the substrate (e.g. a plant leaf) or the wind, some will immediately fall from the substrate to which they have usually attached themselves by fine silken threads (Hattingh, 1941; Whellan, 1954). By doing so they will probably encounter lower level vegetation which is likely to be composed predominantly of grasses and, particularly after recent rainfall (which will be seen to be relevant later), young grasses (Whellan, 1954; Brown, 1962). As well as resulting in a more gentle landing (Whellan, 1954), the threads often break and act as parachutes so that the larvae are carried by the wind and experience far greater dispersal than they would do by walking alone (Hattingh, 1941; Brown, 1962).

A list of food plant species may be found in Brown (1962) with additions in Brown and Dewhurst (1975), Baker (1978) and Yarro et al. (1981). The larvae appear to be able to feed on almost all grasses (family Gramineae) (Brown, 1962) although they do show some preferences, especially for the common weed "star grass" Cynodon dactylon (Yarro, 1982). Yarro (1984) also states that at 25°C and 70%R.H. larvae reared on C. dactylon, Zea mais and Kikuyu grass (Pennisitum clandestinum) develop through five instars while those reared on guinea grass (Panicum maximum) and

Setaria plicatilis develop more slowly and pass through six and seven instars respectively. Cultivated Gramineae on which the larvae have been recorded as feeding include oats (Avena sativum), finger millet (Eleusine caracana), kaffir millet (E. indica), barley (Hordeum vulgare), rice (Oryza sativa), sugarcane (Saccharum officinale), rye (Secale cereale), millet (Sorghum spp.), wheat (Triticum vulgare), maize (Zea mays) and various forage grasses. The most important of these in Africa are, perhaps, maize and the forage grasses (Brown, 1962).

The only other plant family on which African armyworm larvae appear to feed, other than very rarely, are the Cyperaceae (the sedges). In Hawaii, where larval infestations are reported in most years, the armyworm is so often found on Cyperus rotundus (Nut-grass) that it is commonly called the Nut-grass armyworm (Faure, 1943).

Other families, members of which have been rarely observed as host plants, are the Compositae (e.g. sunflower), Convolvulaceae (e.g. sweet potato), Iridaceae (e.g. Montbretia spp.), Leguminosae (e.g. groundnuts), Liliaceae, Malvaceae (e.g. cotton), Musaceae (e.g. banana), Rubiaceae (e.g. coffee) Solanaceae (e.g. potato, tobacco) and Palmae (e.g. Dwarf variety of coconut).

The larvae of S. exempta are usually only seen when they occur in the high densities which result from the concentrated oviposition of a large number of moths in an area. Such infestations, or outbreaks, are commonly composed of larvae at densities of up to 300m^{-2} , although up to $1000\text{ larvae m}^{-2}$ have

been recorded, and may cover several thousand Km² (Tucker et al., 1982). Odiyo (1979) reported an outbreak with a mean density of 28 larvae m⁻² which covered 65 Km² of rangeland. He estimated that during the week of the final instar, they consumed 50 000 Kg dry weight of herbage per day (based on a consumption of 200mg dry weight of maize per larva per day), a feeding rate equivalent to 8000 cattle. It is in these high densities that the larvae inflict significant damage to crops or grasslands, even to the point of completely destroying their host plants in the area (Swaine, 1963), with, frequently, the consequent starvation and death of some or all of the larvae. If this occurs early in the growing season farmers may replant their crop but with a greater risk of failure if the rains are inadequate (Odiyo, 1979). It is in response to starvation that the larvae "march" across the ground from which the common name of armyworm is derived. In fact groups of larvae do appear to move in the same direction - march together - but there is no evidence of true gregarious behaviour (Rose, 1979).

Larvae in outbreaks are typically of the gregaria form (see Ch. 3) and have black bodies and head capsules, with off-white longitudinal body stripes laterally and dorsally. Ventrally they are apple-green. These colours develop fully by the fourth instar, young larvae being pale grey-green in appearance and becoming darker with each moult (Rose, 1979). The larvae may appear particularly black after moulting and pale before the next moult due to expansion of the larval cuticle.

Larvae are also known to occur at such low densities that they are difficult to find (Rose, 1979; Gatehouse, 1986). Faure

(1943) reported a number of fruitless searches for these solitaria form larvae (see Ch. 3) in areas of young grasses, especially Cynodon dactylon, totaling more than 260 man hours. The only solitaria larvae he found on his numerous field trips were one fourth and one fifth instar larva in a dense stand of C. dactylon on the banks of a river during a search lasting 1.08 man hours. Rose (1979) reported finding a few larvae in most years from 1955 to 1977 after extensive searches in Rhodesia, and that small numbers had been recorded in Kenya every year from 1974 to 1977. Others have been found occasionally by entomologists throughout East Africa. Odiyo has also reported low numbers of moths in national network traps over many months of the year in areas where outbreaks have not been reported (Odiyo, unpublished reports, cited in Rose et al., 198-).

Solitaria larvae from low density populations differ in appearance from those found in outbreaks. They vary from green or green and pink to brown with brown head capsules. They also differ in behaviour. Whereas larvae in outbreaks are active and feed high on their host plant low density larvae are sluggish and feed low down in the sward. They also differ in a number of physiological characteristics (see Ch. 3). Faure (1943) described these different larval forms as "phases" by analogy with locusts and it was he who termed the high density form the gregaria phase and the low density the solitaria. He also described intermediate forms between the two extremes and which he termed the transiens phase.

Solitaria larvae may actually be found at quite high

densities during seasons of armyworm outbreaks, provided they are in a thick mat of grasses so that they do not encounter one another in the early instars (Rose, 1979). For example, Whellan (1954) found solitaria at a density of 75 to 150m⁻² and Rose (1979) at densities of 54 and 100m⁻² on pasture.

The egg, larval and pupal developmental periods are very temperature dependent. Hattingh (1941) reports periods of 72h, 28-37 days and 19-21 days at 70°F (21°C) and 28-30h, 10-15 days, and 6-8 days at 90°F (32°C) for eggs, gregaria larvae and pupae respectively. At 60°F (16°C), eggs took nine days to develop and all of the larvae (n=760) died, the last after 27 days. At 50°F (10°C) all the larvae (n=700) had died after only 14 days. Figures by other authors are given by Brown (1962) and are consistent with those of Hattingh, although the data are often incomplete.

In outbreaks the larvae are easily overlooked during the first two or three instars (Swaine, 1963) but, later, they become obvious at outbreak densities and so may seem to have appeared very suddenly. Their development is quite synchronous (Rose et al., 198-) and leads to the great majority of the larvae burrowing down into the soil to pupate over a few days, so that they seem to disappear as rapidly as they appeared. For this reason the armyworm has been given the common name of "mystery worm" in Zimbabwe (Rose, 1979).

Adult eclosion usually occurs during the first half of the night (Rose, et al., 198-). The imagos burrow to the surface, climb any available vertical object on which they hang and inflate their wings. They are capable of flight within

approximately two hours (Brown et al., 1969). The pre-oviposition period has usually been found to be between two and seven days (Whellan, 1954; Brown, 1962) although oviposition on the night after emergence has been reported (Brown et al., 1969). Pre-oviposition period is affected by temperature (Faure, 1943) and Page (1985) has suggested that some of the variance shown is genetic.

Eggs are laid in a mass, often in two or three layers and covered in black hairs from the tip of the female's abdomen. Females may lay one or more batches of eggs in a night. Batches vary in size, typically 200 to 400 eggs (Brown, 1962) on the first and second nights of oviposition, decreasing on later nights to perhaps half a dozen (Page, 1985). Typical fecundities of 200 have been quoted with a maximum of 682 eggs (Brown, 1962) although Page (1985) cites a potential of 1000 eggs. In this laboratory a fecundity of 1200 eggs has been recorded although it is commonly half this number.

The spatial and temporal pattern of occurrence of outbreaks, both within a year and from year to year, has been the subject of intensive investigation with the dual aims of accurate forecasting and control (e.g. Brown et al., 1969)

An excellent sequence of 12 maps, one for each calendar month, showing the frequencies of outbreaks throughout Africa for the years 1940 to 1942 inclusive, is provided by Haggis (1984). Each map shows the number of times an outbreak occurred in each one degree square. An appendix also provides a month by month sequential picture of these 43 years.

The maps show that the armyworm "season" generally begins by December with reports of outbreaks from northern Tanzania or southern Kenya and from Malawi and/or Zimbabwe. The outbreaks become more frequent in these areas in January and become more widely distributed in Tanzania and extend into the Transvaal. In February the outbreaks in the north occur through much of southern Kenya and may now include Uganda, while in the south their incidence is highest in the Transvaal but they may extend throughout the Orange Free State. In March, outbreaks in the south have become less frequent with those that do occur widely scattered across the Transvaal, Orange Free State, Lesotho and extending into Cape Province. In the north the outbreaks appear more concentrated along the Kenyan-Tanzanian border and in Uganda. In later months, outbreaks in the south are infrequent being almost unknown by May although occasionally still occurring in Malawi. In April the outbreaks become spread more evenly across southern Kenya with some occurring in northern Kenya and Ethiopia. They become more common in Ethiopia and less so in Kenya through May, with some occurring in Somalia and, in most years, reach into the Yemen by June. Outbreaks in Kenya are rare by August and declining in Ethiopia and the Yemen where they peter out by October. Reported outbreaks in West Africa are scattered and occur mainly from May to July.

The pattern of incidence of outbreaks is associated with the movement of the Inter-tropical Convergence Zone (ITCZ), the region where the trade winds of the hemispheres meet. The ITCZ moves poleward over land during the summer, monsoon west winds forming between it and the equator. This zone of converging

winds gives rise to seasonal rainfall. As it passes South, the ITCZ produces the "short rains" over East Africa and as it passes North, the "long rains". Thus armyworm outbreaks track the rainy seasons and appear in regions of new growth, not only of grasslands but also of recently planted crops.

A relationship between the severity of the armyworm season (indicated by the number of outbreaks) in East Africa and delayed early season rainfall is conspicuous. Tucker (1984) has found this relationship to be significant, with low October-to-December rainfall preceding severe armyworm seasons and high October-to-December rainfall preceding low armyworm seasons. Hattingh (1941) suggests that this relationship is due to the delayed rains holding up the growth of new grass, which is then available for the young larvae when they hatch. There may also be a destructive element in heavy rains as they knock down and drown young instars and overcast conditions may increase the incidence of disease (Brown and Swaine, 1965).

The occurrence of an outbreak in an area where one was not present at a generation interval before may be attributed to one of two causes. Firstly the build-up of numbers, generation by generation, in a local low density population which, possibly with the benefit of new grass growth following recent rainfall, passes a threshold density of larvae to form the outbreak population. Secondly the increase in local density may be partially, or entirely, due to the immigration of moths from another area.

Hattingh (1941) proposed that armyworm were present in most

outbreak areas the whole year round, having found small outbreaks that had been overlooked by other observers, and that migration of moths over significant distances before oviposition was improbable due to their short, two-to-three day, pre-oviposition period. He therefore believed the former hypothesis as to the origin of outbreaks to be more likely.

Faure (1943), on the other hand, believed that armyworm moths did migrate, because of the sudden appearance of outbreaks, the fact that a second outbreak rarely occurs in the same area, and the unsuitable nature of much of the armyworms range in South Africa during the winter. He concluded that the pre-oviposition period under the outdoor conditions of Pretoria in January would be 91h, calculated from the Blunk formula, rather than the two days of Hattingh and would therefore not preclude migration before oviposition.

The definition of the term migration which has been adopted in this thesis is that of Kennedy (1986). His definition is that of migration as a behavioural process, if one with ecological consequences (Gatehouse, 1987) :- "Migratory behaviour is persistent and straightened -out movement effected by the animal's own locomotory exertions or by its active embarkation on a vehicle. It depends on some temporary inhibition of station-keeping responses, but promotes their eventual disinhibition and recurrence". Thus migration is the action of an individual whereas dispersal is the action of a group. Southwood (1981) has contrasted the two terms by presenting migration as travel from one habitat to another and dispersal as an increase in the mean distance between individuals, whether they stay in the same

habitat or depart from it.

Much circumstantial evidence for the migration of Spodoptera exempta moths has now been accumulated.

Brown et al. (1969) found the longevity of moths to be up to 22 days and their pre-oviposition periods to extend up to 16 days in the laboratory. They reported that moths could take-off at temperatures as low as 13°C and probably maintain flight at temperatures lower than this and so could fly at most temperatures encountered in East Africa. Although they determined the air speed of moths in a wind tunnel to be only 10 Km h⁻¹, they concluded that by travelling on the wind (which was most frequently at 8 to 16 Km h⁻¹ over Nairobi) displacements of more than 100 Km could result from one night's flight, even if the flight was randomly oriented. None of these factors suggested that S. exempta can not undertake prolonged or migratory flight.

These authors then investigated changes in the seasonal distribution of S. exempta by using a system of light traps, meteorological data and records of outbreaks. They concluded that the changes in distribution were dominated by the wind, with the bulk of the population occurring in areas experiencing a rainy season, presumably due to wind convergence concentrating the moths in these areas (see also Rose and Law, 1976; Haggis, 1979, 1984; Blair et al., 1980; Tucker et al., 1982). Behaviour leading to the moths being carried into these rainy areas would be adaptive due to the flush of new grasses available as food for larvae there.

Den Boer (1978) investigated the allele frequencies of six alleloenzymes, which were proved to be polymorphic, from 17 samples of S. exempta. No heterogeneity was detected in the allele frequencies suggesting gene flow caused by extensive migration. Aidley (1974), Gatehouse and Hackett (1980), Parker (1983) and Parker and Gatehouse (1985a and b) used tethered-flight techniques to determine the flight potential of unfed moths and found individuals capable of flying throughout the night (see Ch. 2).

Direct evidence of migration of S. exempta moths has now been obtained from radar and mark/capture studies. Riley et al. (1981, 1983) used radar and infra-red optical detectors at an outbreak site to follow the flight trajectory of recently emerged moths. The moths climbed to a height of several hundred metres and travelled downwind undergoing rapid dispersal (a 10 : 1 difference in aerial density at 14 Km downwind). They were picked up and tracked by a second radar stationed downwind of the emergence site and so followed for a total of more than 20 Km with no indication of descent over this distance.

Rose et al. (1985) marked approximately 166 000 moths at an emergence site by inducing them to feed on dyed molasses. Six moths were later captured in pheromone traps up to 147 Km downwind of the marking site, with a mean displacement of $75 \pm 47(\text{SD})$ Km.

The observed dispersal of moths in these studies, with the observation of Page et al. (1982) that moths may emerge from an outbreak over a period of up to 12 nights, and the variation in flight capacity shown by moths when flight-tested in the

laboratory (Parker, 1983; Parker and Gatehouse, 1985a and b) suggest that dispersal of moths flying from outbreaks may be very important. Gatehouse (198-) stresses, however, that dispersal should not be too great or population densities will drop so low that moths will lose contact with each other (as determined by the range at which a male can detect a calling female). Dispersal from an outbreak may be prevented by rainfall on the night of moth emergence, resulting in a second outbreak in the same place (Rose, 1975). Such outbreaks are likely to be subject to heavy mortality due to the functional and numerical response of predators, parasites and pathogens over the previous generation (Gatehouse, 1986).

The conclusion of this work is that moths flying from outbreaks generally become highly dispersed. However, backtracking from some outbreaks to a previous outbreak using wind direction data on the deduced night of oviposition (Rose et al., 1985; Tucker et al., 1982; Pedgley et al., in prep.) suggests that emerging moths from one outbreak can form a major proportion of the individuals contributing to the formation of another outbreak. Thus, although moths generally become dispersed during migratory flight, some of them may encounter and be reconcentrated by mesoscale wind systems (Blair et al., 1980). For example, intense wind convergence associated with storm outflows can raise aerial densities by an order of magnitude in less than one hour (Pedgley, et al., 1982) and a lesser degree of concentration may occur in rotors associated with topographical features (Pedgley, 1982; Pedgley et al., 1982). Flying moths

have been seen to be brought to ground level by rainfall (Riley et al., 1983; Tucker and Pedgley, 1983; Rose et al., 198-) and these immigrants tend to stay in the area and continue oviposition over the next week (Rose et al., 198-).

By the end of the armyworm season, the dispersal of moths flying from outbreaks and low density populations is likely to result in widespread low density populations over much of the suitable habitat in East and South-eastern Africa (Rose et al., 198-). During the off-season, decreasing habitat quality as much of the habitat dries out will reduce total numbers and will produce a very patchy pattern of habitat availability with pockets of armyworm surviving and continuing to breed in suitable areas such as river valleys, highlands and coastal regions where rainfall occurs sporadically during the off-season supporting green grasses and temperatures are above the threshold for development (Rose et al., 198-).

Rainey and Betts (1979) have suggested previously that the first outbreaks of the new season, the primary outbreaks, are either formed by moths produced either in the north and undertaking a very long distance migration to the south, or moths from "hidden" outbreaks perhaps in Central Africa. This theory of the continuity of the outbreak sequence does not explain the fact that no outbreaks have been found in Central Africa during the off-season. Also the levels of viral disease are seen to build up during the armyworm season from very low levels in the first, or primary, outbreaks to high levels late in the season. This would not be expected from a continuous cycle of high density outbreaks (Brown and Swaine, 1965). The existence of the

solitaria phase is ignored as merely unfortunates which have been left behind by the main population, rather than seen as a form which is well adapted to existence at low density. Finally back-tracking from several primary outbreaks in Eastern Kenya and Tanzania has indicated that the sources of the moths initiating them were the coastal regions of Kenya and Tanzania (Pedgley et al., in prep.). These primary outbreaks appear critical in that they produce large numbers of moths in the air at the same time which may then be concentrated to form the secondary outbreaks, in effect initiating the outbreak sequence. Control measures concentrating on these primary outbreaks may be more practical and effective than later control of the larger, dispersed population which contributes to the widespread secondary outbreaks (Rose et al., 198-).

The present evidence supports the conclusion that the major populations of armyworm during the off-season are present as low density solitaria individuals in regions where suitable habitat persists. The most important of these off-season habitats appear to be in the coastal regions of Tanzania and Kenya and the primary outbreaks at the beginning of the season occur where moths from these areas are carried inland on easterly winds and concentrated by the first storms of the short rains.

Throughout this discussion of the life-history of the armyworm, the role of migration can be seen to be of great importance (Riley et al., 1983). The programme of work reported in this thesis was, therefore, carried out to extend earlier studies of the environmental and genetic factors regulating

migration in the African armyworm in this laboratory (Parker, 1983; Parker and Gatehouse, 1985a and b).

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CHAPTER TWO
Tethered-flight
techniques.

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1. General considerations in tethered-flight studies.

Tethered-flight studies may be conducted to examine physiological or behavioural aspects of insect flight. The parameters of flight under examination will of course depend on the aim of the study and will for a large part determine the design of the apparatus used. Tethered-flight has been used to examine the sources of the energy used for flight (e.g. Clements, 1955), the oxygen consumption during flight (Yurkiewicz, 1967), wing-beat frequency (e.g. Williams and Chadwick, 1943; Cullis and Hargrove, 1972), differences in flight behaviour due to age, sex and mated condition (e.g. Foley, 1985), the response of males to female sex pheromones (Borden and Bennett, 1969) and as an index of the insects' vigour (Smith and Furniss, 1966). Many studies have concentrated on examining the duration of tethered-flights with migration in mind (e.g. Dingle, 1965) with some also measuring the speed and distance covered by the insects on a rotating arm (Hocking, 1953; Atkins, 1961; Cullis and Hargrove, 1972; Foley, 1985).

In many studies the insects are deliberately disturbed to induce and maintain flight e.g. by removal of tarsal contact, blowing or tapping the insect if it stops flying. In these cases the insects are flown to exhaustion which is rarely the cause of the termination of flight in the field (Gatehouse and Hackett, 1980). In other behavioural studies care is taken to disturb the insects as little as possible before or during flight testing to achieve an index of flight capacity which relates to that in the field. In such cases the tethered insects should have a landing

substrate available when not undertaking powered flight but this should not be intrusive when the insect is in flight (Gatehouse and Hackett, 1980; Parker and Gatehouse, 1985a and b).

Of crucial importance as a source of disturbance is the procedure for attachment of the insect to the flight equipment (Gatehouse and Hackett, 1980) which should be as unobtrusive, and as consistent from insect to insect, as possible. A second potential source of disturbance is the presence of the tethered flight equipment close to the flying insect where it might be seen or sensed by the deflection of air currents caused by flight. In particular the actively flying insect should not be able to make tarsal contact with its tether as flight will probably then be inhibited, and will certainly be disturbed (Rowley et al., 1968). Also the attitude of the insect should be that in which it would fly in the field. Tethering in an abnormal attitude may lead to unsuccessful attempts by the insect to steer away from its fixed direction thereby influencing its behaviour, wing-beat frequency, power output, flight speed and duration so that a true index of flight potential will not be achieved (Rowley et al., 1968). Some insects may require some freedom of movement or direction on the tether to obviate this constrained steering behaviour (Gatehouse and Hackett, 1980; Koerwitz and Preuss, 1964) and others a constant head-on flow of air as a stimulus to maintain powered flight (Dingle, 1984).

An insect which flies above the boundary layer - the layer of air near to the ground in which the air speed of the insect is greater than the wind speed and therefore in which the insect is

able to reach any goal under its own power (Pedgley, 1982) - in the field will be subjected to different environmental conditions and sensory inputs in flight than it was before take-off. Atkins (1961) states that the environmental conditions required for take-off e.g. temperature, are often greater than those required for the continuation of flight. Ideally, then, tethered-flight studies in the laboratory should be conducted under environmental conditions normal to the field e.g. air temperatures typical of those at normal flight altitudes for insects flight-tested to exhaustion, and different conditions for flying and landed insects which are able to undertake spontaneous flights.

Individual controlled environment chambers would be necessary for each insect in this latter case and I know of no such study, although environmental stimuli may be very important for the initiation, maintenance and control of power output (which may relate to height attained) of sustained flight. The technical and financial problems associated with such elaborate tethered-flight equipment have proved prohibitive in this study and may continue to do so in others.

2. Tethered-flight equipment.

Flight activity in the laboratory may be indexed in non-tethered insects by recording the activity occurring in a cage (or actograph), for example by the vibration caused by the insect flying into the actograph walls (Leppla, 1976), or by the insect's movement causing either a disturbance in a temperature gradient across the actograph (Macaulay, 1972a,b) or a capacitance change (Grobelaar et al., 1967). In all these cases

there is some ambiguity in that the measured activity may be due to the insect walking, rather than flying, in the actograph. The technique is also unsatisfactory in that flight quickly brings the insect into contact with the walls of the actograph, probably producing an escape response and certainly not permitting sustained, directional flight.

Kennedy and Booth (1963) developed perhaps the most elegant laboratory equipment for indexing insect flight with minimal intrusion to the insect. They used an "air treadmill" to study the photokinetic and phototactic responses of flying aphids. The subject insect was enclosed in a black box with a window at the top. When it took-off from the host leaf on which it was introduced to the box, the light stimulated it to fly (photokinesis) and it flew upwards towards the light (phototaxis). An operator in a blacked-out observation room, and able to see through one side of the box, was then able to maintain the position of the aphid in the centre of the box by controlling the flow of air blown downwards by a fan. The operator controlled a butterfly valve positioned across the air flow, the degree to which the valve was opened (and hence the wind speed and the insects rate of climb) being recorded on a paper chart along a time scale.

The air treadmill was redesigned by Laughlin (1974) to be suitable for insects with as fast a rate of climb as that of honeybees and was used to record flight durations for the Rutherglen bug, Nysius vinitor, by Kehat and Wyndham (1973). However the apparatus is unsuitable for larger insects, for the

measurement of flights of long duration (due to the need for the continual concentration of an operator) or for measurements of the flights of nocturnal insects (since it records only climbing flight towards a light).

The only alternative for the laboratory indexing of flight capacity developed at present is that of tethered-flight. The simplest tethered-flight equipment is a static tether which may be attached to the back of the insect by glue or melted wax (Dingle, 1965). The insect is then, typically, encouraged to fly by removing tarsal contact. Flight duration may be timed until flight terminates, with or without further stimulation. Caldwell (1983 - cited by Dingle (1984) as in press in *Physiol. Entomol.* but not published there) has also examined the effect of juvenile hormone (JH) on the time to take-off of Oncopeltus fasciatus bugs which were initially suspended holding a small styrofoam ball. JH produced a shortening of the time to take-off which Caldwell interpreted as a lowering of flight thresholds, a vital component in the production of any flights.

Riley and Stinner (1985) have automated the recording of flights produced on a static tether by using a microphone placed behind the insect. The displacement of air by the flying insect is detected by the microphone and may be recorded on magnetic tape, where it is available to be played back later, or on paper tape on a time scale chosen for summarising, or examining in detail, any portion of a flight.

Flight-mills are among the most common methods used in both behavioural and physiological studies of insect flight e.g. Hocking, 1953; Green, 1962; Koerwitz and Preuss, 1964; Borden and

Bennett, 1969; Aidley, 1974; McKibben, 1985. They have the advantage of providing a head-on air flow and may provide appropriate visual stimuli of the environment moving backwards relative to the flying insect, all powered by the insect itself. Any change in these stimuli would then be in direct relation to the change in speed of flight of the insect.

Flight-mills have been used to index the flight capacity of insects as different in size as mosquitoes (Rowley et al., 1968; Clarke et al., 1984) and locusts (Krogh and Weis-Fogh, 1952). In all cases of tethered-flight it must be borne in mind that records of flight activity may or may not bear any relationship to the potential flight activity of that insect in the field (Gatehouse and Hackett, 1980; Dingle, 1984; Gatehouse and Woodrow, 1987). Indeed it should be assumed that they do not unless evidence of some correlation with field behaviour (for example the temporal patterning of flights - Gatehouse and Woodrow, 1987) is available. The relationship between tethered- and free-flight durations may be very loose unless the insect undertaking the flight is in migratory-mode (sensu Kennedy, 1975, 1986; see also Dingle, 1984). Under such conditions the insect is relatively unresponsive to vegetative stimuli (stimuli generally associated with somatic or reproductive growth) and may be difficult to distract from its flight. Termination of flight is brought about in the field, and may be brought about in the laboratory, by a resumption of such responsiveness.

The common use of flight-mills to record the intrinsic speed and distance covered by flights, as well as the their duration,

deserves further comment. The speed of flight and distance covered must be heavily dependent on the experimental apparatus due to friction and aerodynamic drag, and also to the inertia of the system - the rotating arm of a flight-mill is under-going a continual change in direction and hence linear acceleration which requires power. Probably for this reason, and to minimise the constraint felt by the insect, Krogh and Weis-Fogh (1952) recommended that the angular velocity of a mill should be kept as small as possible. Attempts have been made to calculate the free-flight speed of an insect based on its tethered-flight speed and measurements of the drag of the flight mill (Hocking, 1953; Aidley, 1974). Such estimates must be used with caution.

As important as the influence of the tethered-flight equipment when comparing free- and tethered-flight is the effect of wind in the field. Wind speed at altitude is often in excess of that attainable by flying insects and may dominate their direction of travel as well as their ground speed. It is only more powerful insects under low wind conditions, and particularly in the (boundary) layer of relatively still air close to the ground which are able to control their direction and speed of travel. Thus an insect which uses the wind as a vehicle will travel at a speed, and cover a distance, related more to the wind speed than to the intrinsic flight speed of the insect. In such insects the rate and duration of climbing flight, taking them out of the boundary layer and into the stronger winds at higher altitudes, may be the most important parameters of flight.

3. Previous equipment used in this laboratory.

Insects on flight-mills are generally unable to land and many fly to exhaustion. This may be suitable for some physiological studies but may be a major factor reducing the correlation between flight activity in the laboratory and the field. Gatehouse and Hackett (1980) described a flight balance which allowed a tethered moth of Spodoptera exempta to take-off and land spontaneously. A wind machine was initially used to provide a head-wind but its omission was not found to produce a discernible difference in flight behaviour. This tethered-flight technique had many of the virtues described above and was used in this laboratory by Parker and Gatehouse (1985a and b).

The technique which was devised by Gatehouse and Hackett (1980) for tethering moths to their flight equipment is very important since it removes the need for any anaesthesia or cold inactivation with their possible influence on the insects' behaviour. This tethering (or mounting) procedure was used unmodified throughout this study and so is described here in detail.

Earlier than eight hours before eclosion the pupal cuticle of a Spodoptera exempta moth turns from a medium brown to a dark chocolate, particularly in the region of the head and thorax. At the same time the cuticle becomes brittle and fragile and may be easily broken with the point of a scalpel blade without damaging the insect inside. From four hours before sunset/lights out of the night of eclosion the moths may be mounted.

Under a binocular microscope, a window is cut in the pupal cuticle over the dorsal surface of the thorax and the hairs and

scales below removed using a small drop of impact adhesive Evostick (Aidley, 1974) applied on the head of a pin. The adhesive is allowed to dry for less than a minute and then peeled away with the hairs and scales attached. A small bracket or mount may then be attached to the thorax. The mount consists of a 3mm length of c.0.40mm i.d. polythene catheter tubing into one end of which has been glued an aluminium foil foot providing a surface of c.1.0mm² for attachment to the dorsal surface of the thorax. A thin layer of glue is applied to the foot of the mount and allowed to dry for approximately one minute. Meanwhile a small drop of glue is applied to the thorax with the pin, equivalent to the area of the foot, and similarly allowed to dry. The mount is then brought into contact with the thorax positioned centrally and with the "toe-end" of the foot posteriorly. The pupa may be lifted immediately using the mount. The whole procedure takes approximately three to five minutes.

Provided that the adhesive has not been applied carelessly and cemented the pupal cuticle to the thorax or mount, the moth is subsequently able to emerge and expand its wings with no difficulty. After the wings have hardened (one or two hours after eclosion) the mount may be seized with forceps and the moth moved between holding containers or attached to the balance without, itself, being touched.

The balance described by Gatehouse and Hackett (1980) had a flight arm which was pivoted on a suspension arm. Both arms were made of stainless steel hypodermic tubing 0.45mm o.d. with bearings of 0.82mm o.d. The moth was simply and securely

attached to the flight arm by pushing the mount over the piece of vertical tubing comprising the front section of the flight arm. The arm was very light (c. 180mg) and being quite short had a small inertia. The thin tube presented only a small profile close to the moth so that intrusion close to the insect was minimised, and joints at the end of the suspension arm and on the front section of the flight arm meant that the insect had some freedom of movement to yaw, bank and move forwards and backwards. Without this freedom, the moths spent much of their flights steering away from the enforced direction of flight and were hence behaving abnormally. Fast movements of the flight arm were damped by a small foil paddle on a side arm suspended in a small plastic pot of liquid paraffin.

The flight arm was balanced across its pivot at the suspension arm but in still air moths were unable to generate enough lift when tethered on the arm to support their own weight. It was therefore necessary to counterweight the arm. Parker (1983) was able to develop a standard counterweight (used by Parker and Gatehouse, 1985a and b) of 60% of the moths weight when it was attached to the balance. This counterweight was enough to enable the flying moth to support its own weight in the absence of a relative wind, but not so much that it became stuck up after losing weight through the experimental period.

The Gatehouse and Hackett (1980) flight balance had a black paper wheel presented to the moth on an arm with a axle so that the wheel could rotate when the moth ran around it. Take-off of the moth was spontaneous. When this occurred a flag on the back of the flight arm dropped out of an infra-red beam which

triggered a solenoid to pull the wheel arm down moving the wheel away from the flying moth. When the moth landed the flag on the flight arm re-entered the infra-red beam, the detector acting as a stop to prevent the arm continuing past the horizontal, the solenoid was turned off and the counter-weighted wheel arm rose over a period of five to ten seconds under the moth. The movement of the wheel arm was damped by the action of a large perspex disc rising and descending in a large pot of liquid paraffin. The interruption of the infra-red beam by the flag on the flight arm also caused a pen to move across a chart on a Rustrak event recorder. Movement of the recorder chart (6in/h) allowed a record of the take-off time and duration of flights throughout an experiment to be made.

The advantages of this tethered-flight technique include the unintrusive and standardised mounting procedure, the spontaneous initiation of flight, the relative freedom of movement of the insect in flight and the ability of the insect to land.

There were however some points of the technique which could be improved. The damping flag on the flight arm occasionally stuck to the side of the damping pot due to surface tension when the fluid level was low so that the arm became stuck up. The moth was then suspended and recorded as flying even if it stopped. Such records could easily be discarded from analysis since the moth was found stuck up in the morning but the loss of moths in this way was inconvenient. Also there must have been some chance that a moth stuck early in the night and might become unstuck later on, leading to a falsely extended flight.

More frequently the wheel arm became stuck, most often in the down position so that the suspended moth, which was not generating any thrust and lift, failed to receive any tarsal contact. When this happened it was common to find that many short flights had been recorded throughout the latter part of the night.

When the moth was flying, the balance had a high power consumption due to the solenoid being on to hold the wheel arm down. Such a high power consumption might make the use of the equipment under field conditions, using a battery power source, impractical.

Lastly, the recording of flights on paper tape meant that the reading of take-off times and flight durations was very time consuming, making anything more than a simple analysis impractical (Clarke et al., 1984). In addition, transferring of data from the tapes to summary sheets by hand must allow for some possibility of human error (Richardson and McNeil, 1987). Some fluctuation in the speed of the Rustrak motors and so chart speed was also noted with the result that take-off times and durations were sometimes recorded with a small degree of inaccuracy.

4. The aims of redesigning the tethered-flight equipment.

During 1983-84 the tethered-flight equipment in this laboratory was redesigned. The main aims of this were :

- [1] to remove as much of the liquid-paraffin damping system as possible. This would have the dual effects of reducing the intrusion of the damping pot in the region of the tethered insect and increase reliability by

removing the main cause of the flight and landing-wheel arms becoming stuck.

[2] the reduction of power consumption by the balances. The initial extreme objective was to make the mechanical action of the flight arm and the corresponding action of the landing-wheel arm powered solely by the flight and weight of the insect. The only power consumed would then be the comparatively small amount required by the electronics of the data recording equipment.

[3] computerisation of data recording. The frequent scanning of balances by a computer with a built-in clock would allow the accurate recording of take-off times and flight durations. The recording of this data on computer file in an appropriate form for further analysis would speed-up the summarising of the data and make more complex analysis feasible.

I am very happy to acknowledge the invaluable help given to me by Mr D. A. Davies of the School of Animal Biology, U.C.N.W., Bangor, both in the design of the flight balances and in teaching me the techniques necessary for their construction. Mr Davies was also responsible for designing and constructing the datalogging interfaces and for writing the datalogging and main data analysis programs. Additional data analysis and plotting programs were written by myself.

5. The moth-powered flight-balance.

An attempt was made to construct a tethered-flight balance constructed of balsa wood which was light enough to be operated by the power of the moth alone. However, this proved impractical.

6. The powered flight-balance.

The starting point of the design was the Gatehouse and Hackett (1980) flight arm. The damping system of this arm comprising a foil paddle from the flight arm reaching into a small pot filled with liquid paraffin had the drawbacks described above. It was thought that the movement of the flight arm in the absence of any damping was too violent in response to a fast movement by the moth. Other methods of damping were therefore investigated.

Air damping using a large horizontal square of photographic film attached to the back of the flight arm was tried. However because air is so much less viscous than liquid paraffin the area of the film needed to produce a significant damping effect was much greater. In fact the area of film needed was so great as to produce difficulties in designing the rest of the flight balance around it and also to add significantly to the weight and inertia of the flight arm.

A flight arm was designed incorporating friction damping. Friction was easiest to impose on the suspension bearing rather than on the vertically-moving sections of the arm. A "brake-shoe" which squeezed the bearing with a constant pressure was impractical, not least because of the necessity of producing a

constant damping effect. A design which could adjust for the effects of wear to maintain this damping would be far too complex. A design was therefore produced which used a weight hanging on the bearing to produce a constant friction. The frictional surface was a hole in a small piece of fibre board to which the weight was attached. However it was found that the weight necessary to produce a significant damping effect was so great as to decrease the freedom of the back-and-forth movement of the flight arm in the horizontal plane, again significantly constraining the movement of the moth.

The fluid damping system of Gatehouse and Hackett (1980) was therefore retained.

The arm was however modified with regard to the counterweighting system. Parker and Gatehouse (1985a,b) had counterweighted using plasticine weighed out to the nearest 5mg and attached at a marker on the appropriate position on the flight arm. This was a very time-consuming process and was replaced by the use of a range of ready-made brass and fuse-wire weights. The appropriate weight was simply chosen and hung on a loop of piano wire built into the flight arm (Fig. 2.1). The counter-weighting point and the moth attachment point on the flight arm were not equidistant from the pivot with the suspension arm. A weight had an effective counterweight of 0.92 times its real value and this should be borne in mind when real counterweight values are referred to in this thesis.

Replacement of the solenoid as the power source for the depression of the wheel arm, with its constant power requirement

Fig. 2.1

Diagram of design of the suspension and flight arms of the motor driven tethered-flight balance, after the design of Gatehouse and Hackett (1980).

a - suspension bearing

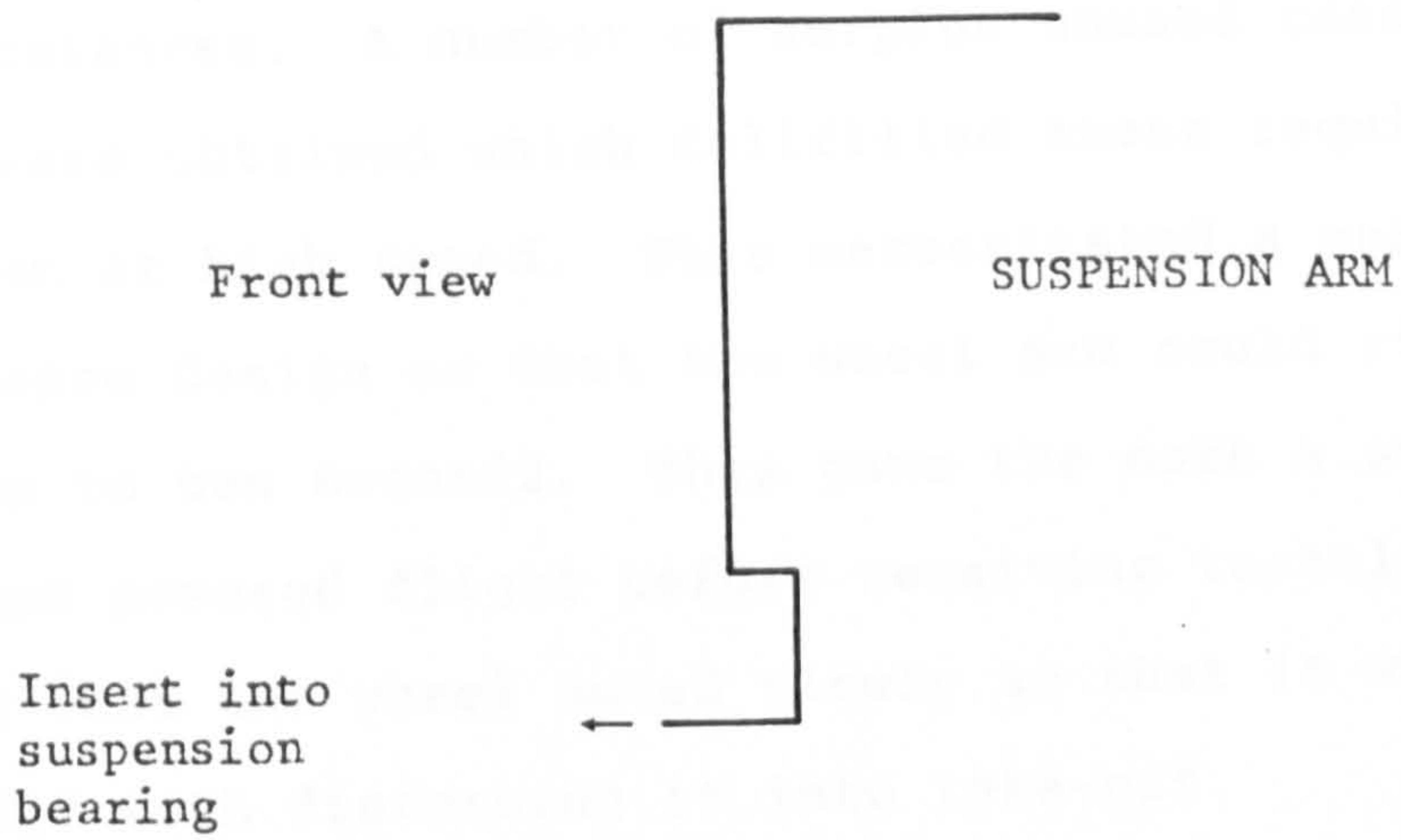
b - moth attachment point

c - suspension bearing

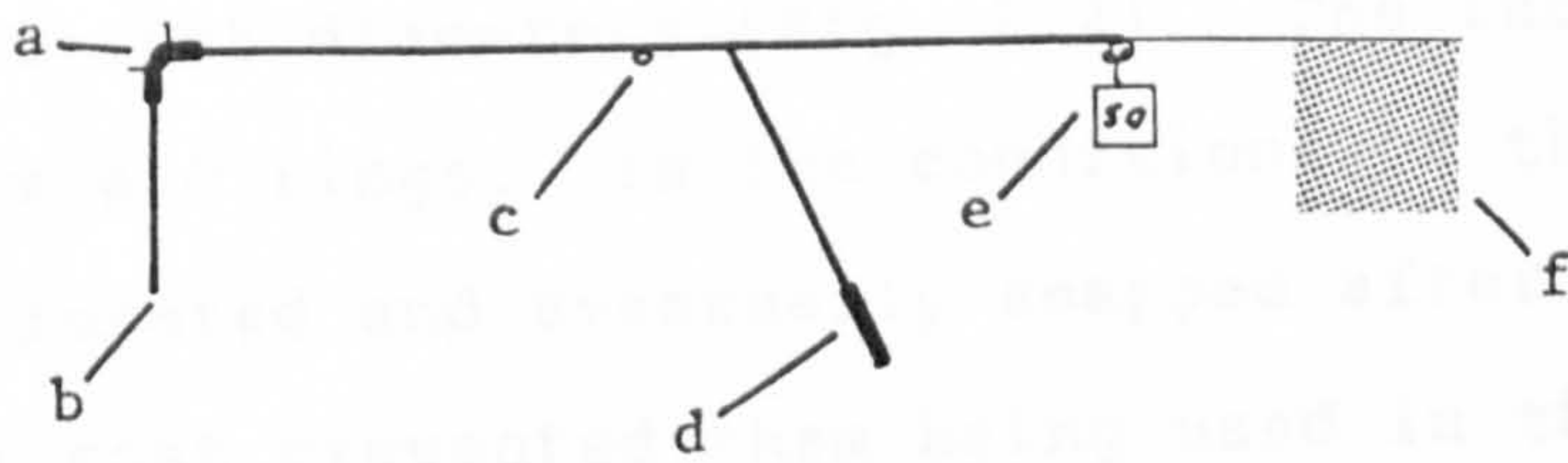
d - damping arm with thick aluminium foil paddle

e - counterweight hanging from loop of piano wire

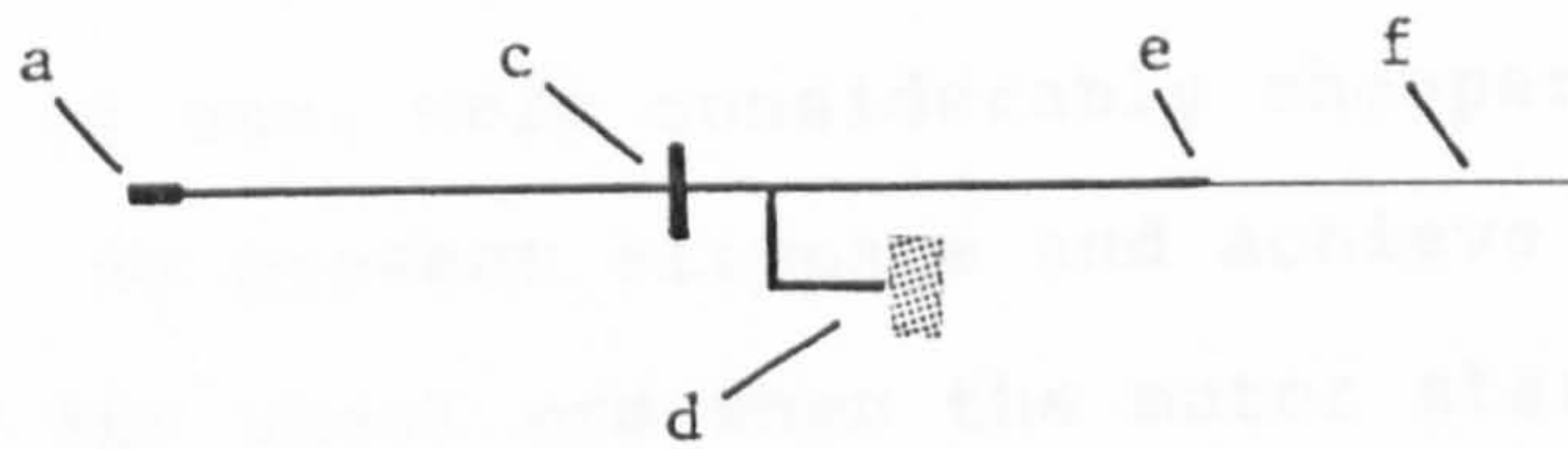
f - light foil flag



View from left side



FLIGHT ARM



View from top

as long as the arm remained depressed, was accomplished with a motor which would operate, and hence draw power, only when the wheel arm was moving. Financial considerations meant that the motors should be cheap and, preferably, small to fit the design of the balances. A number of surplus unused cassette motors were obtained which fulfilled these requirements but which ran at high speed. This necessitated a gearing system in the balance design so that the wheel arm could rise over a period of seven to ten seconds. This gave the moth a small period in which to resume powered flight before receiving tarsal contact and ensured that the wheel moved slowly so that it would not hit the suspended moth disturbing it into take-off.

The gearing system was developed using five, belt-driven, black nylon pulleys on two axles, each wheel consisting of two rims of different diameters (Fig. 2.2). The rubber belts used initially were O rings. In the conditions of the flight room, these deteriorated and eventually snapped after c. eight weeks of use. Their cost prevented them being used in this disposable manner and it was found that rings cut on a lathe from cycle inner tubes ($1\frac{3}{8}$ " diameter) of approx. 1.2mm width were of the correct elasticity, and although they deteriorated after six to seven weeks of use, were considerably cheaper. These were used henceforth. To prevent slippage and achieve an immediate response of the wheel arm when the motor started, it was necessary to replace the final rubber belt-drive with surgical silk secured on both pulleys.

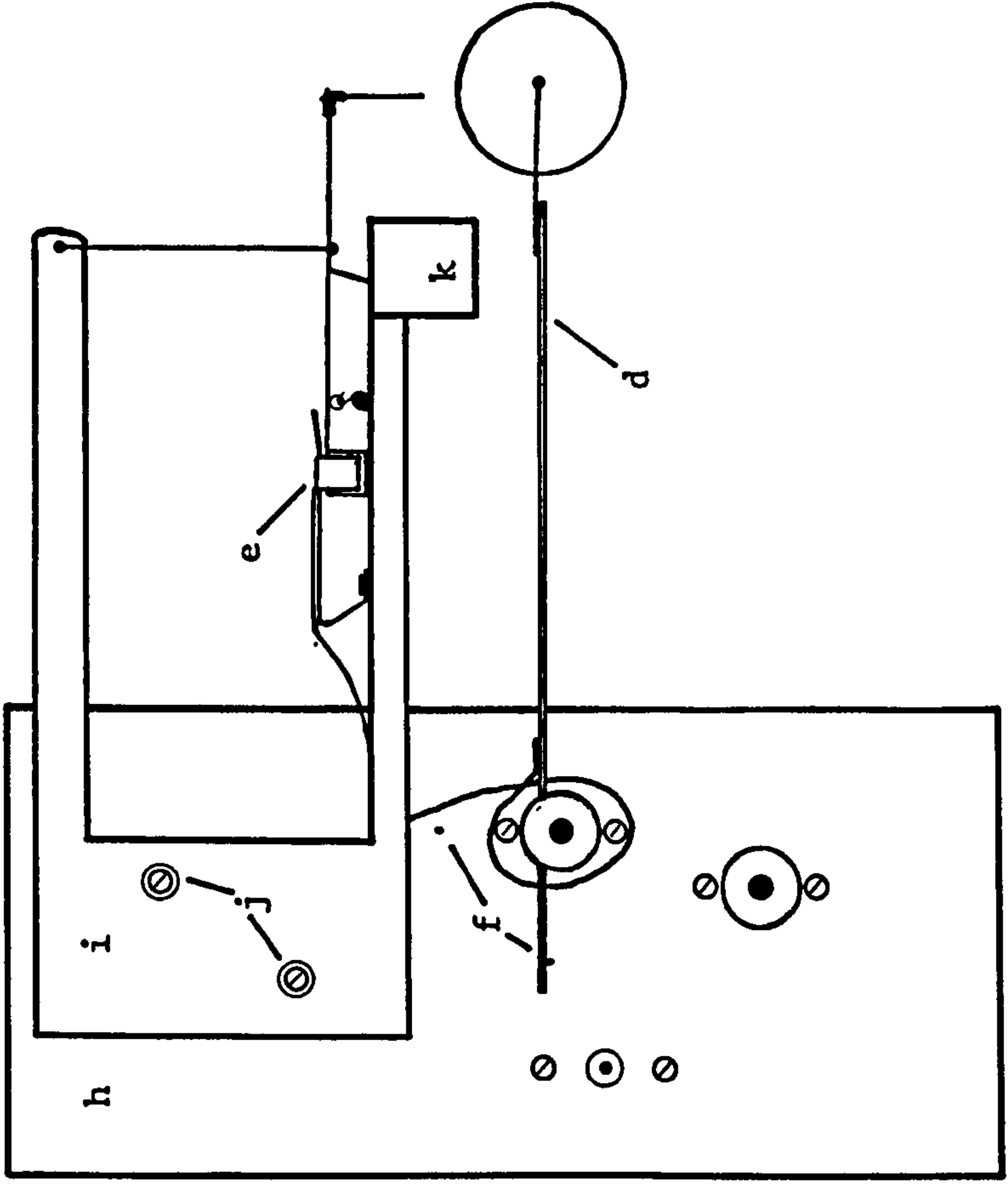
Control of the motor depended on the position of the flight arm as sensed by the flag at the end of the arm interrupting an

Fig. 2.2

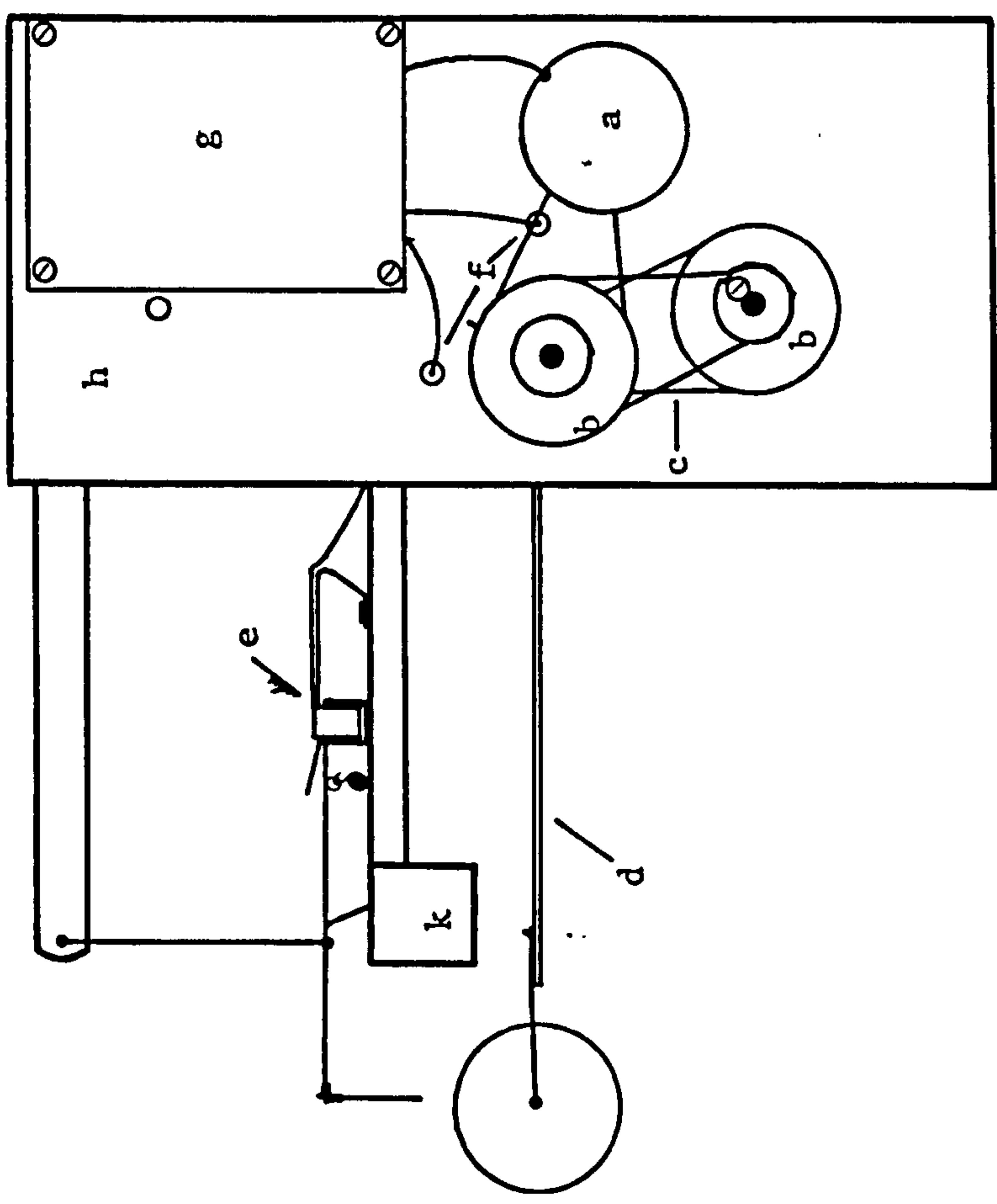
The powered tethered-flight balance, left and right views.

- a - cassette motor
- b - nylon pulley
- c - drive belts
- d - landing-wheel arm
- e - infra-red emitter and detector
- f - pins which act as contact switches
- g - printed circuit board
- h - aluminium frame
- i - U-shaped perspex support
- j - rubber grommets
- k - damping pot

RIGHT SIDE



LEFT SIDE



infra-red beam, and of the landing-wheel arm, as sensed by the completion of a circuit between the landing-wheel arm itself and one of two pins limiting the upper and lower extremes of its movement (Fig. 2.2). The control was exercised by a circuit board mounted on the back of the balance frame. Its logic is summarised below.

Arm position		Landing-Wheel
Flight	Landing-Wheel	Arm Movement
-----	-----	-----
up	up	down
up	intermediate	down
up	down	stop
down	up	stop
down	intermediate	up
down	down	up

The control circuit, motor and gearing system are secured to an aluminium frame (Fig. 2.2). The suspension arm and damping pot are attached to a U-shaped perspex support which is then secured to the aluminium frame by bolts supported by rubber grommets. The grommets damped any vibration from the motor or gearing system so that these would not be felt by the moth. Both the frame and perspex support were painted matt-black to decrease visibility to the attached insect at night.

Moths flying on these flight balances quickly adopted their normal flight posture. In flight, their antennae were pointed forwards, pro- and meso-thoracic legs were folded and meta-thoracic legs extended backwards along the abdomen (Koerwitz and

Preuss, 1964; Gatehouse and Hackett, 1980). Very little time was spent trying to steer-off by turning against the limits of movement of the flight arm bearing. After landing the moths often ran along the landing-wheel before coming to rest. Settled-moths observed at night were usually sitting on the landing-wheel with antennae extended, apparently alert. During the light period, however, they were generally found to have pulled themselves as far down the side of the wheel as the constraint of the tether permitted. In all cases during the light period, moths were found to have folded their antennae along their backs and were relatively unresponsive to disturbance.

7. Data-recording equipment.

The collection of data was performed by a Sinclair ZX Spectrum 48K microcomputer with one or more microdrives for data storage on magnetic tapes. The microcomputer was linked via the Spectrum ZX Interface 1 to a purpose-built interface with a real-time clock.

This equipment was housed in a room c.20m from the controlled temperature room in which the moths were flight-tested. A serial line linked this purpose-built interface with a second interface in the flight room, housing a multiplexor from which individual lines ran to the flight balances. Four lines ran to each balance. These were 12v and 5v lines supplying the motor and electronics respectively, with a ground (0v) and signal line for datalogging. The control circuit was interrogated every second by the computer which sensed whether or not the infra-red

beam was interrupted, and hence whether the moth was landed or was flying.

The equipment was powered from the mains supply in the flight room. A 4Amp mains plug RFI filter/transient suppressor ("The Plug") was used to reduce interference from the mains and the supply was then stepped down to 12v via a transformer. A battery backup (a 12v car battery) was arranged across the power supply and had the capacity to run the apparatus for at least four hours. The battery was permanently attached and so replaced the mains as the power source, with no interruption, when the latter dropped or was cut-off for any reason. Commercial battery backup supplies which cut-in a battery when the mains power dropped can interrupt the power supply momentarily, corrupting the datalogging program running on the microcomputer during a mains failure.

8. Datalogging software.

The software running on the Sinclair ZX Spectrum was written in Pascal using the Hisoft Pascal 4T line editor and compiler. The compiled code runs fast enough on the ZX Spectrum to allow the checking of 128 balances, reading of the real-time clock and updating of the monitor screen to be performed every second.

When a flight begins the take-off time is recorded in the temporary data store in computer memory for that balance channel number. A count is then performed of the "off-up" time. This is an adjustable period, the value of which has been set in the source code of the program at ten seconds for these studies. If

during the off-up time the moth lands again, the count is reset to zero and the small flight is ignored. In this way only continuous flights greater than the off-up time are recorded. This routine ensured that fewer very short flights, which are presumably not related to prolonged or migratory flight capacity, are stored in the databank and hence the size of the memory required for storage is reduced.

Similarly, a moth which has undertaken a flight longer than the off-up time and then lands is counted down for the off-up time. If it takes-off again during this period then the interruption in flight is ignored. This removes small lapses in otherwise continuous flights which do not generally allow time for the landing-wheel to move up and the insect to land. Again the number of flights to be stored in the databank is reduced. Also, considering migratory flight in the field, often at several hundred metres altitude (Riley et al., 1983), short interruptions in the generation of lift would not allow the moth a landing opportunity, so that ignoring short interruptions on the balances may be more realistic. A longer off-up time would give the moth longer to resume flying before the flight is recorded as having terminated. However, it is not practical since a landing opportunity is presented to the moth within ten seconds on the balances. A longer period before the presentation of such a landing opportunity by different gearing of the balances combined with a longer off-up time was considered undesirable because of the possibility that it would result in extension of the length of flights by leaving moths suspended.

When a flight longer than the off-up time has been completed

the flight duration is calculated from the previously recorded take-off time to the beginning of the off-up time for landing. The program algorithm is able to cope with the calculation of flight durations when the landing time appears to be less than the take-off time e.g. a flight from 23.55 to 00.05h.

The balance channel number, take-off time and flight duration are then appended as a single Pascal record to an array of records in computer memory. Up to 1000 or more such flight records may be stored in the array. When the number of records already stored plus the number of moths flying reaches 1000 then the records are saved to microdrive magnetic tape as a sequential file. The action of saving the file takes less than one minute (less than 30s with a newly formatted microdrive tape) and during this period no checking of the flight balances is possible. After the file has been saved checking of the flight balances resumes with the "state" of each balance for the previous second being taken as the same as that of the last time the balances were checked i.e. no change had occurred while saving of the data was taking place.

When saved the data files on tape are assigned the names "one", "two", ..., "nine". No further space is available on one microdrive tape but, if necessary, more files may be saved on a second microdrive although this has never proved necessary in this study. Should so many flights be completed during the experiment that the available space on tape is used up, then the program will terminate the data collection so saving all the data up to that point. Normally the data collection is terminated at

the end of the experiment by pressing the "T" key on the microcomputer. In both cases the remaining flights in progress are then included in the data set as having landed at that time, and the final data file and a master file are saved to tape. This master file contains details of the experiment name (a string assigned at the beginning of the experiment), start and end times of the experiment, the number of flights produced by each moth and readings relating to AtoD facilities (e.g. for recording max. and min. temperatures during the experimental period) not yet implemented.

The data is transferred from Spectrum microdrive tape to 5 1/4" floppy disc on a Gemini Galaxy CP/M microcomputer. The data transfer is conducted along an RS232 serial line by a second facility of the Spectrum data collection program and another program on the Galaxy with handshaking control between them. The Galaxy program uses the master file from the Spectrum to arrange the flight records for each moth (= balance channel) together in sequential order and each set is arranged sequentially through the single data file which is saved to floppy disc. A master file is also saved containing all the information from the original experiment.

The data is saved as Pascal records on the floppy disc for economy of space and processing time and so may not be typed to the screen. The data may be examined by using the purpose-written Replay program version 2.0. This program was written for the Propascal compiler using the Wordstar wordprocessor.

On entry to the Replay program the data filename is requested. The option is then given to examine the data on the

default settings or to go to a menu to change the defaults. By default the program will read the data file and list to the screen all the flights recorded. Flights appear as :-

Moth number	5
Take-off time	19:55:23
Flight duration	00:35:14

A single line separates each flight made by one moth and a double line flights made by different moths.

The parameters which may be reset from the menu are the flight duration window and the day window. The flight duration window may be reset so that only flights above a set low duration and below a set high duration are subsequently output to the screen. Similarly the day window may be used to set values for the times of day between which flights must start if they are to be subsequently output to the screen. The program allows new data files to be chosen and the printer to be activated to print the flight records, but not the program menu, at the same time as they are output to the screen.

The Replay program may therefore be used to look quickly through the details of the flights produced on a particular experimental run. The facilities for choosing flight duration and day windows allow far faster analysis of the data than is possible using Rustrak paper tape.

Replay may only be used to examine the flights produced during one experimental period e.g. one night. However more than one group of moths may be flight-tested during such a period, perhaps a number of different families of moths or even two different species. Also relevant is the flight-testing of one

moth during two separate runs and the need to analyse the flights produced together as one data set. The requirement is to be able to select a part or whole of the data from one experimental run and "merge" the data with that from one or more other runs. Such a facility must involve the assignment of a unique code to each moth so that it is known whether the moth flown on balance 5 from one run is the same as the moth flown on balance 5 from another run (e.g. the same moth flown on two consecutive nights) or not (e.g. two different moths flown on the same balance on two different nights). A program to achieve this was produced and called Merge.

The different format of the master file produced by merge means that the resulting data file cannot be analysed by Replay2 but may be analysed by a further program called R23 (Replay version 23.0). The entry to the program and output to the screen is similar to Replay2 and the menu incorporates the flight duration and day windows already described, as well as other facilities described below.

R23 has the facility to select the moths whose flights are to be analysed or output to the screen by their unique "mothcode". When this facility is chosen from the menu, the mothcodes are presented in a vertical column on the screen. The user is then able to choose the moths to be used by typing "y" or "n" as the cursor descends the column. More than one column is presented if the first is longer than the screen.

A major facility of the R23 program is its ability to perform more complex analysis on the data file. Instead of outputting all the selected (by mothcode, duration and day window)

flights to the screen they may be subjected to four other analyses. The simplest of these is the outputting of only the longest single flight (LSF) produced by each moth. When this option is selected, the setting of the flight duration window is ignored.

The distribution of flights may be examined as frequency histograms in three different ways. The first is a histogram of the frequency of flight durations. Here the classes arranged along the ordinate are ascending flight durations. The second is a frequency histogram of the take-off times of flights. Here the classes of the ordinate are times through the experimental period. It should be noted that the ordinate cannot exceed 24h even if the experimental period does so. In this case the flights taking-off during the period after 24h have elapsed will be superimposed on those of the period before 24h. The third histogram is of moths actually flying during the time classes through the night.

The Galaxy microcomputer does not have a graphics facility as standard so that the histograms mentioned above cannot be plotted on the screen. Instead the data is assigned to the relevant bars of the frequency histogram dependent on the values of the classes chosen. The data is then output to the screen in the form of four columns. The first is the histogram bar number, the second the number of flights assigned to that bar, the third the number of moths contributing to those flights and the fourth the sum of all the durations of the flights, or parts of flights in the case of the last histogram, within the bar. Preceding these columns and separated from them by a blank line are two figures on one row of output. These are the longest single

flight and the sum of all the flights contained within the histogram. To the right of the four columns is appended a fifth containing the times of the beginnings of each histogram bar as a reminder of the ordinate scale chosen.

In each of the three cases of the histograms described above an ordinate must be chosen. The ordinate (or timebase) is determined from the main menu of the program. The ordinate may be of classes of equal width or of differing widths. In the former case the class intervals may be entered by giving the beginning of the first class, the number of classes required and the class width, in the latter case by giving the number of classes and then the low and high values of each class interval.

In all of the cases described above the data is output to the screen and then the user is asked whether the data should also be output to a data file. If this option is requested then the data is output to the file in typable (ASCII) form. The raw flight data output to file in this way is written in the form of mothcode, take-off time and flight duration arranged in three columns. The histograms output to file have only the four columns of processed data described, not the fifth column of histogram bar start times.

The output of typable files then allows the use of other programs for statistical analysis and plotting. The files may be transferred to the U.C.N.W. VAX (VMS v4.6) Minicomputer cluster over a serial line using the Kermit file transfer program. The Minitab (v 5.1) statistical package on VAX has been found quite versatile and particularly useful for regression and polynomial regression analyses.

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CHAPTER THREE
The effect of larval phase
on adult flight

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1. INTRODUCTION

Uvarov (1921) proposed his theory of phases to clarify the confusing existing classification of the genus Locusta (family Acrididae - the short-horned grasshoppers). He examined a large number of live specimens and found many individuals seemingly intermediate between the then recognised species in appearance and morphology. He also gathered information on the distributions and variability of L. migratoria, L. migratorioides and L. danica from many sources and reported laboratory experiments by V. Plotnikov that indicated the forms could interbreed freely. Uvarov concluded that these forms did not represent separate species, that they were not individual aberrations or geographical races as many were found together in the same locality, nor was their occurrence seasonally controlled. He suggested that the forms made up a continuum, at the extremes of which were L. migratorioides and L. danica which he termed the gregarious (or migratorioides) and solitarious (or danica) phases, the transition between them probably being under the control of a combination of genetic and environmental influences. He saw the different phases fulfilling different roles in the maintenance and dispersal of the species; mobilisation and colonisation of new habitat by the more active, swarming gregarious phase and exploitation of such habitats by the solitarious phase.

The primary cause of gregarisation (the formation of the gregarious habit and characters) of locusts has been shown to be crowding of, and hence close contact between, the hoppers (nymphs) (Nolte, 1974). The phase phenomenon has, therefore,

commonly been termed a density-dependent phase polyphenism. Gregarisation may be strengthened over several generations, presumably through maternal effects (Nolte, 1974) as suspected by Uvarov (1921). Also implicated in the phase changes are temperature, humidity, and egg-incubation temperature (Fuzeau-Braesch, 1985).

In addition to L. migratoria a number of other economically important migratory Acrididae have been shown to exhibit a density-dependent phase polyphenism, specifically Schistocerca gregaria, Nomadacris septemfasciata, Doeiostaurus maroccanus, Locustana pardalina, Calliptamus italicus and Chortoicetes terminifera (Nolte, 1974; Retnakaran and Percy, 1985). The phenomenon has also been demonstrated in a number of non-migratory Tettigonidae (bush-crickets) and some Phasmatiidae (elongate stick-insects) (Fuzeau-Braesch, 1985) as well as in some Lepidoptera (butterflies and moths).

Gruys (1970) has reviewed the effects of larval rearing density in many Lepidoptera. He has concluded that where different rearing densities result in a larval colour difference the higher density larvae are consistently the darker form. Also higher density larvae are usually more active and show less cryptic behaviour. Peters and Barbosa (1977) also suggest that larvae reared at higher density have a greater tolerance of unpalatable foods and have faster and more synchronised larval and pupal development rates.

No colour difference between adults reared at different densities has been found, perhaps because of the holometabolous

Simmonds and Blaney (1986) have recently shown that gregaria larvae in their experiments had a higher feeding rate than solitaria, although the gregaria actually spent as much, or less, time feeding. The result was an overall shorter development time for gregaria than solitaria (measured from the first instar to eclosion).

Other physiological differences have been found between solitaria and gregaria larvae. Lactic acid production depends on activity and it is therefore not surprising that gregaria contained higher lactic acid titres than solitaria. Gregaria also contained lower concentrations of uric acid in their blood, contained more fat as both larvae and pupae and less water as larvae (Matthee, 1945). Electrophoretic results have also suggested that gregaria larvae contained fewer proteins and glycoproteins than solitaria (Khasimuddin, 1981).

Faure (1943) examined adults derived from larvae reared as gregaria and solitaria. He found no difference in adult size, shape of the wings or colouration. He also found no evidence of physiological differences (although how such differences were sought is not stated) but concluded that this did not mean that physiological differences did not exist.

Gunn and Gatehouse (1987) have recently examined the influence of larval phase on metabolic reserves, fecundity and longevity of Spodoptera exempta moths. They found a far greater (3.5 to 6.1 times) abdominal glyceride content at emergence in the gregaria, but no differences in total protein levels of the thorax or abdomen, nor haemolymph glyceride, carbohydrate or

proportions of tri-, di-, and mono-glycerides. While similar protein levels suggest that larvae of the two phases process similar amounts of food, the lower abdominal glyceride content of the solitaria suggests that larvae of this phase are utilising carbohydrate in their food for lipid synthesis to a lesser extent than the gregaria.

When female moths were fed distilled-water, solitaria had only half the weight-related fecundity of gregaria but when fed sucrose, their fecundity was comparable. There was no difference between levels of metabolic reserves in the eggs themselves. Thus the weight-related fecundity of water-fed moths reflects the glyceride content of the larvae from which they were derived and, with the results of the sucrose-fed moths, suggests that, provided the moths have access to water, fecundity is limited by the lipid stores or carbohydrate source available (Gunn and Gatehouse, 1987).

Glyceride reserves also act as the fuel for flight (see Ch. 5). S. exempta is known to undertake prolonged, migratory flights which although they may be wind assisted must entail a significant drain on these energy stores. The greater energy reserves of moths reared as gregaria larvae suggest that these individuals may possess a greater flight capacity than those reared as solitaria.

Gatehouse (1979) investigated the flight capacity of moths derived from separately maintained solitaria and gregaria cultures at the K.A.R.I. and I.C.I.P.E. laboratories in Kenya and found a difference between the phases. Gregaria larvae produced a higher proportion of female moths whose longest flight

was longer than three hours ($P < 0.02$). In males, gregaria larvae produced a significantly higher proportion of moths with longest flights greater than nine hours ($P = 0.035$; total $n = 76$ approximately equally divided between sexes and phases). However, Parker and Gatehouse (1985b) subsequently discovered that flight capacity was under genetic control. Offspring tended to resemble their parents and the proportion of long-fliers (moths giving at least two hours of flight composed of individual flights of at least 30 mins) could be increased or decreased in a population in response to selection. Since the insects used by Gatehouse (1979) came from different cultures and were probably of different genetic backgrounds any difference in flight capacity which had been attributed to phase could have been due to a different genetic capacity for flight.

This investigation was planned to examine the effect of larval phase on adult flight using a split-sib experimental design i.e. sibling groups were divided between the treatments for phase.

2. MATERIALS AND METHOD

2.1 Insect material

The insects used were derived from a sample collected at Samburu, Kenya, and brought back to Britain as pupae on 2nd June 1984. Adults from this parental sample were mated randomly as single pairs and larvae reared gregariously to produce the F1 generation of moths used in this investigation. This procedure allowed the eggs of badly-diseased moths, which died early, to be identified and removed from the rearing programme since transmission of disease from generation to generation via the oocytes is known in S. exempta (Swaine, 1966).

2.2 Flight-testing

In all cases the flight-testing procedure was as previously described in chapter 2. Moths of both sexes were mounted between 1400 and 1700hrs on D0 (the day before the night of emergence). They were attached to the balances between 1400 and 1530hrs on D1 (the day after the night of emergence) and flights recorded over N1 (the first night after emergence) from 1700 to 1000hrs the next morning. All moths were starved and unmated until flight-testing had been completed. Ten flight balances were available during this experiment. Data recording was performed using the computer data-logging system previously described in Ch. 2.

Flight-testing was performed under conditions of $30 \pm 4^{\circ}\text{C}$ and $73 \pm 7\%$ R.H., cycling diurnally. Main lighting was provided by Thorn 75/85W Artificial Daylight fluorescent tubes. An artificial dawn and dusk of c.45 mins. was provided by tungsten lights controlled by a dimmer circuit resulting in a photoperiod

of approximately 13L:11D. The heating effect of the tungsten lighting contributed to the diurnally cycling temperature regime and to the corresponding changes in relative humidity.

2.3 Experimental procedure

The F1 moths were flight-tested as described. Those with the greatest flight capacity were chosen for mating. Flight capacity is known to have a genetic basis (Parker and Gatehouse, 1985b). The intention of this selection was, therefore, to increase the incidence of prolonged flight in the gregaria phase as a basis on which any decrease due to rearing larvae in the solitaria phase could be judged. Moths were mated as single pairs in 500ml Kilner jars, each containing a small plastic pot with cotton wool saturated with distilled water. A crumpled piece of filter paper was also supplied as a convenient substrate for oviposition, although eggs were also laid on the filter paper lined floor and lid of the jar and, less frequently, on the glass walls of the jar. Eggs were collected and food pots changed daily.

The eggs laid by each female each day were divided into two approximately equal groups. This usually involved an egg batch laid on filter paper being divided by tearing the filter paper and placing each half in a plastic pot. Where the eggs to be used had been laid on the glass jar these were left in situ until hatching. One to 20 hours after hatching the larvae were divided into the two treatments using a fine paint brush. Larvae of this age spin silken threads making it easy to pick

them up using a brush without actually touching the larvae themselves. Division of egg batches between the two treatments - a "split-sib" experimental design - ensured that the two samples were of comparable genetic background.

Larvae to be reared in the gregaria phase treatment were set up initially at a density of 60 per 500ml Kilner jar until the fourth instar and then at a density of 20 per jar until pupation. In the solitaria phase treatment larvae were reared individually in 60ml plastic pots from the first instar. From the fourth instar the tight plastic lids of these pots were replaced by ones which had small perforations for ventilation and to reduce condensation. All larvae were reared on leaves from four to six-week-old maize plants, renewed daily and provided in excess of the quantity consumed in each 24 hour period. Larval rearing conditions were $30 \pm 3^{\circ}\text{C}$ and $66 \pm 6\%$ R.H.

During the sixth instar all larvae were examined and those with other than obviously gregaria colouration in the gregarious treatment and solitaria colouration in the solitarious treatment were discarded.

All pupae were sexed one to three days before eclosion. Pupae from gregaria larvae were kept in groups, and those from solitaria alone, under the larval rearing conditions until the mounting procedure. The moths were mounted and flight-tested as described.

An F3 generation, offspring of some F2 long-flying parents, was reared and flight-tested in the same way.

3. RESULTS

The distribution of the durations of the longest single flights (LSFs) produced by both phases and sexes is positively skewed (Fig. 3.1). Davis (1980) has suggested that all distributions of insect tethered flight durations can be expected to be positively skewed in this way and proposed a number of reasons to explain this phenomenon. When examined the distribution of the sum of all flights (SAF) also proved to be skew. A logarithmic transformation was attempted. Table 3.1 shows that none of the resulting distributions are significantly different from normal with the exception of the SAF distribution for female gregaria (Kolmogorov-Smirnov : $D=0.1741$, $n=63$, $0.02 < P < 0.05$). Analysis of variance (AOV) was thought to be robust enough to cope with this extent of non-normality in a distribution with this sample size and so was used for the analysis of both LSF and SAF normalised data.

Two-way AOV for unbalanced data (different numbers in each cell) of LSF (Table 3.2) indicates a significant effect of phase ($P < 0.001$) and a significant interaction term ($P < 0.02$) with sex but no significant effect of sex alone ($P > 0.50$). The AOV for SAF (Table 3.3) provides a similar result (phase $P < 0.001$; sex, $P > 0.50$; interaction $P < 0.05$). It is therefore apparent that sex does not determine LSF or SAF but that phase does do so and that the two sexes differ in their response to phase.

Differences due to phase within sibling groups of the same sex may be investigated diagrammatically by adapting the technique of Via (1984). The responses to phase are shown diagrammatically in Fig. 3.2 (for LSF) and Fig. 3.3 (for SAF) for both sexes.

Fig. 3.1

The distributions of the durations of the longest single flights (LSFs) produced by moths of each sex when reared either crowded (as gregaria) or alone (as solitaria). Note that the groups of flight durations on the ordinate of each frequency histogram are not of equal size.

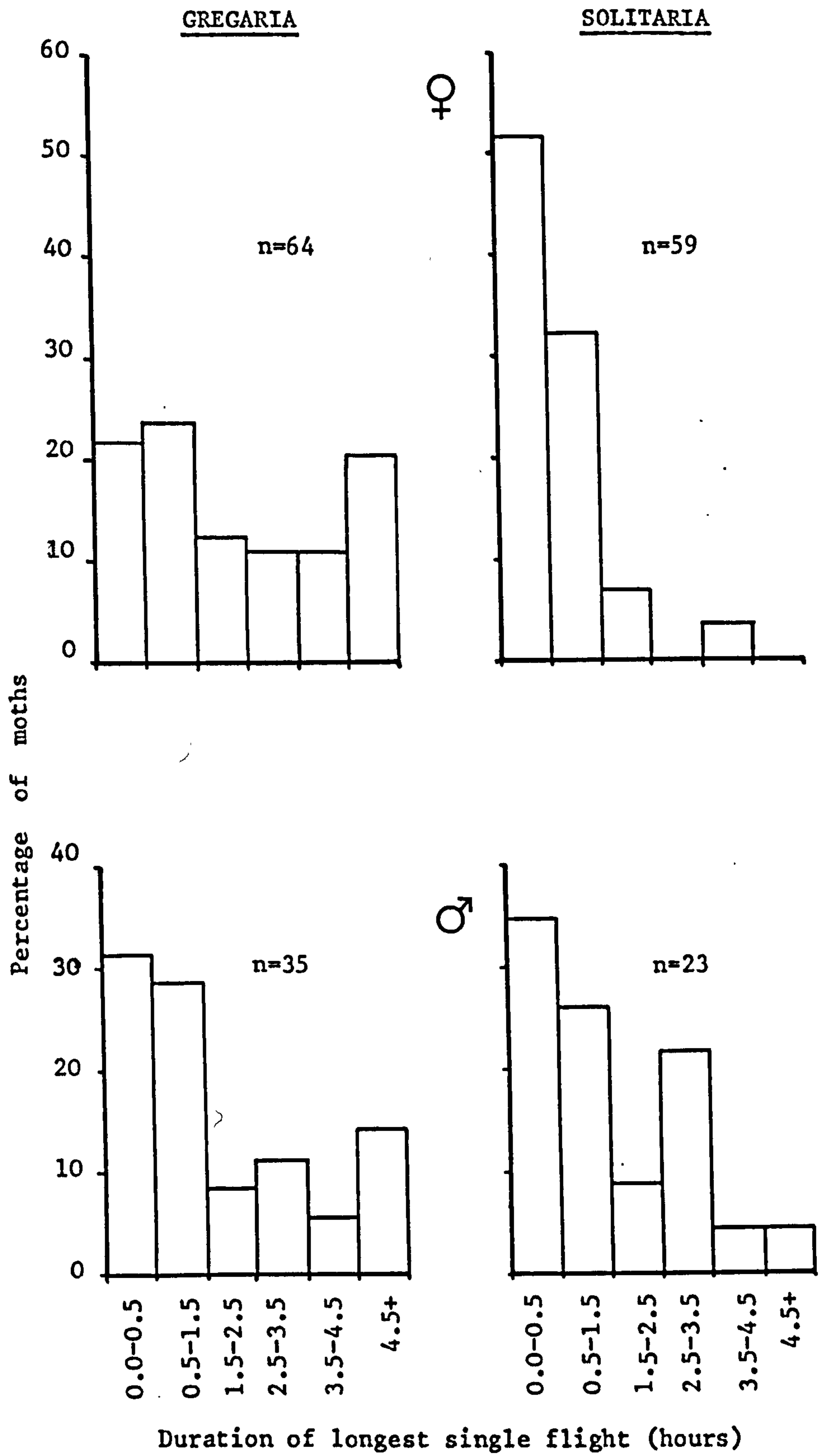


Table 3.1.

Results of Kolmogorov-Smirnov tests for differences from normality of log transformed flight duration distributions (both longest single flight (LSF) and sum of all flights (SAF)) of female and male adults which had been reared as gregaria or solitaria larvae.

The mean and standard deviation of each sample are presented, with the sample size (n), the test statistic (D1) and the probability (P) of being incorrect if the distribution is said to differ from normal.

	Mean	SD	n	D1	P

lg(LSF)					
Females					
Gregaria	3.7544	0.5548	63	0.1196	>0.20
Solitaria	3.2199	0.4314	58	0.0852	>0.50
Males					
Gregaria	3.5612	0.5988	34	0.0984	>0.50
Solitaria	3.5211	0.6124	22	0.1331	>0.50

lg(SAF)					
Females					
Gregaria	4.0807	0.4428	63	0.1741	<0.05
Solitaria	3.7141	0.3688	58	0.1070	>0.50
Males					
Gregaria	3.9005	0.4460	34	0.1824	>0.10
Solitaria	3.8849	0.4533	22	0.2413	>0.10

Table 3.2.

Two-way unbalanced analysis of variance (AOV) of flight duration (lg(LSF)) data. Treatments are sex and larval phase. Degrees of freedom (DF), sum of squares (SS) and mean squares (MS) are given for the analysis. Also given is the test statistic (F) and the significance level (P) for each term.

Source	DF	SS	MS	F	P
Sex	1	0.0856	0.0856	0.2998	>0.50
Phase	1	6.3839	6.3839	22.360	<0.001
Interaction	1	2.2636	2.2636	7.9285	<0.02
Residual	173	49.3983	0.2855		
Total	176	58.1314			

Table 3.3.

Two-way unbalanced analysis of variance (AOV) of flight duration (lg(SAF)) data. Treatments are sex and larval phase. Degrees of freedom (DF), sum of squares (SS) and mean squares (MS) are given for the analysis. Also given is the test statistic (F) and the significance level (P) for each term.

Source	DF	SS	MS	F	P
Sex	1	0.0043	0.0043	0.0242	>0.50
Phase	1	2.9217	2.9217	16.4233	<0.001
Interaction	1	1.1414	1.1414	6.4160	<0.05
Residual	173	30.7848	0.1779		
Total	176	34.8522			

Fig. 3.2

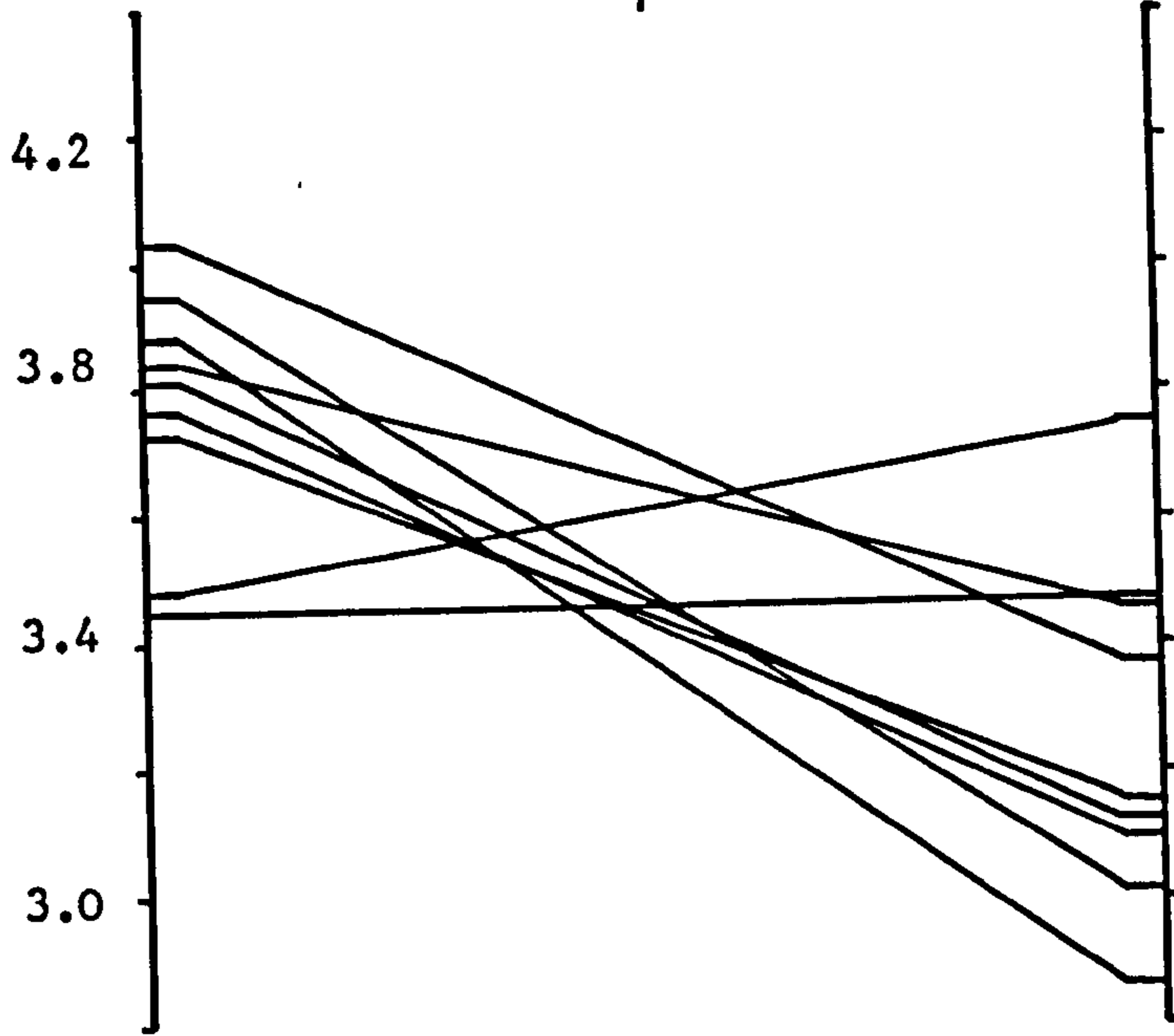
Diagrammatic comparison of the two treatment groups of each family in the split-sib experimental design. The treatments were rearing as crowded larvae (gregaria) or alone (solitaria). Data are family means of $\lg(\text{LSF})$. Males and females are presented separately.

GREGARIA

SOLITARIA

♀

Mean lg(LSF) for each family



♂

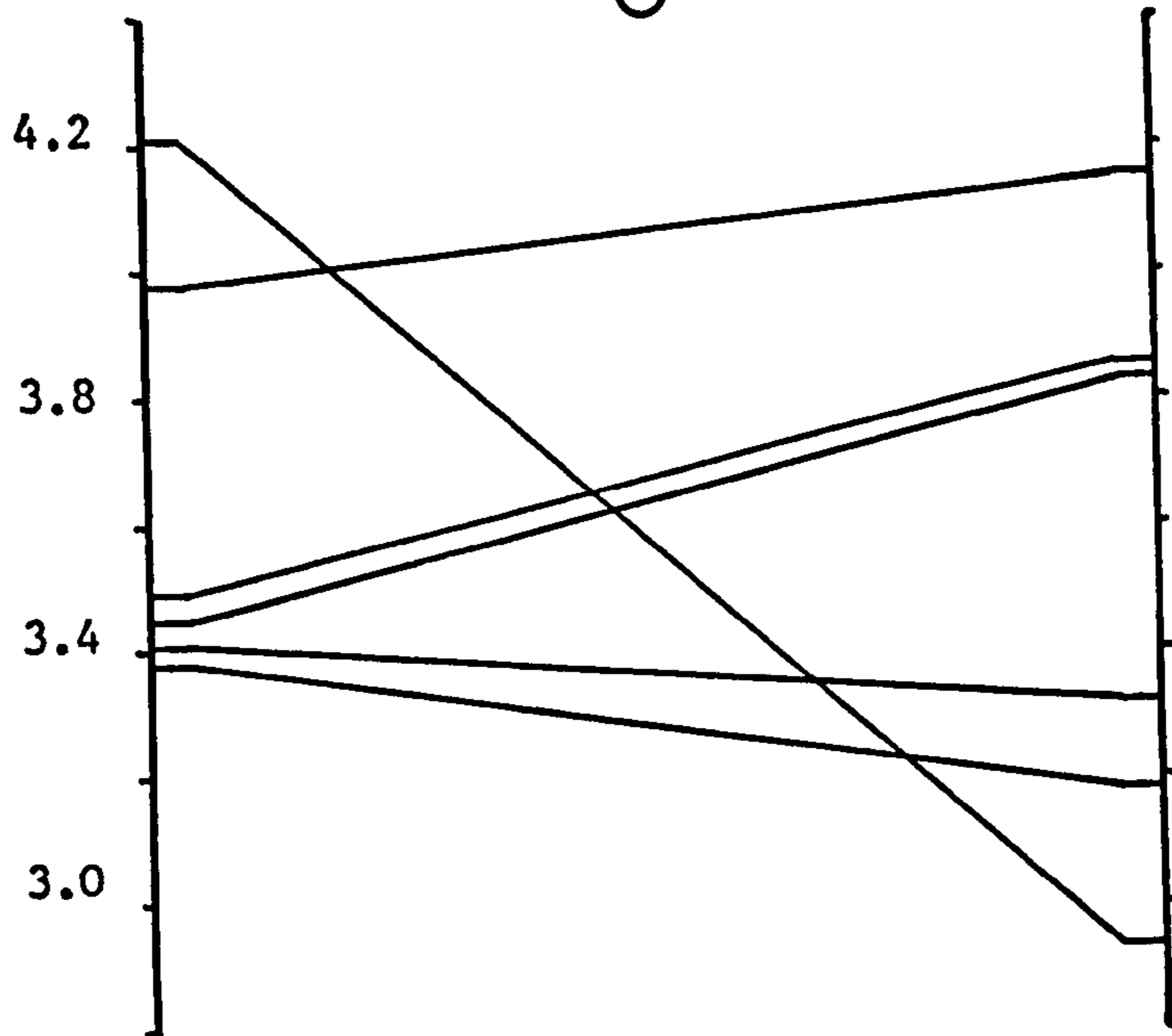


Fig. 3.3

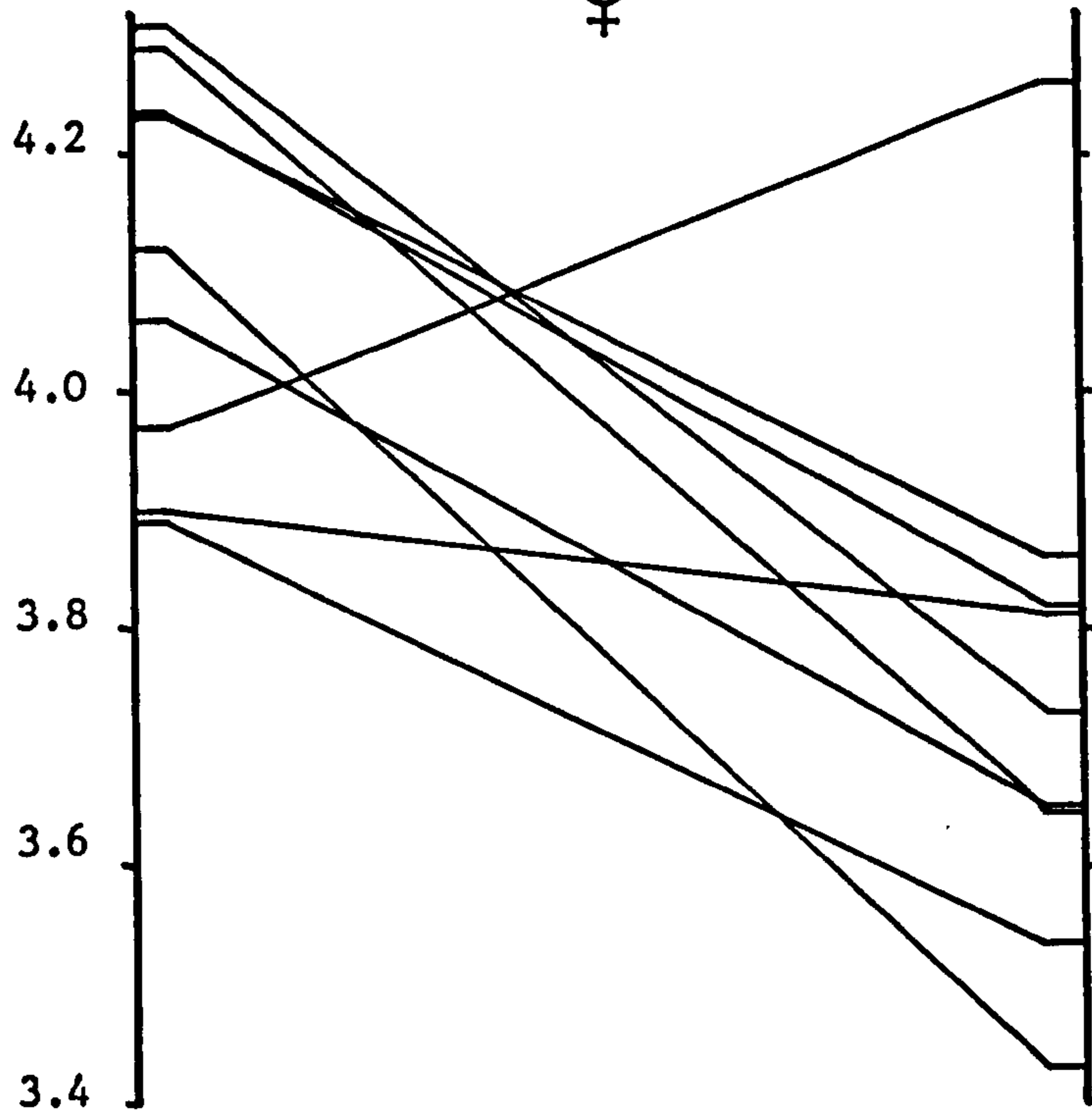
Diagrammatic comparison of the two treatment groups of each family in the split-sib experimental design. The treatments were rearing as crowded larvae (gregaria) or alone (solitaria). Data are family means of $\lg(\text{SAF})$. Males and females are presented separately.

GREGARIA

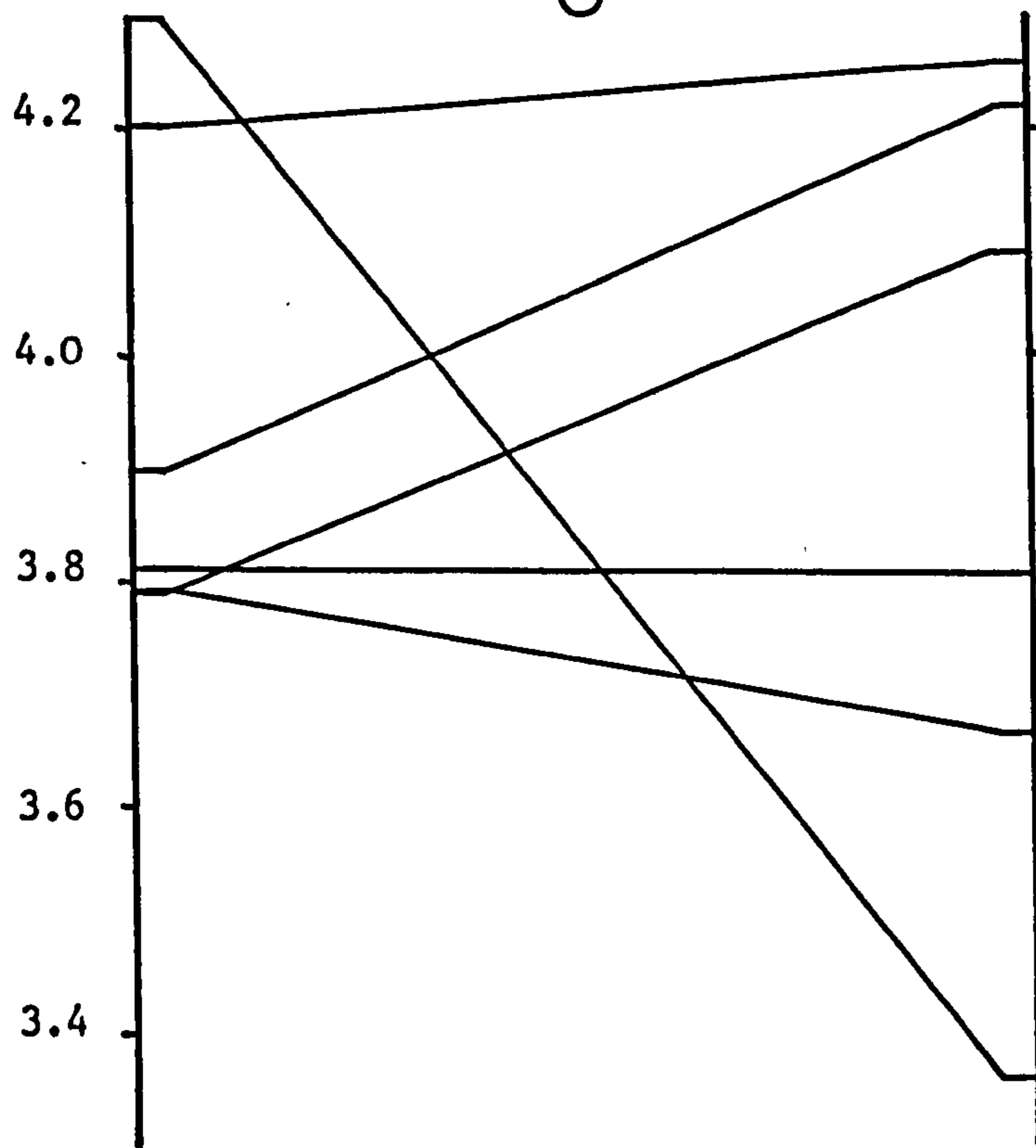
SOLITARIA

♀

Mean lg(SAF) for each family



♂



For both LSF and SAF a clear trend is apparent in females with gregaria having a greater flight capacity than solitaria. For LSF seven families show this trend strongly, one shows virtually no change and one the reverse change. In SAF all but one family shows the trend, the exception showing the reverse trend.

For males no consistent effect of phase is apparent with the flight performance of different families showing no change, increasing and decreasing with the difference in phase for both LSF and SAF.

The use of family means may remove any effect of different numbers in each single sex sibling group. The difference between the means of these family means for the two phases may be tested using a one-tailed paired-sample t-test. Such tests are highly significant for both LFY and SAF (LFY : $n=9$, $t=3.6316$, $P<0.005$; SAF : $n=9$, $t=3.5697$, $P<0.005$). Similar tests for males are not significant (LFY : $n=6$, $t=0.4365$, $P>0.50$; SAF : $n=6$, $t=0.3753$, $P>0.50$).

Fig. 3.1 shows the flight duration frequencies of the two sexes and phases and illustrates the marked difference between the phases in females and similarity between the phases in males. A small difference in the proportion of males giving flights greater than 3.5h may be apparent (8.6% of solitaria and 20.0% of gregaria) although not significant with the numbers flight-tested in this experiment.

Other results, to be presented later in this thesis, suggest a qualitative difference between flights which begin before and after midnight. A reanalysis of the LSF data was performed in

the light of this information, in case flights beginning during one period were affected by phase and this effect was being masked by flights beginning during the other period which were not.

In examining flights beginning after midnight it was found that some moths had produced no flights. In these cases a logarithmically transformed LSF is meaningless. Omission of these values from the analyses might lead to a bias e.g. if a greater proportion of one phase produced no flights after midnight than the other. Therefore an arbitrary LSF of 10s was assigned in each case, giving a logarithmically transformed value of one, and the analysis performed including these values.

AOV of LSF beginning before midnight (Table 3.4) demonstrates a significant effect of phase ($P < 0.001$) and a significant interaction term ($P < 0.02$) with an insignificant effect of sex ($P > 0.50$) similar to those analyses performed at any time of night. AOV of LSF after midnight (Table 3.5), in contrast, demonstrates no significant effect of sex or phase nor a significant interaction term ($P > 0.50$, $P > 0.20$, $P > 0.10$ respectively). Thus there is evidence of an effect of phase on flights beginning before midnight, and that the two sexes respond differently to phase. There is, however, no evidence of an effect of phase on flights beginning after midnight for either sex. A two-tailed paired-sample t-test performed for male LSFs beginning before midnight shows that there is no significant difference between the means of the family means for the two phases ($n=6$, $t=1.5046$, $P > 0.10$). Hence there is no evidence that

LSFs in males, before or after midnight, depend on phase.

Table 3.4.

Two-way unbalanced analysis of variance (AOV) of flight duration ($\lg(\text{LSF})$) data for flights beginning before midnight only. Treatments are sex and larval phase. Degrees of freedom (DF), sum of squares (SS) and mean squares (MS) are given for the analysis. Also given is the test statistic (F) and the significance level (P) for each term.

Source	DF	SS	MS	F	P
Sex	1	0.2878	0.2878	0.7349	>0.50
Phase	1	5.6712	5.6712	14.4821	<0.001
Interaction	1	3.1591	3.1591	8.0672	<0.02
Residual	173	67.7394	0.3916		
Total	176	76.8575			

Table 3.5.

Two-way unbalanced analysis of variance (AOV) of flight duration (lg(LSF)) data for flights beginning after midnight only. Treatments are sex and larval phase. Degrees of freedom (DF), sum of squares (SS) and mean squares (MS) are given for the analysis. Also given is the test statistic (F) and the significance level (P) for each term.

Source	DF	SS	MS	F	P
Sex	1	0.3302	0.3302	0.9059	>0.50
Phase	1	0.6625	0.6625	1.8176	>0.20
Interaction	1	1.0711	1.0711	2.9426	>0.10
Residual	173	63.0551	0.3645		
Total	176	65.1189			

4. DISCUSSION

The results of these experiments have been analysed previously and published (Woodrow et al., 1987). For this paper, a non-parametric analysis was chosen due to the highly skewed nature of the data. There was no reason to believe that the distribution of flight durations would easily transform to normal and the analysis software had not been developed to a stage where transformations could easily be made. The data handling and analysis software has since been improved so that flight data can be transformed quickly and simply. The data in this investigation proved to be log-normally distributed with the exception of SAF for female gregaria which was just significantly different from normal ($0.02 < P < 0.05$). This difference was not thought to be so great as to invalidate the use of an analysis of variance.

The distributions of LSFs show great variability under the controlled environmental conditions of the laboratory. Such variability could reflect a number of factors; firstly, uncontrolled environmental factors, secondly, variance inherent in the behavioural assay of flight capacity in the laboratory (Gatehouse and Woodrow, 1987) and, thirdly, genetic differences in the capacity for flight. The genetic determination of prolonged flight has been demonstrated by Parker and Gatehouse (1985b, see Ch. 1 : General Introduction) and dictated the design of these experiments which is based on matched genetic samples (full sibs) split between the two treatments for phase. Ideally equal numbers of full sibs would have been flight-tested in each treatment for each sex, requiring only a simple balanced two-way

AOV. In fact, differential mortality and numbers of each sex between treatments and logistical considerations in making maximal use of the flight-balances meant that unequal numbers of full sibs have been flight-tested in each treatment. An unbalanced two-way AOV was therefore used and, in addition, a graphical analysis adapted from that of Via (1984). Via's analysis is a graphical construction of the norms of reaction i.e. the mean phenotype of each sex of each full-sib group under the two treatments. A sloping line connecting the two treatments of a full-sib group indicates an environmental effect, differences in the elevation of the lines genetic variation, while non-parallelism indicates genotype-environment interaction.

A significant difference between the phases in the AOV could have resulted from a phase-related difference in flight capacity, or from the different numbers of moths in each treatment for each single-sex sib group since more genetically long-fliers could have been flight-tested in one treatment and more genetically short-fliers in the other. The use of family means in the graphical representation of norms of reaction removes this possible source of error. The consistent slope of the lines for females of most families may then be seen. The t-test provides an additional quantitative indication of the difference between the means (across treatments) of the family means (within treatments).

In this study family means from gregaria and solitaria treatments of each sex are plotted on the two vertical axes and their paired nature illustrated by a joining line. The slope of

each line reflects the difference in flight capacity due to the difference between the treatments, and the elevation of each line the genetic capacity for flight of each group of full sibs of each sex.

The difference in flight capacity of females reared as different phases is clearly demonstrated. Females from the gregaria treatment have a greater flight capacity in terms of LSF and SAF than do females from the solitaria treatment. There is some evidence from non-parallelism in the graphical analysis of genotype-environment interaction, however, given the variability inherent in the behavioural assay of flight-capacity and the family sample sizes the existence and extent of the interaction must be uncertain.

In marked contrast to the females, no difference is apparent in flight capacity of the males from the two treatments. A number of explanations are possible. There may be no real difference in the flight capacity of males from the two treatments. Alternatively, tethered flight recorded on this apparatus may not provide a reliable index of flight in males; perhaps the technique is too intrusive for use with this sex which appear to be more sensitive to disturbance. Lastly, males may differ in their phase-related flight capacity only for flights beginning during some particular part of the night. Other results presented in this thesis have indicated a qualitative difference between flights beginning before and after midnight (see Ch. 4). A re-examination of the data for males on this basis did not reveal any difference in flight capacity between the treatments either for flights beginning before or

after midnight (see above). Thus, either there is no difference in the flight capacity of males reflecting larval phase or the tethered-flight technique does not provide a reliable index of the capacity for prolonged (migratory) flight in males.

The flight capacity of females was also re-examined on the basis of flights beginning before and after midnight. This has revealed no phase-related difference in LSF beginning after midnight, but a very significant difference in LSF beginning before midnight (see above). This result confirms the qualitative difference between flights beginning before and after midnight which has been shown elsewhere (see Ch. 4). The possible relationship of these qualitatively different flights to the field situation is discussed later in this thesis.

Only one other investigation of the effect of phase on the flight behaviour of a noctuid moth has been published. This study, by Hill and Hirai (1986), of Mythimna separata used larvae reared as groups up to the second or third instar. Only then were larvae separated into isolated (one per 113cm³ petri dish) or crowded (50-200 per 3400cm³ plastic box) treatments. No indication was given of the ancestry of the isolated or crowded larvae and it is inferred that no attempt was made to match the treatment groups genetically. Crowded and solitary larvae were sorted according to colour categories (on a scale of one to five) in the final instar and the former were placed in petri dishes in groups of five. Solitary larvae were found to be mainly from colour categories one and two, with some from category three, whereas larvae reared in crowds fell into categories four and

five, with some from category three.

Although not stated explicitly, it is inferred that moths from each treatment were used, irrespective of their larval colour, so that moths from larvae with colours from the whole phase continuum were used. Moths from colour category three were, therefore, present in both treatments. This contrasts with this study of S. exempta where only larvae of clearly gregaria or solitaria colouration were included in the experiment, all transiens larvae being discarded before pupation.

Female moths of M. separata were flight-tested either on a flight-balance derived from the design described by Gatehouse and Hackett (1980) or freely suspended on a wire with activity recorded on a smoked kymograph drum (after Hwang and How, 1966).

Flight activity on the flight-balance revealed no difference between the phases. The criterion used was total flight activity (Sum of All Flights (SAF) in this thesis). It should be noted that a high SAF may result not just from one or more prolonged flights but also from many short flights. Hill and Hirai's study is therefore an examination of the relationship between phase and total activity, whereas this study stresses the relationship between phase and prolonged flight capacity.

Hill and Hirai found a pattern of flight activity for M. separata similar to that obtained for S. exempta in this laboratory. A large peak of activity at dusk was followed by a small second peak in the fifth hour of scotophase, and a broader and higher hump of flight activity over the eighth to tenth hours. No dawn peak of flight activity was recorded. This pattern recorded for M. separata reflected that observed in the

field. Hsia et al. (1963) observed a pattern of nocturnal activity in moths of M. (cited as Leucania) separata observed from, and trapped on, ships in the Gulf of Chili and the Yellow Sea. Nocturnal activity began at 1700h with peaks at approx. 2000 and 0400h, corresponding to the peaks at the beginning, and eight to ten hours after the beginning of scotophase. No peak at dawn is mentioned. The correspondence of flight activity recorded in the laboratory with that observed in the field is evidence for the validity of the flight-testing technique (Gatehouse and Woodrow, 1987).

Data recorded on the kymograph revealed no pattern of flight activity through the night in terms of the proportion of time spent flying in three-hourly periods, possibly because the lack of provision of tarsal contact is likely to enhance flight activity obscuring any such pattern. Moths reared crowded flew for significantly less time than moths reared isolated when flight-tested in this way. Moths of M. pallens were also flight-tested using the kymograph and again those reared crowded were found to fly significantly less than those reared isolated. Because of the lack of any pattern of flight activity comparable to that observed in the field, the relevance of these results as indices of flight capacity in the field is more uncertain.

A further study of M. separata using larvae reared isolated and crowded from hatching in a split-sib design and flight-testing moths derived only from larvae at only the extremes of the phase continuum might reveal further information.

In the field, low density populations of S. exempta larvae

in the solitaria phase are now believed to persist in areas of suitable habitat over much of the species range throughout the year (Rose, 1979). Because of their procrypsis, cryptic behaviour and low density they are very difficult to find and it may be presumed that both their appearance and behaviour are maintained by the selective pressure of predators and parasitoids.

Gatehouse (1986) has suggested that S. exempta and possibly other species of leaf-feeding and migratory continental noctuid moths whose larvae feed on ubiquitous host plants, are specifically adapted to existence at these low population densities. Such low densities may be maintained at each generation by dispersal by flight, the extent of which is under genetic control and subject to selection imposed by the spatial and temporal heterogeneity of the suitable habitat. In general the costs in fitness terms associated with dispersal would be minimal due to the very widespread nature of suitable host plants, especially during the rainy season.

Gregaria larvae are characteristically associated with high density outbreaks during the rainy season (Haggis, 1986; see also Ch. 1 : General Introduction). Under crowded conditions the larvae must be subject to higher mortality due to the functional response of predators and parasitoids (e.g. Gruys, 1970) and increased incidence of disease (Brown and Swaine, 1965). The larvae may also deplete their food supply to such an extent that some caterpillars starve (Brown, 1962) , a mortality factor selecting against slower-developing individuals.

The black colouration of gregaria larvae and their habit of

feeding high on their host plant in direct sunlight have been interpreted as adaptations to increase body temperature, speed-up metabolic rate and therefore complete development in a shorter time (Rose, 1979). However, it should be noted that evidence of a difference in development time under the microenvironmental conditions selected by gregaria and solitaria larvae in the field is sadly lacking. In effect the larvae at high density are unable to hide in space and so must do so in time by developing as fast as possible to pupation. The abandonment of procrypsis and cryptic behaviour in achieving this faster development may emphasise their ineffectiveness under high-density conditions.

Larvae in one outbreak have usually developed from the oviposition of moths present in a high density over a period of a few consecutive nights (Page, 1985; Gatehouse, 1988). Their development is quite synchronous leading to emergence over a few nights. . Since higher mortality can be expected at the high densities characteristic of outbreaks than at low densities, it would seem reasonable to deduce that dispersal of the moths emerging from an outbreak to achieve low densities would be very important. In very approximate terms, if both moths from a low density population and moths from an outbreak would gain maximal advantage by dispersing down to a similar density before oviposition, then the scale of dispersal would have to be greater for moths from the outbreak. This greater scale of dispersal might be achieved by a generally greater flight capacity, or greater range of flight capacities. However an additional factor might be expected to offset the dispersal from outbreaks, at

least for some moths. Outbreaks are formed by the concentration of flying moths by mesoscale wind systems such as storm outflows and topographically induced eddies which act to concentrate flying insects (Brown et al, 1969; Blair et al, 1980; Pedgley, 1982). If further dispersal is inhibited e.g. by the onset of sexual maturity (Page, 1985) or rainfall (Riley et al, 1983) then mass oviposition often occurs. When compared with a short-flier, a moth which flies for longer should have a greater probability of being caught in a concentrating wind system and so contributing to the formation of an outbreak, with its attendant detrimental effects on the moth's fitness. Thus increased flight expression may not necessarily ensure that the moth will reproduce within a population of low density.

A further factor is introduced by the area covered by the source outbreak. A small area will necessitate only small scale dispersal to achieve a low density. Dispersal of moths from the centre (or upwind edge) of a very large outbreak will necessitate a far greater scale of dispersal. The result would be unpredictable variation in the selection for flight capacity from generation to generation.

Overall, the implication of this discussion is that the solitaria phase is the primary larval form of S. exempta. The familiar black gregaria caterpillar is seen as an adaptation to achieve accelerated development under the adverse circumstances of a high density outbreak where procrypsis and cryptic behaviour are ineffective in containing mortality and contact between larvae enhances the spread of disease. Dispersal from the outbreak to a safely low density population - but not too low

since when at a very low density moths would be unable to find each other for mating (Gatehouse, 1987) - may be achieved by the greater flight capacity of female moths in the gregaria, compared with the solitaria form.

If the tethered-flight capacity of male moths is accurately indexed by the technique used here, it would seem that larval phase has no effect on male flight capacity. One possible explanation of this is that the strategy of male moths is not to disperse down to an optimal density as previously described for females. Rather the main element of their strategy is likely to be to locate and mate successfully with any female, provided that she then lays her eggs in an area which will sustain their offspring. A pattern in which flight is interrupted by landings so enabling males to perceive and respond to any female sex pheromone present at ground level may be more appropriate for male moths. The pattern of flight, if this occurs, may depend little for its efficiency of scanning the habitat for females, on whether the male emerged from a high density outbreak or a low density population. This problem may be open to investigation by mathematical modelling.

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CHAPTER FOUR

The genetic regulation
of tethered-flight durations

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1. INTRODUCTION

Knowledge of the migration and dispersal of insects, and how they are regulated, is important not least because many migratory insect species are very effective pests of crops (Joyce, 1981; Stinner et al., 1983). Polymorphisms associated with insect mobility by flight are well known (e.g. Guthrie, 1959; Harrison, 1980). Polymorphism, that is intraspecific discontinuous variation (Harrison, 1980), may result from genetic differences - genetic polymorphism - due to the presence of loci where variant alleles are present at intermediate frequencies (Falconer, 1981). Alternatively, polymorphism may result from environmental effects - polyphenism (Shapiro, 1976). The age of an adult may also effect the morph it expresses e.g. young termite (Isoptera) reproductives are winged until they have completed their mating flight when the wings are shed. Sexual dimorphism is also known e.g. Kimyra and Masaki (1977) - see below.

Flight polymorphisms may be conveniently divided into three categories. These are polymorphisms of wing structure, those of flight muscle, and those of flight behaviour amongst individuals which all appear fully capable of migratory flight. Polymorphisms of wing structure and flight muscle are comprehensively reviewed by Harrison (1980) and Dingle (1985), with physiological aspects discussed by Johnson (1974).

The most obvious polymorphism is that of wing size. This may be simply the possession or lack of wings, under environmental and genetic control, as in some aphid clones which differ in their sensitivity to environmental cues (Dixon, 1985). In other insects the polymorphism may be represented by classes

of individuals with different wing lengths, involving one or both pairs of wings (Harrison, 1980; Dingle, 1985, Table 7 and Section 8.2; see also Denno et al., 1985; Fujisaki, 1985; Solbreck, 1986; Ritchie et al., 1987). A seasonal and sexual dimorphism has been found by Kimyra and Masaki (1977) in the vapourer moth, Orgyia thyellina. All male moths were normal winged forms but wing form in females depended on photoperiod at constant temperature (20°C) such that, in the field, females eclosing in summer had normal wings and those eclosing in autumn had atrophied wings.

Polymorphism of flight muscles may be found to be due to either a failure of the flight muscles to develop after eclosion in some individuals, or to degeneration (histolysis) of the flight muscles at a later stage in adult life, either before or after flight has occurred (reviewed by Johnson, 1974). Failure of the muscles to develop may be associated in some cases with aptery (Dingle, 1980) and histolysis with shedding of the wings as occurs in the sexual stage of termites. Development of wings and development and maintenance of flight muscles is believed to constitute a cost to the insect in terms of fitness (Zera, 1984; Roff, 1984b, 1986a)

Southwood (1962) has suggested that the level of migratory movement (which he defined as movement taking the animal out of the habitat inhabited by the population to which it belonged) is related to the stability of the habitat, being greatest in those species with the most temporary habitats. He produced evidence to substantiate this hypothesis from a review of the major taxa of terrestrial Arthropoda. The implication was that, in general,

apterous species should be found in stable habitats, while macropterous species should occur where habitats are transient. Dingle (1980, Table II) has summarised the characteristics of the wing polymorphism and habitats of a number of species of aquatic water striders (Gerridae) supporting Southwood's conclusions in this particularly well-studied group. Many polymorphic species found in habitats whose quality fluctuates are able to respond to environmental cues (e.g. temperature, photoperiod) indicating seasonal changes or those (e.g. host plant availability or quality, crowding) preceeding imminent habitat deterioration, by changes in the proportion of the morphs produced. The flight threshold of apparently flight-capable individuals may also vary inversely with the proportion of macropters in the population (Fairbairn and Desranleau, 1987). However, Fairbairn (1986) has also shown that in at least one species of Gerrid (Gerris remigis) the proportion of macropters that undertook long-distance flight in the field appeared very small. Indeed during the season of maximum movement by both macropterous and apterous morphs the macropters were not capable of flight having histolysed their flight muscles very early in the season.

As well as environmental effects on wing polymorphism, genetic effects are apparent from the high degree of variation within environmental treatments. In particular, different aphid strains (Sutherland, 1970) and clones (Lamb and MacKay, 1979) have been shown to vary in the proportion of different wing morphs produced in response to standard environmental stimuli.

Studies of the genetic basis of wing polymorphism have largely concentrated on differentiating between single locus or

polygenic control. Roff (1986a) has reviewed the literature on wing-dimorphic insects and has proposed that both forms of inheritance can be responsible for the production of distinct wing forms, assuming a general threshold model. He postulated that wing production is suppressed when some hormone, perhaps juvenile hormone, exceeds a threshold level during a critical stage in development. He also argued that an increasing proportion of brachypters in a population may be more often produced by a greater fitness of the brachypterous form (as indicated by a higher fecundity and earlier reproduction in females) than by emigration of the macroterous form.

Jackson (1928) investigated the alary dimorphism of samples of the weevil Sitona hispidula obtained from two Scottish localities. Those from Invershin bred true for macroptery (no brachypters were seen in this area), but those from Swordale maintained a level of only 6-9% macroptery. Single-pair crosses produced results entirely consistent with single-locus, two-allele, control of the polymorphism, with brachyptery dominant. A similar mechanism may also be present in the carabid beetle Pterostichus anthracinus (Lindroth, 1946) although this evidence is not conclusive due to the small number of offspring (52) obtained from his seven crosses.

Klausner et al. (1981) discovered a brachypterous mutant in a laboratory culture of Oncopeltus fasciatus. The character behaved as a "single recessive Mendelian unit", not related to sex but with some variation between brachypterous individuals, indicating the presence of modifiers. Although it is of interest

that a single mutation can produce brachyptery, this seems to be of little relevance to the field situation where no brachypters or heterozygotes for this trait have been found.

Vepsäläinen (1978) suggested that morph frequencies in Gerris could be controlled by a combination of environmental effects and a single-locus genetic switch, and proposed a threshold model for the mechanism. Harrison (1980) and Zera et al. (1983), however, point out that the experimental design and interpretation of the data were not rigorous - in particular, that females used in the study were field-collected and may have mated prior to collection with a male of unknown morph type - leaving the results inconclusive and the model unsubstantiated.

Solbreck (1986) has crossed true breeding lines of brachypterous and macropterous morphs of the lygaeid bug Horvathiolus gibbicollis. The F1 generation obtained were all of the brachypterous morph and the F2 showed a ratio of macropters to brachypters not significantly different from one to three, indicating monogenic control with brachyptery dominant.

Other studies have demonstrated genetic control of flight polymorphisms which cannot be based on a single-locus, two-allele model.

Zera et al. (1983) found that crosses of macropters, or of apterous morphs, could produce offspring of either type in the gerrid Limnoporus canaliculatus. Crosses between macropters and apterous morphs gave a proportion of macropters intermediate between the within-morph crosses. Some influence of sex was also apparent in morph determination. Similarly, Harrison (1979) found that crosses within macropterous or brachypterous morphs

produced offspring of both types in the field cricket, Gryllus pennsylvanicus. Roff (1986c) also found the genetic control of wing dimorphism in the sand cricket, Gryllus firmus, to be polygenic with micropterous parents producing a higher proportion of micropterous offspring than macropterous parents. He also estimated the heritability of the trait as 0.62 and 0.68 for males and females respectively, and by a second method as 0.55 in males and females with no indication of maternal effects under the given rearing conditions.

The response of the proportion of macropters in a population to selection has been examined by Mahmud (1980) for the planthopper Laodelphax striatellus when reared on wheat. He increased the proportion of both male and female macropters in one generation by breeding only from macropterous parents. However, a second generation of selection failed significantly to increase the proportion further.

Dingle (1985) reported that Honek (1976a,b) selected for macroptery in the bug Pyrrhocoris apterus under long-day conditions and raised the proportion of macropters from 20% to 90% in 29 generations. Selection under short-day conditions also increased the proportion of macropters from 0% to 70% although entry into diapause under such conditions was unaffected by the selection. Dingle (1985) also reported that macropters of P. apterus develop little or no flight muscle and are flightless. Ritchie et al. (1987) have reported a similar, apparently flightless, macropterous morph of the acridid Chorthippus parallelus produced under long-day conditions. They do not

comment on its flight-muscle development but state that females mate later and are less fecund than brachypters. The role of wing polymorphism in these insects is clearly difficult to understand and Ritchie et al. postulate some role other than flight for macropterism in C. parallelus.

Flight behaviour is obviously dependent on the presence of the flight apparatus but, within species where all individuals appear capable of flight, as well as within apparently flight-competent morphs, differences in flight behaviour have been reported. Differences in flight duration may be quantified in the laboratory by tethered-flight techniques (see Ch. 2) and differences in flight threshold (readiness to fly) may also be quantified (e.g. Kidd and Cleaver, 1984, 1986).

Studies of the variation in flight ability, whether environmentally or genetically controlled, within the flight-capable macropterous morph of a polymorphic species are rare (Gatehouse, 1988). Shaw (1970) has demonstrated an effect of parental and offspring crowding on offspring flight behaviour in alates of the aphid Aphis fabae. Crowding in both cases increased the proportion of migrants (flying before parturition) compared with fliers (flying after parturition) and non-fliers. Using the same terminology, Kidd and Cleaver (1984) have shown that in alatae dissected before reproduction or flight, those reared under high density conditions, and hence mainly migrants, had fewer, and less advanced, embryos than low density reared, mainly flier, alatae of the same weight. They also showed that the flight performance after take-off of migrants was comparable with that of fliers (Kidd and Cleaver, 1986). Post-take-off

free-flight duration was found to depend on alate size - small alatae flying for longer - and therefore indirectly on host plant quality. In the field crowding (controlling take-off) and host plant quality (controlling prolonged flight) are probably synchronous leading to greater migratory flight with declining habitat quality.

Fairbairn and Desranleau (1987) have recently examined the variation in flight threshold, measured on an ordinal scale, within macropters of four species of Gerridae. They found variation within species and highly significant differences between species for both overwintered and summer-born macropters. They concluded that flight ability depended not only on the proportion of macropters in these species but also on the flight ability of macropterous individuals.

The flight behaviour of monomorphic macropterous species has been more thoroughly studied than that of macropters of polymorphic species. Such studies have concentrated on the use of tethered-flight techniques to examine flight durations, either by grouping individuals into flight categories (e.g. Rose, 1972 for Cicadulina; McAnelly, 1985 for the grasshopper Melanoplus sanguinipes; Parker and Gatehouse, 1985a,b for Spodoptera exempta) or by analysis of the flight durations themselves always revealing a strongly positively skewed distribution of flight durations (e.g. Rose, 1972; Johnson, 1976; Davis, 1980; Dingle, 1980).

The capacity for prolonged flight commonly depends on age, often peaking after the completion of cuticle sclerotisation and

before reproduction begins (Dingle, 1980). This variation in flight behaviour may lead to errors of classification in the laboratory where individuals are flight tested at only one age (Gatehouse, 1988) particularly with insects which have a long pre-reproductive, and hence flight period e.g. Oncopeltus fasciatus, Mythimna separata.

Environmental regulation of flight behaviour has been reported in species from a number of orders (review by Dingle 1985, Table 6).

In other reports a genetic regulation of flight behaviour has been demonstrated. For example Sharp et al. (1983) achieved significant responses to selection for and against "flight propensity" (measured in terms of sensitivity to disturbance) in the fruit flies Anastrepha suspensa and Ceratitis capitata. A number of examples are available from known migratory species. The North American grasshopper Melanoplus sanguinipes is known to make migratory flights both in swarms and in non-swarmling populations (McAnelly, 1984; McAnelly and Rankin, 1986). Initial indications of a genetic basis to tethered flight capacity came from differences between three geographically separated field-collected populations. These differences were maintained at significant levels for at least one generation in the laboratory and in one case into the fourth generation. Crosses between the most and least active strains produced a population with a proportion of long-fliers (flying for longer than 55 mins.) close to the least active parental strain, indicating that genes

producing long flight may be "somewhat recessive" (McAnelly, 1985).

The association between parental and offspring tethered-flight performance in the planthopper Cicadulina mbila has also indicated a genetic component in the determination of flight capacity (Rose, 1972). Flight performance appears to be polygenically inherited and is associated with a dimorphism of body length without change in wing length, short-bodied morphs giving longer flights. Rose suggested that seasonal changes in the frequency of these morphs occur by natural selection. The short-bodied morphs with lower wing-loading and greater flight capacity would be favoured in the dry season because of their greater ability to reach suitable patchily distributed host plants. The greater fecundity of the long bodied morphs would give this form selective advantage in the wet season when host plants are more uniformly distributed. In fact, during the flight season (from the end of the wet season) a higher proportion of short bodied forms were found settling on cereal crops (50-94%), while irrigated grasses were found to contain more long-bodied forms (86%).

The regulation of flight behaviour in the bug Oncopeltus fasciatus has often been studied, and particularly the association of flight with other life history traits (Dingle, 1966, 1968, 1980; Palmer, 1985). Intense selection for tethered flight performance under long-day conditions raised the proportion of long fliers (flying for more than 30 mins.) from 30 to 60% in females and 20 to 68% in males in one generation

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(Dingle, 1968). Positive selection for wing length also increased the proportion of long fliers (Palmer, 1985) and Rankin (1978) has shown that the timing of maximal flight activity can be delayed by four generations of selection.

Tethered flight durations in the bug Lygaeus kalmii have also been shown to exhibit genetically controlled variation. Caldwell and Hegmann (1969) investigated the heritability of flight durations from offspring on parent regressions using appropriately transformed data. They achieved values of 0.2 and 0.4 from regressions on male and female parents respectively, and interpreted the higher latter value as indicative of maternal effects.

Evidence for the genetic control of flight behaviour in Lepidoptera is limited to a few examples. Wellington (1964) reported observations of qualitative changes in the behaviour of colonies of the Western Tent Caterpillar, Malacosoma pluviale, and in the adults derived from them, with the succession of generations in the same habitat patch. He recognised the behaviour of caterpillars as "active" or "inactive" (to the point of being "...too sluggish to leave their tents to feed") and moths also as "active" (strong flying, often "towering up" to tree top level before continuing in level flight) or "inactive" (only able to make short distance low level flights). He found that inactive moths produced a high proportion of inactive offspring with a few active individuals able to travel further before oviposition, the latter in turn having a higher proportion of vigorous individuals amongst their progeny. Vigour was unrelated to predation or density of colonies in a habitat. He

concluded that vigour was genetically determined and that the migration of active individuals from a habitat decreased the mean vigour of the remaining population. Although this was advantageous for the successful colonisation of new habitats and for continued "local exploitation" in the short term, he attributed the adverse effects he observed to the maximum favourability of the local environment being maintained for three or four years. Gatehouse (1988) has pointed out that colonies of M. pluviale are composed entirely of siblings posing the question of the role of kin selection.

Gatehouse (1988) has also reviewed reports of the genetic determination of flight in the spruce budworm, Choristoneura fumiferana, and the tent caterpillar, Malacosoma disstria. A model was proposed by Campbell (1962, 1966) of two types of X chromosome controlling life history characters, including flight, which assumed the pre-reproductive migration of smaller, less fecund females. The reverse was found to be true in M. disstria and the assumption was not substantiated for C. fumiferana by field evidence.

Gilbert and Singer (1973) studied two populations of Euphydryas editha (called JR and DP) where the adults of one (DP) were noticeably more mobile. They collected DP larvae and released them within the JR population area. The adults of this sub-population appeared to be more ready than the JR population to fly over trees and shrubs and so to disperse. They inferred, although their results were certainly not conclusive, a genetic component in the control of flight behaviour in this butterfly

species.

Blair (1978) flight-tested adults of Agrotis ipsilon and A. segetum in actographs in the laboratory. He assigned the tested moths to "active" or "inactive" categories based on the number of 30 min. periods of continuous activity during one night and found no difference between the activity of the sexes but that A. ipsilon was significantly the more active species. By mating single active and inactive pairs of both species Blair found that the offspring of active parents were not significantly different from their parents, whereas the offspring of inactive parents were significantly less active. He concluded the presence of a significant genetic component to the variation in activity and that the heritability of the inactive character was greater than that of the active.

Parker and Gatehouse (1985a,b; see also Parker, 1983) examined the control of tethered flight capacity in adults of Spodoptera exempta reared as gregaria phase larvae. They (Parker and Gatehouse, 1985a) found indications of a genetic influence on adult flight through the occurrence of groups of "long-fliers" (moths giving a total of at least two hours flight on N1 composed of flights of at least 30 mins. duration) at generation intervals in both control and treatment samples in experiments designed to investigate the influence of food quality and availability and crowding on flight. The proportion of long fliers in a population was then shown to respond to bidirectional selection. The proportion of long flying females rose from 38 to 75% in three generations with selection imposed for only two and remained above 70% for all subsequent generations where selection

was imposed. Males also responded to selection for flight although less rapidly, the proportion of long fliers not exceeding 60% until the 10th generation (8 generations of selection). Selection against flight was less successful over the initial generations probably because short fliers from the long-flight line were initially bred back into the short-flight line on the assumption that flight was under monogenic control. Later selection against flight in which the lines were isolated was more successful decreasing the proportion of long fliers to 20-40% in females and 0-15% in males.

Heritability estimates were also made (Parker and Gatehouse, 1985b, Parker, 1983) from offspring on parent regressions. The regression of mean offspring on mid-parent values was significant giving an overall heritability of 0.40. Regressions of single sex of offspring on single sex of parent were also significant, with heritability values significantly higher for regressions on fathers than those on mothers (0.71-0.89 c.f. 0.50-0.55). This may indicate some sex-linkage in the inheritance of flight capacity or it may be an artefact due to differences in the reliability with which the tethered-flight equipment indexes migratory flight in the two sexes (Gatehouse, 1986). The data used in these estimates were based on the sum of all flights longer than 30 mins. for each moth, any individual not producing a flight of at least 30 mins. duration being assigned a value of 30 mins. The distribution of these data was not normal but they were not transformed for the estimation of heritability because "no suitable transformation could be found" (Parker, 1983).

It can be concluded from these results that there is genetic, probably polygenic, control of flight behaviour in S. exempta with some suggestion that the inheritance of flight may be related to sex.

This investigation seeks to confirm and investigate further the genetic basis of flight behaviour in S. exempta.

2. MATERIALS AND METHOD

2.1 Insect material

Spodoptera exempta moths used in the investigation of the genetic regulation of flight were derived from four field-collected samples.

1. K strain - collected from an infestation at Kabarnet, Kenya at the beginning of June 1985. Brought back to Britain as pupae on 7th June 1985.

2. KT strain - collected from infestations in the Tana River delta, Kenya at the end of December 1985. Brought back to Britain as pupae on 4th January 1986.

3. L strain - collected from the field as 5th and 6th instar larvae at Lukenya, 30km east of Nairobi, Kenya, fed on cut mixed grasses in the laboratory until pupation on 4th and 5th February 1986 and brought back to Britain on 9th February 1986.

4. N strain - collected from the field as 6th instar larvae at Grant's Ranch, northwest of Nanyuki Kenya, fed on mixed grasses until pupation on 7th to 10th June 1986 and brought back to Britain on 14th June 1986.

All strains were reared through one generation in the laboratory before adults were used for flight testing and selection. It was thought that pupae transported from Kenya to Britain would have been subjected to stresses which could be expected to have biochemical, physiological and behavioural effects in the adult stage. Also these adults were derived from larvae which had developed under unknown feeding and other environmental conditions and so would, in any case, not be

directly comparable with their laboratory reared offspring. A further major consideration was the control of disease brought into the laboratory with new material. Isolating field-collected adults as single pairs in breeding jars, and their offspring from single egg batches in rearing jars, proved an effective way of limiting the spread of any disease and allowed diseased individuals to be identified and eliminated from the culture (see below).

2.2 Flight-testing

In all cases the flight-testing procedures were as previously described (in Ch. 2). The data-logging program was set so that only flights of at least ten seconds duration were recorded (offup time = 10s).

Previous selection experiments (Parker and Gatehouse, 1985b) had been performed on the basis of flight-testing on the night after emergence (N1) only. The initial three generations of selection of the K strain were flight tested for both N0 and N1. It was hoped that this would increase the reliability with which moths were classified according to their flight capacity. This was based on the assumption that a moth which has a high genetically-determined flight potential might not express this potential fully every night. It would, therefore, be less likely to be mistakenly categorised if flown for two nights instead of only one. However, flight-testing for a second night appeared to impose an unacceptable level of stress on moths under the laboratory conditions in this investigation. This was

particularly true under the high temperature conditions in the flight-testing room during the summer of 1985 (see below). Moths flight-tested for two nights sometimes appeared exhausted on the morning of D2, with their wings not completely folded at rest and occasionally with their proboscis extended. The impression was also gained - not surprisingly - that moths generally fed more readily when placed on the food pot on D2 if they had been flown for two nights. Furthermore, with only 16 balances available, the constraint on the sample size of moths flown each generation became severe when moths were flown for two nights. During the fourth generation of selection of the K strain, the procedure was therefore changed and subsequent moths only flight-tested on N1.

Where flight-testing was continued for two nights the procedure for attaching moths and counterweighting, previously described in Ch. 2, was followed. Moths flight tested for N1 only were attached to the flight balances on the afternoon of D1, between 1500 and 1630hrs, using a 70% counterweight.

2.3 Experimental procedure

Larvae were reared in the gregaria phase as previously described in Ch. 2, with the following exceptions. Larvae and pupae were kept in a room maintained at $30 \pm 2^{\circ}\text{C}$, $63 \pm 7\%$ R.H. with a photoperiod of 12L:12D. Larvae were reared at a density of 60-80 per 500ml jar until the fourth instar for all strains, when the density was reduced to 25 per jar (K and KT strains) or 20 per jar (L and N strains) until pupation. One or two of the larvae in a jar may have died before pupation so reducing the density to a small extent but jars in which a larger

number succumbed to disease were discarded, the jar and contents being sterilised at 170°C.

It proved impossible to maintain control over daytime temperature in the flight-testing room during the summer as the cooling system was unable to counter the effects of direct sunlight on the flat roof immediately above it. An attempt was made to reduce heating by insolation by painting the roof with white reflective paint but with limited success. During the initial three generations of selection of the K strain (July to October, 1985) the temperature in the flight room increased through the day up to 34°C within an hour after dark and fell through the night down to 23°C within an hour after dawn. For later selections e.g. KT strain (February to June, 1986) a cycling temperature was maintained but over a lower range from 20°C at night up to 27°C during the day. The room temperature did not rise above 27°C during the summer of 1986.

Males as well as females were flight-tested. After flight-testing moths chosen for breeding on the basis of their flight performance were immediately set up with food as described in Ch. 2 and with a mate as soon as one became available. Adult breeding jars were kept in the larval rearing room. All adults were fed 10% w/v sucrose to increase their longevity (Gunn and Gatehouse, 1985) and so allow greater flexibility in choosing breeding pairs from moths flight-tested several nights apart. Eggs were collected and the food pot replaced every two days.

2.4 Selection procedure

Selection was imposed on the parental population of each strain

and on subsequent generations on the basis of flight performance, in attempts to produce "long-" and "short-flying" lines. For the long-flying line the 10-20% of moths with the greatest LSFs were chosen for mating and, similarly, for the short-flying line the 10-20% of moths with the smallest LSFs. These criteria were flexible and could be varied with low numbers in a generation to allow at least six pairs of moths to be set up for breeding in each line. Mating extra pairs also made some allowance for the production of infertile eggs and moths becoming stuck in copulo. Further selection unrelated to flight capacity was imposed by the occurrence of disease in the larval stage. These latter three sources of mortality had the result of enabling some moths to become successful parents when others with greater LSFs did not.

Obvious parameters for the analysis of the flight performance of each moth are the longest single flight (LSF), the sum of all the flights (SAF), and the sum of all the flights made which are longer than a critical duration (Parker and Gatehouse, 1985a). The choice of the critical duration is however arbitrary and so this criterion was avoided and analysis performed using LSF and SAF.

2.5 Estimates of heritability

The phenotypic variance of a character (V_p) expressed by an individual may be divided into a number of components. These are environmental variance (V_e), additive genetic variance (V_a) and non-additive genetic variance (V_n - comprising dominance and interaction variances) (Falconer, 1981). Environmental variance

is simply that variance produced by the environment on the given genotype. Additive genetic variance is that variance produced by genes which behave additively i.e. where the "value" of a genotype with respect to several loci is the sum of the values due to the individual loci. Non-additive genetic variance is the variance due to all other genetic effects such as the dominance effect of some genes over others and interaction effects between genes.

The proportion of V_p which is due to V_a is known as the (narrow sense) heritability of the character, h^2 . Hence

$$h^2 = \frac{V_a}{V_p}$$

Heritability effectively describes the degree of resemblance between parents and offspring and may be estimated by the strength of that relationship. For a number of families, the heritability of a character may be estimated by a regression of the mean offspring values on the mid-parent values. The heritability is given by the slope of the regression line. A complication would be introduced if the variance of the character were not equal for the two sexes, but this is not the case here (e.g. KT strain : variance ratio test - $\lg(\text{LSF}) - F=1.264, n=32, n=40; \lg(\text{SAF}) - F=1.110, n=32, n=40$). Ideally offspring means should be weighted according to the phenotypic correlation between the offspring in the families to compensate for different numbers of offspring in the calculation of the regression. However the weighting has little effect on the precision of the estimate unless the number of offspring varies considerably and the procedure was not performed in this analysis.

Narrow-sense heritability values are given where the slope of the regression line is significantly different from zero.

The resemblance between offspring and one or other parent can also be examined by mean offspring on single parent regression. In this case the value of the heritability is found by doubling the slope of the regression line (Falconer, 1981).

A requirement for regression analysis is that, for any value of X, there exists in the population a normal distribution of Y values and that these were sampled at random. A normally distributed data set was therefore needed.

Estimates of heritability depend not only on the character in question but also on the population and the environmental conditions to which the individuals are, and have been, subjected (more variable conditions reduce heritability) (Falconer, 1981). Environmental conditions have therefore been maintained as constant as possible throughout this study. This constraint also requires that interpretation of laboratory results in terms of behaviour of wild moths under field conditions must be undertaken with caution.

3. RESULTS

Previous work on the genetics of flight by Parker and Gatehouse (1985b) involved the designation of each moth as a "long-" or "short-flier" on the basis of its flight performance. A moth was a long-flier if it produced more than two hours of flight composed of individual flights longer than 30 mins, when flight-tested on N1. The response to selection for flight was then measured as the percentage of long-fliers in each generation.

The computerised data-logging and analysis capability in this investigation has allowed the distribution of flight durations to be examined and the response to selection, as well as the selection differential, to be based on the flight performance of each moth.

3.1 Distribution of flight durations of unselected moths

The distribution of flight durations produced by the four unselected, parental populations of flight-tested moths was examined.

The frequency distribution of the longest single flights (LSFs) produced by the moths from each population is shown in Fig. 4.1. It can be seen that the distribution of these flights is strongly positively skewed for all four populations. The first bar of each histogram includes all flights less than 30 mins (1800 s) duration. For all four populations more than half of the LSFs are within this range of durations (60, 67, 58 and 51% for the K, KT, L and N populations respectively).

The power of statistical analyses of such data would

Fig. 4.1

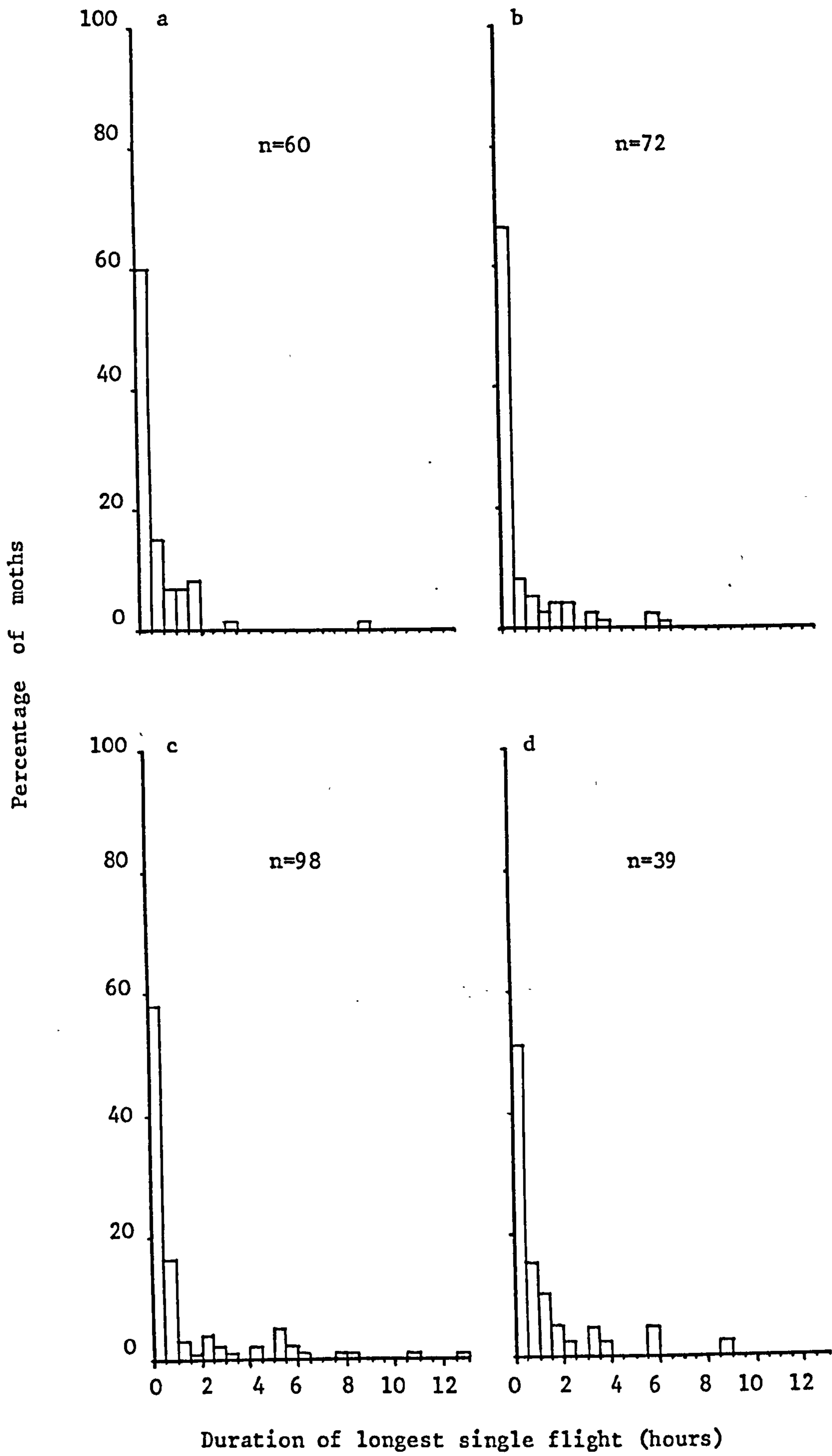
Frequency distributions of the longest single flights produced by moths of the unselected, parental generations of the four strains.

a - K strain

b - KT strain

c - L strain

d - N strain



be increased if they could be transformed to approximate to the normal (Gaussian) distribution. Parametric tests could then be used with a reduced probability of committing a type II error (not rejecting the null hypothesis when it is, in fact, false - Zar, 1984). The meaningful calculation of population means and their standard errors is then also possible. Both the square root and \log_{10} transformations were examined and it was found that the latter was appropriate in this case. The distributions of the transformed data sets are shown in Fig. 4.2. None are significantly different from normal (Kolmogorov-Smirnov, K : $D=0.1136$, $P>0.05$; KT : $D=0.0985$, $P>0.05$; L : $D=0.0679$, $P>0.15$; N : $D=0.0877$, $P>0.15$ (where p is the probability of being incorrect if the population is said to be not normal)).

A similar examination was made of the distribution of the sum of all flights (SAFs) produced by moths of the four populations. Again the distribution of flight activity is strongly positively skewed with approximately half of the moths flying for a total of less than 1.5 hours (K : 45%, KT : 56%, L : 56%, N : 41%, Fig. 4.3). Logarithmic transformation of these data produced distributions not significantly different from normal (Kolmogorov-Smirnov, K : $D=0.0916$; KT : $D=0.0592$; L : $D=0.0692$; N : 0.1215; $P>0.15$ for all populations; Fig. 4.4).

Logarithmic transformation of both LSFs and the SAFs may therefore be used to normalise these data.

Fig. 4.2

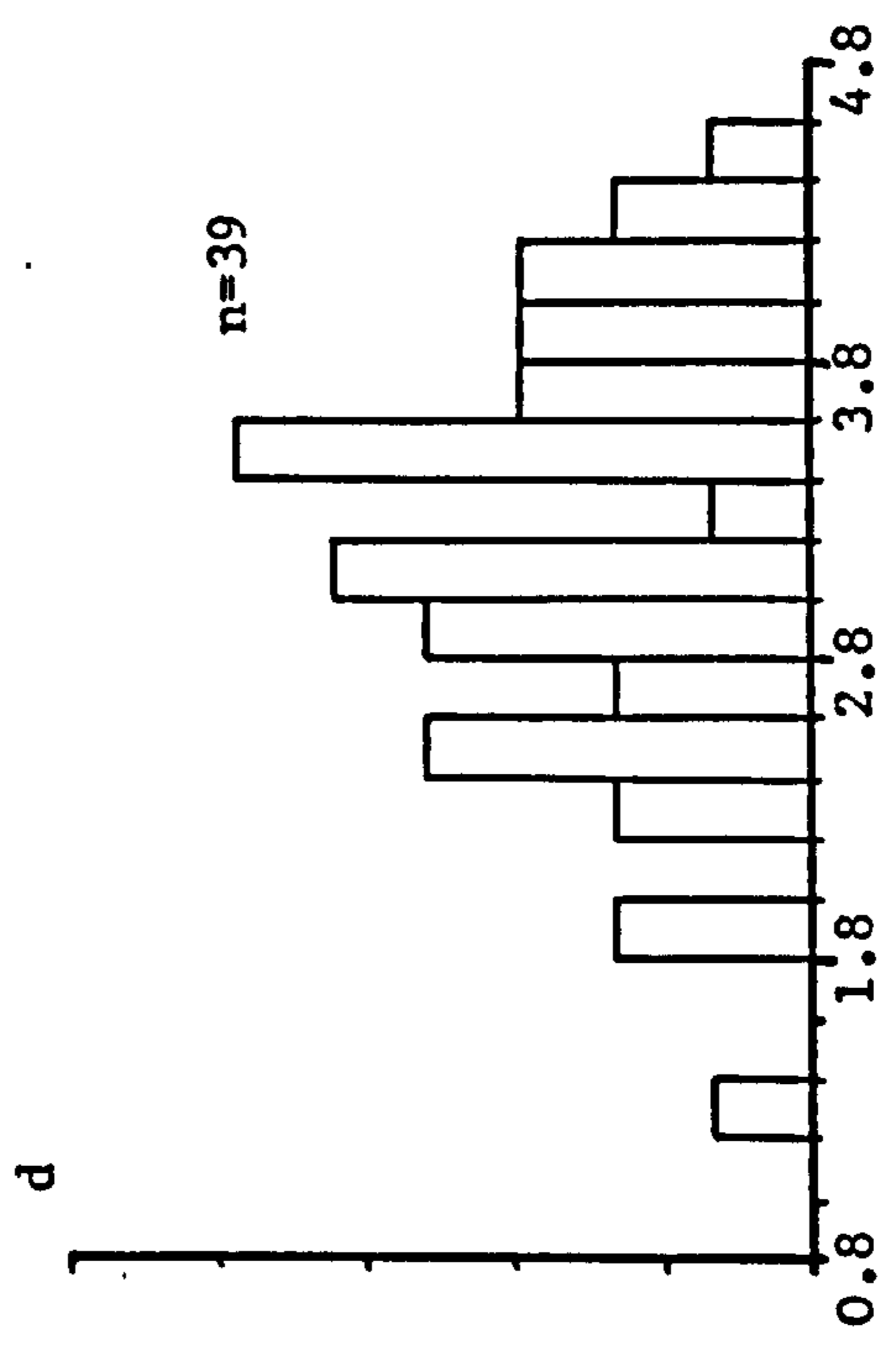
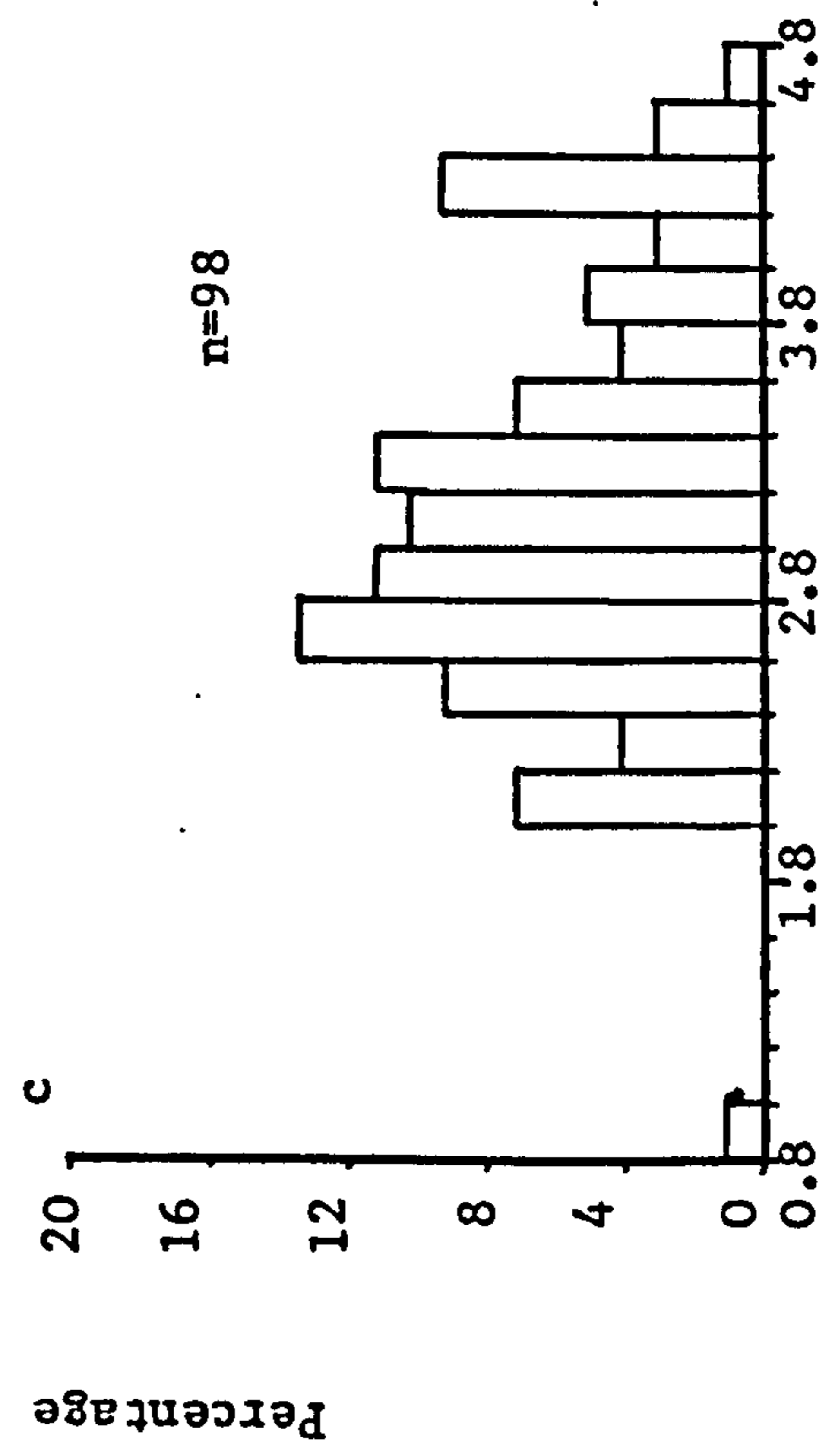
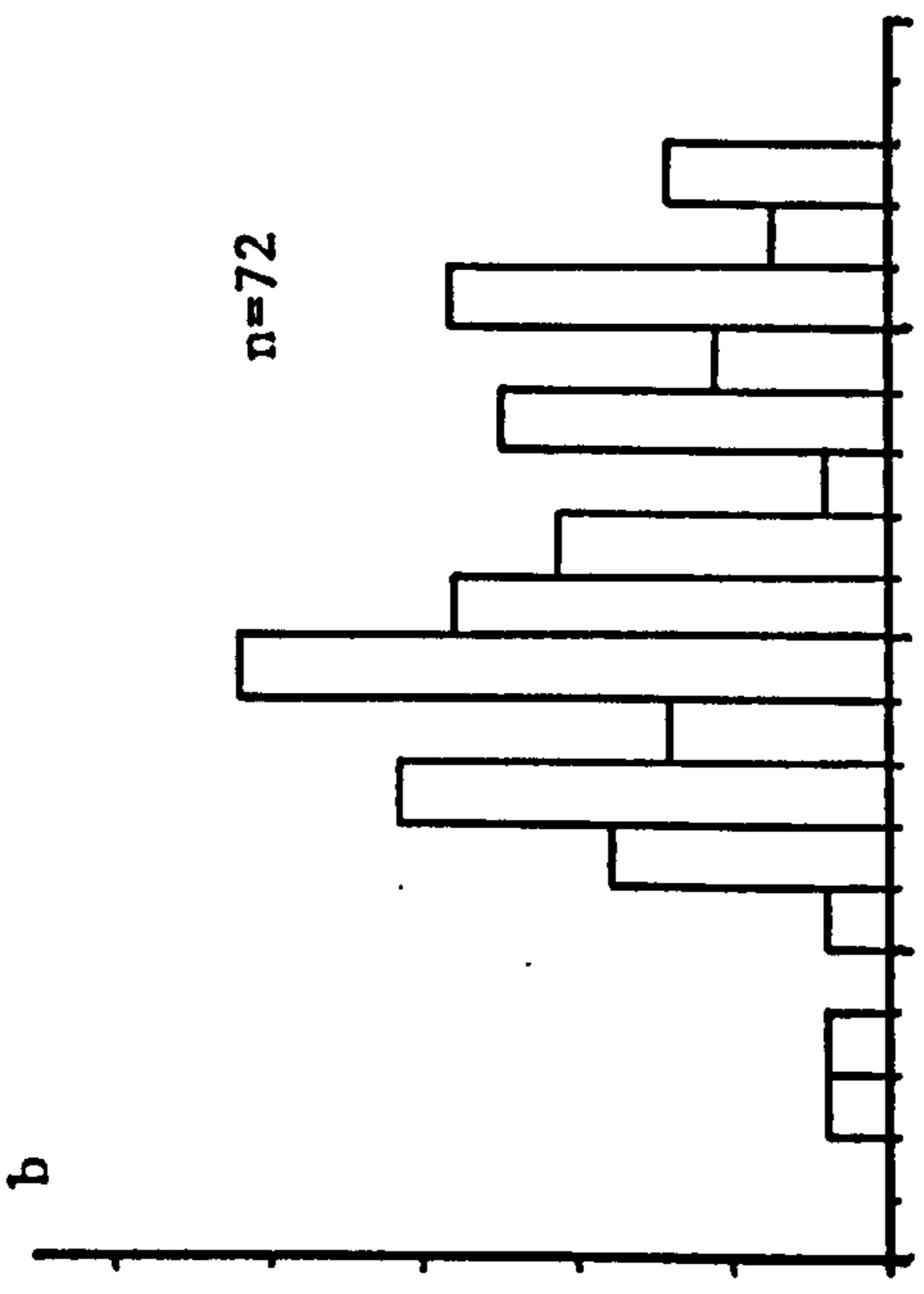
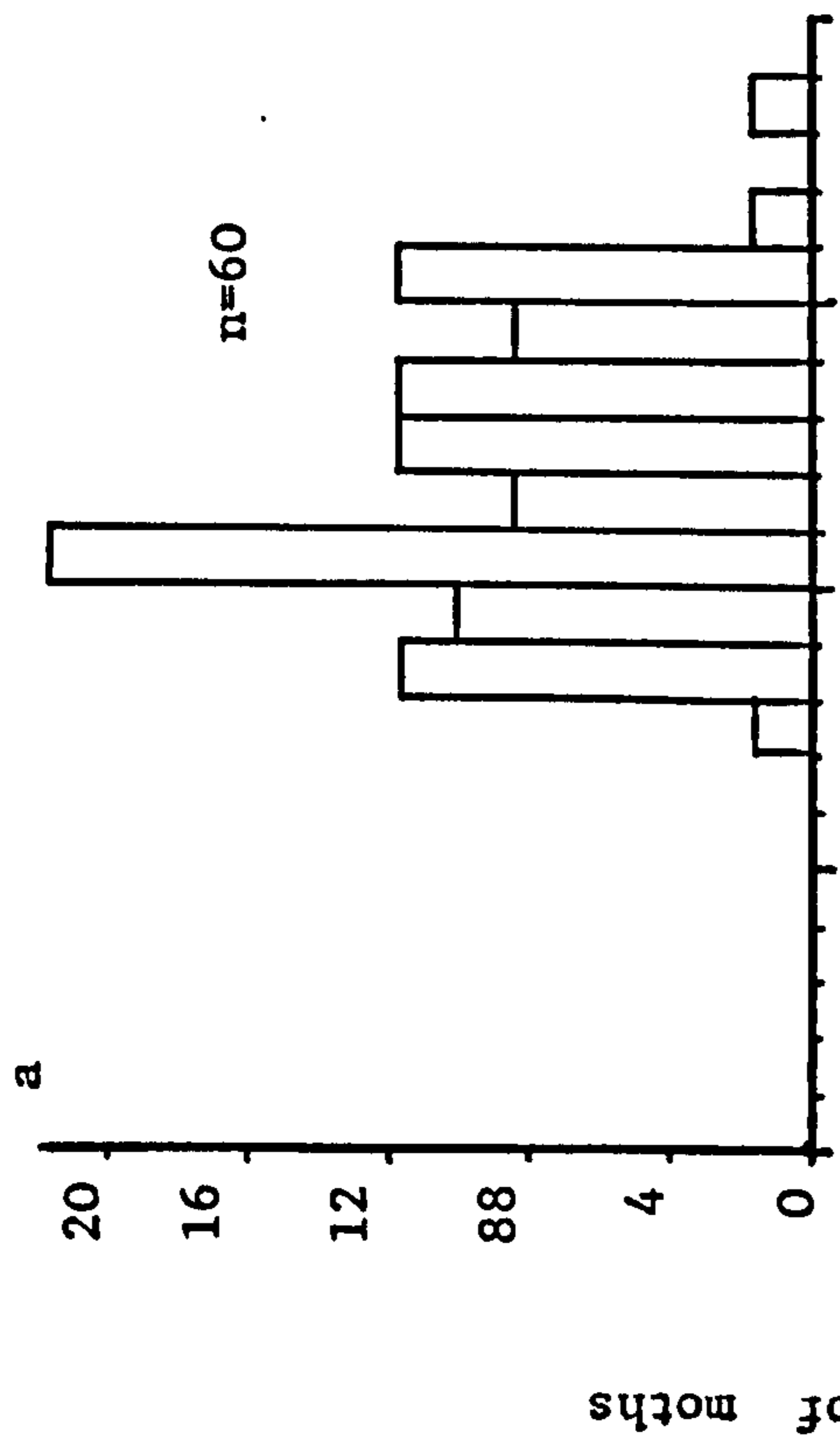
The data presented in Fig. 4.1, the longest single flights produced by individuals of the unselected, parental generations of the four strains, were log-transformed and are presented here. None of the distributions of the log-transformed longest single flights were significantly different from normal.

a - K strain

b - KT strain

c - L strain

d - N strain



Lg(Longest single flight (LSF))

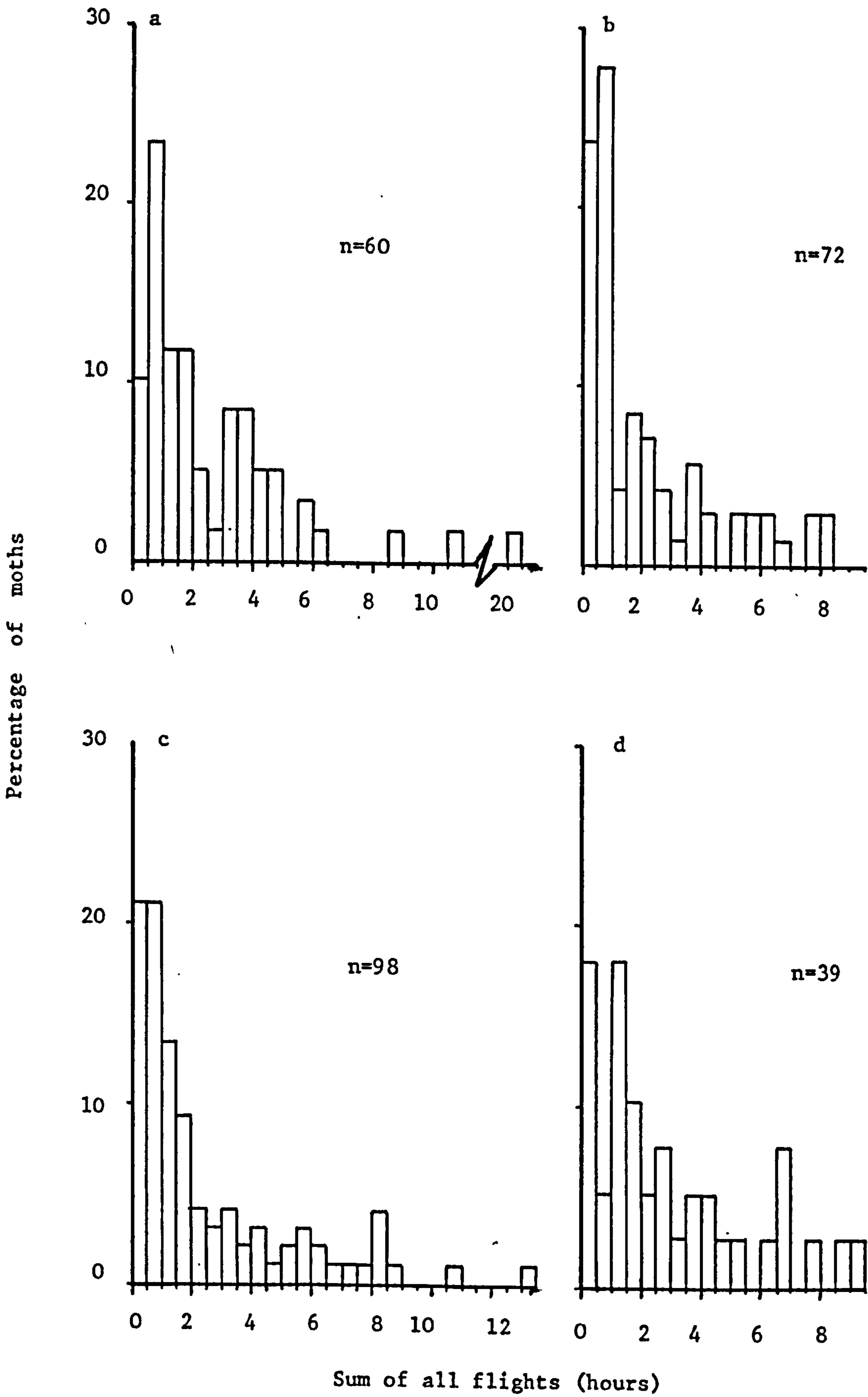


Fig. 4.4

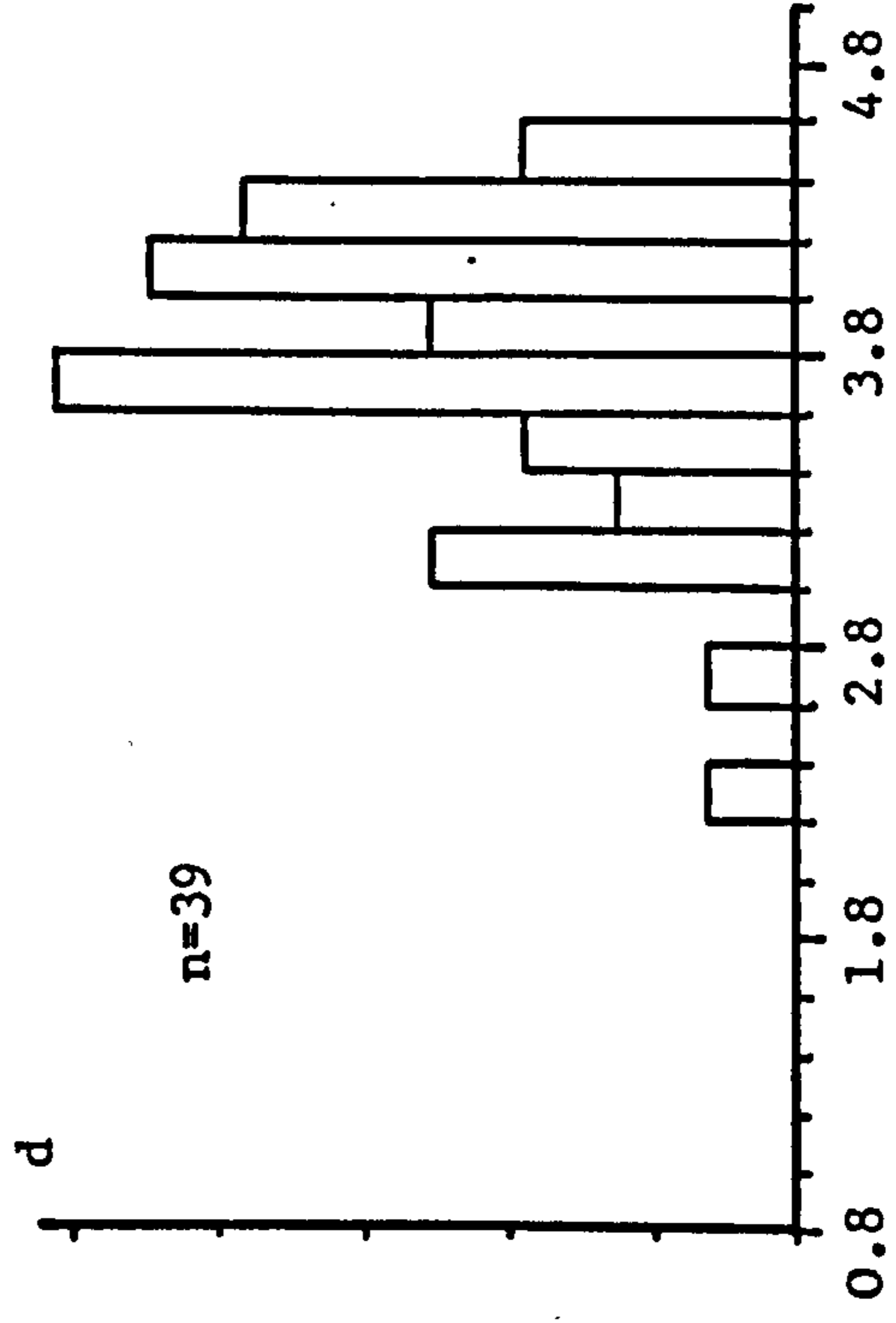
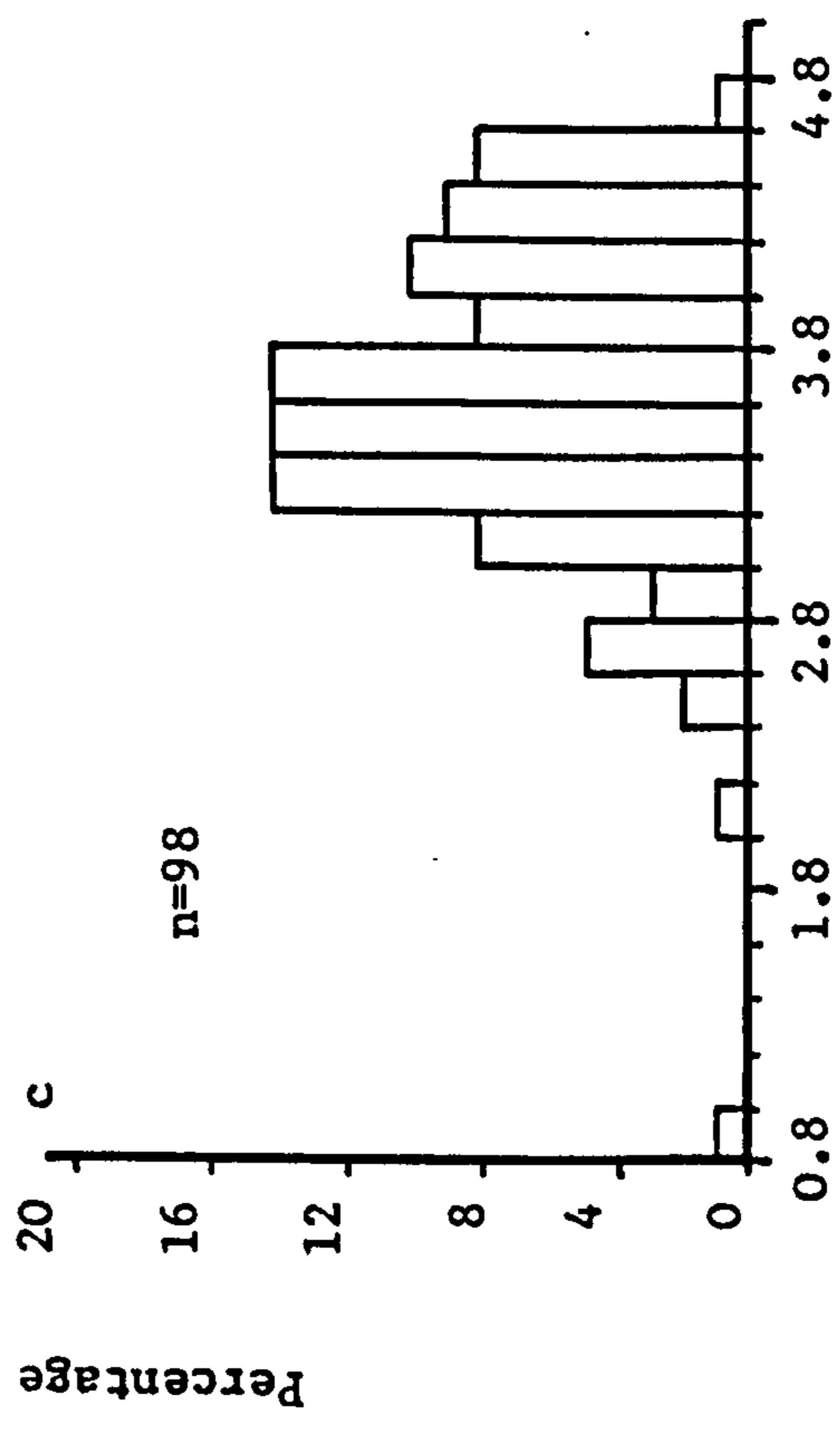
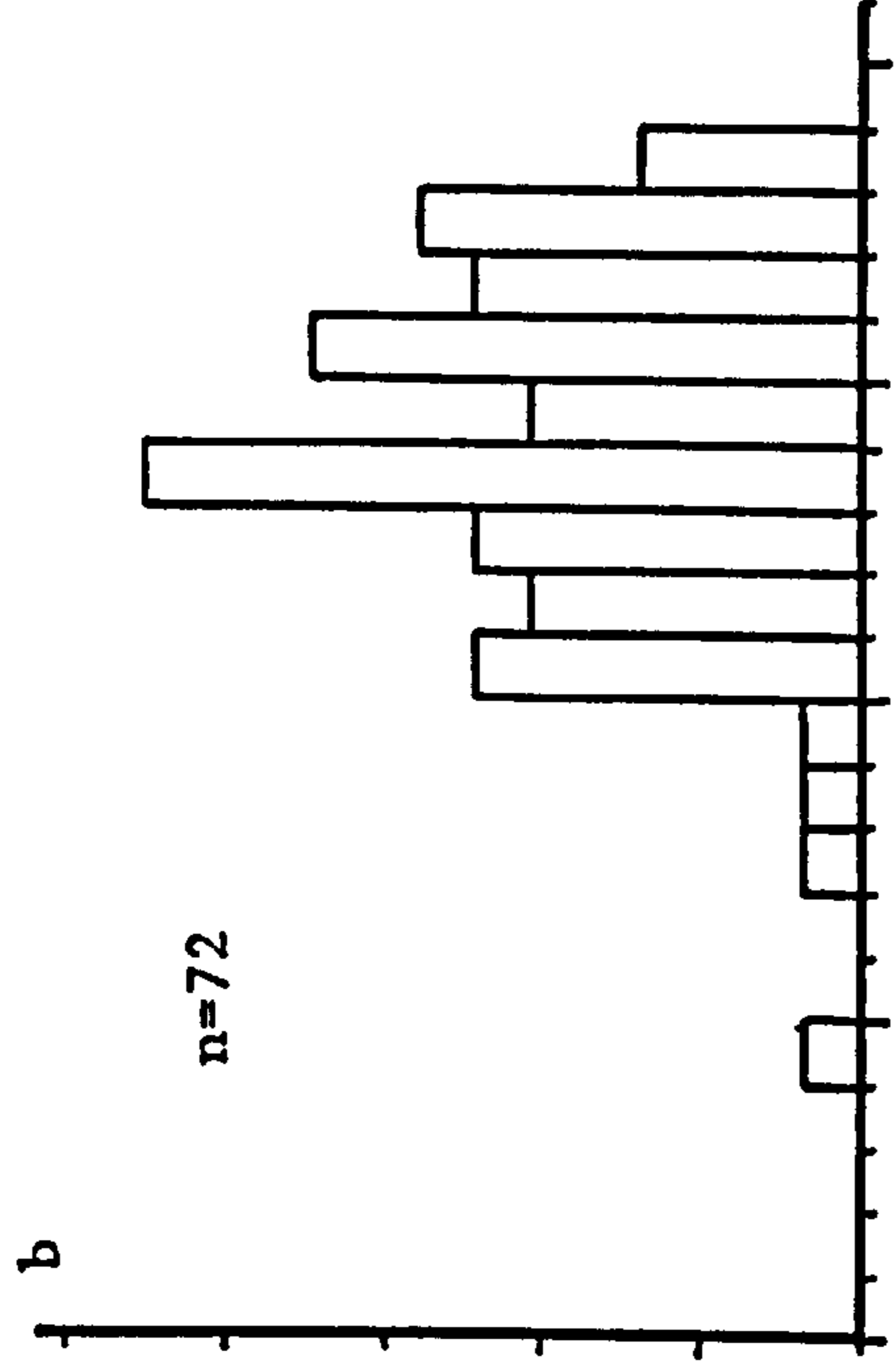
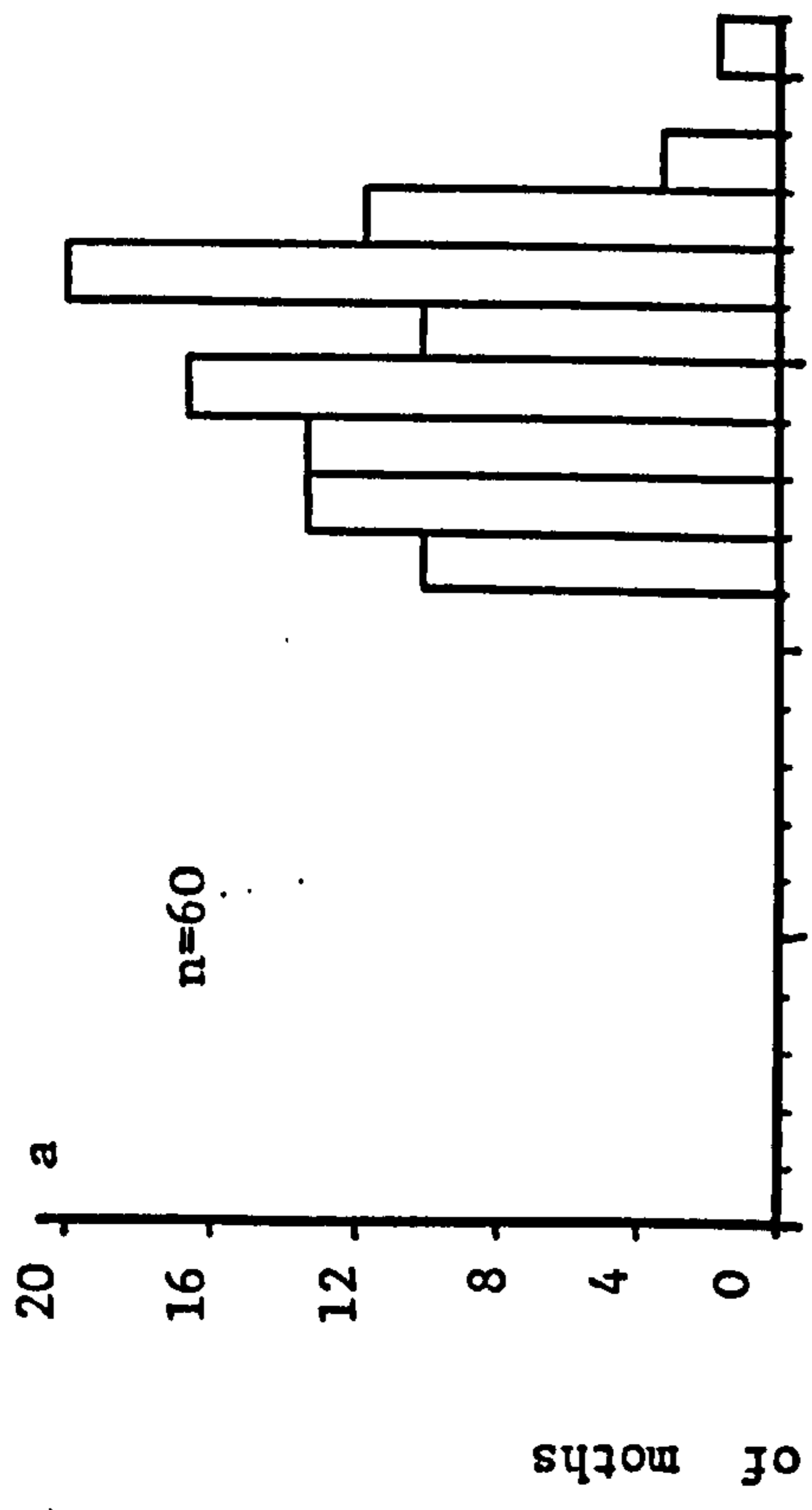
The data presented in Fig. 4.3, the sum of all flights (SAF) produced by individuals of the unselected, parental generations of the four strains, were log-transformed and are presented here. None of the distributions of the log-transformed SAFs were significantly different from normal.

a - K strain

b - KT strain

c - L strain

d - N strain



Lg(Sum of all flights (SAF))

3.2 The response to selection

3.2.1 The measurement of selection

The response to selection can be shown as a plot of response against generation number. Parker and Gatehouse (1985b) did this when they measured the response as the proportion of "long-fliers" in each generation (see above). Falconer (1954, 1981) criticised this approach since the selection differential applied will probably vary from generation to generation and between the lines selected for and against the trait. He suggested that a better representation of the response to selection is provided by a plot of total response against the cumulated selection differential.

In practice, the appropriately transformed (logged) data enable the response to selection to be plotted simply as the mean for each generation. The selection differential is the mean value for the chosen parents minus the generation mean. Given that some parents will have more or less surviving offspring than others in the next generation, this differential should be weighted as :

$$\text{Weighted selection differential} = \frac{\text{Sum} \left\{ \left\{ \begin{array}{l} \text{Parental} \\ \text{value} \end{array} \right\} - \text{generation mean} \right\} \times \text{no. of offspring} \right\} \text{ for all parents}}{2 \times \text{total no. offspring in the next generation}}$$

Falconer (1954) states that, if the response to selection continues at approximately the same rate, regression equations may be calculated and lines plotted through the points of the high and low lines, giving estimates of the average response per unit of selection. He called this ratio the "realised

heritability, h^2 ".

Such plots often show an assymetry of response to selection between the high and low lines. Since differences due to generation interval, selection differentials or scale of measurement have already been removed, observed assymetry may be due to inbreeding depression, unequal frequency of the alleles favouring the high and low lines in the base population or directional dominance of the alleles (Falconer, 1954).

3.2.2 The K strain

3.2.2.1 Initial generations flown for N0 to N1.

Selection for flight produced an increase in both the $\lg(\text{LSF})$ (Fig. 4.5) and the $\lg(\text{SAF})$ (Fig. 4.6) measured over both nights for both generations of selection. However, under both criteria, the increase for the low line was greater than that for the high line. At this time there were few moths in the selected generations of the low line (six in the F1 and 9 in the F2 generations). Four pairs were initially set up from the parental generation, from which two males died and their females (which did not oviposit on the next night and were therefore assumed not to have mated) were mated with other males. One of these females subsequently died without ovipositing and one of the other pairs produced larvae which were so heavily infected with disease that they were destroyed. The offspring from the two remaining pairs were also diseased and the next generation comprised only six adults. From these two pairs were set up which produced larvae with some disease present such that, once again, only nine adults

Fig. 4.5

The K strain.

The response to selection is plotted against the cumulated weighted selection differential imposed. Moths from the first two generations of selection were flight-tested for two nights and selection imposed both for and against flight. The line selected for decreased flight performance exhibited a greater flight capacity than that of the line selected for increased flight (see text). After two generations the lines were mixed and selection imposed for a further two generations, this time on the basis of flight-testing on only the first night following the night of emergence. The line selected for increased flight capacity maintained its flight performance and that selected for decreased flight dropped rapidly.

- ◇ - parental generation
- - generation resulting from selection for increased flight performance
- - generation resulting from selection for decreased flight performance

Flight capacity was measured on the basis of the longest single flight (in seconds).

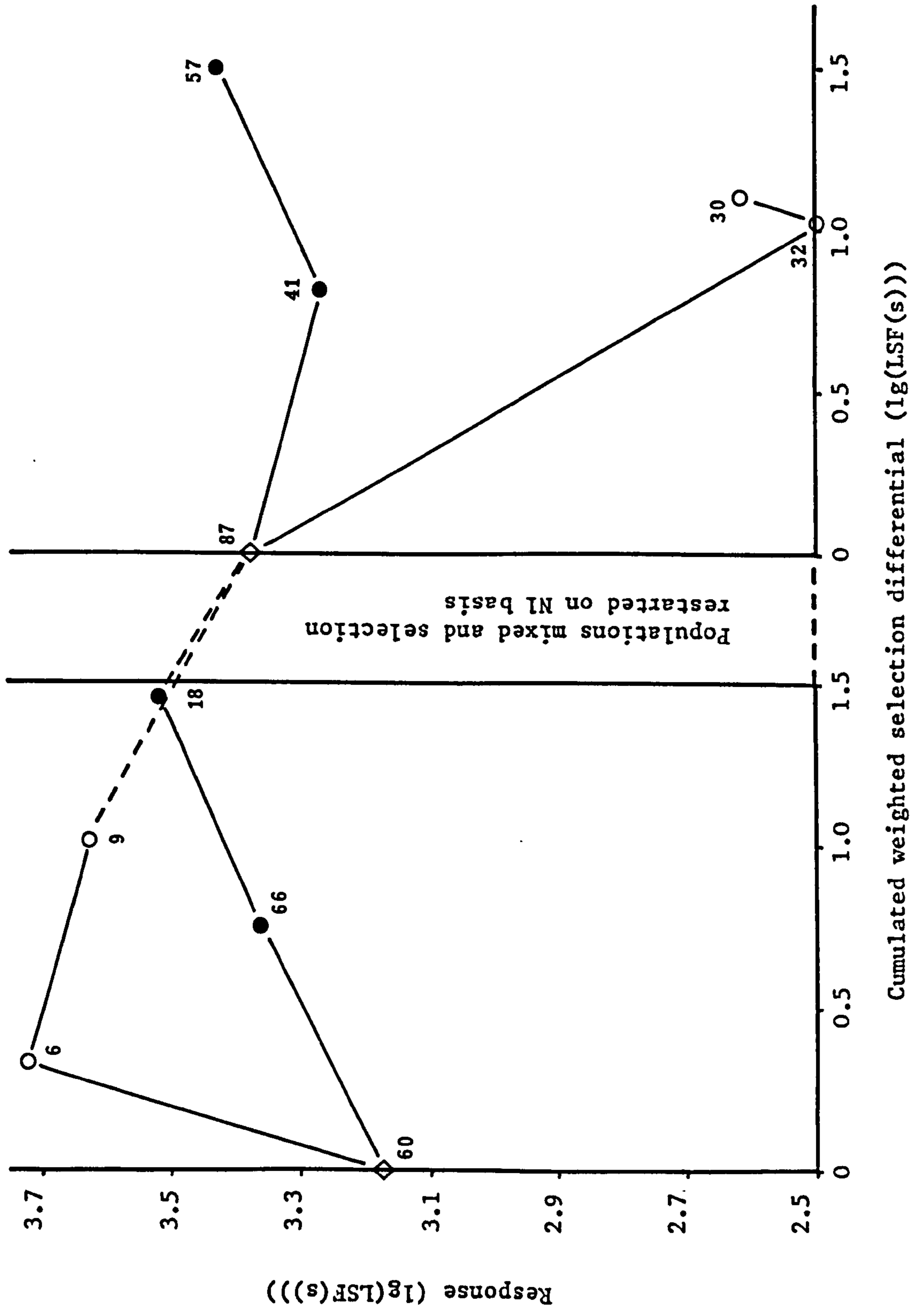


Fig. 4.6

The K strain.

The response to selection is plotted against the cumulated weighted selection differential imposed. Moths from the first two generations of selection were flight-tested for two nights and selection imposed both for and against flight. The line selected for decreased flight performance exhibited a slightly greater flight capacity than that of the line selected for increased flight (see text). After two generations the lines were mixed and selection imposed for a further two generations, this time on the basis of flight-testing on only the first night following the night of emergence. The line selected for increased flight capacity maintained its flight performance or perhaps increased it slightly and that selected for decreased flight dropped rapidly.

- ◇ - parental generation
- - generation resulting from selection for increased flight performance
- - generation resulting from selection for decreased flight performance

Flight capacity was measured on the basis of the sum of all flights (in seconds). The number of individuals in each generation of each line is indicated.

Fig. 4.3

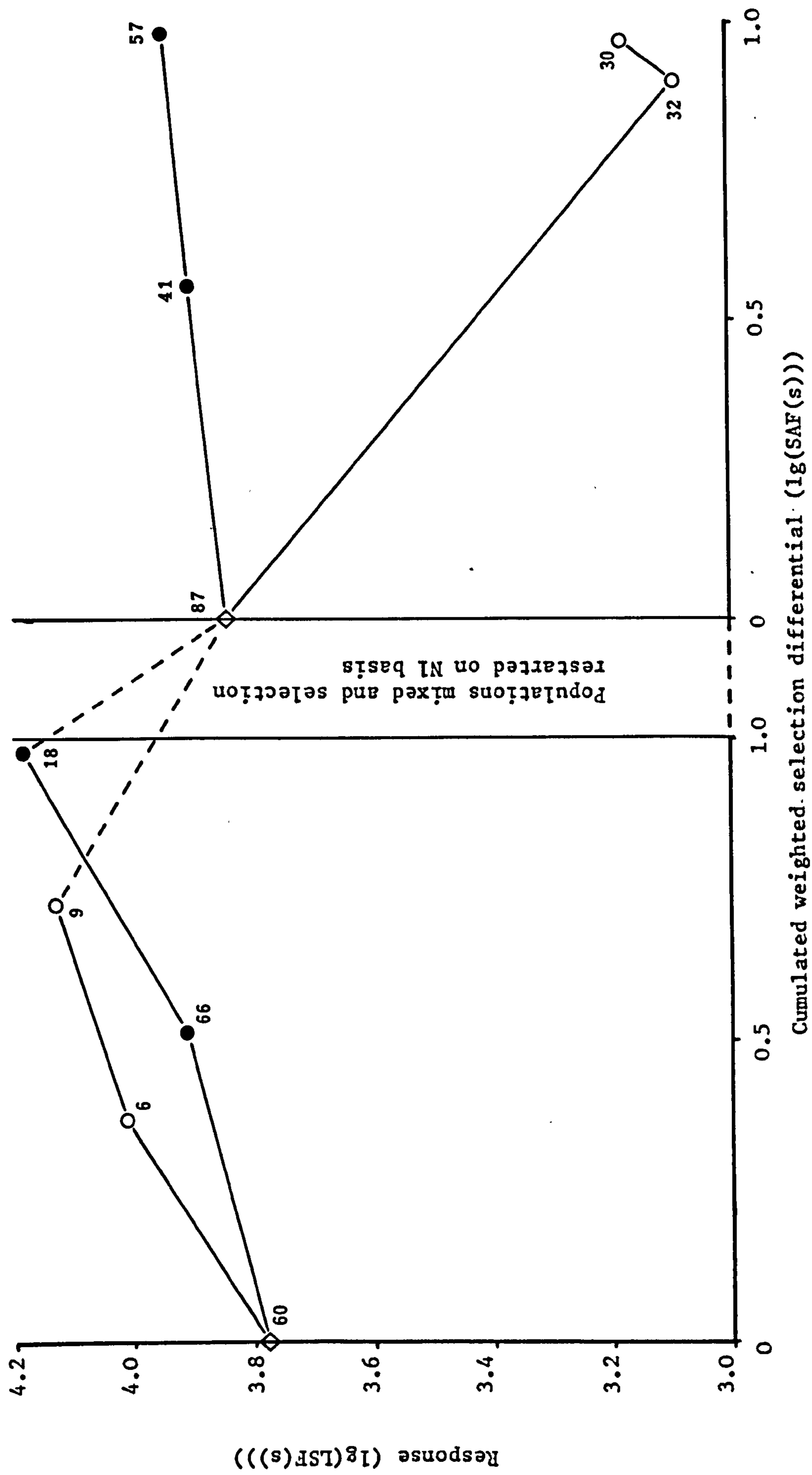
Frequency distributions of the sum of all flights (SAF) produced by moths of the unselected, parental generations of the four strains.

a - K strain

b - KT strain

c - L strain

d - N strain



were produced in the next generation.

During this summer period there were also problems controlling the temperature in the flight-testing room with temperatures reaching 34°C within an hour after dark (see above). It is unclear, however, how the higher temperature or the high incidence of disease could result in a greater flight capacity in a line selected for lower flight. It therefore seems likely that the high flight performance resulted from an incorrect classification of one or more of the parents from the initial generation.

It was also proving difficult to flight test as many moths as it was possible to rear and mount because each moth occupied a flight balance for two nights. All these considerations led to the decision to restart the selection by breeding the last selected generation of both high and low lines (K4) together irrespective of their flight performance. The resulting (K5) generation was treated as a parental population and high and low lines selected from it on the basis of flight performance on N1 only.

3.2.2.2 Later generations flown for N1 only.

Generations K5 to K7 were flight-tested for N1 only. Temperatures in the flight room were lower at this time (up to 27°C during the day) and the numbers flight-tested in each generation of each line did not drop below 30 individuals.

The flight performance of the low line in this case fell rapidly under strong selection from K5 to K6. Only a very small

selection differential against flight, measured as $\lg(\text{SAF})$ or $\lg(\text{LSF})$, was imposed on the K6 generation of the low line and the K7 generation showed a small increase in response. The high line also decreased in $\lg(\text{LSF})$ from K5 to K6 but much less than the low line, and increased from K6 to K7. $\lg(\text{SAF})$ increased slightly but consistently from K5 to K6 and K6 to K7.

3.2.3 The KT strain flown for N1 only

Selection for increased flight performance was followed in this strain for only two generations (Fig. 4.7). The third generation consisted of only 18 individuals. No eggs laid by the selected pairs proved viable probably due to disease.

When assessed in terms of $\lg(\text{LSF})$ the response to selection over the two generations was remarkably consistent. A regression line through the points has a slope giving a realised heritability of 21.5%.

Selection for decreased flight performance continued for five generations (Fig. 4.8). Both the selection differential imposed at each generation and the change in response were relatively consistent. The realised heritability of decreasing flight performance was estimated from the slope of the regression line at 24.7%.

In contrast, similar figures obtained for the heritability of the high and low lines based on $\lg(\text{SAF})$ show quite a different picture. The heritability for the high line is quite small at 10.5% and for the low line much greater at 36.3% indicating that there is an asymmetry in the responses of the two lines to selection based on this criterion.

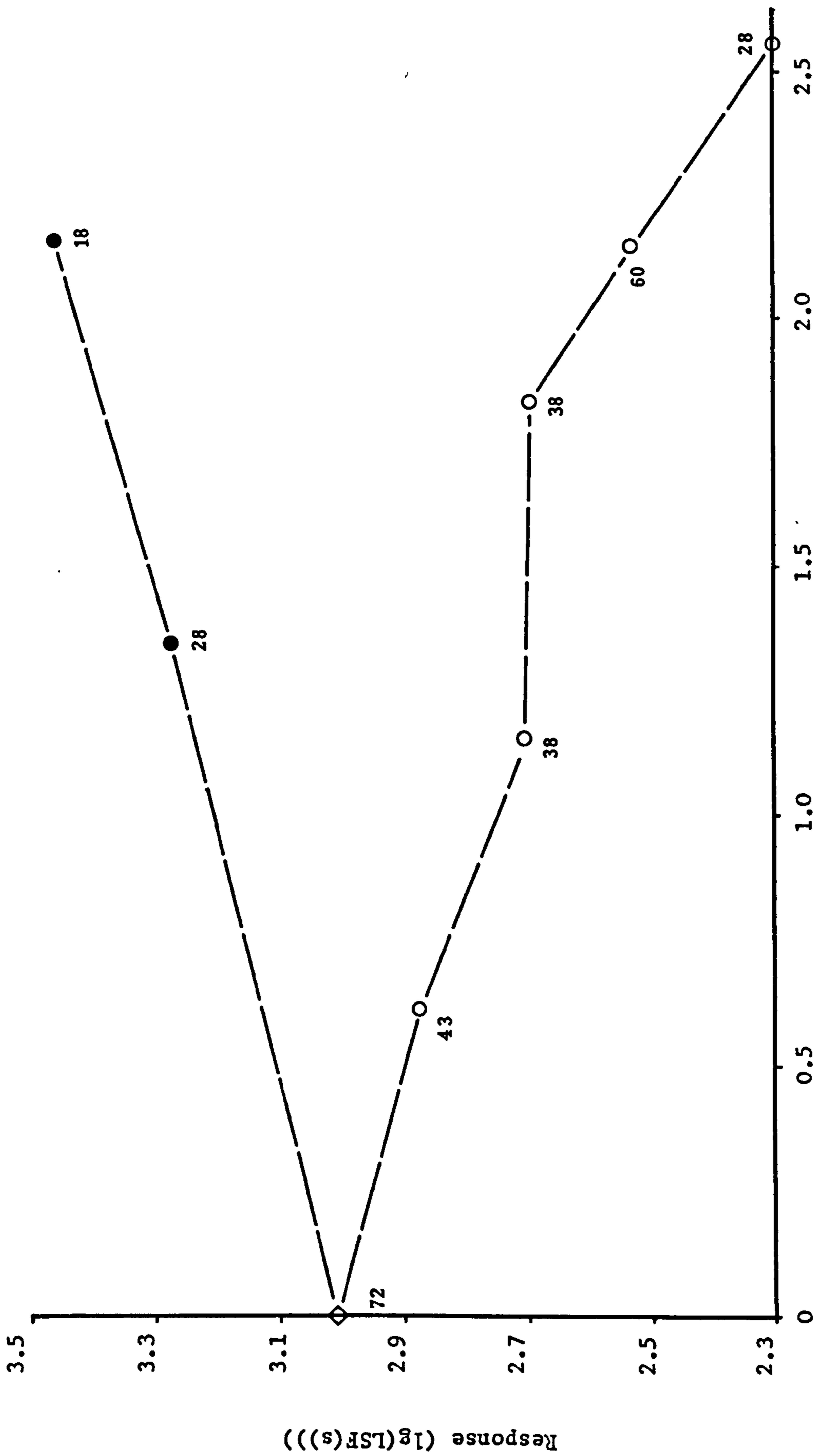
Fig. 4.7

The KT strain.

The response to selection is plotted against the cumulated weighted selection differential for selection imposed for increased and decreased flight over two and five generations respectively.

- ◇ - parental generation
- - generation resulting from selection for increased flight performance
- - generation resulting from selection for decreased flight performance

Flight capacity was measured on the basis of the longest single flight (in seconds). The number of individuals in each generation of each line is indicated.



Cumulated weighted selection differential (lg(LSF(s)))

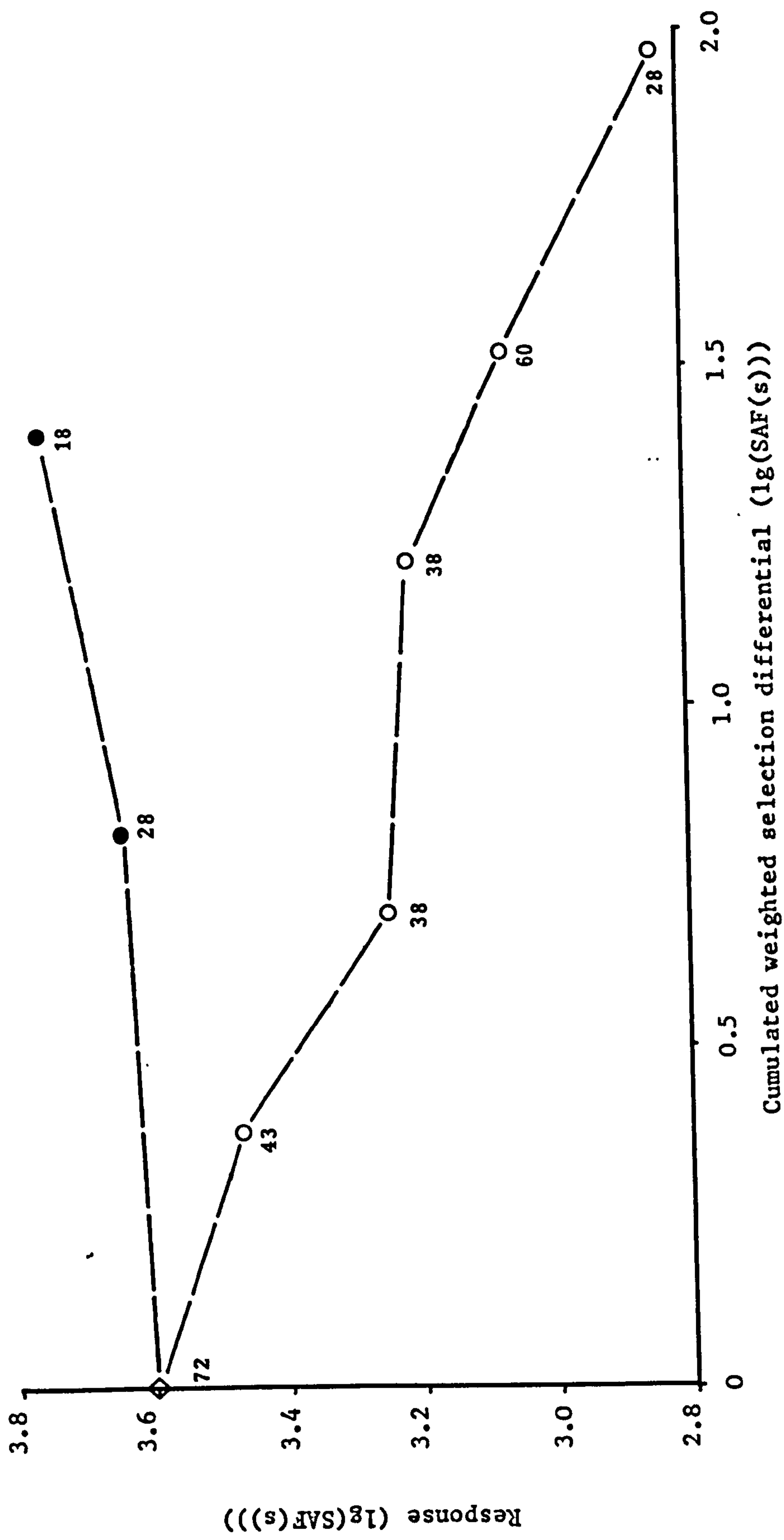
Fig. 4.8

The KT strain.

The response to selection is plotted against the cumulated weighted selection differential for selection imposed for increased and decreased flight over two and five generations respectively.

- ◇ - parental generation
- - generation resulting from selection for increased flight performance
- - generation resulting from selection for decreased flight performance

Flight capacity was measured on the basis of the sum of all flights (in seconds). The number of individuals in each generation of each line is indicated.



3.2.4 The L strain flown for N1 only.

The high line in this strain had selection imposed for eight generations and the low line for four generations. Both high and low lines gave a good initial response to selection in the expected direction when assessed as $\lg(\text{LSF})$ (Fig. 4.9) or $\lg(\text{SAF})$ (Fig. 4.10).

Regression lines placed through all the points of each line gave the estimates of realised heritability shown in Table 4.1. The relatively high values of heritability for the low line are due to a very rapid response to selection over the first generation followed by a reduced intensity of selection over subsequent generations. The low levels of flight expressed did not allow greater selection to be imposed.

The response to selection over the first generation can be separated from that of the subsequent generations if care is taken with the interpretation of the results. The realised heritabilities for the first generation of selection and subsequent generations (derived from a line joining the first two points and a fitted regression line for the second and remaining points) are given in Table 4.2. None of the regressions are significant due to the small number of data points and the shallow gradients of the lines of best fit. However, it is obvious that the change in the response due to selection over the initial generation of selection is very rapid whereas that over subsequent generations is very small, if real at all.

Fig. 4.9

The L strain.

The response to selection is plotted against the cumulated weighted selection differential for selection imposed for increased and decreased flight over eight and four generations respectively.

- ◇ - parental generation
- - generation resulting from selection for increased flight performance
- - generation resulting from selection for decreased flight performance

Flight capacity was measured on the basis of the longest single flight (in seconds). The number of individuals in each generation of each line is indicated.

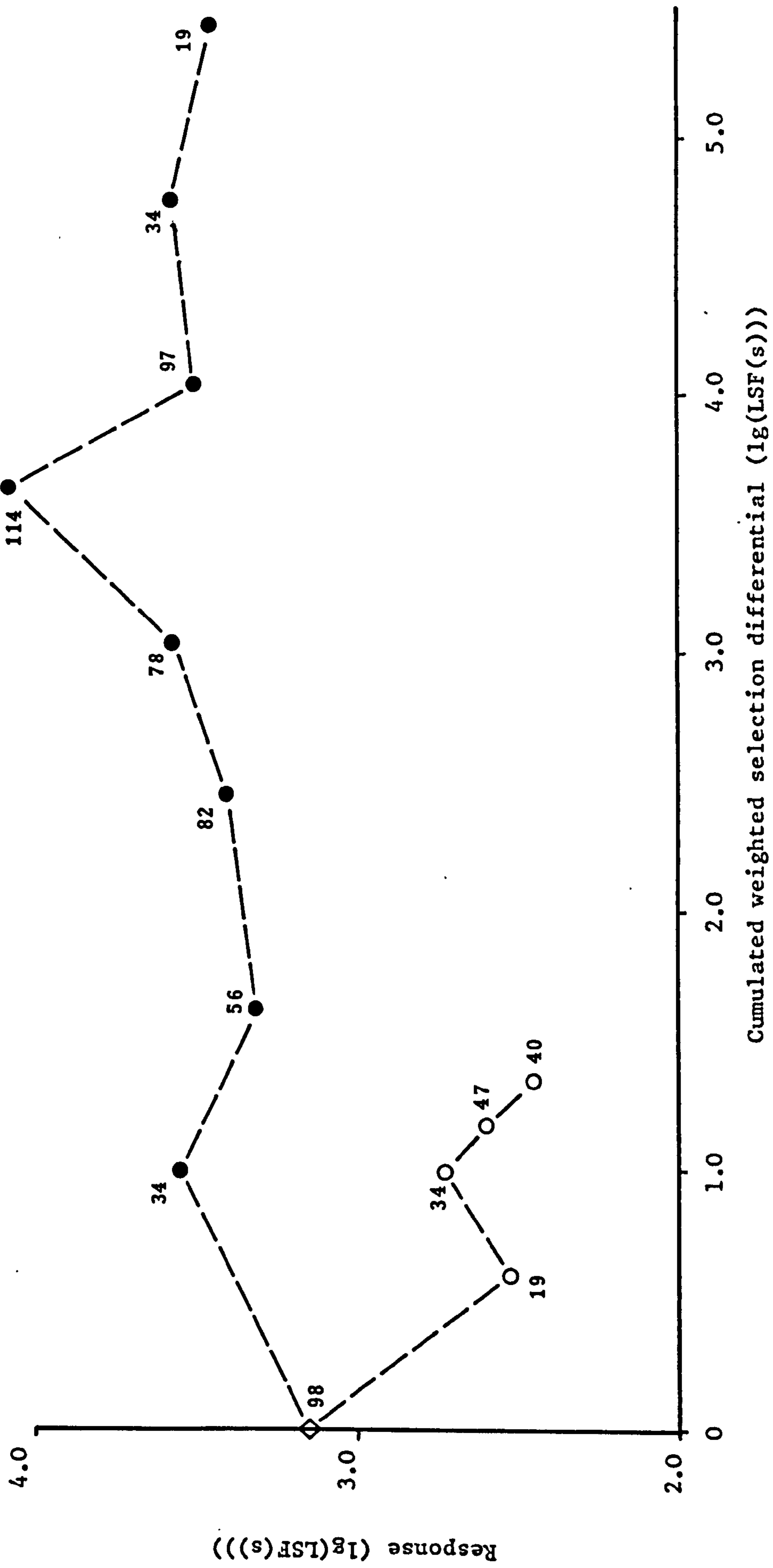


Fig. 4.10

The L strain.

The response to selection is plotted against the cumulated weighted selection differential for selection imposed for increased and decreased flight over eight and four generations respectively.

◇ - parental generation

● - generation resulting from selection for increased flight performance

○ - generation resulting from selection for decreased flight performance

Flight capacity was measured on the basis of the sum of all flights (in seconds). The number of individuals in each generation of each line is indicated.

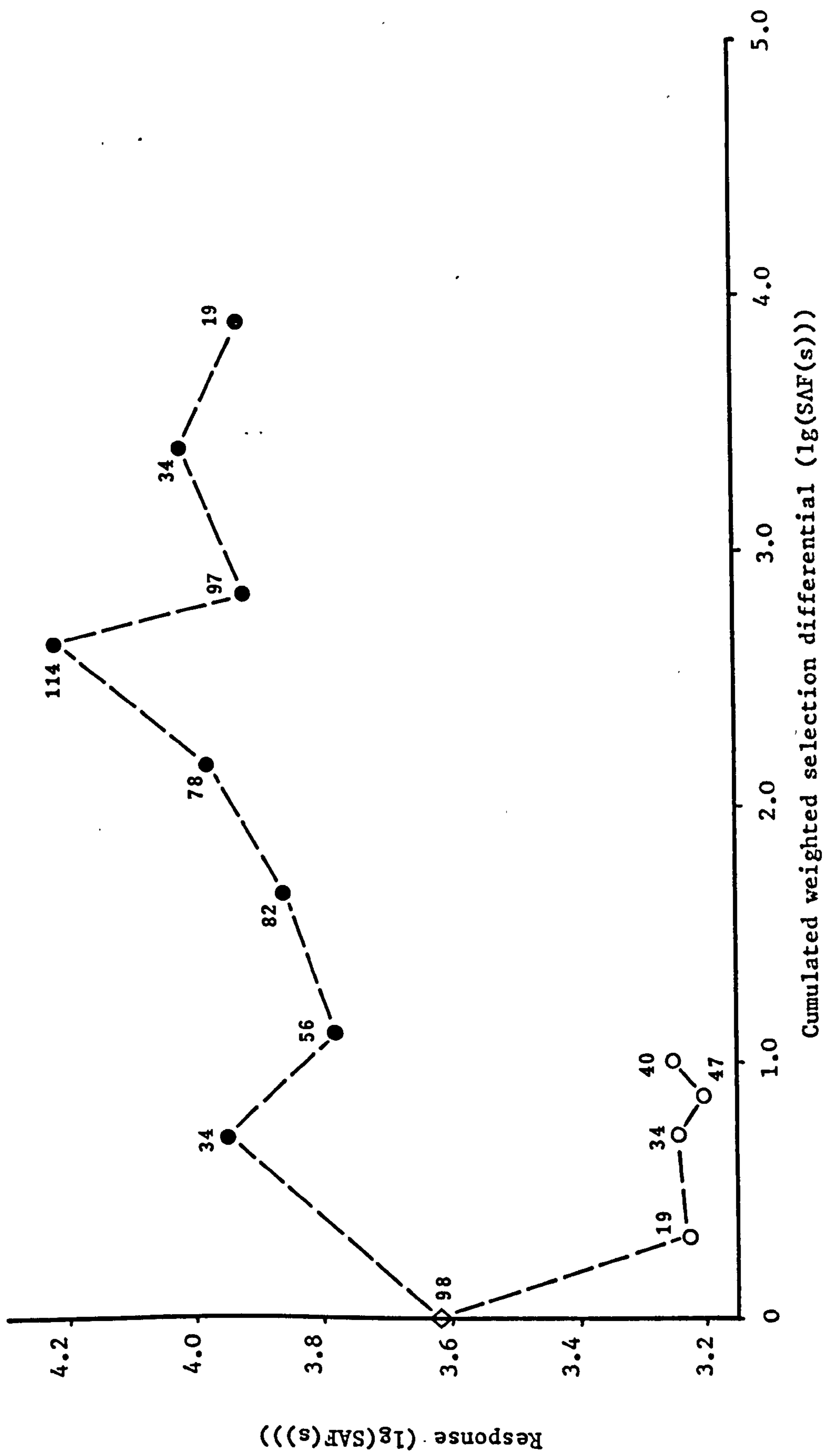


Table 4.1.

Coefficient (r), F values and significance levels (P) for regression analyses performed on plots of the response to cumulated weighted selection differentials imposed for and against flight (high and low lines) on moths of the L strain. Flight capacity was measured in terms of lg(LSF) and lg(SAF).

		Flight capacity	
		lg(LSF)	lg(SAF)

	r	0.854	0.766
low	F	8.079	4.259
	P	>0.05	>0.10

Line	r	0.510	0.579
high	F	2.457	3.523
	P	>0.10	>0.103.

Table 4.2.

The slope (m) of lines joining the parental and first selected (F1) generations of lines of the L strain for plots of the response to selection against the cumulated weighted selection differential applied for and against flight.

Also the coefficients (r), F values and significance levels (P) for regression analyses and the slope (m) of the line of best fit for the F1 and remaining generations.

Flight capacity was measured in terms of lg(LSF) and lg(SAF).

Lines		Flight capacity	
		lg(LSF)	lg(SAF)

low m		1.053	1.245
1st generation			
high m		0.402	0.482

r		0.768	0.182
F		0.125	0.068
low	P	>0.25	>0.25
m		0.065	-0.015
Remaining generations			
r		0.195	0.311
F		0.240	0.064
high	P	>0.25	>0.25
m		0.021	0.038

2.5 The N strain flown for N1 only

Selection for increased flight performance proceeded for three generations. $Lg(LSF)$ showed an increase for the first two generations with a very small drop for the third (Fig. 4.11). $Lg(SAF)$ showed an increase for all three generations (Fig. 4.12). In both cases the greatest increase per unit of selection differential took place over the first generation.

A second line was subjected to selection for increased flight over the first generation. The selection differential was less than that imposed on the first line in terms of $lg(LSF)$ (Fig. 4.11) and $lg(SAF)$ (Fig. 4.12) and the change in the response also less. The rate of change of response was greater for the second line than the first when measured in terms of $lg(LSF)$ but less in terms of $lg(SAF)$. The direction of the selection imposed on the second line was then reversed for the second generation resulting in a reversal in the direction of change in the response for both $lg(LSF)$ and $lg(SAF)$. Finally selection was reversed again, being imposed in the direction of increased flight performance, and was followed by an increase in the response.

3.2.6 The repeatability of the response to selection

The response to selection of the strains may be compared by plotting responses against cumulated selection differentials for all four on the same graph (Fig. 4.13). Only those generations flight-tested for N1 alone have been included in the case of the K strain.

It is apparent from this diagram that a consistent feature

Fig. 4.11

The N strain.

The response to selection is plotted against the cumulated weighted selection differential for selection imposed for increased flight performance over three generations. A second line is selected for increased, decreased and, finally, increased flight performance over three consecutive generations. Because the first generation is selected for flight the line is plotted as one selected for increased flight capacity and when selection is imposed for decreased flight capacity in the second generation this is indicated as a negative selection differential for increased flight i.e. the line dog-legs to the left on the diagram.

- ◇ - parental generation
- - generation resulting from selection for increased flight performance
- - generation resulting from selection for decreased flight performance

Flight capacity was measured on the basis of the longest single flight (in seconds). The number of individuals in each generation of each line is indicated.

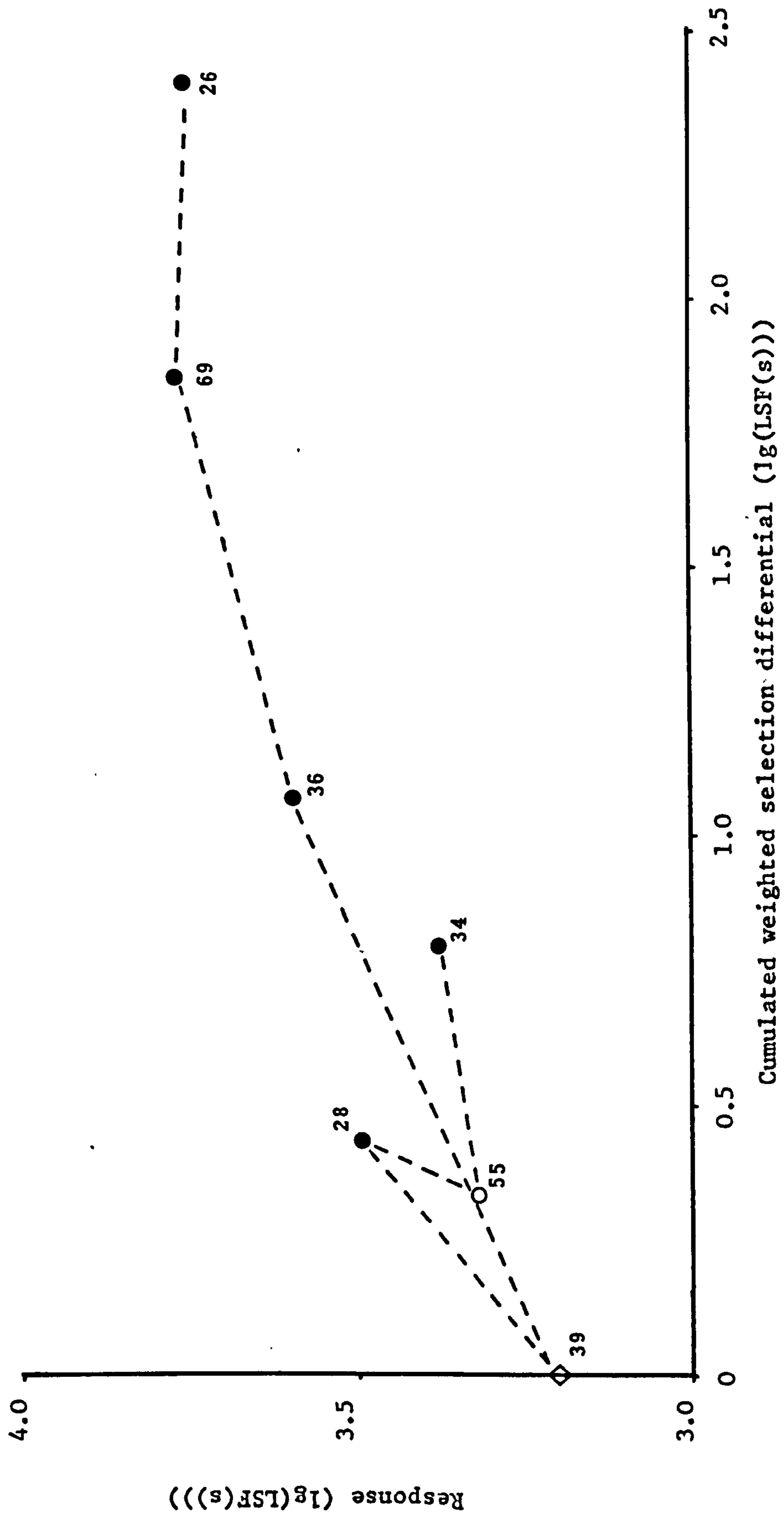


Fig. 4.12

The N strain.

The response to selection is plotted against the cumulated weighted selection differential for selection imposed for increased flight performance over three generations. A second line is selected for increased, decreased and, finally, increased flight performance over three consecutive generations. Because the first generation is selected for flight the line is plotted as one selected for increased flight capacity and when selection is imposed for decreased flight capacity in the second generation this is indicated as a negative selection differential for increased flight i.e. the line dog-legs to the left on the diagram.

◇ - parental generation

● - generation resulting from selection for increased flight performance

○ - generation resulting from selection for decreased flight performance

Flight capacity was measured on the basis of the sum of all flights (in seconds). The number of individuals in each generation of each line is indicated.

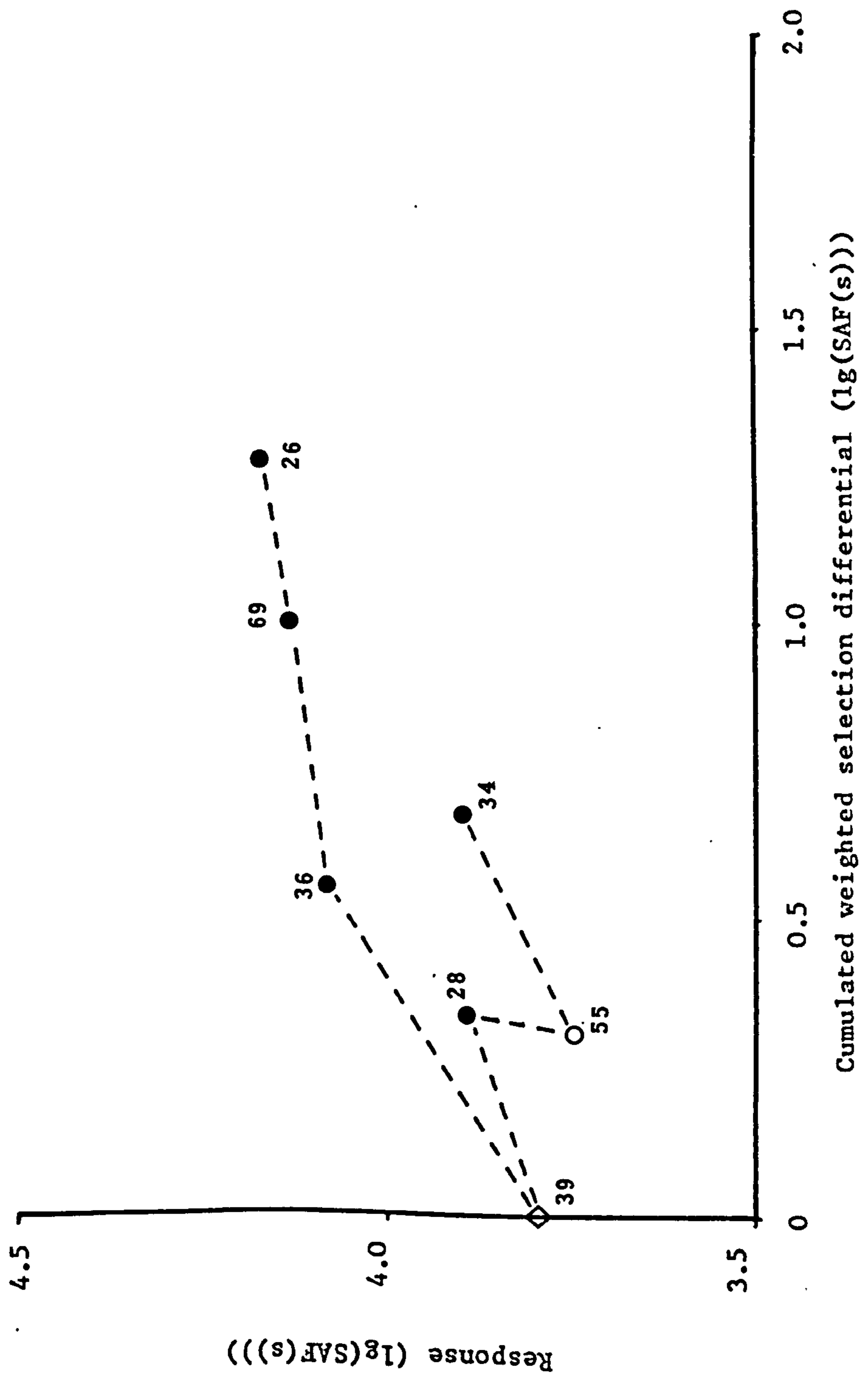


Fig. 4.13

The response to selection is plotted against the cumulated weighted selection differential for all four strains on the same graph so that the repeatability of the response may be examined.

generation

● - generation resulting from selection for increased flight performance

○ - generation resulting from selection for decreased flight performance

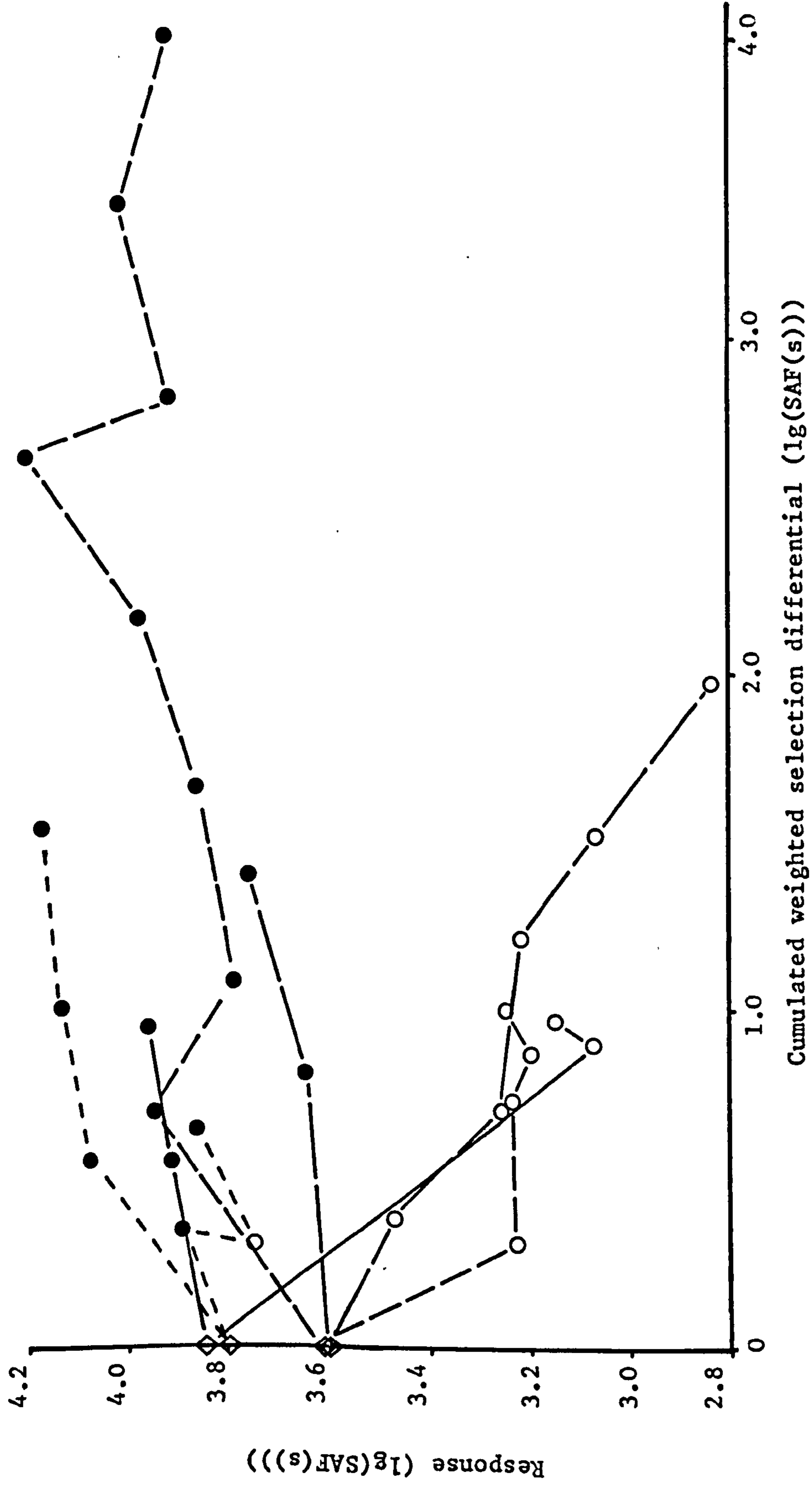
————— - K strain

——— ——— - KT strain

----- - L strain

- - - - - - N strain

Flight capacity was measured on the basis of the sum of all flights (in seconds). The number of individuals in each generation of each line is indicated.



of the lines selected for and against flight is an assymetry in their response. The rate of change of response is generally greater when selection is imposed against flight than when it is imposed for flight, particularly over the first generation of selection of a line.

Also apparent is the consistency with which a change in the response occurs in the same direction as the selection was imposed. Over 29 generations of selection the direction of the change in the respose has followed that of the direction of the selection 23 times, with two others being small positive increases in the response of low lines ($<0.1 \lg s$) after small negative selection differentials ($<0.15 \lg s$) had been applied.

There is a great deal of variation in response apparent between the four strains, both in their parental and selected generations. There are a number of potential reasons for this variation. Firstly, the genetic makeup of the parental generations may have differed significantly. Secondly, random drift may have acted to cause further differences between these gene pools. Thirdly, there will be variation in the measured flight durations due to uncontrolled environmental factors, particularly microenvironmental factors. Fourth, and perhaps most important, is the variation inherent in any behavioural data other than simple push-button reflexes (Kennedy, 1969). Fifthly, sampling error may be present in the estimation of the generation means.

It is interesting that the parental generation with the highest response is that of the K strain which had been subjected

to some previous selection (on the basis of N0 to N1), the majority of which was positive for flight. Very close to this is the response of the parental generation of the N strain with an apparent gap between these and the parental generations of the KT and L strains. A one-way analysis of variance of the N, KT and L parental generations (the K strain is not considered comparable having already been subjected to some selection) in fact indicates that there is no significant difference between these means ($F=1.59$, $DF=2$, 206 , $P>0.10$).

3.3 The nature of early and late flights

Peaks of flight activity have been observed in populations of S. exempta emerging from outbreaks using an Aldis lamp beam (Rose and Dewhurst, 1979), radar and an infra-red device (Riley, et al., 1981; 1983). Major and consistent peaks occur at dusk, from c. 21.00 to 24.00h, and at dawn. Radar evidence (Riley et al., 1981; 1983) using a radar overlooking an emergence site has suggested that the dusk peak of activity is due a mass migratory flight. Moths were observed to ascend well above their boundary layer to an average maximum altitude of 420m agl (Riley et al., 1983). Many moths were recorded flying at the altitude of the strongest mean wind (nine to ten ms^{-1}) and so would have maximised their ground speed. It is not known if this selection of the altitude of strongest winds is deliberate and a usual phenomenon or if it was an accident on this occasion. The overlooking radar had a maximum detection range of 2.3 Km for objects of 0.5 cm^2 cross-section. A second "down-range" radar of the same type positioned c.15 Km down-wind of an outbreak was

used to continue following the emigrants which, while in range of this radar, showed no sign of descending and may be presumed to have travelled at least 18-20Km.

Some moths appeared to enter nearby trees early in the night before taking-off again later, possibly on emigration flights (Rose and Dewhurst, 1979). Groups of these moths sometimes took-off simultaneously (in plumes) which could be seen on radar. These moths were never seen on the down-range radar and so probably flew for only a few kilometres. Even so their flights had taken them out of the outbreak area and so may be termed migratory in the sense of Southwood (1962). Moths taking-off in the peak of activity before sunrise did so on only short flights, as the flights were always finished by the end of the twilight period (Riley et al., 1983). This pattern of flight activity has also been observed in tethered-flight studies by Gatehouse and Hackett (1980), Parker and Gatehouse (1985a,b) and has been reported elsewhere in this thesis.

The apparent qualitative differences in flights in the field beginning at different times of the night, together with the demonstrated additive genetic component to the variance of tethered-flight, prompted an examination of the heritability of the duration of tethered-flights beginning at different times of the night in the laboratory.

A preliminary account of the differences in the heritability of flight duration - between early (starting before midnight) and late (starting after midnight) flights has been published by Gatehouse and Woodrow (1987). Their analysis was based on

untransformed data from the L strain and they calculated estimates of heritabilities from mean offspring on mid-parent flight duration regressions. The narrow-sense heritability of the duration of flights beginning before midnight (1600 to 2400h) was found to be 0.51 whereas that for flights after midnight (2400 to 0800h) was found to be 0.08.

However, because regression analysis assumes a normal distribution of the data and random sampling (see above) the data have now been normalised as described. Unfortunately this log transformation introduces a complication. Where a moth has not produced any flights longer than ten seconds (the minimum duration of flights recorded by the apparatus) beginning in the period under analysis, its flight duration (LSF or SAF) is zero. Logarithmic transformation of zero is minus infinity and meaningless in this context so that the calculation of mid-parent or mean offspring values, when one or more of the individuals have a flight duration of zero, becomes impossible.

One solution to this problem is to assign an arbitrary value of flight duration greater than zero to these moths. A suitable value might be ten seconds, giving a transformed value of one. An alternative value which could be assigned with a similar chance of being "correct" is one sec. giving a transformed value of zero. It was decided that the arbitrary nature of any such value assigned to a moth with no recorded flight duration, and the large effect that the size of this value has on the transformed value (and hence the calculation of mid-parent and mean offspring values), was unsatisfactory.

The alternative solution which was adopted was to treat the

value for moths with no recorded flight as a missing value. The mid-parent and mean offspring values involving such moths must then be excluded from the data set and calculations of regressions and plots of the data based only on moths giving at least one flight greater than ten seconds. The significance of the regressions may be reduced by the omission of a number of data points but this was thought preferable to their inclusion where errors had been introduced by the arbitrary assignment of flight duration values.

In plotting the response to selection against the cumulated weighted selection differential this approach was impossible as calculation of generation means would have been rendered impossible. In these analyses the assignment of an arbitrary flight duration to a moth which had produced no flights was necessary and a duration of one second and hence a transformed value of zero was chosen.

Mean offspring on mid-parent regression analyses are very time consuming and so have only been calculated for the KT and N strains (using $\lg(\text{LSF})$ and $\lg(\text{SAF})$) and the L strain (using $\lg(\text{SAF})$) for flights beginning within both the early (1600 to 2400h) and the late period (2400 to 0800h) of the night. The mean offspring on mid-parent regression equations for each analysis are shown in Table 4.3. Also shown are F values, number of data points (n), the significance of each regression (P) and, where possible, estimates of narrow-sense heritability (h^2). Significant regressions were calculated for $\lg(\text{LSF})$ and $\lg(\text{SAF})$ based on early flights for the KT strain ($P < 0.001$ for both) but

Table 4.3.

Regression equations, F values, number of data points (n), significance of the regressions (P) and estimates of narrow-sense heritability (h^2) for mean offspring on mid-parent regression analyses for both lg(LSF) and lg(SAF) measured before and after midnight for the KT and N strains. Also for lg(SAF) measured before and after midnight for the L strain.

Strain	Flight Para- meter	Time	Regression Line	F	n	P	h^2
KT	lg(LSF)	Early	MO = 1.66+0.394MP	16.46	23	<0.001	0.394
		Late	MO = 2.02+0.189MP	1.73	20	>0.20	-
	lg(SAF)	Early	MO = 1.64+0.469MP	28.31	23	<0.001	0.469
		Late	MO = 2.16+0.240MP	3.10	20	>0.05	-
L	lg(SAF)	Early	MO = 1.36+0.561MP	42.08	39	<0.001	0.561
		Late	MO = 2.38+0.237MP	5.00	28	<0.05	0.237
N	lg(LSF)	Early	MO = 2.58+0.218MP	3.23	18	>0.05	-
		Late	MO = 1.49+0.440MP	11.96	12	<0.01	0.440
	lg(SAF)	Early	MO = 2.31+0.342MP	3.51	17	>0.05	-
		Late	MO = 2.41+0.264MP	2.84	12	>0.10	-

MO = Mean Offspring

MP = Mid-Parent

the regressions based on late flights were not significant ($P > 0.20$, $P > 0.05$). The L strain also had a significant regression for $\lg(\text{SAF})$ based on early flights ($P < 0.001$) with a less significant regression for late flights ($P < 0.05$). The only regression which was significant for the N strain was that for late flights based on $\lg(\text{LSF})$ ($P < 0.01$).

3.4 Sex-related heritability of flight durations

The regression of single-sex offspring flight durations on those of one parent allows the investigation of sex linkage in the inheritance of flight durations. Since the heritability of flight durations has already been shown to be significant only for the period before midnight for the KT strain, and is far more significant for this period for the L strain, these regressions were performed only on the data from this period for these two strains. For the N strain, $\lg(\text{LSF})$ measured after midnight is the only significant regression so single-sex regressions were also performed for the period after midnight for this strain.

The heritability values for flight duration of offspring on one parent are calculated as twice the slope of the regression line (Falconer, 1981). The heritability values, significance of the regressions and number of data points for data before midnight are shown in Table 4.4 (for the KT strain), Table 4.5 (for the L strain) and Table 4.6 (for the N strain). No single-sex regressions of the N strain after midnight proved to be significant, with $P > 0.20$ in all cases.

Table 4.4.

Estimates of narrow-sense heritability (h^2) from single-sex offspring on one parent regression analyses for flights beginning before midnight for the KT strain. The heritability is calculated as twice the slope of the line of best fit where the regression is significant.

Flight capacity was measured in terms of $\lg(\text{LSF})$ and $\lg(\text{SAF})$.

		Parents	
		Female	Male
Offspring	Female	$h^2 = 0.768$	$h^2 = 0.642$
		$P < 0.05$	$P < 0.05$
		$n = 27$	$n = 27$
	Male	$h^2 = -$	$h^2 = 0.646$
$P > 0.50$		$P < 0.02$	
	$n = 24$	$n = 24$	

		Parents	
		Female	Male
Offspring	Female	$h^2 = 0.984$	$h^2 = 0.662$
		$P < 0.005$	$P < 0.01$
		$n = 27$	$n = 27$
	Male	$h^2 = 0.954$	$h^2 = 0.536$
$P < 0.01$		$P < 0.05$	
	$n = 24$	$n = 24$	

Table 4.5.

Estimates of narrow-sense heritability (h^2) from single-sex offspring on one parent regression analyses for flights beginning before midnight for the L strain. The heritability is calculated as twice the slope of the line of best fit where the regression is significant.

Flight capacity was measured in terms of $\lg(\text{SAF})$.

		Parents	
		Female	Male
Offspring	Female	$h^2=0.886$	$h^2=0.642$
		$P<0.001$	$P<0.001$
		$n=58$	$n=51$
	Male	$h^2=1.234$	$h^2=0.794$
$P<0.001$		$P<0.001$	
		$n=54$	$n=50$

Table 4.6.

Estimates of narrow-sense heritability (h^2) from single-sex offspring on one parent regression analyses for flights beginning before midnight for the N strain. The heritability is calculated as twice the slope of the line of best fit where the regression is significant.

Flight capacity was measured in terms of $\lg(\text{LSF})$ and $\lg(\text{SAF})$.

		Parents	
		Female	Male
Offspring	Female	h^2 - P>0.10 n=23	$h^2=0.744$ P<0.02 n=22
	Male	h^2 - P>0.05 n=22	$h^2=0.980$ P<0.01 n=21

		Parents	
		Female	Male
Offspring	Female	h^2 - P>0.10 n=22	$h^2=0.920$ P<0.02 n=22
	Male	h^2 - P>0.10 n=21	$h^2=0.880$ P<0.02 n=21

3.5 The response to selection before midnight

The responses of $\lg(\text{LSF})$ and $\lg(\text{SAF})$ to selection for and against flight in the L strain were re-examined in the light of the greater narrow-sense heritabilities found for flights beginning before midnight (Figs 4.14 and 4.15). It can be seen that the decrease in $\lg(\text{LSF})$ and $\lg(\text{SAF})$ between the F1 and F2 generations of the high line apparent in the original analysis also occurs in flights beginning before midnight. This coincides with, and appears to be due to selection against flight before midnight being imposed at this time. The reversal of selection was accidentally imposed as two parents chosen for breeding had produced very long flights after but not before midnight.

The re-examination of flights before midnight for the low line show that flight only increased when selection was accidentally imposed for longer flight between the F2 and F3 generations.

3.6 The flight duration distributions of generations after selection for flight

An analysis of the distribution of $\lg(\text{LSF})$ in the lines selected for prolonged flight has revealed what appears to be a discontinuity (Fig. 4.16). A bimodal distribution is apparent in the F1 generation of each strain. The mathematical analysis of bimodal distributions presents problems (Harding, 1949) but it was possible to examine these generations further by the use of the graphical analysis technique described by Harding (1949) and Southwood (1966 and refs), and used by Rose (1972).

Normal probability paper is used to separate the two main

Fig. 4.14

The L strain.

The response to selection is plotted against the cumulated weighted selection differential for selection imposed for increased and decreased flight over eight and four generations respectively.

◇ - parental generation

● - generation resulting from selection for increased flight performance

○ - generation resulting from selection for decreased flight performance

Flight capacity was measured on the basis of the longest single flight beginning before midnight (in seconds). The number of individuals in each generation of each line is indicated.

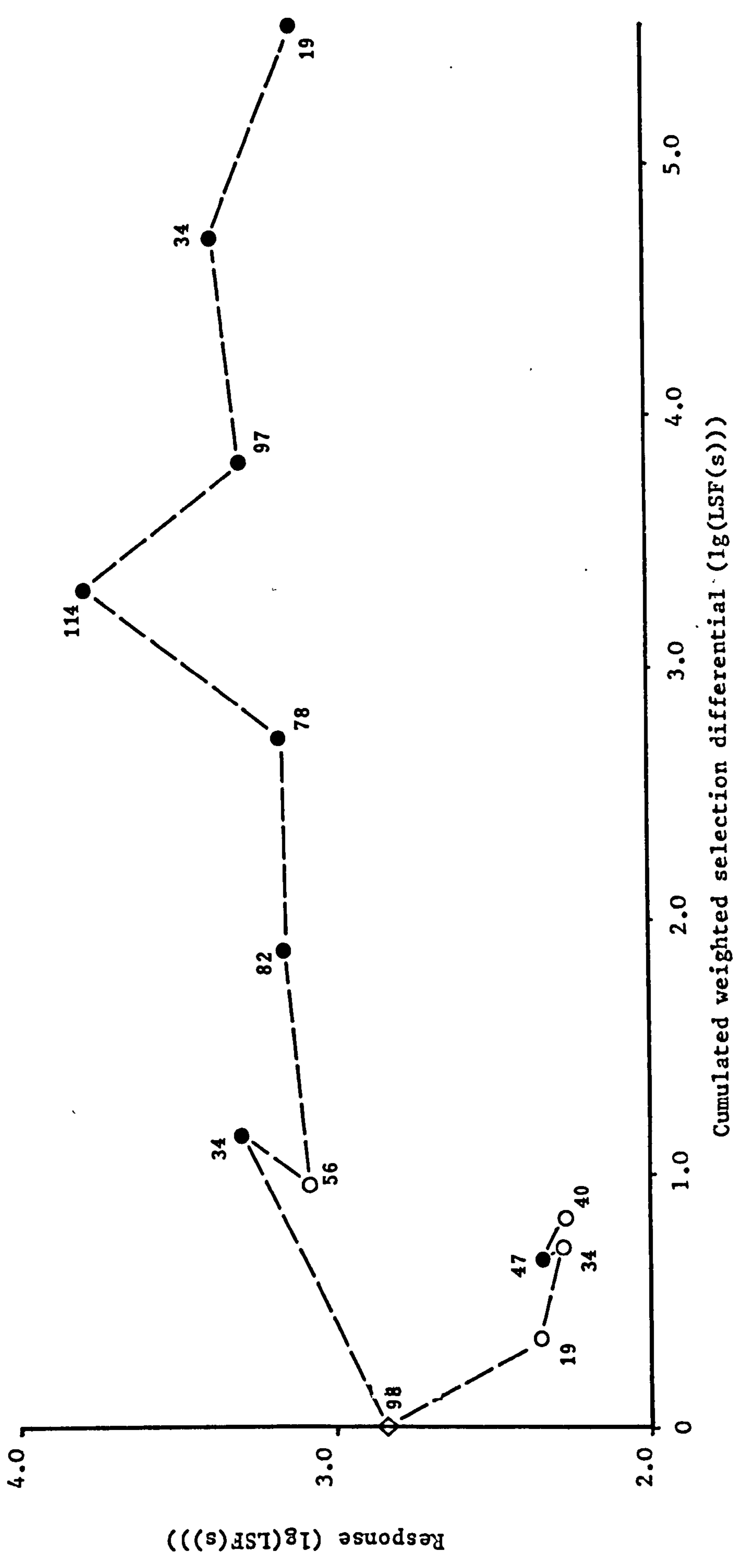


Fig. 4.15

The L strain.

The response to selection is plotted against the cumulated weighted selection differential for selection imposed for increased and decreased flight over eight and four generations respectively.

- ◇ - parental generation
- - generation resulting from selection for increased flight performance
- - generation resulting from selection for decreased flight performance

Flight capacity was measured on the basis of the sum of all flights beginning before midnight (in seconds). The number of individuals in each generation of each line is indicated.

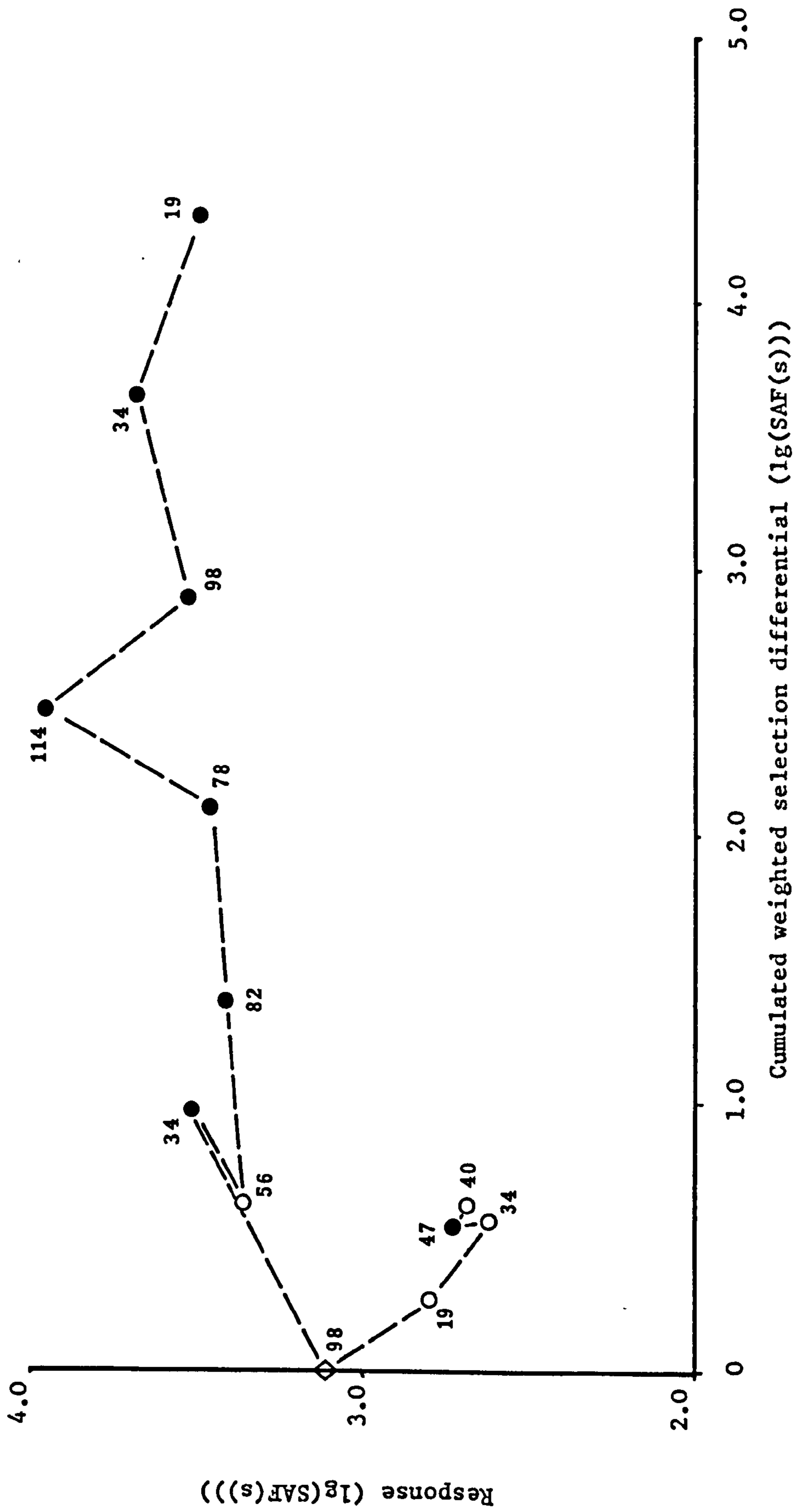
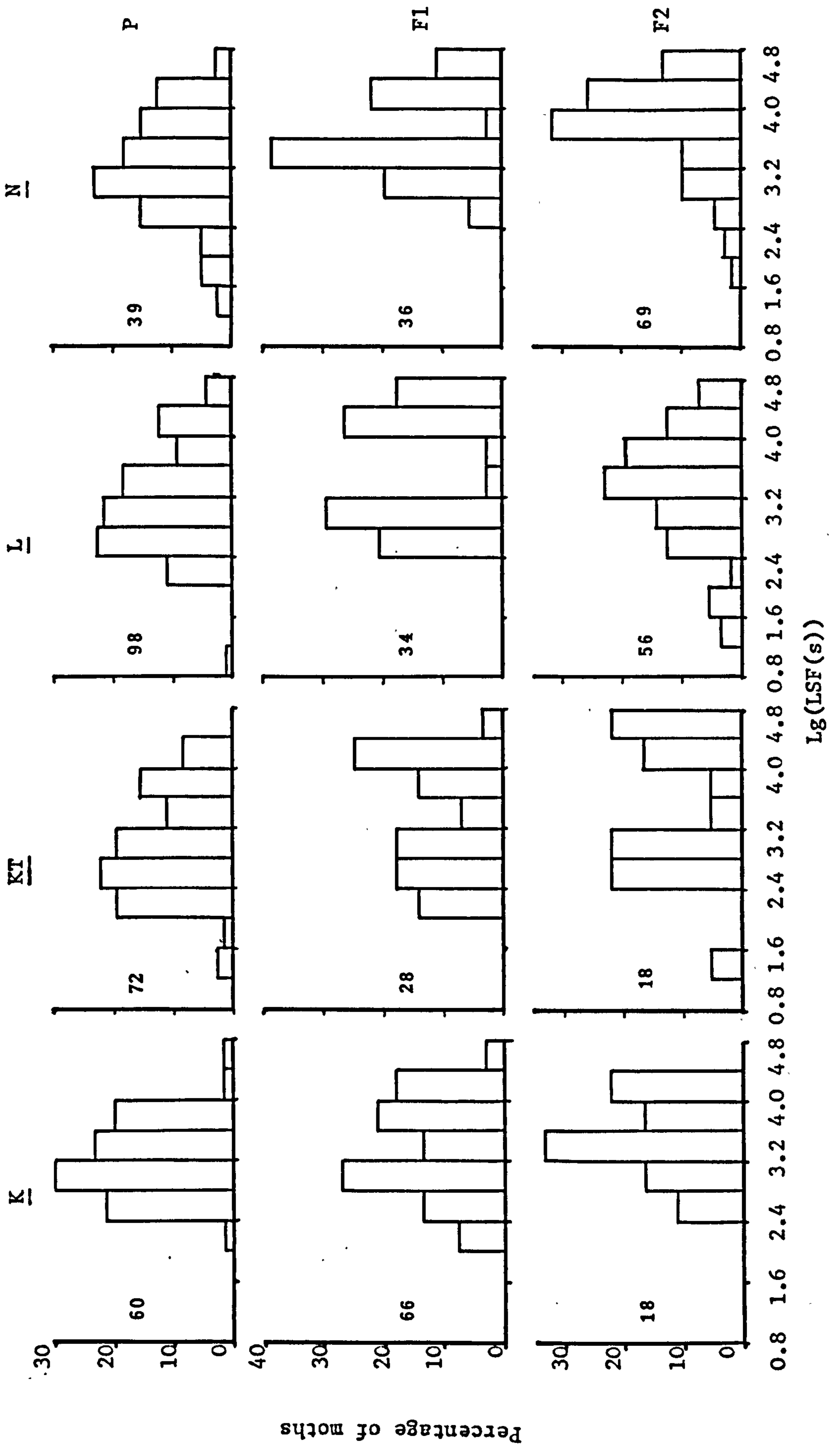


Fig. 4.16

Frequency distributions of $\lg(\text{LSF})$ for the parental (P) and first two generations (F1 and F2) of lines selected for increased flight capacity of the four strains. The diagram illustrates the bimodality present in, principally, the F1 generation of all four of the lines selected for flight.



categories of each distribution and to enable the mean and standard deviation of each category to be derived (Fig. 4.17a-d). If the data points are arranged in order of increasing value they may then be plotted by their value on the arithmetic axis and the proportion of the total population so far included in the plot on the probability axis which has its lowest value coincident with the lowest value of the arithmetic axis (i.e. the first point of 20 will represent 5% of the population and so should be plotted at 2.5% with the second at 7.5% and the third at 12.5%). The number of modes in the total population is indicated by the number of points of inflexion in the resulting curve - two modes for one point of inflexion, three modes for two points of inflexion, etc...

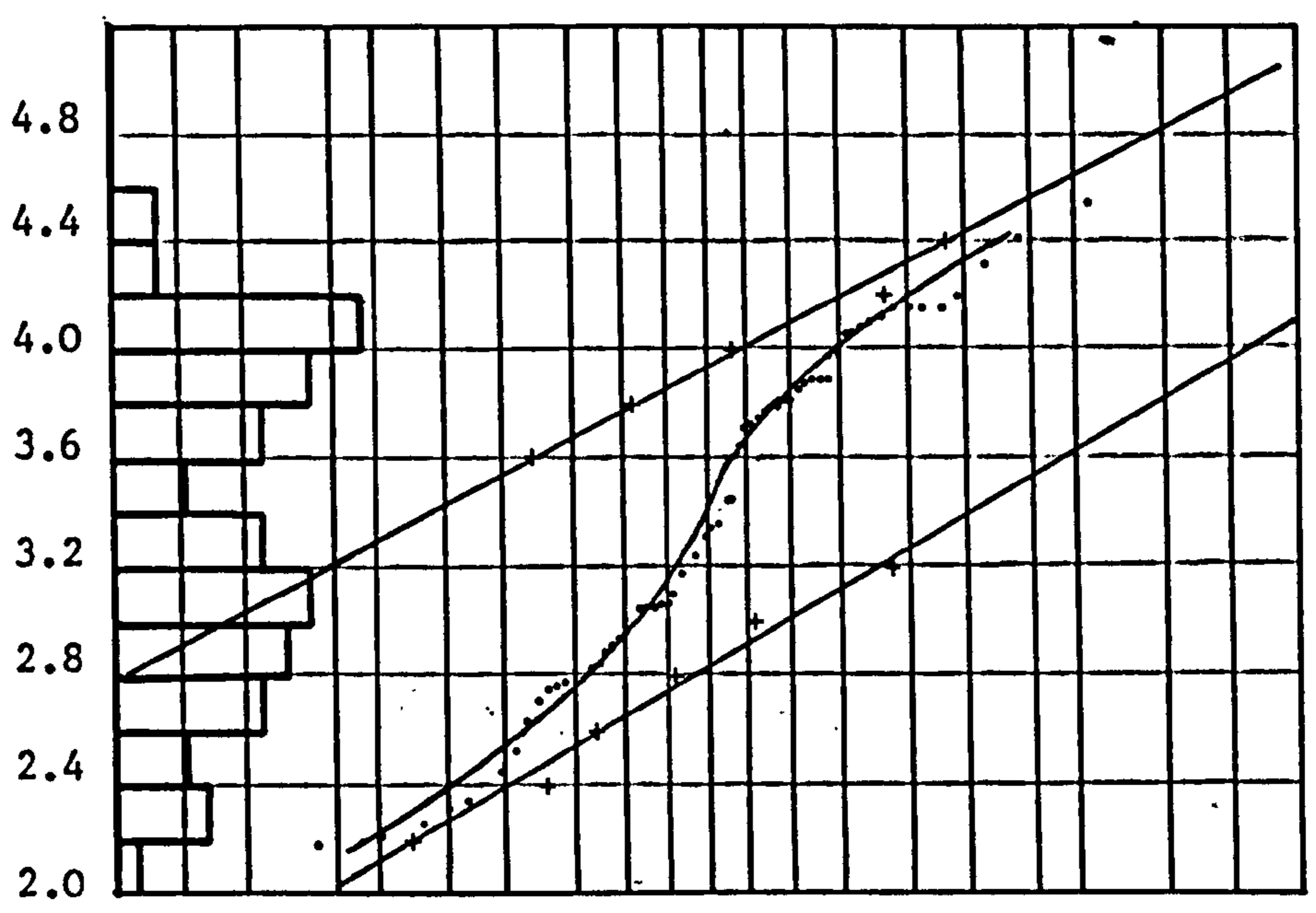
For two modes the modal categories may be separated by plotting each side of the point of inflexion separately. Each data point is plotted as its value (arithmetic axis) and twice the proportion of the population which it encompasses (as above) on the nearest of the two probability axes. Lines of best fit may then be drawn by eye through these two groups of points. Finally the resultant of these two lines is determined by choosing values on the arithmetic scale which are encompassed in both lines. The resultant is then the mean of the probability values for the two lines where they intersect the arithmetic value. The resultant may be plotted as a curve through the original data points. The best resultant curve is sought by moving the two lines of best fit, thus changing the shape of the curve. When the curve fits the original data as well as

Fig. 4.17a,b

Analysis of the bimodality present in the F1 generation of each of the lines selected for increased flight performance using normal probability paper (see text for method). Means and standard deviations of the two modal categories may be derived.

	Mean	SD
a. K strain -	2.84	0.34
	3.92	0.32
b. KT strain	2.59	0.33
	3.92	0.40

a



$Lg(LSF(s))$

b

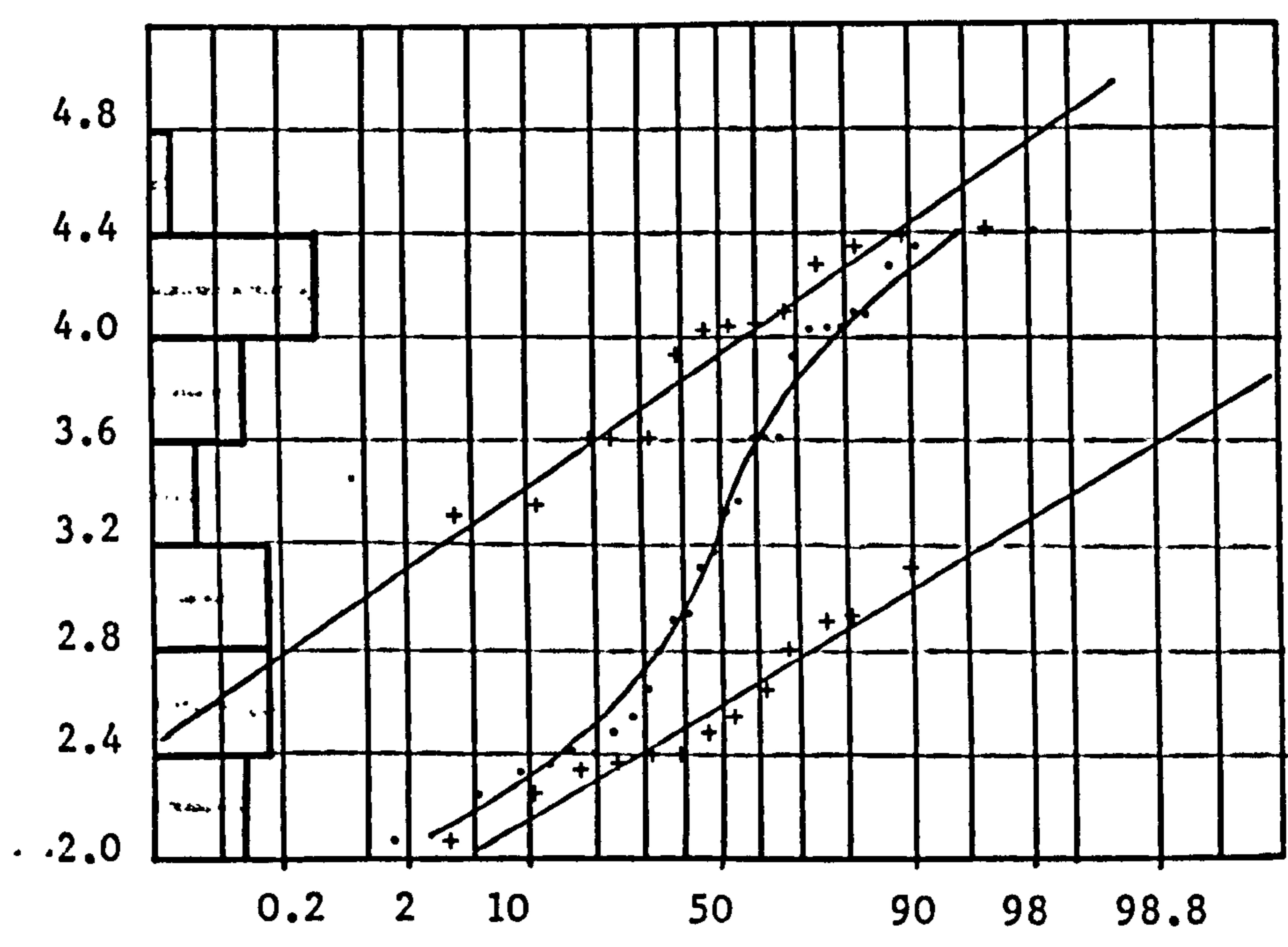
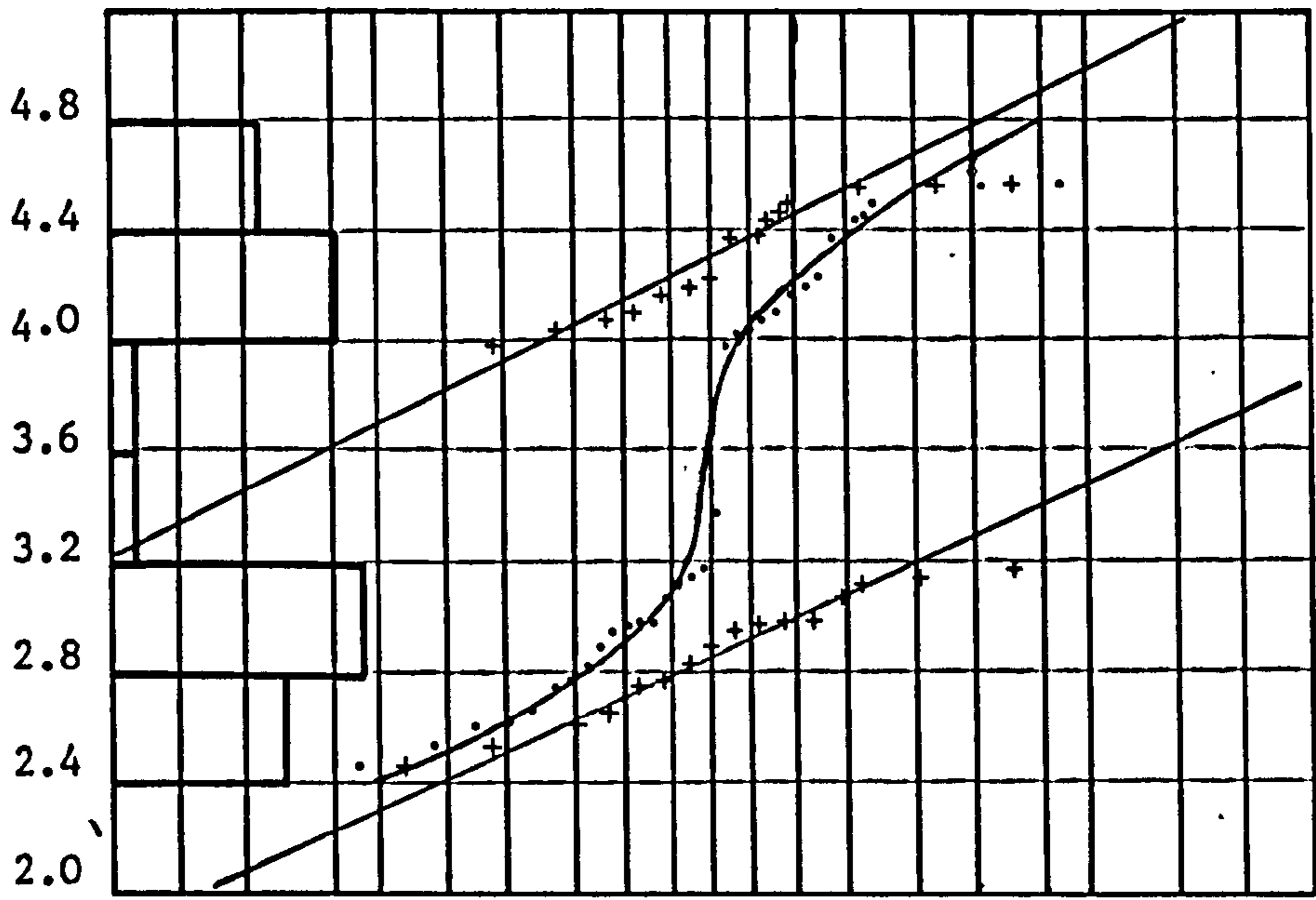


Fig. 4.17c,d

Analysis of the bimodality present in the F1 generation of each of the lines selected for increased flight performance using normal probability paper (see text for method). Means and standard deviations of the two modal categories may be derived.

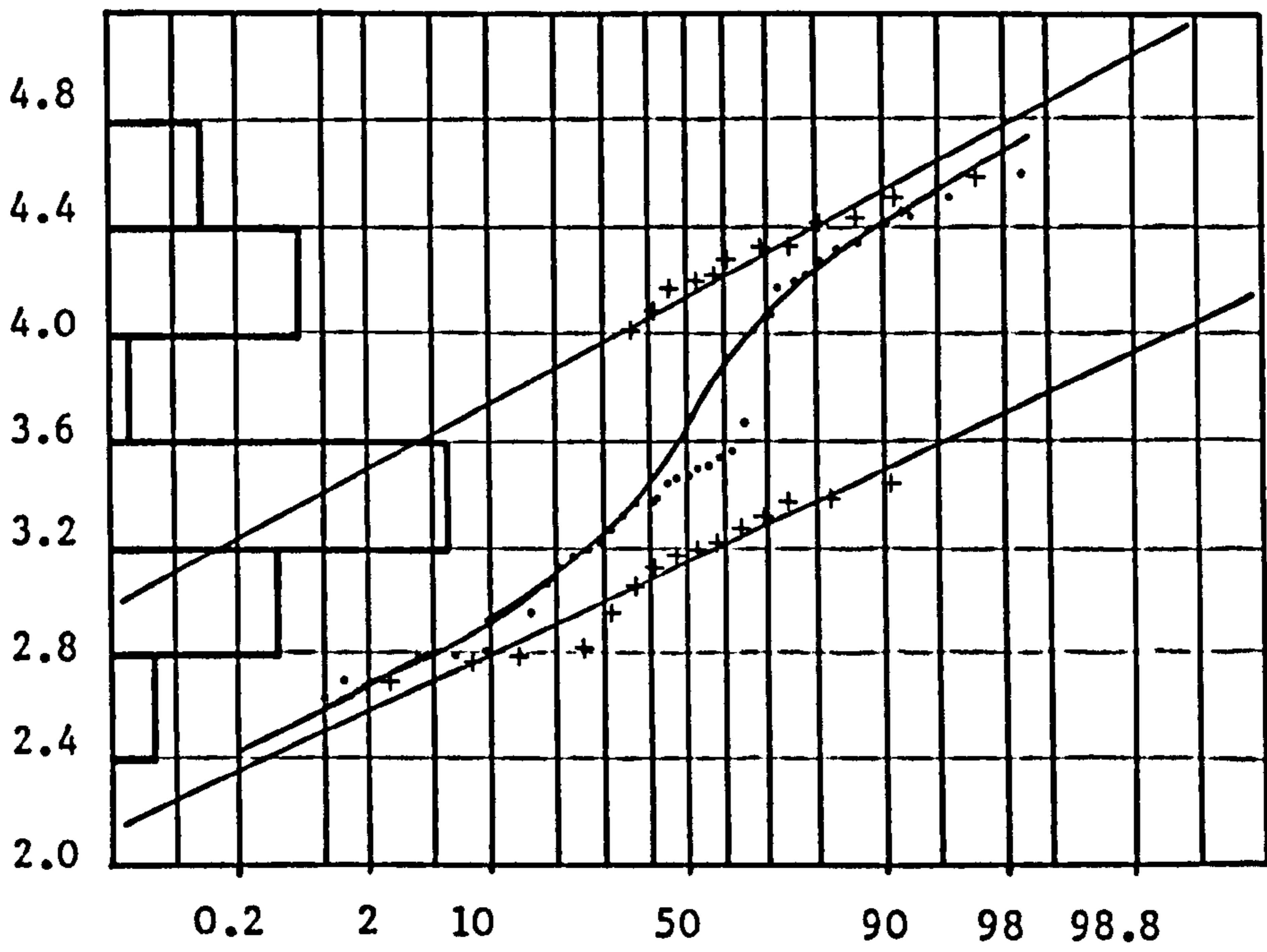
	Mean	SD
a. L strain -	2.88	0.26
	4.31	0.30
b. N strain	3.15	0.27
	4.13	0.32

c



$Lg(LSF(s))$

d



possible, judged by eye, the mean of each of the two straight lines may be determined from the value at the 50% probability line and the standard deviation from half the difference between the values at 15.87% and 84.13%. These means and standard deviations are given in Table 4.7.

The bimodality is not obviously present in any subsequent generations (Fig. 4.16 and 4.18), nor is it found in selected generations of the low line (Fig. 4.19). Means of the flight durations for the low modal categories in Table 4.7 are in the range 2.59 to 3.15 (6.5 to 24 mins) with those in the high modal categories in the range 3.92 to 4.31 (2h 20mins to 5h 40mins). Those for selected generations of the low line of the L strain are in the range 2.46 to 2.67 (4.8 to 7.8 mins) and F2 generation onwards of the high line in the range 3.32 to 3.88 (34mins to 2h 6mins).

Correlation analyses of $\lg(\text{LSF})$ and pharate adult weight were performed for the first selected generation of the four strains of this study. No relationship between body weight and flight performance was found (K : $r=0.220$, $n=66$, $P>0.05$; KT : $r=-0.159$, $n=28$, $P>0.20$; L : $r=-0.007$, $n=34$, $P>0.50$; N : $r=-0.002$, $n=36$, $P>0.50$) (Fig. 4.20).

For strains which have responded well to selection it is apparent that the logarithmic transformation suitable for unselected generations may be too strong for later generations. Fig. 4.18 illustrates the response to selection in the distributions of successive generations of the high line of the L strain from F3 onwards (P, F1 and F2 generations are shown in Fig. 4.16). The increase in incidence of prolonged flight can be

Table 4.7.

The means (and standard deviations) of the two modal categories which are apparent in the first generation of each strain selected for greater flight. Flight capacity is measured as $\lg(\text{LSF})$.

Strain	Lower category	Higher category
K	2.84 (0.34)	3.92 (0.32)
KT	2.59 (0.33)	3.92 (0.40)
L	2.88 (0.26)	4.31 (0.30)
N	3.15 (0.27)	4.13 (0.32)

Fig. 4.18

Frequency distributions of $\lg(\text{LSF})$ for the third to eighth generations (F3 to F8) of the line of the L strain which was selected for increased flight capacity. The diagram illustrates the response to selection over the F3 to F6 generations. There is no apparent evidence of a bimodality in these distributions.

Percentage of moths

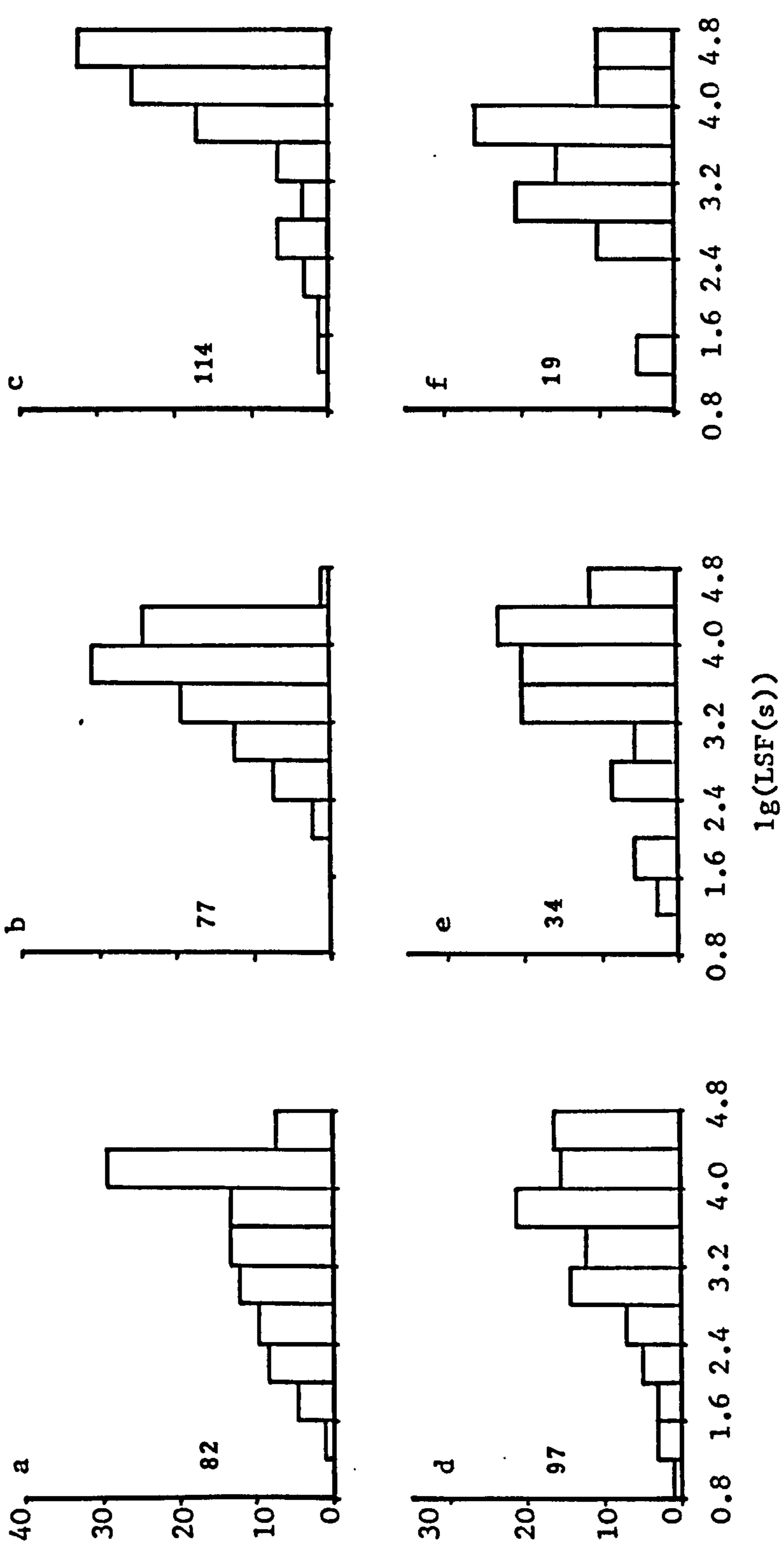


Fig. 4.19

Frequency distributions of $\lg(\text{LSF})$ for the first to fourth generations (F1 to F4) of the line of the L strain which was selected for decreased flight capacity. There is no apparent evidence of a bimodality in these distributions.

Percentage of moths

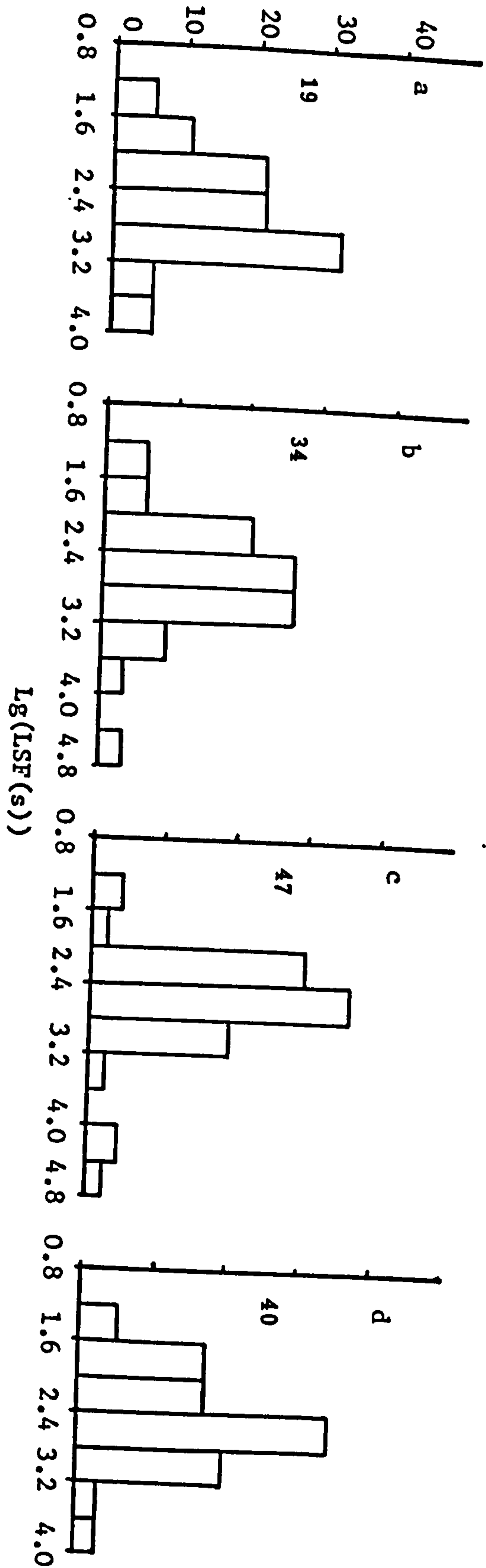
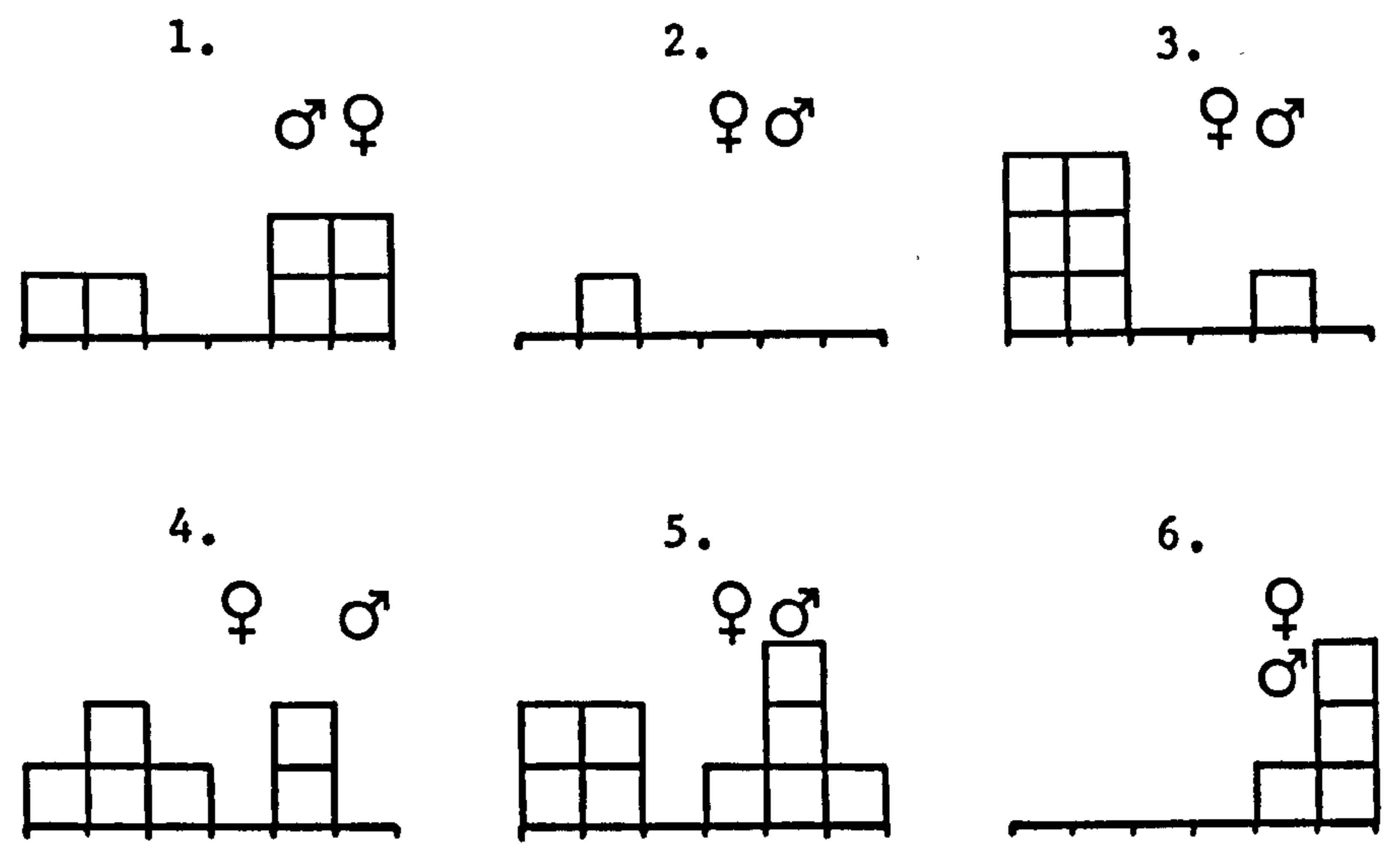


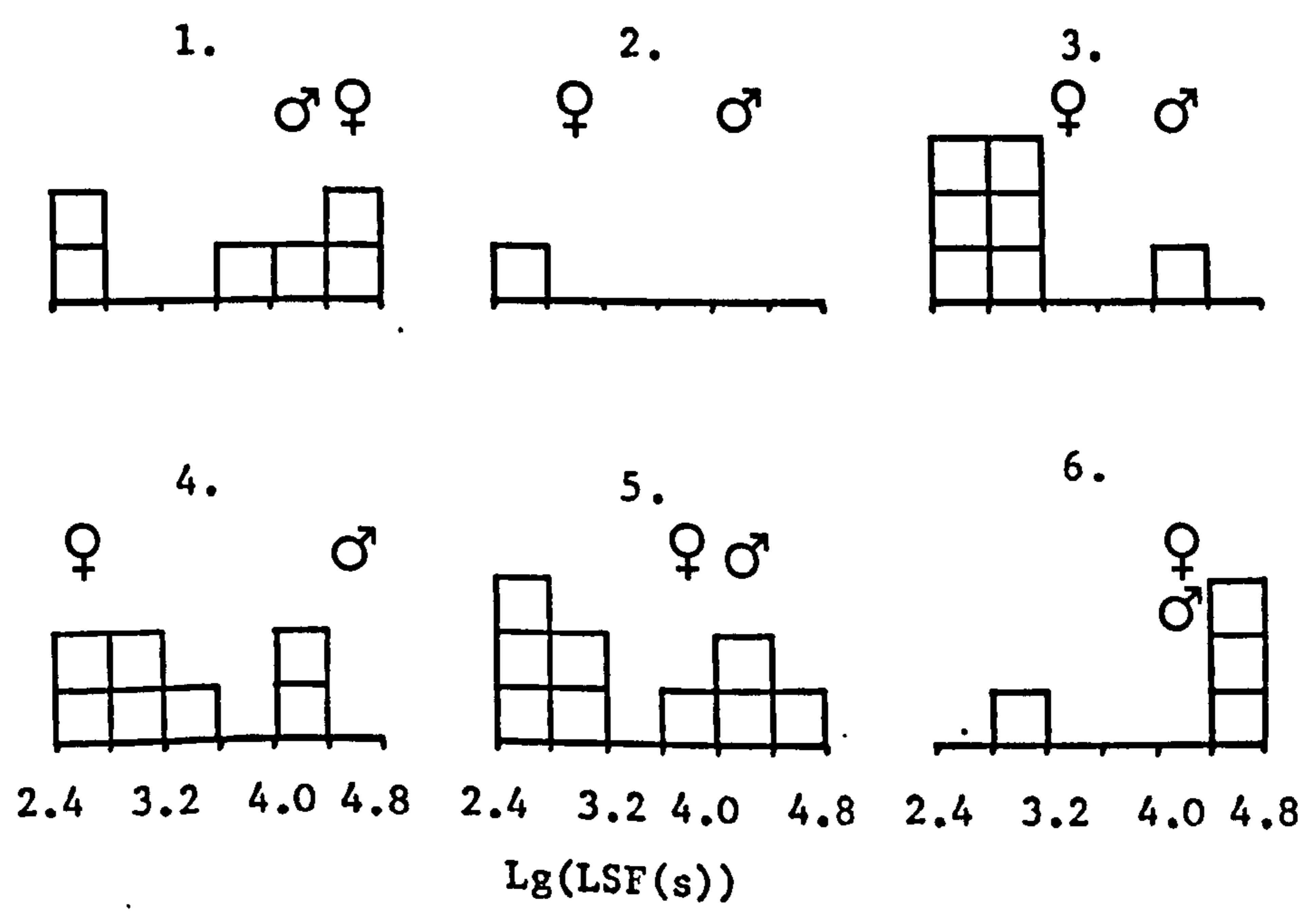
Fig. 4.20

Frequency distributions of $\lg(\text{LSF})$ for the offspring of the six families which make up the F1 generation of the L strain line which was selected for increased flight capacity. One square represents one individual. Also indicated by male and female symbols are the flight capacities of the parents. The diagram illustrates that short-flying offspring may be produced by even the longest-flying parents.

a



b



followed until the F6 generation after which it declines. Unfortunately the low line had died out before the F6 generation so it is impossible to say whether or not the decline might have been due to some environmental influence e.g. change in food plant quality causing a simultaneous change in the two lines.

The high line terminated at the F8 generation because no viable eggs were laid. This was thought to be due to disease, the presence of which might have affected the flight behaviour of the F8 adults. If this generation is omitted an estimate of realised heritability from a regression line through the points of the high line has a value of 11.3% although the regression is not significant ($P > 0.10$). If the disease was present in the F7 generation, as may be indicated by the declining numbers in this generation, then the behaviour of the adults might also be affected here. Omitting this generation produces an estimate of heritability of 14.7% although again the regression is not significant ($P > 0.10$).

4. DISCUSSION

4.1 The response to selection

With the exception of the first few generations of the K strain which were flight-tested for N0 and N1 selection for and against greater flight capacity produced a response in the same direction at least over the first few generations. This confirms the previous findings of Parker and Gatehouse (1985b) that flight expression in S. exempta is under genetic control.

Fig. 4.20a illustrates the distribution of lg(LSF) for the offspring of the six families which make up the F1 generation of the high line of the L strain. Also indicated are the lg(LSF)s for the parents of the families. Fig. 4.20b illustrates the same families categorised on the basis of lg(LSF) before midnight. From these figures of typical families it can be seen that some short flying offspring are produced by even the longest flying parents e.g. families one and six. It can also be seen from Fig. 4.19 that crosses of short-flying parents can produce some long-flying offspring. It may therefore be concluded that the control of lg(LSF) is polygenic in nature.

Roff (1986b) suggested that the polygenic control of wing dimorphism would be favoured by natural selection. Given a single locus, two allele system with brachyptery (B) dominant the proportion of macropters from all possible crosses are 0% (BB x any other), 25% (Bb x Bb), 50% (Bb x bb) and 100% (bb x bb). Changes in the frequency of macropters will occur in a population following emigration, immigration and selection, but these changes are rarely likely to be optimal in terms of being able to

resist invasion by some alternative strategy. A polygenic mode of inheritance permits more numerous and variable trajectories (changes in the proportion of macropters from generation to generation depending on the genetic constitution of the starting population - e.g. an impregnated immigrant female - and the heritability of the trait under the current environmental conditions). Roff also postulated an intermediate heritability, probably regulated by genotype-environment interactions, for a population which inhabited a number of differing habitats and therefore having different optimal rates of emigration at each site. His argument seems equally applicable to behavioural aspects of flight.

In this study, an exception to the expected response was observed in the K strain over the first two generations of selection. This may have been influenced by the poorly-controlled environmental conditions or the extra stress imposed by flight-testing over an additional night (N0). However, as discussed above, it seems more likely to have been due to the incorrect classification (the tethered-flight behaviour inaccurately reflecting the genotype) of one or two of the small number of parents selected for breeding of the low line from the parental generation, hence producing an increasing selection differential rather than the intended decreasing one.

The very fast response of the high and low lines of the L strain, for both lg(LSF) and lg(SAF), over the first generation of selection is followed by no significant response to further selection when flights beginning at any time of night are

considered (Table 4.2). This might be interpreted as indicating either that the additive genetic variance remaining in the two lines after one generation of selection is a very small proportion of the phenotypic variance, or that selection is no longer being effectively imposed. However, if the figure is replotted using only those flights beginning before midnight (see below) it can be seen that the response of both $\lg(\text{LSF})$ and $\lg(\text{SAF})$ follows the direction of selection over all four generations of selection of the low line and the first five generations of selection of the high line (Figs 4.14 and 4.15). The increase in response is particularly high from the fourth to the fifth generations and is followed by a decrease against the direction of selection from the fifth to the sixth generations, down almost to the level of the fourth generation. A small increase in response follows from the sixth to the seventh selected generations before it decreases once again against the direction of selection from the seventh to eighth generations.

The poor survival of the last generation and the failure to produce viable eggs may be indicative of inbreeding depression or disease in the culture. S. exempta may be susceptible to bacterial attack as well as fungal and the well known viral "wilt disease". The latter may be due to a nuclear polyhedrosis virus (NPV) which is characterised by liquefaction of the larval body contents, the skin becoming thin and fragile, so bursting after death with resulting spread of the disease by contamination of food plants. A second type of viral disease is that of cytoplasmic polyhedrosis in which the larva becomes flaccid, shrivels and dries up after death, so being less infective than

the former. Diseases of S. exempta, along with predators and parasites found in the field and their potential as control agents, are discussed by Brown (1962).

NPV has been endemic in the cultures of S. exempta in this laboratory. In addition a disease began to be noticed in July 1985 which may therefore have been introduced with the K strain in June 1985. The disease presented symptoms in the larvae very similar to NPV, suggesting that it was related, with the exception that it produced a bright red colouration dyeing the larval contents. It also appeared to increase the mortality of adults which had previously not exhibited any symptoms at approximately three or four days old. These adults were also coloured red internally, particularly their muscular tissue.

The last generation of the L strain high line were the offspring of three pairs from the previous generation. Four other pairs had failed to produce viable eggs and one of these had later become stuck in copulo. The previous generation had also shown signs of infertility, viable eggs being obtained from nine of 16 mated pairs. The proportion of mated pairs which produced viable eggs from the parental generation to the last generation are : 0.88, 0.75, 0.78, 0.83, 0.46, 0.33, 0.56, 0.42, 0.0. It may be thought that either a pathogen or an inbreeding effect causing a reduced viability may have had a detrimental effect on adult flight behaviour over the last two or three generations even when no symptoms were evident. In this case the results of the first five generations of selection would indicate a greater realised heritability. However, the greatest flight

activity was recorded from the generation which had the smallest proportion of viable pairs before that of the last generation (0.33) so that this seems unlikely.

4.2 The repeatability of the response to selection

It has been pointed out in the results section of this chapter that the response consistently follows the direction of the imposed selection, in fact doing so in 23 out of 29 generations of selection. Of the six cases which did not do so five occurred during the selection of the L strain and one the K strain. If this data from the L strain is reanalysed on the basis of only those flights beginning before midnight (see below) then these five examples are reduced to two. Although the other strains have not been reanalysed it seems likely that the proportion of generations where the response of flights before midnight has followed the direction of selection is greater than 23 out of 29 and provides some indication of the consistency of the response to selection.

Some discussion has also been made of the causes of variation between strains in their response to selection. It should be emphasised that in the laboratory study of a behaviour such as flight a high degree of variation in the expression of the behaviour is to be expected because of the inevitably intrusive nature of the techniques employed. Behaviour has been defined by Kennedy (1969) as the integrated functioning of the whole animal in its environment with special reference to its movements and so incorporates a large number of intrinsic (e.g. genes, nervous system, endocrine system, rhythm generators, age,

reproductive status) and extrinsic (e.g. temperature, sunlight, availability of food or a mate) factors, both present and past. An introduction to the subject of insect behaviour is given by Matthews and Matthews (1978).

Gatehouse and Woodrow (1987) have suggested that tethered-flight may only provide a satisfactory index of prolonged flight in the field during the suppression of the individual's responsiveness to vegetative stimuli during migratory flight (Kennedy, 1986) and that for any confidence to be placed in the index as reflecting free-flight behaviour at least some indication of a correspondence of one aspect of the behaviour (e.g. temporal patterning) is required.

4.3 Asymmetry of the response to selection

A consistent feature of the bidirectional selections (K, KT and L strains) was the greater rate of response of the low lines compared with the high line and thus their higher realised heritabilities (Figs 4.5-4.10, 4.13-4.15). No judgement can be made on the N strain where the "low" line was not selected strongly and consistently against flight. An asymmetry of response to selection may be caused by differences due to generation interval (if the response is assessed after a period of time for both lines), selection differential (in a plot of response against generation interval) and scale of measurement (Falconer, 1954). The effects of the first two of these possible causes are removed by the plot of response against cumulative weighted selection differential, so that they cannot be the cause

of any asymmetry here. The effect of scale of measurement has been removed by log transformation which normalises the data. In later generations of selection for flight in the L strain this transformation appears too strong (Fig. 4.18) which could cause an apparent decline in the rate of increase of the response. Only the first few generations of selection should therefore be considered when looking for an asymmetry of response.

The K and KT strains both show a marked asymmetry of response on the basis of $\lg(\text{LSF})$ and $\lg(\text{SAF})$ using flights from any time of night (Figs 4.5, 4.6, 4.7, 4.8). The response of the first few generations of the L strain is also asymmetrical though to a lesser degree. When this strain is examined on the basis of flights beginning before midnight (Figs 4.14, 4.15) the asymmetry is at least as obvious as in the K and KT strains.

The remaining possible causes of such an asymmetry cited by Falconer (1954) are inbreeding depression (the depressive effects of inbreeding acting to decrease the trait and thereby aiding selection against it and hindering selection for it), unequal frequencies of alleles favouring the high and low lines in the parental population (if 90% of the alleles favour the high line then selection in this direction can only increase the allele frequency by 10% of the total but selection against the trait can increase the frequency of alleles favouring the low line by 90%), or directional dominance of at least some of the alleles (so that increasing the allele frequency favouring the high line by 10% increases the trait by 10% whereas increasing the allele frequency favouring the low line by 10% increases the trait by more than 10%). Inbreeding depression seems unlikely in this

case as the asymmetry was apparent over the first generation and moths were usually outbred.

Falconer (1954, p34) concluded, from a comparison of theoretical response curves and experimental results, that "sufficient cause of the observed cases of asymmetry can be found either in unequal initial gene-frequencies or in directional dominance or more probably in a combination of these two.". He concludes that he would "expect asymmetrical response to be a common feature of many quantitative characters when selection is applied.".

This has an important bearing on the conclusions which may be drawn from estimates of the narrow sense heritability of flight capacity and other life history characters. It is tempting to interpret an estimate of narrow-sense heritability in terms of the potential response to selection without considering the direction of that selection. The presence of an asymmetry, by definition, indicates that this response will be greater than predicted in one direction and less than predicted in the other. The implication in this study is that the potential for increasing the flight capacity of a population is not as great as first interpretation of narrow-sense heritability estimates would indicate.

4.4 The nature of early and late flights

Examination of the heritabilities of $lg(LSF)$ and $lg(SAF)$ for the KT strain (Table 4.3) shows that the durations of flights beginning before midnight have significant heritabilities

(lg(LSF) : $h^2=0.394$, lg(SAF) : $h^2=0.469$). The heritability of lg(LSF) and lg(SAF) based on flights beginning after midnight were however not significant.

Similarly the estimated heritability of lg(SAF) for the L strain is far more significant and has a higher value before midnight than after midnight (before : $P<0.001$, $h^2=0.561$; after : $0.025<P<0.05$, $h^2=0.237$). This difference is significant (comparison of regression slopes : $t=16.98$, $DF=63$, $P<0.001$).

Thus a significant proportion of the phenotypic variance in lg(LSF) and lg(SAF) of flights beginning before midnight is additive genetic variance and they are therefore able to respond to selection. In contrast additive genetic variance is only a small component of the phenotypic variance of flights beginning after midnight. This suggests a qualitative difference between flights beginning before and flights beginning after midnight.

That long-distance migratory flight appears usually to begin before midnight in the field has already been discussed in this chapter. It is plausible that the tethered-flights showing additive genetic variance are the laboratory equivalent of long-distance migratory flights in the field. Since heritability is dependent on the environmental conditions this only suggests that long-distance migratory flights in the field may show additive genetic variance and short flights may not.

In long-distance migratory flight a major determinant of the distance travelled by a moth, and hence the dispersal of a population, will be the time spent flying and so genetic variance in flight time will determine the degree to which a population is effective in scanning the habitat for suitable sites for

colonisation. In trivial and "pluming" flights the scope for genetic variation in the regulation of flight time is much less simply because the flights are much shorter. In this case the variation which is inherently present in a complex behaviour such as flight (see above) may be a more important determinant of distance travelled, and hence dispersal of the population. In all cases of flights reaching above the boundary layer the distance travelled will depend to a large degree on the direction and strength of the winds encountered by the moth.

The N strain contrasts with the KT and L strains (Table 4.3). The heritability of $\lg(\text{SAF})$ is not significant either before or after midnight. The heritability of $\lg(\text{LSF})$ is also not significant before midnight but is significant after midnight (before : $P > 0.05$; after : $P < 0.01$, $h^2 = 0.440$). Because this strain differed so markedly from the KT and L strains it is examined in further detail in the analysis of sex-related heritability below.

4.5 Sex-related heritability of flight performance

Regressions of single-sex offspring on one parent were performed for $\lg(\text{LSF})$ and $\lg(\text{SAF})$ based on flights before midnight for the KT and L strains. Estimates of narrow sense heritability could then be derived as twice the gradient of the regression line (Falconer, 1981).

For the KT strain (Table 4.4) the regression of female offspring on mothers gave the highest value of heritability both for $\lg(\text{LSF})$ and $\lg(\text{SAF})$. This regression was also the most significant for $\lg(\text{SAF})$ ($P < 0.005$). The regression of male

offspring on mothers was also very significant for $\lg(\text{SAF})$, giving a high value of heritability, but was not significant for $\lg(\text{LSF})$ so that no estimate of heritability could be made. Regressions of both sexes of offspring on fathers were also significant giving lower estimates of heritability than those on mothers.

Therefore, for this strain, total activity before midnight ($\lg(\text{SAF})$) of both sexes of offspring is more dependent on mother than father. But longest single flight ($\lg(\text{LSF})$) for each sex of offspring depends most strongly on the same sex of parent (greater significance of the regressions and values of heritability).

For the L strain (Table 4.5) all regressions based on $\lg(\text{SAF})$ before midnight are significant at $P < 0.001$. The highest values of heritability are again for those regressions on mothers.

Examination of the N strain showed that, in contrast to the picture obtained from the mean offspring on mid-parent regressions before and after midnight, when divided into single sex regressions none were significant for the period after midnight but some were significant before midnight. These significant regressions were for both sexes of offspring on fathers for both $\lg(\text{LSF})$ and $\lg(\text{SAF})$ (Table 4.6). Thus both total flight activity and longest single flight before midnight depend only on fathers but not significantly on mothers.

The picture from the single-sex offspring on one parent regressions of the N strain - some significant regressions before midnight but none after midnight - is consistent with that from

the mean offspring on mid-parent regressions of the KT and L strains. This suggests that the mean offspring on mid-parent regressions based on flights during the whole night for the N strain are anomalous. It is relatively easy to see how two significant relationships (e.g. female offspring and male offspring on male parent) could be masked by two non-significant ones (e.g. female offspring and male offspring on female parent) to produce a non-significant relationship (e.g. mean offspring on mid-parent for flights beginning before midnight). However, it is harder to see how a significant relationship (mean offspring on mid-parent for lg(LSF) beginning after midnight ($P < 0.01$)) could be produced from the combination of four non-significant relationships (single-sex offspring on one parent for lg(LSF) beginning after midnight) other than by chance.

Therefore all three strains show evidence of sex-related flight capacity. Parker and Gatehouse (1985b; see also Parker, 1983) also found evidence of sex-related flight in selection experiments for flight capacity on one strain of S. exempta. Their heritability estimates, based on untransformed flight durations, were significantly ($P < 0.001$) higher for both sexes of offspring regressed on fathers than on mothers (0.71-0.88 on fathers, 0.51-0.54 on mothers).

Thus, while flight capacity in S. exempta seems to be consistently sex-related, the sex of parent upon which flight depends more strongly varies from strain to strain. This may easily be explained by the presence of flight-related genes, either directly involved in flight control or as modifiers

(Robinson, 1980), on the sex chromosomes (the female is the heterogametic sex in Lepidoptera). Variation in the presence of these genes between the strains could then produce the observed variation in the relatedness to each sex.

It is also possible that the tethered-flight technique indexes flight of the two sexes differently. Males are generally more alert and susceptible to disturbance than females and this may be reflected in their tethered-flight behaviour. This topic has been more fully discussed in Ch. 3.

Dingle (1968) demonstrated the contribution of additive genetic variance to the variation in flight capacity of the milkweed bug, Oncopeltus fasciatus, by imposing selection and recording a change in the proportion of bugs giving flights longer than 30 mins. He did not, however, measure heritability or indicate the presence of a relationship between the response to selection and sex. Caldwell and Hegmann's (1969) estimates of the heritability of flight behaviour in the bug Lygaeus kalmii have a somewhat lower value from regressions of all offspring on each sex of parent than those recorded in this study (0.41 on mothers and 0.20 on fathers) with the difference again indicating a relationship with sex.

4.6 Discontinuous flight distributions

An examination of the distributions of $\lg(\text{LSF})$ has revealed a discontinuity present in the first generation resulting from selection for increased flight performance in all four strains. This discontinuity may also be found in the second generation selected for flight in the KT strain.

Discontinuous distributions of morphological characters associated with flight are well known, wing polymorphism being the most conspicuous example (see introduction). There are, however, very few published analyses of the distribution of tethered flight durations. Caldwell and Hegmann (1969) obtained a skew distribution for the flights produced by Lygaeus kalmii. Rose (1972) also obtained skewed tethered flight distributions for Cicadulina spp. flown on pins. Log transformation of his data produced bimodal frequency distributions similar to those obtained here. For both C. mbila and C. storeyi the de-transformed means of the two modal categories, designated short- and long-fliers, were 15s and 501s. Flight ability in Cicadulina was also found to be correlated with body size, long-fliers having shorter bodies. This was interpreted as an adaptation to decrease body weight and hence decrease wing loading, facilitating dispersal of the adult. It suggests that a balance may be maintained by different selection under different conditions; a long-bodied short-flying morph being favoured due to its greater fecundity in favourable grass habitats and a short-bodied strong-flying morph favoured by its greater flight ability when habitats are dry (Rose, 1972).

No significant correlation was found between $\lg(\text{LSF})$ and pharate adult weight for the bimodally distributed generations. This agrees with the conclusion of Parker and Gatehouse (1985a) who found no relationship between female moth weight on D1 and flight performance on N1 in terms of broad flight duration categories. No adaptation to decrease wing loading in moths with high flight capacity is therefore apparent.

The phenomenon of a bimodal distribution of flight capacity may have a number of explanations. Firstly the bimodality may have occurred by chance. This seems unlikely since it is present in the F1 generation of all four strains with a consistent inter-modal value of 3.2 to 4.0 and with a combined sample size of 164.

Secondly the discontinuity may be an artefact produced by the tethered-flight technique. This also seems unlikely due to its consistent occurrence only in the F1 generations of each strain. This fact, and that these generations were flight-tested at different times, also seems to rule out an environmental cause of the bimodality.

Thirdly, it may be a real genetic phenomenon. The possibility of Mendelian control of flight behaviour has been discussed and discarded. However it is possible that a gene is present in each strain which has a large effect in relation to the residual variation (a major gene). A parental population may be imagined which would have a small proportion of individuals with such genes which determined long flight. If selection was then imposed for flight these individuals might make up a large proportion of the parental sample. The offspring would then be composed of individuals with and without the major gene in numbers of the same order, and might then show a discontinuous distribution. Further selection for flight would increase the proportion of individuals in the population with the gene producing an apparently unimodal distribution. This distribution would be expected to have a mode at the level of that of the upper modal category of the bimodal distribution, or above. This

is not the case in the results of this study. The large samples in the F2 generations of the L and N strains show that the mode lies at a value between the modes found in the F1 generation.

Lastly, a bimodal distribution might be expected from a "threshold character" (Falconer, 1981; see also introduction to this chapter). Variance shown within each phenotypic class would be environmentally produced so that an implication of this explanation is that selection within each morph should have no effect. This can be seen not to be the case here, for example in the L strain (Figs 4.16, 4.18).

Thus, although not entirely satisfactory the explanation which best fits the observed data is that of a polygenic system where one gene has a large effect compared with the residual variation. Further work is needed to confirm or reject this explanation.

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CHAPTER FIVE
Flight and fecundity

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1. INTRODUCTION

"The primary functions of the adult stage of insects are reproduction and, in many species, dispersal" (Slansky and Scriber, 1985). Both of these functions, dispersal (and/or migration) and reproduction are heavily dependent on stored metabolic reserves. In females the extent of egg production commonly depends on the success of the larva in attaining its ideal body weight before pupation, especially in those species in which the adult either does not feed or consumes only nectar (Slansky and Scriber, 1985). The role of adult food in nectar feeders may be simply the supply of water necessary for sustaining adult life and/or enabling egg development. It may also provide an energy source for metabolism (both these factors perhaps influencing fecundity indirectly by their effect on longevity). Finally it may form a supply of energy and amino acids for egg production.

The potential reproductive effort of an adult insect at emergence is the sum of the fraction of total body nutrients at emergence together with the fraction of adult intake devoted to reproduction (Boggs, 1981). The division of reserves between reproduction, locomotion and other processes e.g. body maintenance, are fundamental considerations directly influencing fitness. As Roff (1977) says : "If egg production and flight share the same energy reserves flight will diminish the number of eggs an insect can produce".

Active flight is an economical mode of transport for insects in terms of energy expended per unit distance travelled, but is expensive per unit time (Kammer and Heinrich, 1978). These

authors have estimated the efficiency with which energy input to the flight muscles is converted to useful aerodynamic work at only 6%. It is not therefore surprising that the metabolic rates of actively flying insects are the highest known (Weis-Fogh, 1961).

The main substrates for energy metabolism in insects are protein, carbohydrate and lipid. Protein has been found to be a major substrate in only a few species (Bursell and Slack, 1976 and refs; Weeda et al., 1980 and refs) whereas both carbohydrates and lipids have been shown to be important in many. Before the investigation of some dipteran muscles revealed a proline metabolism Beenackers (1969) categorised insect flight muscle into three types on the basis of their metabolism. Those muscles that oxidised only carbohydrate, those that oxidised only fatty acids, and those capable of both.

Intensive study of flight muscle in Locusta migratoria (Jutsum and Goldsworthy, 1976) has shown that carbohydrate is the predominant energy source for the first 20-30 mins of flight. Lipid is rapidly mobilised from the fat body, under the control of adipokinetic hormone, AKH, released from the corpora cardiaca. The rate of lipid utilisation rises from zero in the first few mins to $35\mu\text{g min}^{-1}$ after 15 to 30 mins reaching $85\mu\text{g min}^{-1}$ during the second 30 mins of flight. Flight speed reflects the fuel used; it is high when carbohydrate is being metabolised slowing to a cruising speed after c.20mins. That this difference is due to the fuel utilised has been shown by injection of AKH to mobilise lipid before take-off (Goldsworthy et al., 1979).

Locust flight metabolism has been reviewed by Beenackers et al. (1981).

A similar transition from carbohydrate to lipid flight fuels has been shown in Aphis fabae (Cockbain, 1961). However, in the Brown Planthopper, Nilaparvata lugens, carbohydrate metabolism may continue for some hours with, in addition, lipid utilisation beginning almost as soon as flight is initiated (Padgham, 1983). Other insects have been shown to be capable of utilising fat-body reserves and metabolising an external carbohydrate source for flight, either directly (Spodoptera frugiperda, Van Handel and Nayar, 1972) or after conversion to lipid (Danaus plexippus, Brown and Chippendale, 1974). Kammer and Heinrich (1978) suggested that in general adult Lepidoptera which feed may have a higher glycolytic capacity than those which do not and so be able to utilise both carbohydrate and lipid.

Lipid is particularly suitable as an energy reserve for sustained flight. When metabolised, lipid can produce the same energy from half the mass, and less volume, than carbohydrate (Chapman, 1982; Beenackers, 1969). Beenackers (1969) also points out that greater quantities of metabolic water are produced from lipid compared with carbohydrate, which is of possible benefit in forestalling desiccation in some insects. Examples of insects which metabolise lipid for flight include the Australian plague locust, Chortoicetes terminifera (Hunter et al., 1981), the corn leaf aphid, Rhopalosiphum maidis (Liquido and Irwin, 1986), the brown planthopper, Nilaparvata lugens (Chen, 1983; Padgham, 1983) and the cowpea weevil Callosobruchus maculatus (Nwanze et al., 1976) as well as many Lepidoptera (Domroese and Gilbert, 1964;

Van Handel, 1974; Kammer and Heinrich, 1978; Ziegler and Schulz, 1986).

During the larval stage, S. exempta has been shown to accumulate large quantities of lipid which are held in the abdominal fat body of the adult (Gunn and Gatehouse, 1986). Water is necessary for female S. exempta to hydrate and mature their eggs (Gunn and Gatehouse, 1985). These authors have also shown that when a source of carbohydrate (10% w/v sucrose) is available to the adult females, their fecundity may be increased, especially in moths derived from small, poorly-fed larvae. The sucrose is used to synthesise lipid and to supplement protein reserves (Gunn and Gatehouse, 1986). A further effect of feeding sucrose rather than water is to increase the moths longevity, although the oviposition period is not extended (Gunn and Gatehouse, 1985).

Gunn and Gatehouse (1986) present a notional reserves budget suggesting that the amount of lipid used in egg production is far less than that available in a female moth at eclosion even accounting for structural lipids, the excess, they suggest, being available for flight. Any trade-off between the reserves used for flight and egg production, in the absence of a source of carbohydrate available to the adult, is fundamental to understanding the life-history strategy of this migratory species. Effects of depletion of reserves by flight may also be observed in other life history traits e.g. longevity (Boggs, 1981; Haynes, 1985).

The ability of adult S. exempta to utilise a source of

carbohydrate to restore depleted lipid reserves after prolonged flight is a vital consideration, not only from the viewpoint of the reproductive success of the moths after migratory flight, but also from the viewpoint of the build-up of population numbers and hence the formation of pest outbreaks.

This chapter describes a laboratory investigation of the effect of tethered flight on the fecundity of S. exempta females subsequently fed water or provided with a source of carbohydrate.

2. MATERIALS AND METHOD

2.1 Insect material

This investigation was performed in two halves, experiments A and B. Experiment A examined the effect of flight on the fecundity of moths which were subsequently fed with distilled water. The insects used were derived from samples collected in Samburu and Margarini, Kenya and brought back to Britain as pupae. This population was in its eighth generation of laboratory culture at the beginning of this experiment.

Experiment B investigated the effect of flight on the fecundity of moths subsequently fed 10% sucrose. This experiment used insects similarly derived from a sample collected at Lukenya, Kenya and brought back to Britain as pupae. This population was in its seventh generation of laboratory culture at the beginning of this experiment.

2.2 Flight-testing

In all cases the flight testing procedure was as described previously in Ch. 2. Female moths were flown either for N0 to N1 inclusive or N0 to N2 inclusive. Flight testing continued throughout the intervening days, although day-time flight activity is very low. Moths which eclosed before c.1630h on day zero were attached to the flight balances between c.1730 and 1800h. The majority of moths eclosed by 2200h. Therefore, if needed, more moths were weighed and attached to the balances between 2230 and 2330h. These moths were manipulated by the light of a pencil-beam head-torch so as to minimise disturbance to them and to the moths already on the balances.

Flight testing was suspended from c.0930h every morning for the moths to be reweighed and the appropriate counterweight recalculated at 65% of body weight. Flight-testing was resumed as soon as this was done. The counterweight is smaller than that used when moths were attached to the apparatus in the afternoon to account for the additional loss of weight which occurred during the day. Fully flight tested moths were immediately set up with a male and food as described below.

2.3 Experimental procedure

Larvae were reared on leaves of four to six week-old maize plants which were renewed daily and provided in excess of the quantity eaten in 24 hours. The larval and pupal stages were kept at $30 \pm 2^{\circ}\text{C}$, $63 \pm 7\%$ R.H. and a photoperiod of 12L:12D. Larvae were reared in the gregaria phase at a density of 60-80 per 500ml jar until the fourth instar when the density was reduced to 20 per jar until pupation.

All pupae were weighed between one and five hours prior to eclosion when the cuticle had turned dark brown and become thin (Gatehouse and Hackett, 1980). These weights are described below as pharate adult weights since the pupal cuticle before eclosion represents less than 1.5% of the total pupal weight. This measure of weight was chosen to exclude variation between moths due to their meconium being voided at different times after eclosion (Gunn and Gatehouse, 1985).

The female moths in experiment A were divided into two groups. One group was flight tested N0-N1, the other group N0-

N2. All females in experiment B were flight tested N0-N2. Flight testing was carried out under conditions of $24 \pm 4^{\circ}\text{C}$ and $64 \pm 14\%$ R.H. Daylight fluorescent tubes provided the main lighting with tungsten bulbs controlled by a dimmer circuit providing an artificial dawn and dusk and resulting in a photoperiod of approximately 13L:11D. The tungsten lights contributed to the heating of the room so that the temperature dropped gradually through the night, with a consequent increase in humidity, reaching a minimum at dawn.

On the morning after flight testing, or the morning after emergence in the case of unflown controls, the female moths were placed in a 500ml jar with a male. They were provided with a small plastic pot containing cotton wool saturated with either distilled water or a 10% w/v (Bolton et al, 1979) sucrose solution. In the case of flown moths, the mount was removed with no detrimental effect on the moths. Experience had previously shown mounts occasionally stuck in the cotton wool, leaving the moth trapped upsidedown on the pot. A crumpled piece of filter paper provided a convenient resting and oviposition substrate, but eggs were also laid on the filter paper-lined floor, lid and, less often, on the glass walls of the jar.

If possible males were at least 36 hours old so that they were likely to be sexually mature and ready to mate. Dead males were replaced and, in addition, females which did not lay eggs by the second day after the first male was introduced had a second male added to their jar in case the first male was defective in some way and unable to mate.

The food pot was replaced every day. Any eggs were removed

and either counted immediately or frozen at -20°C and counted later. Dead females were dissected to determine the number of spermatophores present and, if possible, the cause of death.

Ideally experiments A and B would have been performed at the same time on the same generation of moths. This was impossible because the limited supply of maize prevented enough moths being reared at the same time. Also only 16 flight balances were available to fly moths. With each moth being flown for at least two nights, not enough could have been flown for the whole investigation. Also a few moths were lost from the experiments - becoming stuck in copulo or being unable to lay eggs because of meconium blocking the genital orifice.

3. RESULTS

A total of 164 female moths were flown, divided between treatments as shown in Table 5.1.

Both experiments A and B had, as one control, an unflown sample of moths which were subsequently fed on distilled water. When the fecundity of each of these controls was plotted against pharate adult weight significant regressions were obtained (A: $b=13.0$, $F=31.8$, $P<0.001$; B: $b=9.2$, $F=63.3$, $P<0.001$). A significant regression was also found for sucrose-fed moths ($b=7.79$, $F=33.7$, $P<0.001$). It was therefore possible to use weight-related fecundity (fecundity per 100mg pharate adult weight) for further analysis. Weight-related fecundities, longevities and spermatophore counts were compared between treatments using the Mann-Whitney U Test (Zar, 1984). A comparison of these data between the water-fed unflown controls shows no significant differences between experiments A and B (Fec : $P=0.18$, Long : $P=0.34$, Sperm : $P=0.38$). Comparisons may therefore be drawn between the other treatments in the two experimental groups with a degree of confidence. The results from experiments A and B are therefore discussed together.

Flight activity is presented in hours. Analysis of the effect of flight activity on other life history characters has been performed for total flight activity (sum of all flights) and the sum of long (>30 min.) flights by individual moths.

3.1 Longevity

Combining the unflown water-fed control groups from experiments A and B ($n=45$) it was found, from a regression of

Table 5.1.

The number of moths (n) in treatments of experiments A and B. Weight related fecundity (no. eggs per 100mg pharate adult weight), longevity (days) and number of spermatophores are given as mean±SE for each treatment. A superscript indicates that the distribution of the data is significantly different from normal the difference from normality (P), median, minimum and maximum values of the data being given below the table.

Expt	Period Flown	Food	n	Weight Related Fecundity	Longevity /days	Number of Spermatophores
A	N0-N1	D/W	34	388.2±33.1	6.1±0.2	1.5±0.2
	N0-N2	D/W	15	279.5±61.1	6.3±0.3	1.3±0.2
	N/F	D/W	20	674.0±35.1	6.5±0.3 ^b	1.9±0.3
B	N/F	D/W	25	599.1±30.4	6.7±0.2	1.4±0.1
	N/F	Suc	27	735.7±35.6	8.3±0.4 ^c	2.0±0.2
	N0-N2	Suc	43	651.9±17.9 ^a	9.8±0.2	1.8±0.2 ^d
		P	Median	Minimum	Maximum	
a -	<0.01		677.6	355.8	830.7	
b -	<0.05		6.0	5.0	10.0	
c -	<0.01		8.0	5.0	16.0	
d -	<0.01		2.0	1.0	5.0	

longevity on pharate adult weight, that larger moths lived longer ($b=0.024$, $F=15.1$, $P<0.001$). When unflown sucrose-fed moths from experiment B were examined no such relationship was found between longevity and pharate adult weight ($b=0.0141$, $F=1.27$, $P>0.50$).

Within experiment A flight-tested moths were compared with the unflown control to see if flight-testing had an effect on longevity, irrespective of the moths' flight performance. In moths flown for two nights and for three nights there was no significant difference between the flight-tested groups and the control (N0-N1 : $P=0.28$; N0-N2 : $P=0.92$).

The longevity of moths flight-tested N0-N1 and fed water did not depend on either total flight activity ($b=-0.106$, $F=3.36$, $P>0.10$) or on the sum of long flights (flights > 30 mins.) ($b=-0.126$, $F=3.72$, $P>0.10$). In moths flight tested N0-N2 however, longevity did depend on total activity ($b=-0.192$, $F=23.3$, $P<0.001$). There was also a significant regression on the sum of long flights ($b=-0.227$, $F=18.2$, $P<0.002$).

Within experiment B, water- and sucrose-fed unflown controls had significantly different longevities ($P=0.0013$), with sucrose-fed moths living longer (Table 5.1). Also within sucrose-fed moths in experiment B, the control and flight-tested individuals had significantly different longevities ($P<0.0001$), with flown moths living longer (Medians : unflown=8, flown=10 days).

The longevity of moths flight-tested N0-N2 and fed sucrose (experiment B) did not depend on total flight activity ($b=0.0604$, $F=0.82$, $P>0.50$) or on the sum of long flights ($b=0.120$, $F=1.55$, $P>0.20$).

3.2 Characteristics of flight

The largest sample of moths flight-tested N0-N2, those subsequently fed sucrose (experiment B, n=43), was used to examine the characteristics of flight over this period for unfed moths.

3.2.1 Flight activity

The flight activity which occurred during N0, D1-N1 and D2-N2 is presented (Fig. 5.1a,b and c) as a percentage of the total activity possible during consecutive 15 min. periods of each day i.e. number of moths (43) x number of seconds in each 15 min. period.

Little activity is apparent during D1 and D2. Both dusk and dawn peaks of activity are clear for N0, N1 and N2 (less than 43 moths are represented for the dusk peak of N0 because not all had emerged, but data from those that had are plotted on the same scale). One other peak is apparent on N0 at approximately 0200h. There are a number of other peaks on N1 at c.2030, 2230, 2400, 0145 and 0345hrs. It appears that these peaks of activity occurred at approximately 2h intervals through the night. Activity was generally higher on N1 than during N0 and higher during the second half of N1 than the first.

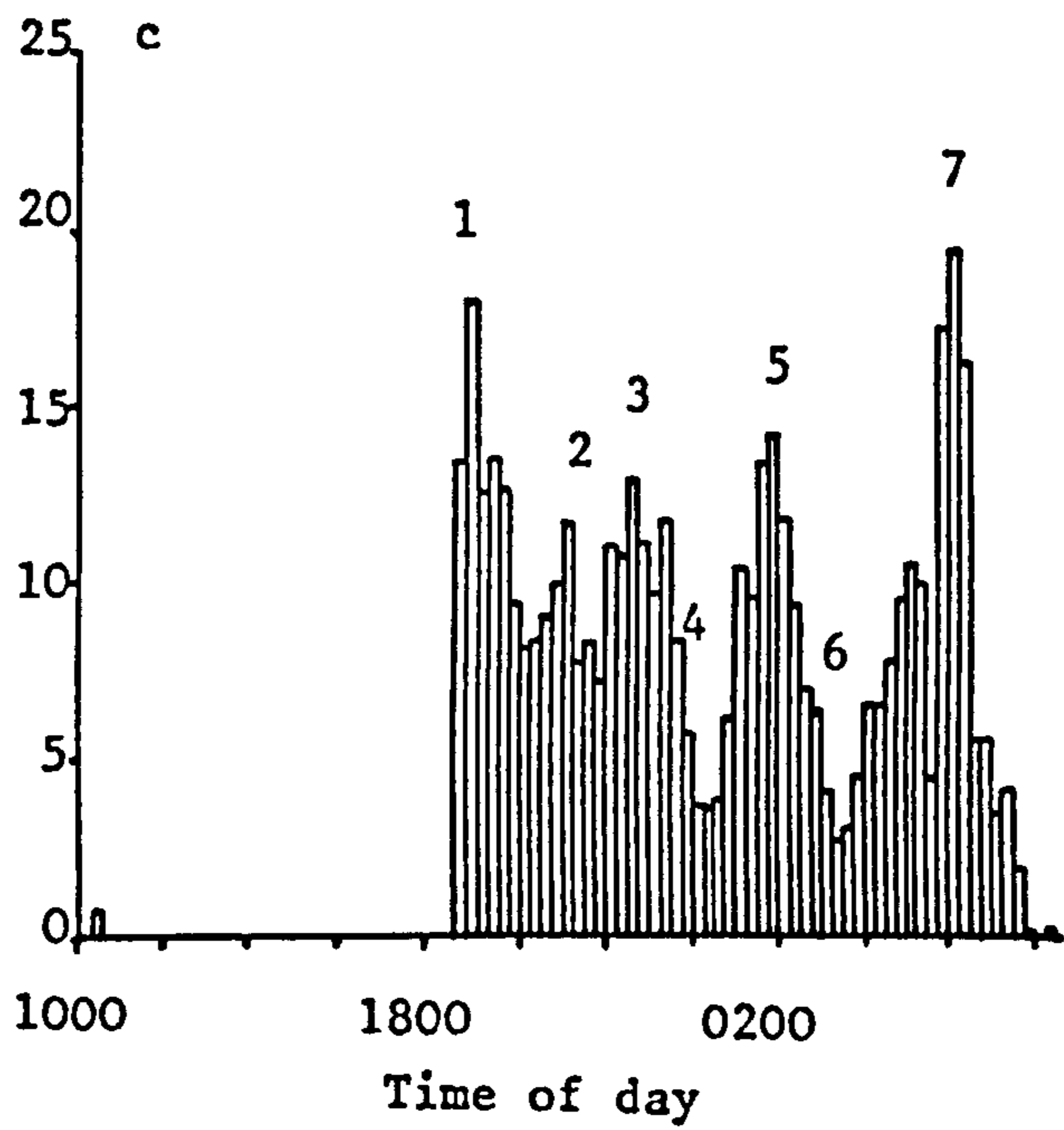
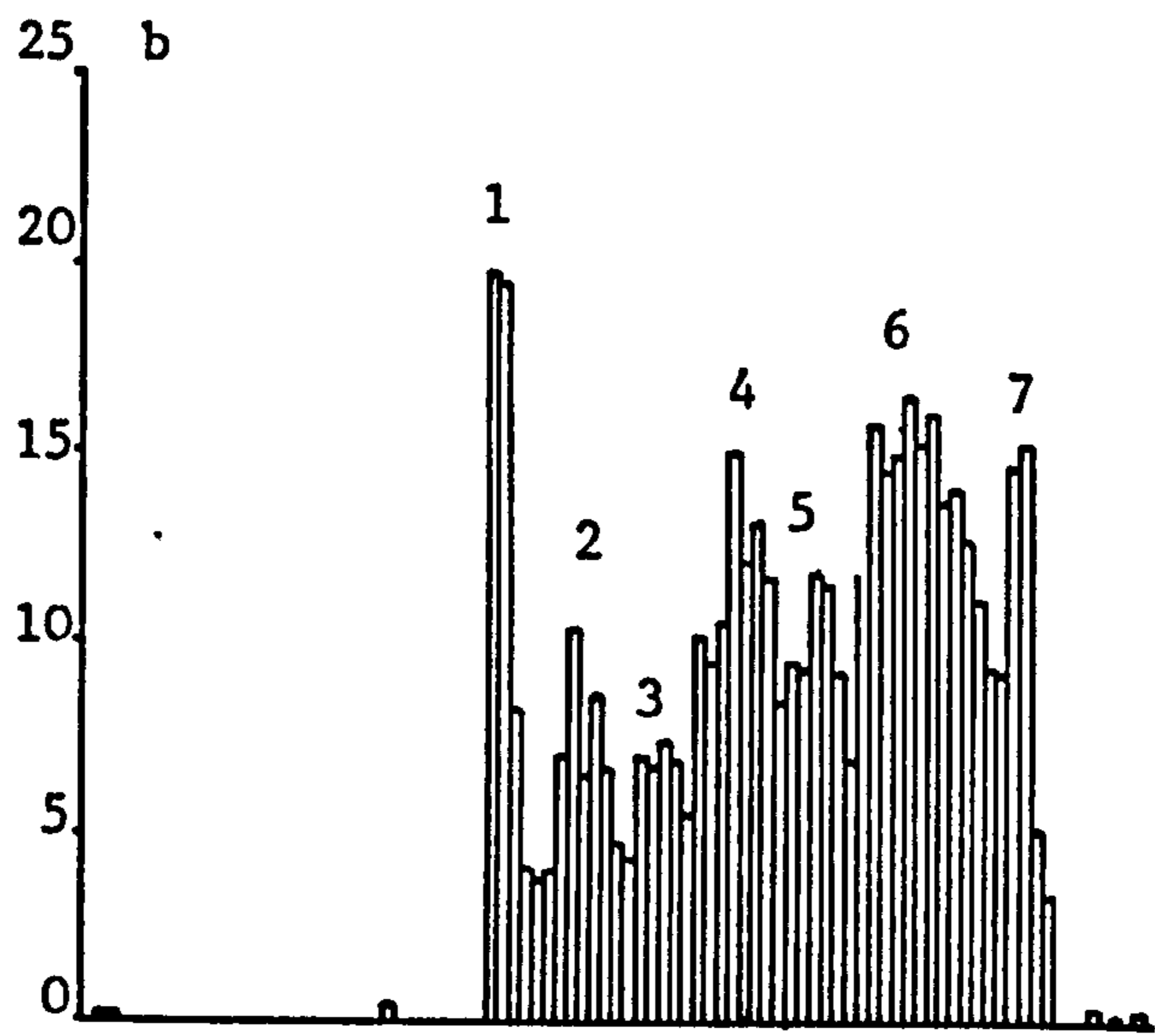
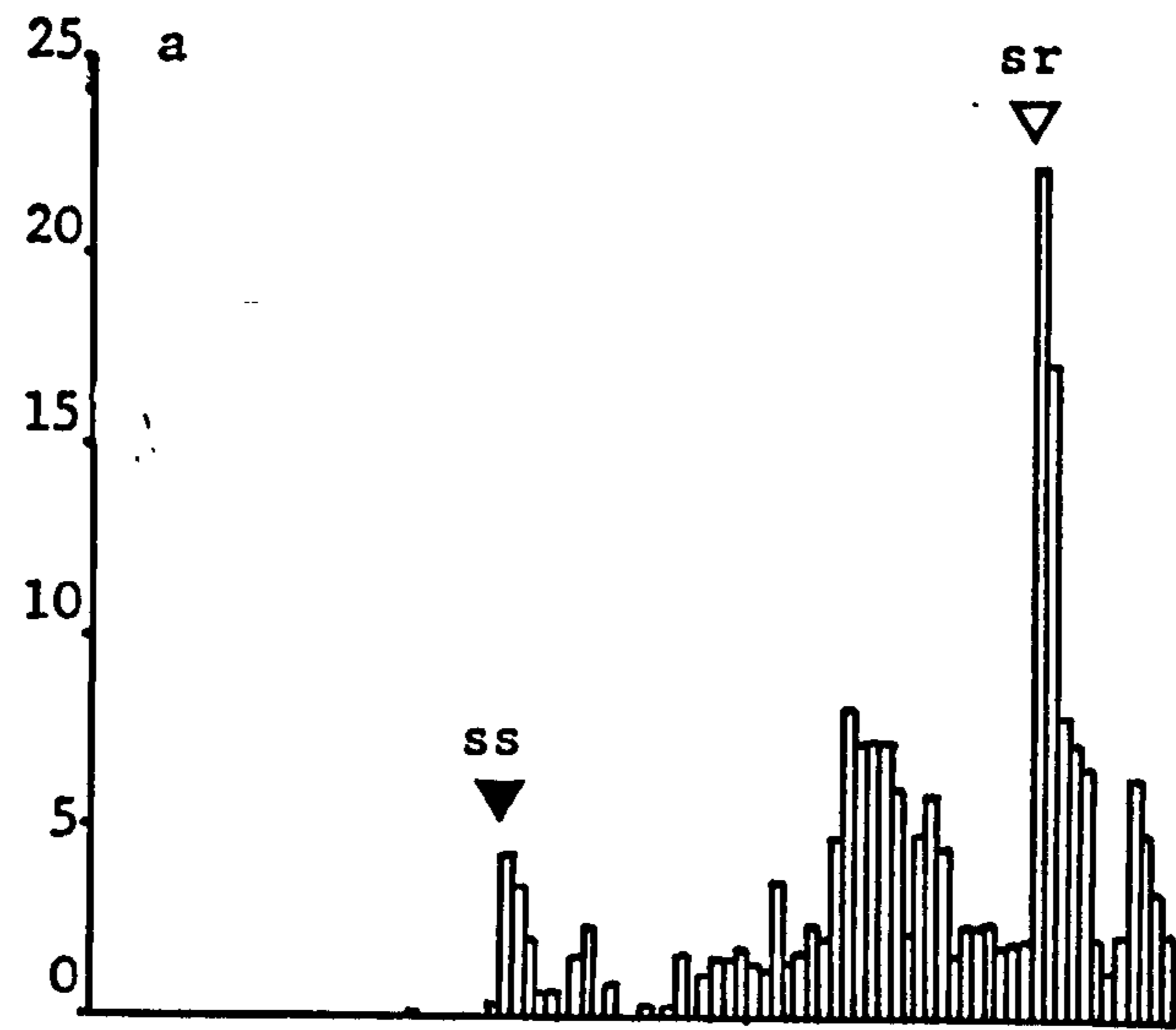
During N2, similar peaks are apparent to those present on N1 at 2115, 2245 and 0200hrs with a possible peak at 0515hrs. It is very noticeable that the two highest peaks of N1 (excluding the dusk and dawn peaks) at 2400 and 0345hrs are absent on N2.

It is also possible to examine the percentage of the total possible activity occurring which is due to moths flying on long

Fig. 5.1

Frequency histogram of the flight activity which occurred, as a percentage of the total activity possible, during consecutive 15 min. periods of each day i.e. number of moths x number of seconds in each 15 min. period. The moths used were those (n=43) flight-tested N0-N2 and subsequently fed sucrose. Fig. 5.1a presents flight activity which occurred during N0, Fig. 5.1b that which occurred during D1-N1 and Fig. 5.1c, D2-N2.

Percentage of total possible activity



(>30 min.) flights. The pattern of such "sustained" flight activity can be seen in Fig. 5.2a,b and c for N0, D1-N1 and D2-N2 respectively. By comparison between Figs 5.1 and 5.2, the flight activity pattern due to short (<30 min.) flights may also be inferred.

The small amount of sustained flight which occurred on N0 took place late in the night from 0145 to 0415 and 0600 to 0900hrs. On N1 sustained flight began at dusk. There was then a small peak of activity from 2215 to 0015hrs and a larger one from 0215 to 0515hrs. Much of the overall activity observed at this latter time of night was due to this sustained flight. In contrast on N2, the highest levels of sustained flight occurred before 0015hrs with a drop to zero for 30 mins. followed by lower levels of activity.

It should be emphasised that few moths produced long (>30 mins) flights on any of the three nights. The number of moths contributing to the tallest peak on each night were two, six and four for N0, N1 and N2 respectively. The data for sustained flight is therefore based on few moths and would probably present a clearer picture if this section of the investigation were repeated with a larger sample.

3.2.2 Time of take-off

Figs 5.3a,b and c show the number of flights beginning during 15 min. intervals from 1000 to 0900hrs on N0, D1-N1 and D2-N2 respectively.

On all three nights the dusk and dawn peaks of take-off are very obvious. The dawn peak is larger than the dusk peak for N1

Fig. 5.2

Frequency histogram of the prolonged flight activity (composed of flights of at least 30 mins duration) which occurred, as a percentage of the total activity possible, during consecutive 15 min. periods of each day i.e. number of moths x number of seconds in each 15 min. period. The moths used were those (n=43) flight-tested N0-N2 and subsequently fed sucrose. Fig. 5.2a presents flight activity which occurred during N0, Fig. 5.2b that which occurred during D1-N1 and Fig. 5.2c, D2-N2.

Percentage of total possible activity

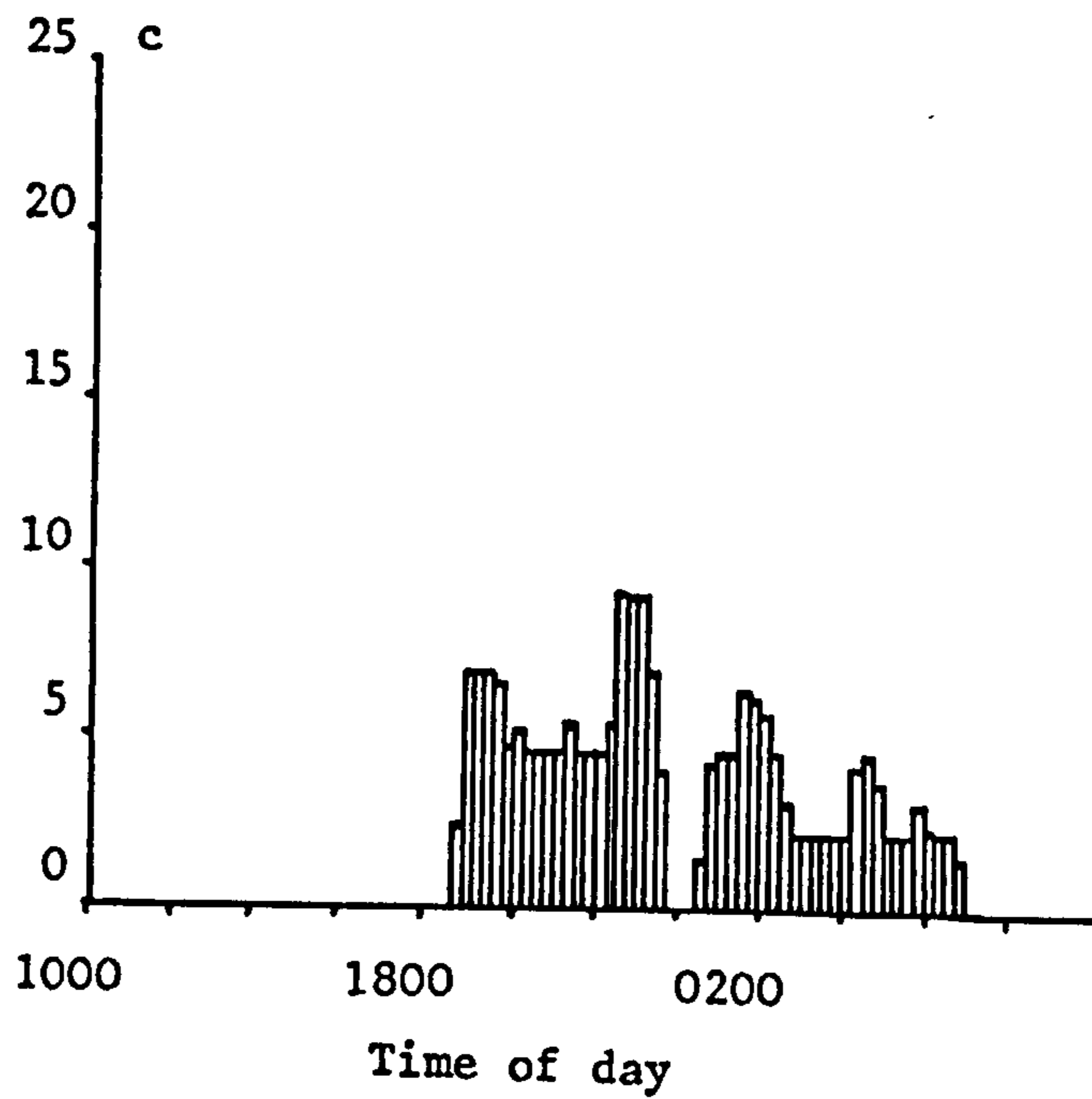
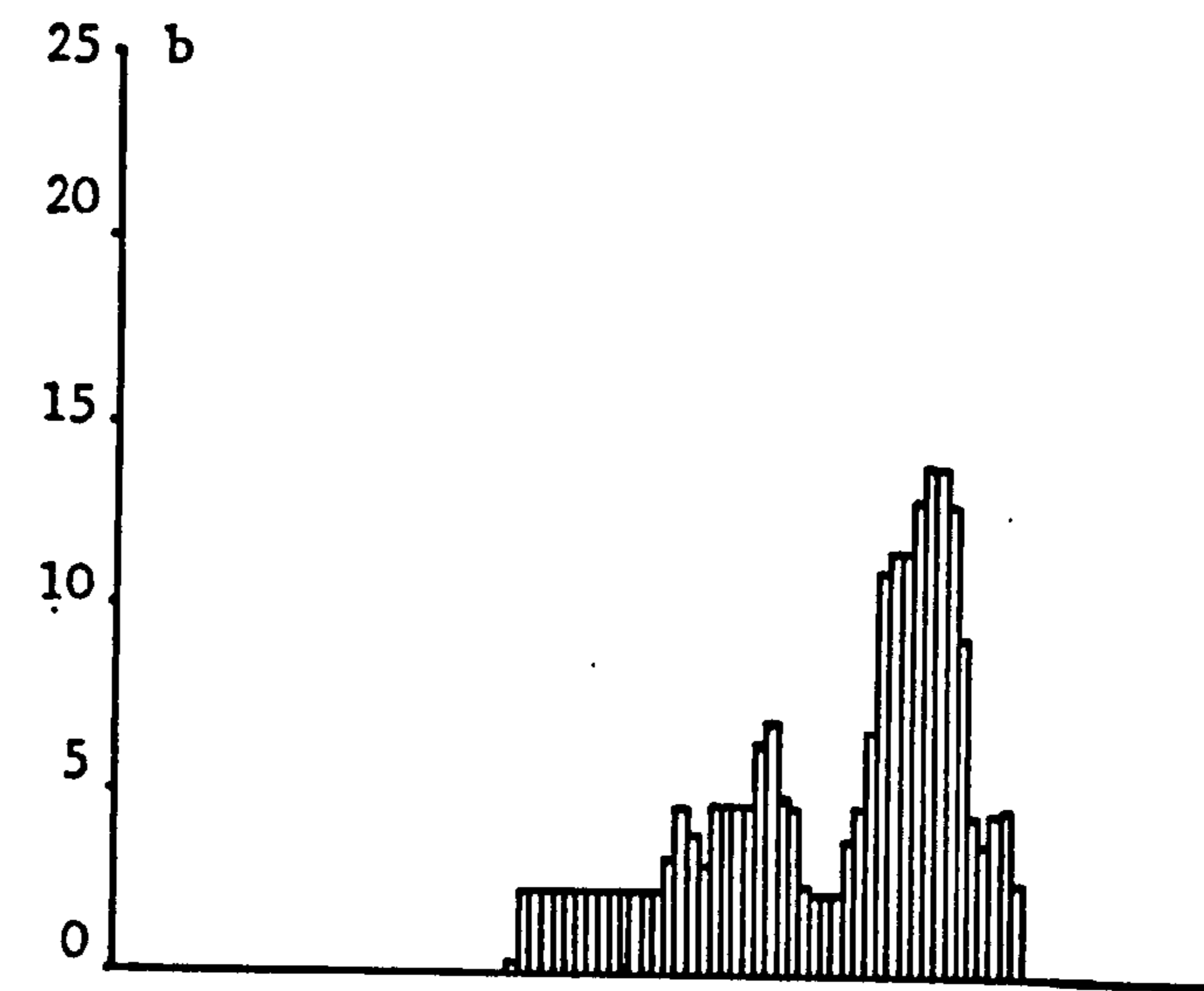
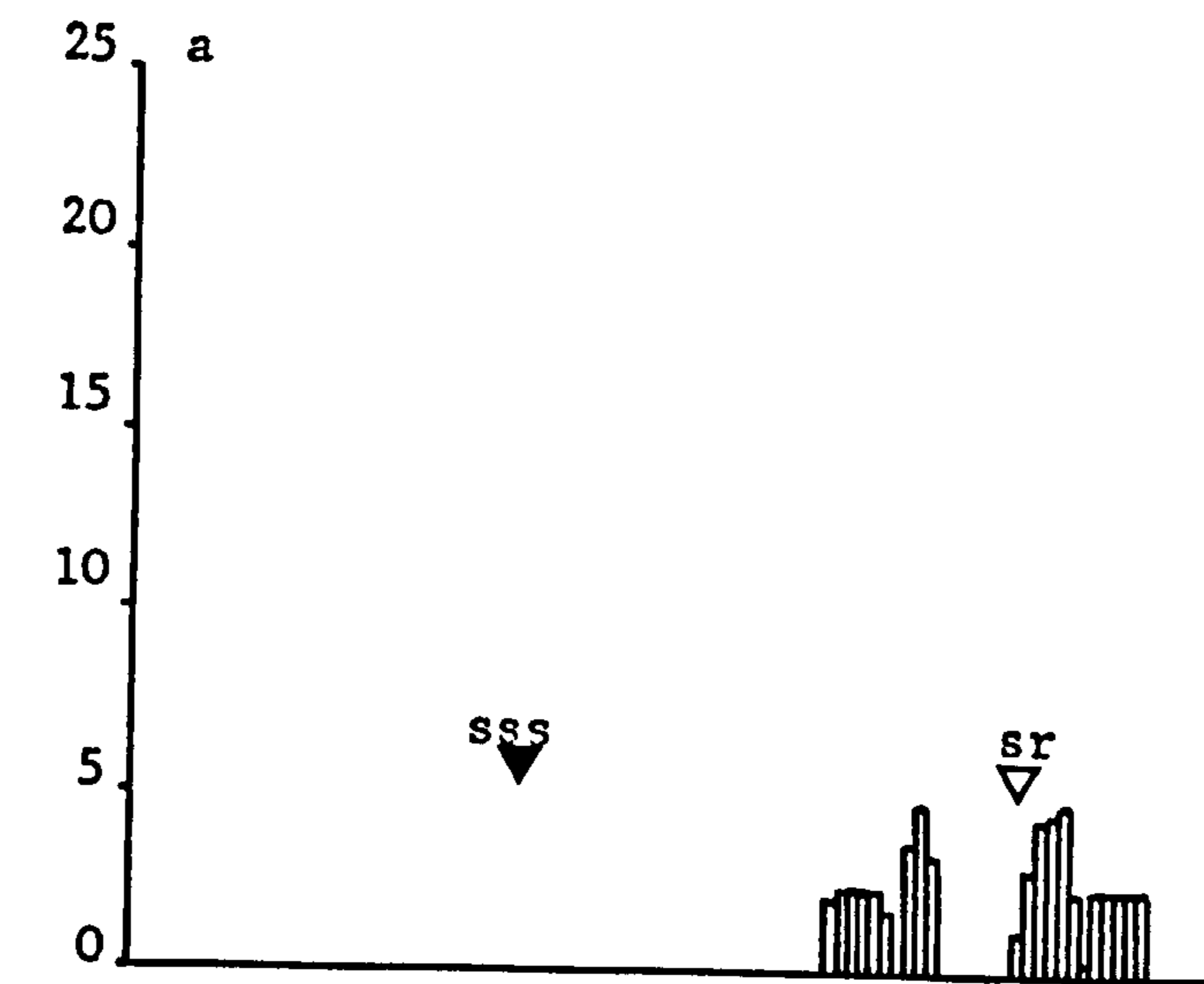
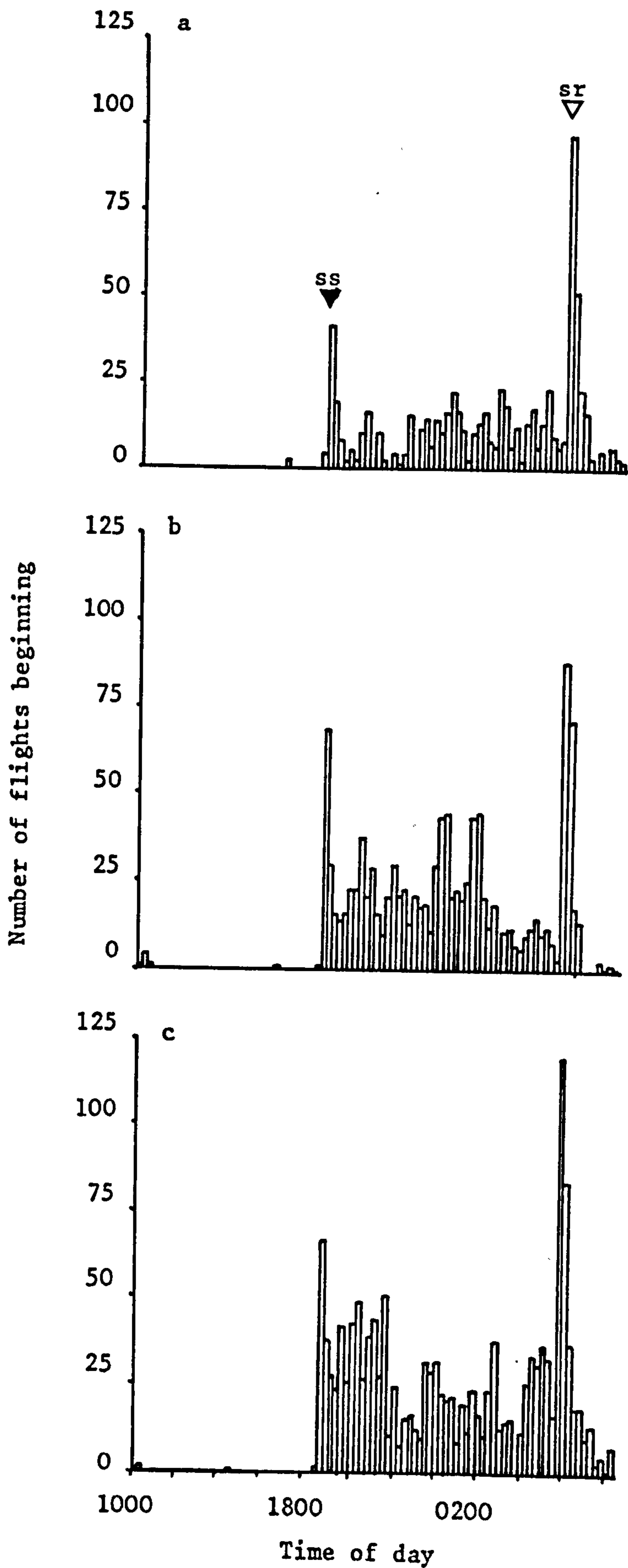


Fig. 5.3

Frequency histogram of the number of flights beginning during consecutive 15 min. periods of each day from 1000 to 0900h. The moths used were those (n=43) flight-tested N0-N2 and subsequently fed sucrose. Fig. 5.3a presents the number of flights beginning during N0, Fig. 5.3b those which began during D1-N1 and Fig. 5.3c, D2-N2.



and N2 (different numbers of moths are present for dusk and dawn on N0 because of the pattern of emergence - see above). The dawn peak on N2 may be larger than that on N1. Other peaks of take-off are visible on N1 at 2030, 2200, 0015, 0200 and possibly 0445hrs. Similar peaks are visible on N2 at 2030, 2145, 2345-0030, 0300 and 0515hrs. Compared with N1 more flights appeared to begin post-dusk (<2200hrs) and pre-dawn (>0430hrs) on N2, with less flights beginning in the middle part of the night.

The distribution of times of take-off on long flights for N0, D1-N1 and D2-N2 are shown in Fig. 5.4a,b and c. Few long flights were produced by the 43 moths (N0 - 7, N1 - 16, N2 - 15). Some long flights occurred on all three nights, similar numbers on N1 and N2 but fewer on N0. There was no significant difference (Fisher's Exact Test, $P=0.083$) between the number of long flights beginning in the latter part of N1 (13/16 flights begin after midnight) compared with N2 (8/15 flights begin after midnight).

3.3 Mating frequency

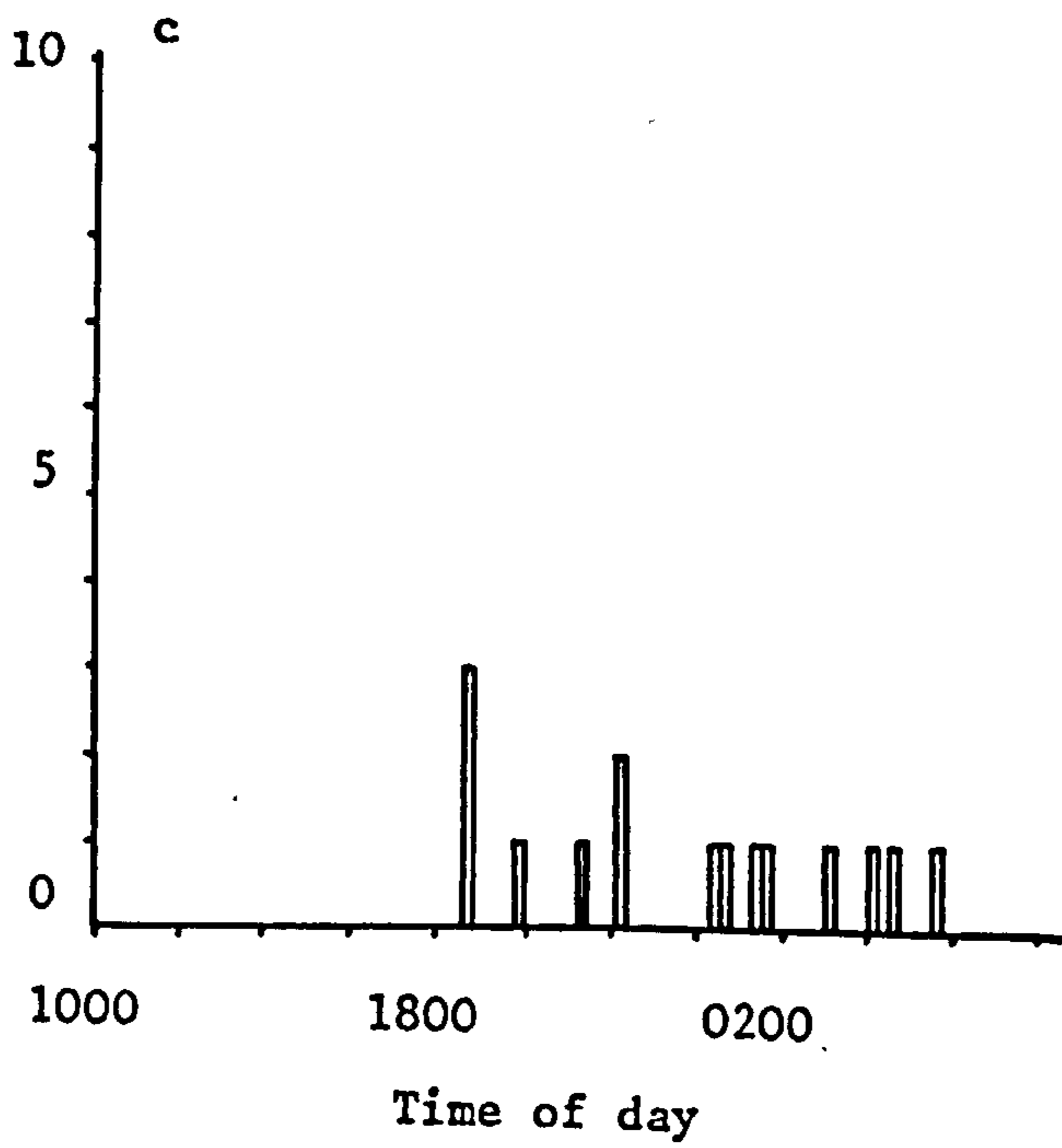
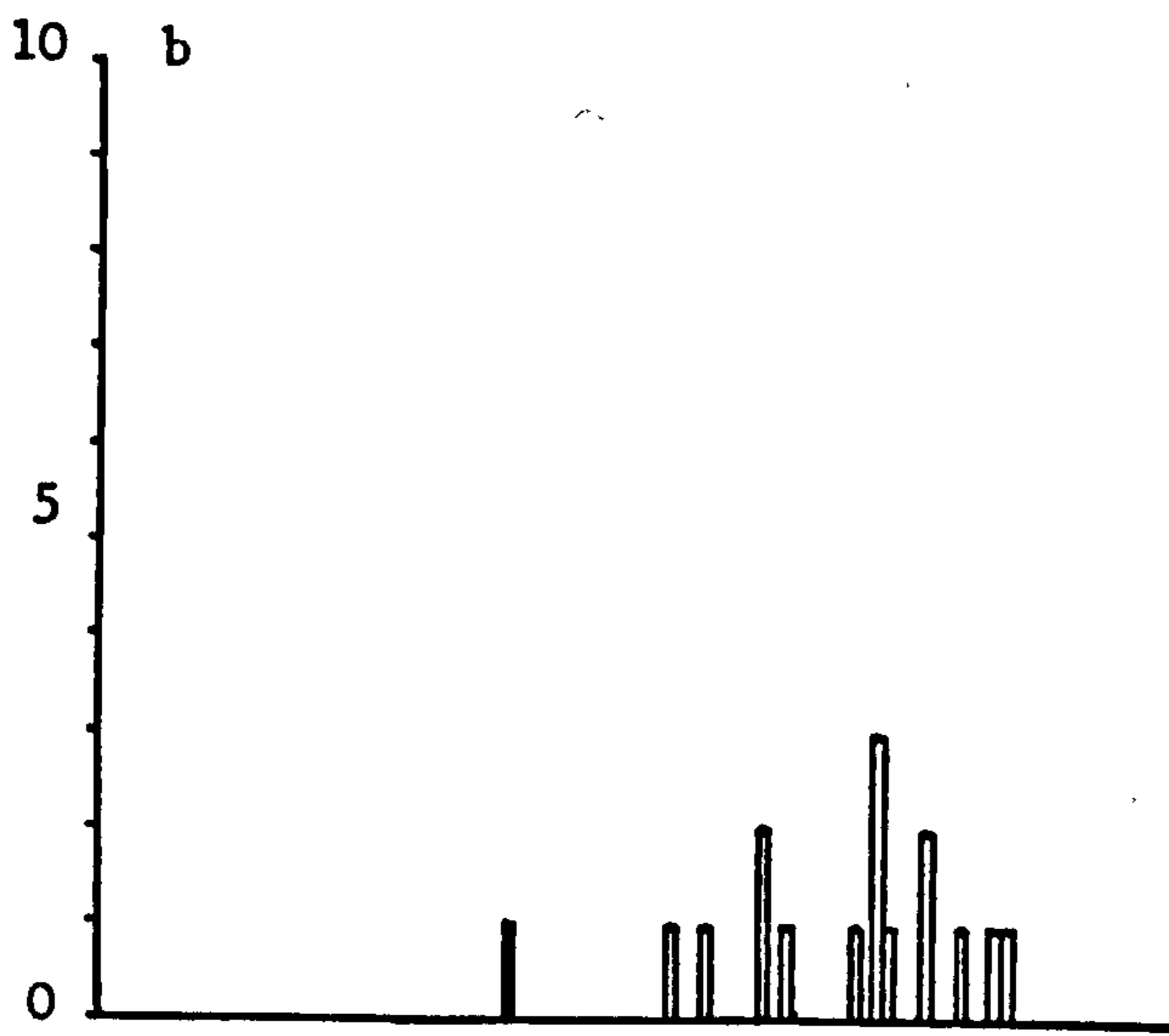
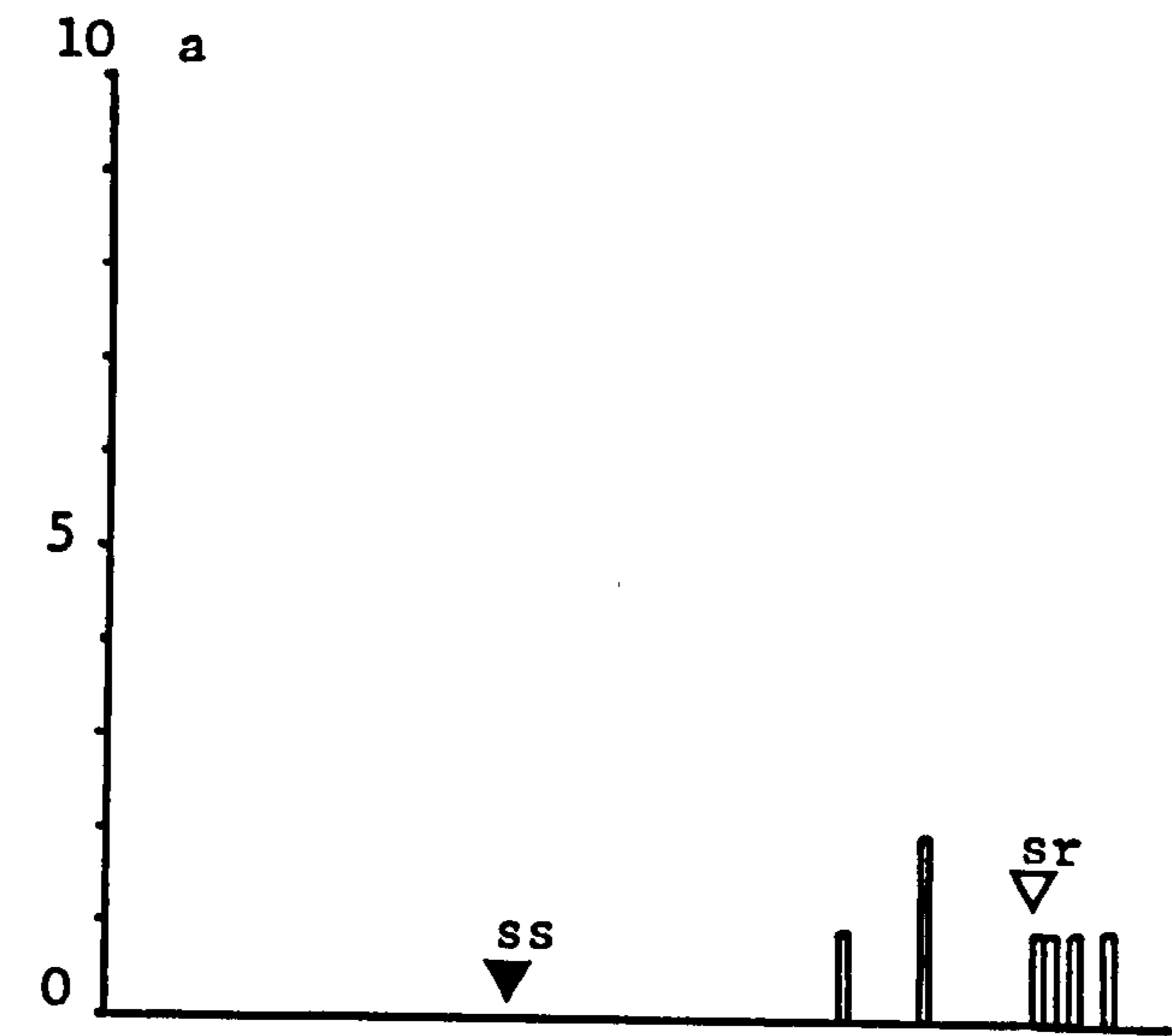
The number of times a female had mated during her life was determined by counting the number of spermatophores present in the bursa copulatrix of the dissected abdomen (Table 5.1).

Mating frequency was compared within experiment A, in females flight-tested for N0-N2 irrespective of flight activity, and in unflown control moths ($P=0.26$). A significant difference was observed when unflown moths fed sucrose or water were compared (Expt. B, $P=0.04$, Medians : sucrose=2, water=1). There

Fig. 5.4

Frequency histogram of the number of prolonged (greater than 30 mins duration) flights beginning during consecutive 15 min. periods of each day from 1000 to 0900h. The moths used were those (n=43) flight-tested N0-N2 and subsequently fed sucrose. Fig. 5.4a presents the number of flights beginning during N0, Fig. 5.4b those which began during D1-N1 and Fig. 5.4c, D2-N2.

Number of long flights beginning



was also a significant difference between flown and unflown moths fed sucrose in this experiment ($P=0.03$, Medians : flown=1, unflown=2).

There was no relationship, in unflown water-fed moths, between the number of spermatophores and pharate adult weight ($b=0.0017$, $F=0.08$, $P>0.50$, $n=45$) or the number of spermatophores and longevity ($b=0.162$, $F=1.58$, $P>0.20$, $n=45$). There was also no relationship between weight-related fecundity and the number of spermatophores ($b=15.3$, $F=0.39$, $P>0.50$, $n=45$). The highest and lowest weight-related fecundities were achieved with only one mating.

3.4 Pre-oviposition period

The relationship between pre-oviposition period, the interval between eclosion and the beginning of egg-laying, and flight activity was examined. Correlation analyses were performed for the three flight-tested treatments. In all cases there was no indication of a significant relationship between pre-oviposition period and either total flight activity or the sum of long flights (Table 5.2).

There was also no evidence of a relationship between pre-oviposition period and longevity in the combined water fed unflown controls ($r=0.22$, $P>0.10$) but a relationship was apparent for the sucrose-fed unflown control ($r=0.487$, $P=0.01$). The significance of this last relationship is due to one moth which had a pre-oviposition period of six days and lived for 16 days. Removing this moth reduces the correlation coefficient to 0.223 and the significance of the correlation to $P>0.20$.

Table 5.2.

The coefficients (r) and significance levels (P) for correlations between pre-oviposition period and flight activity (Total activity or Sum of long (> 30 mins.) flights) for the three flight-tested treatments.

Treatment		Water fed		Sucrose fed	
		N0-N1	N0-N2	N0-N2	
Total Activity	r	0.28	0.27	0.13	
	P	>0.05	>0.20	>0.20	
Long Flights	r	0.19	0.15	0.07	
	P	>0.20	>0.20	>0.50	

3.5 Fecundity

Initially, the effect of flight-testing on the subsequent weight-related fecundities of water-fed moths was examined irrespective of flight performance (Experiment A, Table 5.1). Moths flight-tested N0-N1 are significantly less fecund than those of the unflown control group ($P < 0.0001$, Medians : unflown=651.3, flown=380.1). Similarly, moths flight-tested N0-N2 are significantly less fecund than the control ($P = 0.0001$, Medians : unflown=651.3, flown=267.7), with a lower median (but not significantly lower, $P > 0.05$) than the group flown for only two nights.

A comparison of treatments from experiment B (Table 5.1) indicates that, in moths which have not been flight-tested, feeding sucrose enhances the weight-related fecundity compared with water-fed moths ($P = 0.0032$, Medians : sucrose fed=756.8, water fed=617.1). For sucrose-fed moths, weight-related fecundity is decreased by flight-testing for N0-N2 compared with an unflown control ($P = 0.0125$, Medians : unflown=756.8, flown=677.6).

The main purpose of this investigation was to examine the effect of flight activity on the subsequent fecundity of water-fed and sucrose-fed moths. In the expressions which have been derived for these relationships below, the following abbreviations have been used :

Fec	Fecundity (no. of eggs)
Wt	Pharate adult weight (mg)

WtRlFec	Weight related fecundity (no. of eggs per 100mg pharate adult weight)
TotAct	Total activity (Sum of all flights in hours)
LFlts	Sum of long (>30 mins. duration) flights (hours)

3.5.1 Moths flight-tested N0-N1 and fed water

Due to a power failure, the records of the flight activity of two of the moths flown N0-N1 were not complete. These moths have been necessarily excluded from analysis of flight activity, reducing the size of this treatment to 32.

Weight-related fecundity was plotted against total flight activity (Fig. 5.5) and a linear regression calculated ($F=18.3$, $P<0.001$). The expression for this line was :

$$\text{WtRlFec} = 558.5 - 31.5\text{TotAct}$$

A curve in the best-fit regression line was sought using stepwise polynomial regression (Zar, 1984) but no significant improvement was obtained over the simple linear regression ($F=0.98$, $P>0.50$).

Weight-related fecundity was also plotted against the sum of long flights (Fig. 5.6). Here a second order polynomial provided the line of best-fit ($F=10.2$, $P<0.01$) indicating a non-linear relationship. The expression for this line was :

$$\text{WtRlFec} = 585.2 - 95.7\text{LFlts} + 6.54\text{LFlts}^2$$

These expressions may be expanded so that fecundity is derived from pharate adult weight as well as flight activity. The full expressions are :

$$\text{Fec} = -66.1 + 6.28\text{Wt} - 44.3\text{TotAct}$$

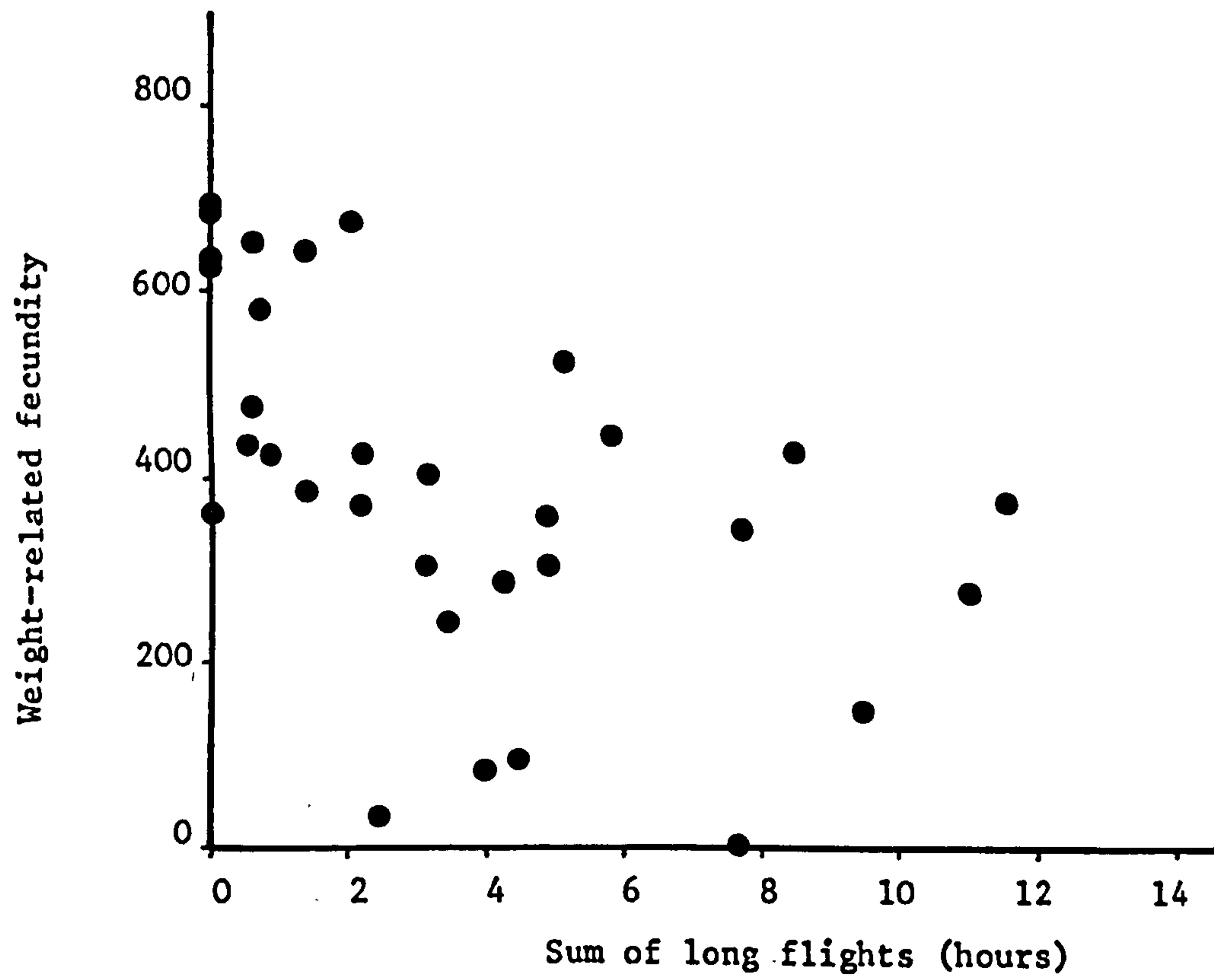
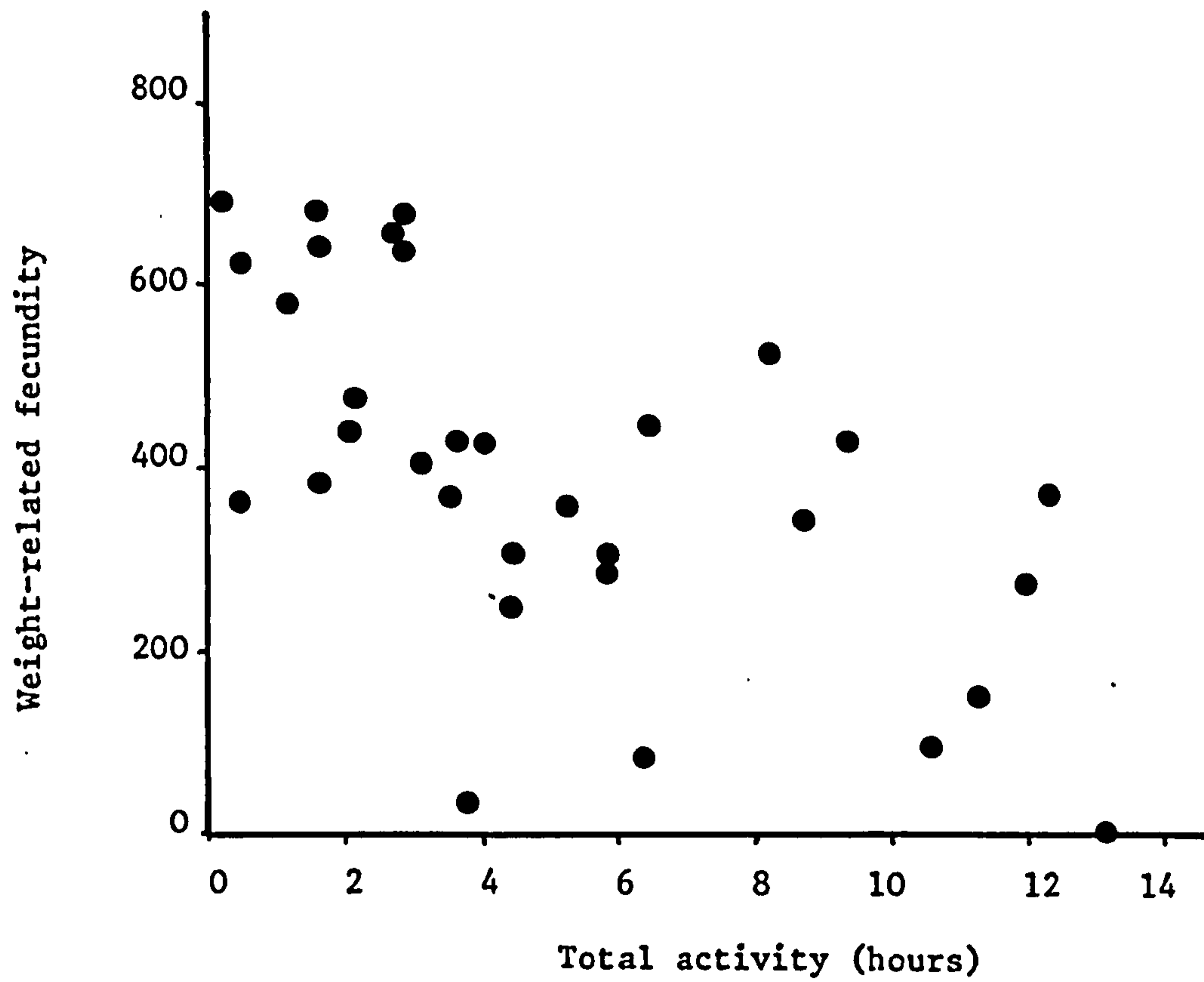
$$F=16.1, P<0.001$$

Fig. 5.5

A plot of weight-related fecundity (fecundity per 100mg pharate adult weight) against total activity (the sum of all flights produced) for moths flight-tested for N0-N1 and subsequently fed water.

Fig. 5.6

A plot of weight-related fecundity (fecundity per 100mg pharate adult weight) against the sum of long (greater than 30 mins duration) flights for moths flight-tested for N0-N1 and subsequently fed water.



and

$$\text{Fec} = -35.4 + 6.22\text{Wt} - 121.1\text{LFlts} + 7.79\text{LFlts}^2$$

$$F=10.5, P<0.001$$

3.5.2 Moths flight-tested N0-N2 and fed water

The relationship between weight-related fecundity and total flight activity can be seen in Fig. 5.7. The line of best-fit is a second order polynomial where :

$$\text{WtRlFec} = 685 - 131\text{TotAct} + 6.39\text{TotAct}^2$$

$$F=33.3, P<0.001$$

The second order polynomial for weight-related fecundity regressed against sum of long flights (Fig. 5.8) is not significantly better than the simple linear regression :

$$\text{WtRlFec} = 394 - 42.6\text{LFlts}$$

$$F=8.76, P<0.02$$

As before these expressions can be expanded so as to define fecundity in terms of weight and flight activity :

$$\text{Fec} = -301 + 9.23\text{Wt} - 164\text{TotAct} + 7.32\text{TotAct}^2$$

$$F=35.6, P<0.001$$

$$\text{Fec} = -1823 + 19.1\text{Wt} - 208\text{LFlts} + 13.3\text{LFlts}^2$$

$$F=26.9, P<0.001$$

3.5.3 Moths flight-tested N0-N2 and fed sucrose

Regression analysis of weight related fecundity on total activity produces a line the slope of which is not significantly different from zero (Fig.5.9, $b=-9.68$, $F=3.25$, $P>0.10$). A similar result is obtained from a plot of weight-related fecundity against the sum of long flights (Fig.5.10, $b=-8.29$, $F=1.05$, $P>0.50$).

Fig. 5.7

A plot of weight-related fecundity (fecundity per 100mg pharate adult weight) against total activity (the sum of all flights produced) for moths flight-tested for N0-N2 and subsequently fed water.

Fig. 5.8

A plot of weight-related fecundity (fecundity per 100mg pharate adult weight) against the sum of long (greater than 30 mins duration) flights for moths flight-tested for N0-N2 and subsequently fed water.

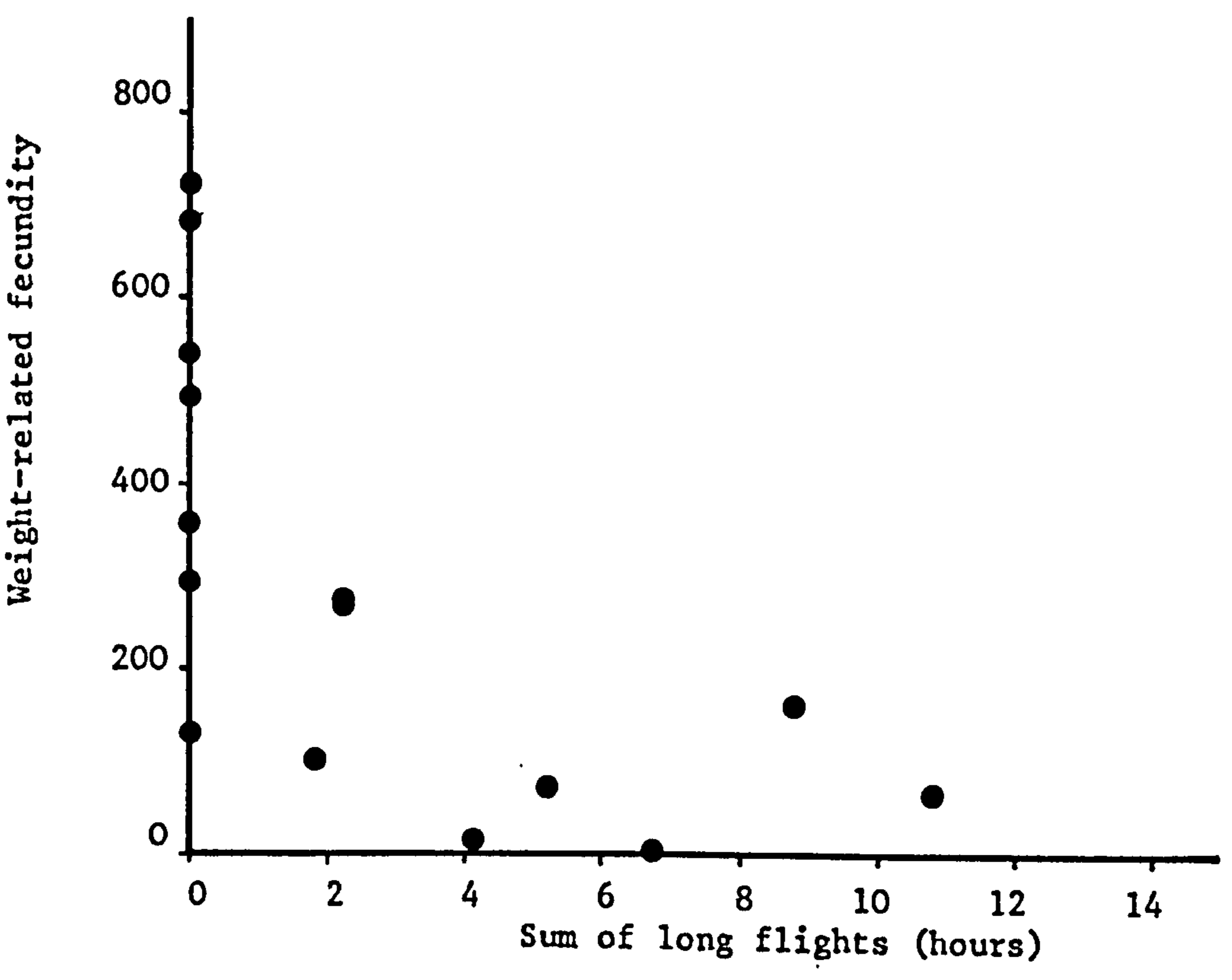
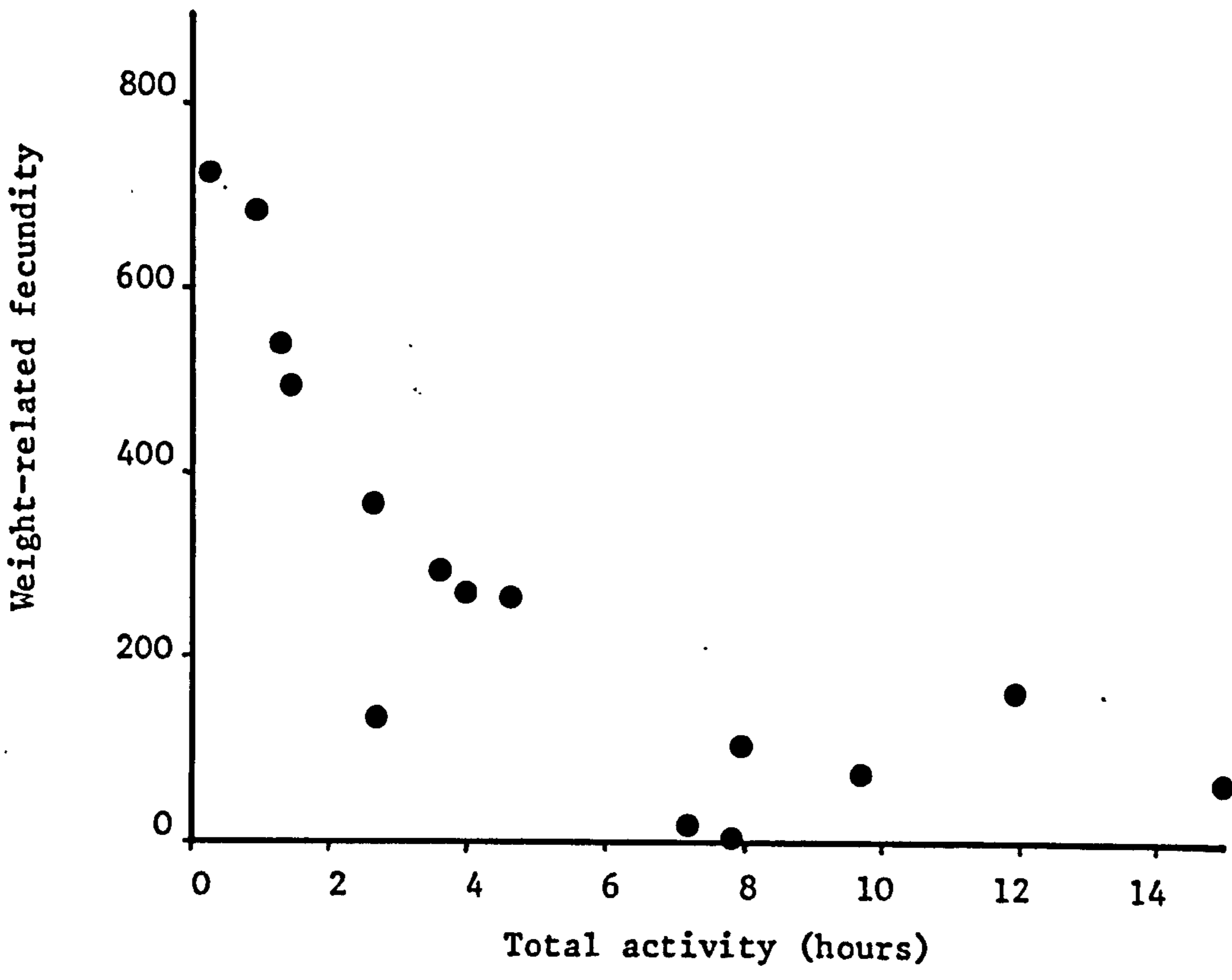
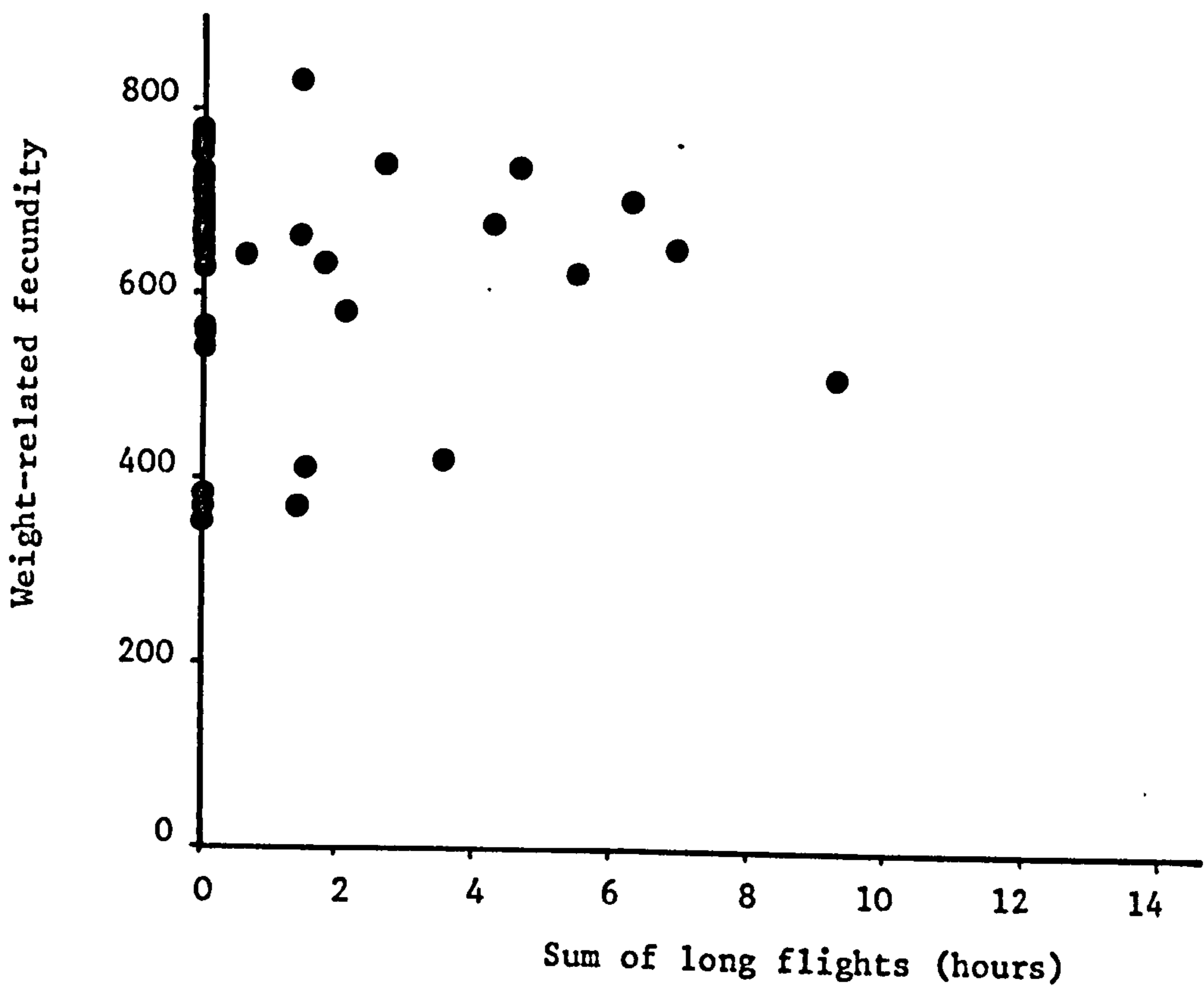
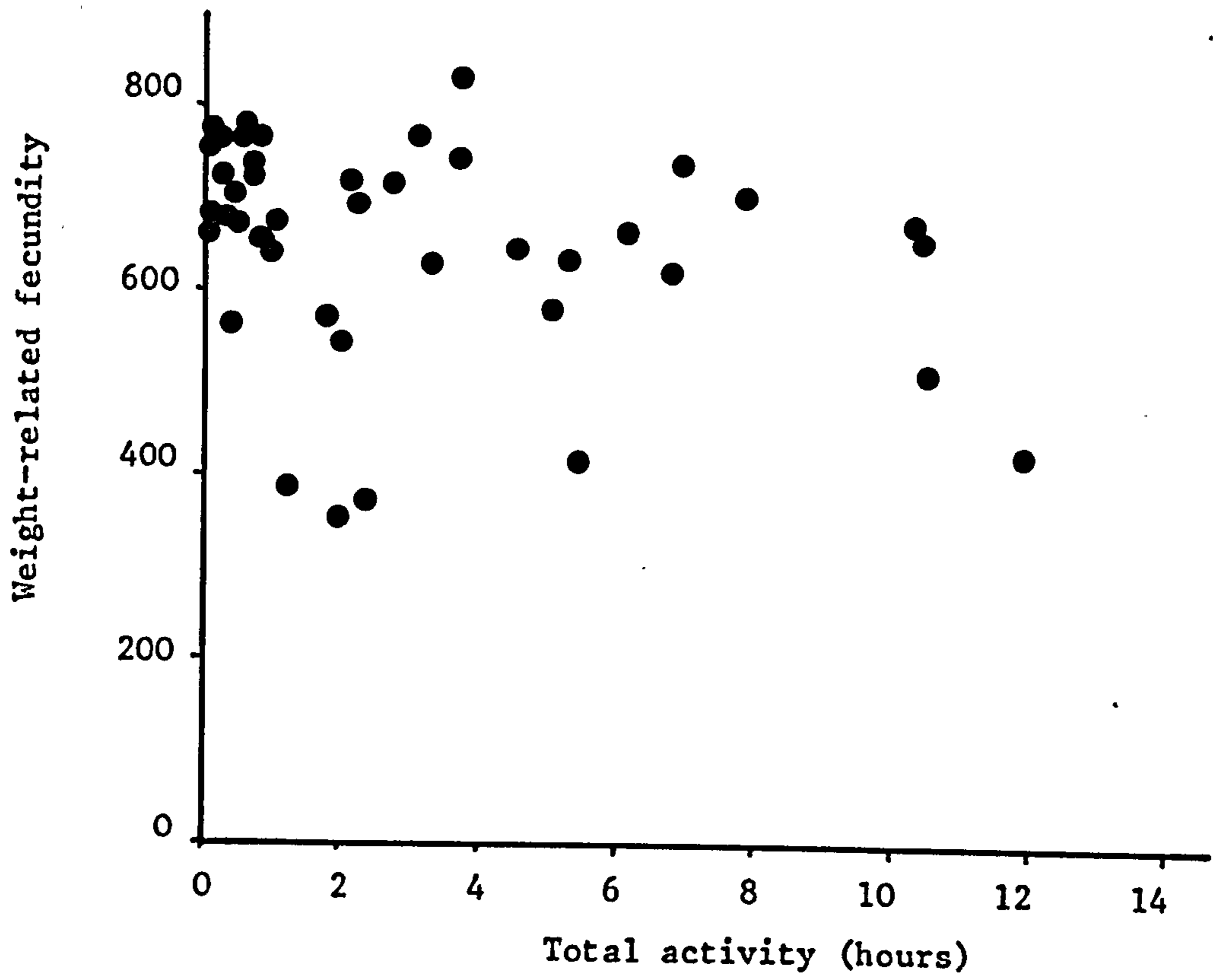


Fig. 5.9

A plot of weight-related fecundity (fecundity per 100mg pharate adult weight) against total activity (the sum of all flights produced) for moths flight-tested for N0-N2 and subsequently fed sucrose.

Fig. 5.10

A plot of weight-related fecundity (fecundity per 100mg pharate adult weight) against the sum of long (greater than 30 mins duration) flights for moths flight-tested for N0-N2 and subsequently fed sucrose.



4. DISCUSSION

4.1 Longevity

The results of this investigation confirm the findings of Gunn and Gatehouse (1985) that unflown moths fed 10% w/v sucrose live significantly longer than those fed distilled water. The dependence of longevity on moth weight has been shown to be significant for water-fed but not for sucrose-fed moths. The absence of a relationship between longevity and weight in unflown moths fed sucrose has also been reported by Gunn and Gatehouse (1985). It seems reasonable, as they suggest, that sucrose in the adult diet can be used for maintenance thereby prolonging life when larval carbohydrate reserves have been exhausted in egg production. The relationship for water-fed moths may indicate that larger moths have more reserves per unit weight of metabolising tissue, which are available for body maintenance.

The beneficial effect of a carbohydrate source on longevity has been observed in other insects. Examples include irradiated (sterile) male boll weevils, Anthonomus grandis grandis (Boheman) (Haynes, 1985); bollworm, Heliothis zea (Boddie); tobacco budworm, H. virescens (F.) and cotton leafworm, Alabama argillacea (Hubner) (Lukefahr and Martin, 1964). For other examples see Jensen et al (1974), Leather (1984), Lukefahr and Griffin (1956), Murphy et al (1983), Preuss (1963) and Shorey (1963).

Flight activity may impose an additional stress on female moths, shortening their lives if they are subsequently fed only water. It is interesting that this relationship is very strong for moths flight-tested N0-N2 but is not present for moths

flight-tested N0-N1. It cannot be said that the actual process of flight-testing for a third night imposes an unacceptable stress on the moths since the longevity of both flown groups, irrespective of flight performance, are not significantly different from the unflown control (Table 5.1). Rather it is the flight activity expressed on this additional night which is the source of the stress. The stress may be imposed by water loss with no external source of water available although this may be partially offset by metabolic production of water from lipid metabolism (Beenackers, 1969).

Regressions of longevity on total flight activity in moths flight tested for three nights were produced separately for the time periods N0-N1 and for D2-N2. While longevity did depend on total flight activity during D2-N2 ($b=-0.342$, $F=7.23$, $p<0.05$) this was less significant than the regression on total activity for N0-N1 ($b=-0.253$, $F=18.1$, $p<0.002$). Therefore, once the stress due to flight activity in D2-N2 has occurred, the moth's previous history of flight activity also becomes important in determining its lifespan. Longevity depends most significantly on the total flight activity over the whole flight testing period ($b=-0.192$, $F=23.3$, $p<0.001$) when moths are flown for three nights.

Since longevity was related to weight in unflown water-fed moths, multiple regression equations were calculated for the relationship between longevity, flight activity and weight for the treatment of flown moths fed water.

For total flight activity :

$$\begin{array}{l} \text{Longev} = 4.93 - 0.205\text{Acty} + 0.0190\text{PhAdWt} \\ \text{(days)} \qquad \qquad \qquad \text{(h)} \qquad \qquad \qquad \text{(mg)} \\ \qquad \qquad \qquad \qquad \qquad \qquad \qquad \qquad \text{(F=13.1, p<0.01)} \end{array}$$

Or for sum of long flights :

$$\begin{array}{l} \text{Longev} = 1.81 - 0.291\text{Acty} + 0.0404\text{PhAdWt} \\ \text{(days)} \qquad \qquad \qquad \text{(h)} \qquad \qquad \qquad \text{(mg)} \\ \qquad \qquad \qquad \qquad \qquad \qquad \qquad \qquad \text{(F=18.0, p<0.005)} \end{array}$$

Moths flight-tested N0-N2 and fed sucrose live longer than unflown moths fed sucrose, irrespective of their flight activity. Since flight activity itself has no significant effect on the longevity of sucrose-fed moths this effect must depend on the delay in mating opportunity and feeding (and hence egg maturation) incurred by the flight-testing treatment. This delay in the beginning of the oviposition period with a subsequently increased longevity implies that egg development and oviposition (with the associated mobilisation of reserves) determine the onset of senescence and death. Ellis and Steele (1982) observed a similarly increased longevity in Spodoptera littoralis when mating was forcibly delayed. Virgin females and those not mated until eight days after emergence lived the longest (means of 17 and 18 days respectively) with earlier matings progressively reducing the lifespan (7.5 to 10.5 days for those mated 0 or 1 day after emergence). Collatz and Wilps (1985) also found that virgin female blowflies, Phormia terrae novae, lived longer (by 40% of the mean) than mated flies.

4.2 Characteristics of flight

Peaks of flight activity and take-off are apparent at dusk and dawn for flights of all durations but not when only those

flights longer than 30 mins are considered. Other peaks of flight activity on N1 (Fig. 5.1) are quite regularly spaced through the night, although they vary in amplitude, which may indicate an endogenous rhythm. An alternative would be a disturbance in the flight-testing room occurring with this period. Evidence of such disturbance could not be found.

It is interesting to note that peaks 4 and 6 on N1 are not present on N2; in fact activity at these times on N2 is lower than at any other time during the night. This suggests that peaks 4 and 6 on N1 are due to one or more behaviours which involve flight and that these behaviours do not occur on N2. Alternatively, or in addition, the two troughs on N2 are due to sedentary (non-flight) behaviours occurring at these times and which do not occur on N1. Dreisig (1986) has stated that, in general, nocturnal moths forage and oviposit during the early part of the night, calling and mating in the later part, with the timing of flight activity adapted to ecological factors. S. exempta has been observed calling in the latter half of the night in the field (Dewhurst, 1984) and in the laboratory (Page, 1985; E. Han, personal communication). Thus it may be calling behaviour (or attempted calling) which is suppressing flight, resulting in one or both of the troughs on N2.

Comparison of Figs 5.1b and 5.2b shows that the fourth total activity peak on N1 is partially formed by a peak in activity due to long flights. This is shown to an even greater extent in the sixth peak which is composed of predominantly long flights.

A midnight peak of activity has been observed in the field

by Rose and Dewhurst (1979). They used a vertically pointing aldis beam in the area of emergence from an outbreak and counted the number of moths flying through the beam in three one min. periods every 30 mins. They attributed this peak of activity to moths which had emerged after dusk, flying into nearby trees to settle for the night. A slightly later peak, labelled peak 5, recorded on N0 in this study may represent this post-emergence peak of Rose and Dewhurst. Two peaks of activity recorded in this study, peaks 4 and 6, on N1 were not seen by these authors. This is not surprising since at this time of night Rose and Dewhurst would probably have been observing the behaviour of only those moths which had recently emerged, i.e. on N0., and at were at low altitude.

Observations of flight activity have also been made in the field by Riley et al (1980, 1983) using mobile, scanning radars overlooking and downwind of an outbreak. The density of insects at 70m above ground level less than 1km downwind of the outbreak site showed more peaks through the night. Particularly apparent are peaks at dusk, 2200-2300h, 0300-0400h and a small peak at dawn. High density plumes of moths were observed taking off throughout the night. Fig. 5.11 is taken from Riley et al (1983) and shows that, for the night of 5-6th April 1980, these started after 2100h, occurring at intervals until just before dawn. They often appeared to be grouped around the major peaks of activity. Rose and Dewhurst (1979) suggested that moths emerging after 2000h make only local flights on N0 at approximately 2300h and dawn, which corresponds well with the recorded activity in the laboratory. They further suggest that

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these moths emigrate from the habitat on the following night, which would be the activity observed by the radar studies. The peaks of activity recorded in this study on N1 and N2, including peaks 4 and 6, may represent the peaks of activity occurring in the field and recorded by the radar, including the observed pluming behaviour.

4.3 Mating frequency

The observation that unflown moths fed sucrose mate more than those fed water may reflect the formers' greater longevity. However, in unflown water-fed moths, there was no relationship between mating frequency and longevity. Jensen et al. (1974) found that female soybean looper moths, Pseudoplusia includens (Wlk.), lived longer and mated more frequently when fed 10% honey solution ad lib. or cotton nectar than when they were fed water or starved. They also found that those adults given food for two days and then water only had comparable longevities and frequencies of mating to those supplied food continuously.

Unflown and flown (N0-N2) water-fed moths do not differ in mating frequency, while similar treatments fed sucrose do, with the unflown group mating more. This could suggest that mating occurs more readily earlier in the life of the adult (but see previous paragraph). However the number of matings does not influence the fecundity of the moth and it is known that a female may lay her full complement of eggs after having mated only once (Gunn and Gatehouse, 1985). Mating frequency may be strongly influenced by laboratory conditions (especially confinement with

a male in a 500ml jar) and have little relation to field conditions. It is impossible to remove the effect on mating frequency of the males' willingness to mate. Also, the significance values obtained for differences in mating frequency are not very extreme ($P=0.03$ and 0.04) so that the possibility of a type I error (invalid rejection of the null hypothesis; Zar, 1984) cannot be excluded.

4.4 Pre-oviposition period

The pre-oviposition period is often postulated as the time most suited to migration in the life of an insect. This has been suggested for S. exempta (Brown et al., 1969) with the implication that the pre-oviposition period may be prolonged to allow migration to occur.

Page (1985) observed an influx of moths into an area where mating and oviposition subsequently took place and found that the arriving moths were generally in "pre-arrested" or "arrested" oocyte development. He concluded that moths migrate during the period of pre-arrested development (when the near-terminal oocytes are 0.12-0.22mm in diameter) and during arrested development (near-terminal oocytes 0.24-0.34mm diameter). He also found that arrested development could continue at least up to N3 in laboratory reared moths ($n=100$) and N4 in field collected moths ($n=307$).

Female S. exempta moths delay egg-laying until late in their lives if they are unmated and may or may not then lay a small number of infertile eggs before death. Thus moths flown in this investigation which would not have arrested the development of

their eggs, or would have done so for only a short period, have had their pre-oviposition periods forcibly extended by the lack of food and a male until D2 or D3. A relationship between the natural pre-oviposition period and flight activity would be concealed by this extension. Moths with a normally short pre-oviposition period could be responsible for the possible calling behaviour on the flight balances on N2 (see Section 4.2. Characteristics of flight).

4.5 Fecundity

The strong relationship between fecundity and pharate adult weight has been observed in female S. exempta by Gunn and Gatehouse (1985). Miller et al. (1983) report a similar relationship in Callosamia promethea with a correlation coefficient of 0.99.

The observed effect of increasing the weight-related fecundity of female S. exempta moths by feeding them sucrose rather than water has been reported previously by Gunn and Gatehouse (1985). A small effect was generally apparent in moths from larvae fed ad lib. but the increase was only significant when the females' larval diet was restricted. The larvae in this investigation were maintained ad lib. This result, in conjunction with those of Gunn and Gatehouse, confirms that this effect is marginal in moths derived from well-fed larvae.

The effect of flight-testing moths subsequently fed water is to decrease their weight-related fecundity. This effect is also significant, but less marked, for sucrose-fed moths indicating

that feeding on sucrose enables the moths to compensate to some degree for the stress imposed by flight-testing. That they are not able to compensate fully for this stress suggests that not all of the detrimental effect is due to use of fuel reserves. Further, since weight-related fecundity for flight-tested moths fed sucrose does not depend on flight activity, this detrimental effect is due to the testing procedure itself and not to the activity of the moths.

Moths flight-tested for N0-N1 or N0-N2 and fed water in this investigation have no energy source available to them as adults and are therefore unable to restore the lipid reserves used as a substrate for flight (Gunn and Gatehouse, 1986). Hence, for these moths, weight-related fecundity may be seen to depend to a large degree on flight activity. There is no plateau of weight-related fecundity before the decrease with increasing flight activity, indicating that there is no excess of lipid stores above that which can be used to develop eggs i.e. solely available as flight fuel. This finding contrasts with the prediction of the notional energy budget of Gunn and Gatehouse (1986) who suggested that only one third of the lipid content of a female at eclosion would later be incorporated into her eggs and that much of the excess is available as flight fuel. The results presented here rather suggest that lipid is not present greatly in excess of that required for egg development (as well as other functions not related to flight).

The relationship between weight-related fecundity and total flight activity is linear for moths flown N0-N1 and fed water. For these moths the relationship of weight-related fecundity and

the sum of long flights is a quadratic curve. A similar, but more acute curve is apparent for the total flight activity of moths flown N0-N2 and fed water. This also appears to be the case for the sum of long flights for these moths although a polynomial expression fits this curve no better than does a straight line.

The curve of these last three graphs illustrates a very interesting phenomenon. Moths which are very active suffer far less of a decrease in fecundity than would be predicted by extrapolation from moths of low activity.

Liquido and Irwin (1986) flight tested corn leaf aphids, Rhopalosiphum maidis, suspended from a human hair and measured their lipid contents after flight. They found a linear relationship between the percentage lipid content (dry weight) and flight duration up to eight hours. Thereafter they found three alates which flew for c.10.5, 11.5 and 14.5 hours without further reduced lipid. A polynomial described the resultant curve significantly better than a straight line. If lipid is accepted as the limiting factor on weight-related fecundity in flight tested S. exempta, then the plots described in this study are similar.

There must, however, be some doubt as to the accuracy of the flight duration of the three very long flying alates in the experiments by Liquido and Irwin, although this is not mentioned by the authors. Tethered flight was measured by continuous observation by the investigator, with a stopwatch, for the entire flight period. Even given accurate recording of these flight

durations, a curve would be produced if the very long flying alates contained a very large quantity of lipid before flight and then utilised it for flight at the same rate as the others in the sample. This would necessitate a correlation between very high lipid content and very long tethered flight. Liquido and Irwin, however, interpret the curve as indicating a transition from the use of lipid to a "non-lipid", presumably carbohydrate, flight fuel, although it is difficult to reconcile energetically the use of lipid before carbohydrate (see Section 1. Introduction).

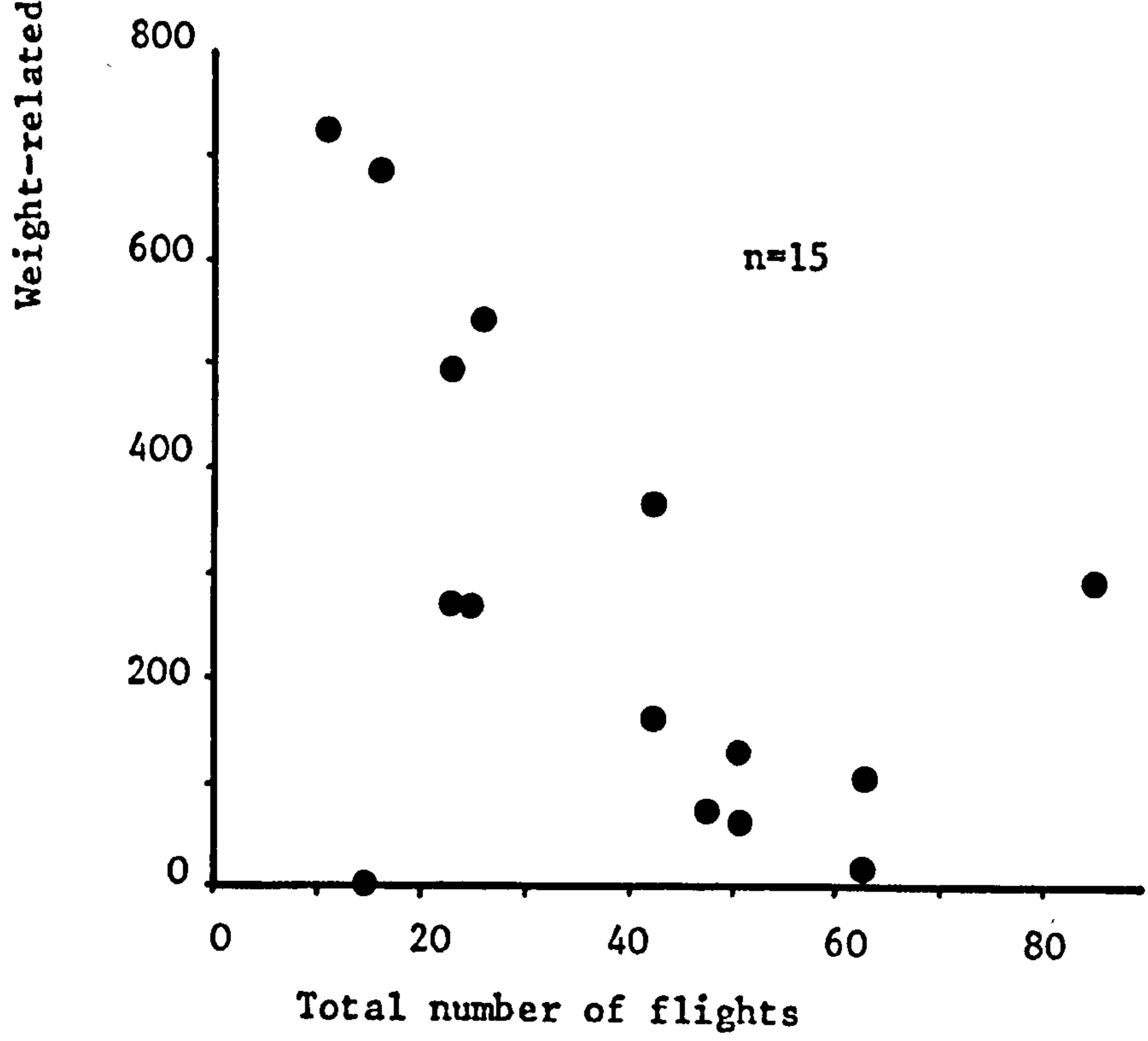
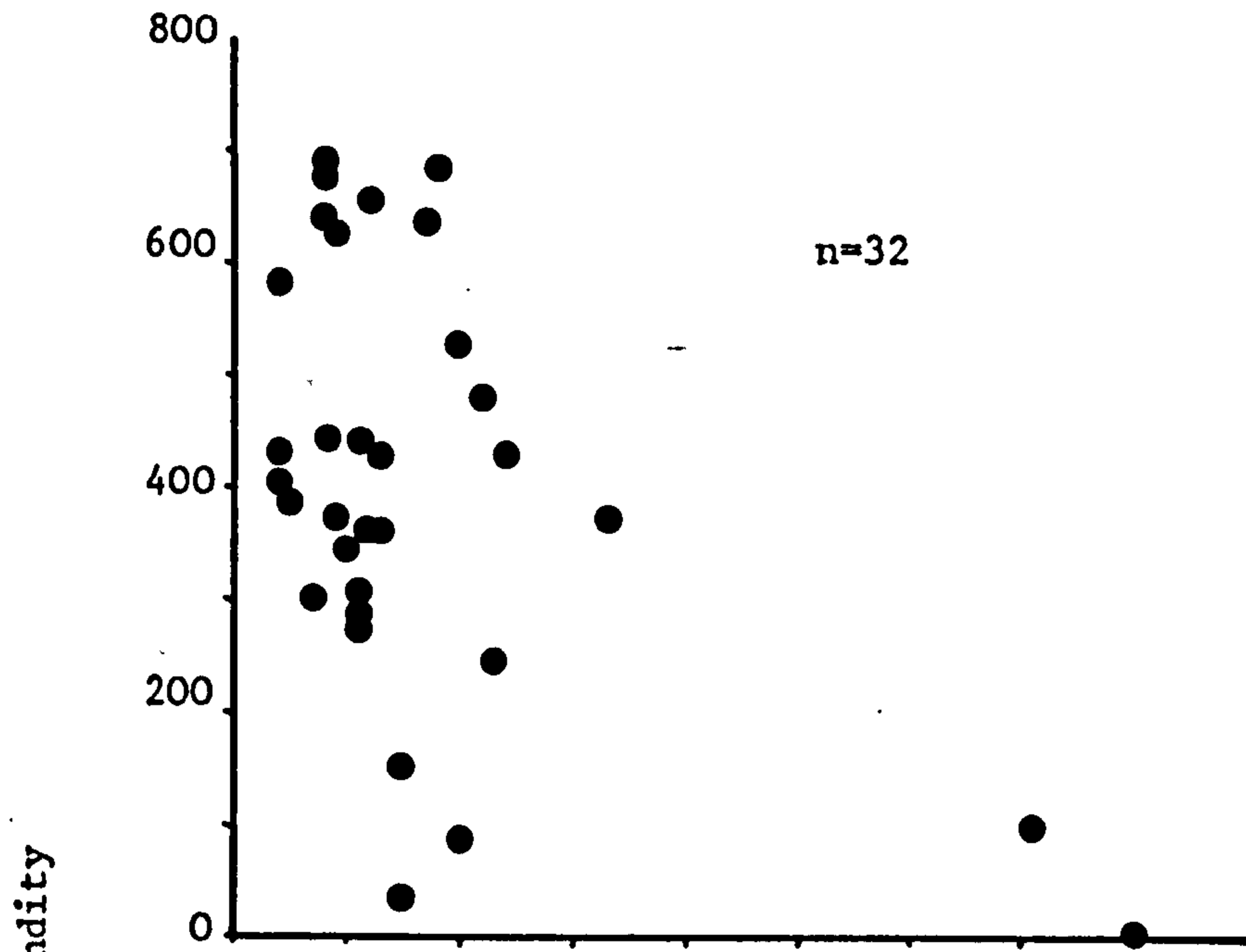
Such an explanation is inappropriate in the case of S. exempta where carbohydrate is present in only very small quantities (Gunn and Gatehouse, 1986; A. Gunn, personal communication). One reason why high activity moths perform better than they "should" may be that the cost of flying is not a constant during a flight, but decreases with increasing time since take-off i.e. long flights are cheaper per unit time than short flights.

A preliminary examination of this hypothesis was attempted by plotting weight-related fecundity against the number of flights produced by each moth. An expensive period at the beginning of each flight, for example caused by more powerful, climbing flight, followed by very cheap flight might produce a significant regression. In fact this regression is significant for moths flown N0-N1 ($b=-5.83$, $F=10.5$, $P<0.01$, Fig. 12a) but not significant for moths flown N0-N2 ($b=-5.87$, $F=5.2$; $P>0.05$, Fig. 5.12b). The latter plot actually appears to reveal a relationship with the exception of one moth with very low weight-related fecundity which must decrease the significance of

Fig. 5.12

Plots of weight-related fecundity (fecundity per 100mg pharate adult weight) against the number of flights produced by moths :

- a. flown N0-N1 and subsequently fed water.
- b. flown N0-N2 and subsequently fed water.



the regression.

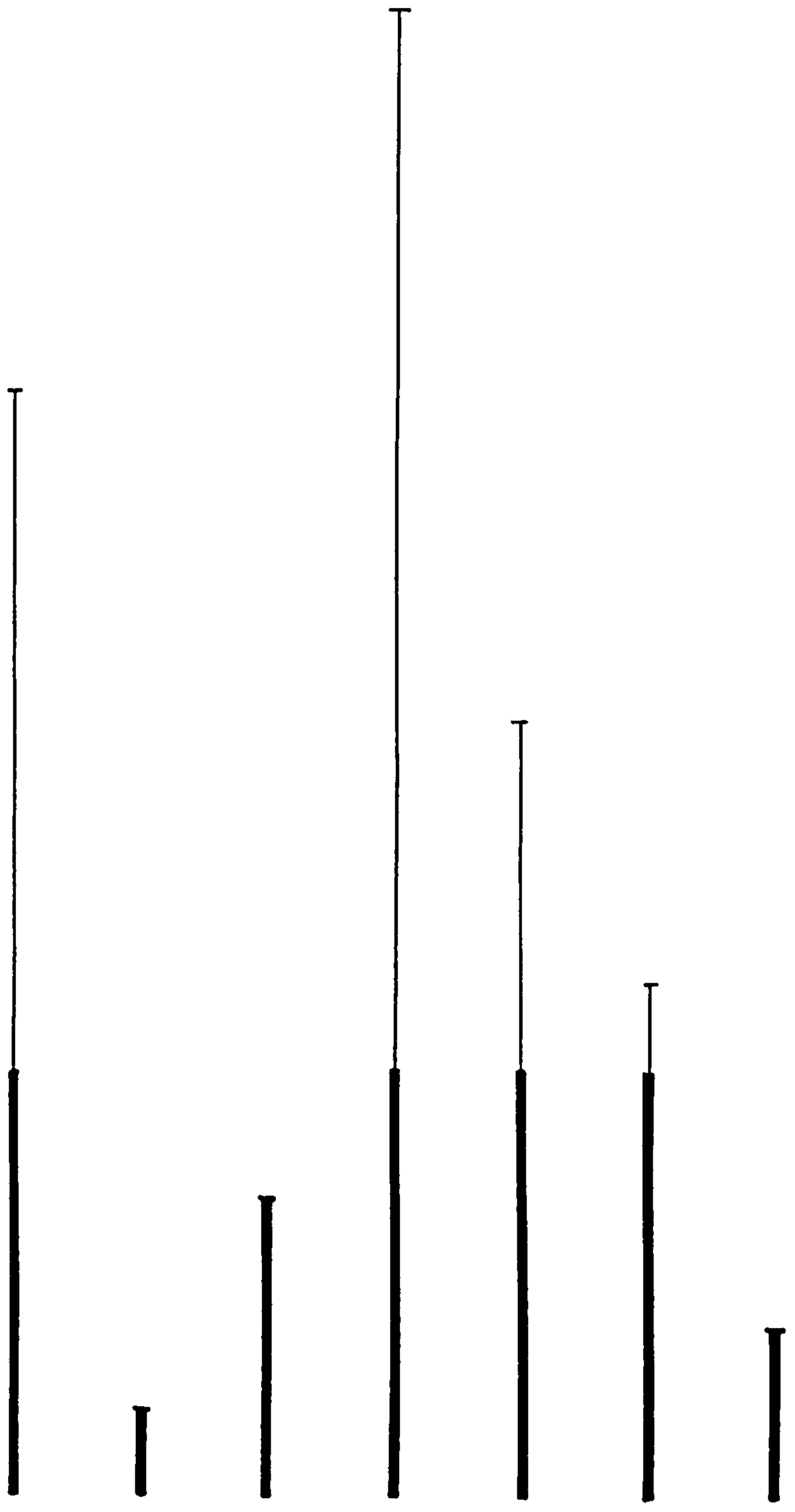
An attempt was made to refine this analysis. In the simplest terms, a flight might be imagined to consist of an early "expensive" period of flight (possibly due to the greater energy consumption of a climbing flight and/or the high energy cost of a pre-flight "warm-up" period (Beenackers, 1969)) followed by cheaper "cruising" flight. The transition from the expensive phase to cheaper flight can initially be assumed to be instantaneous, with the period from take-off to the transition (the "expensive period") a constant for all flights by all moths (Fig. 5.13). Cost within the expensive and cheap periods of flight is also assumed to be constant. The period of expensive flight is then summed for all flights of each moth i.e. all flights shorter than the expensive period are summed, together with the value of the expensive period for each flight longer than the expensive period. A regression of weight-related fecundity on the sum of expensive flight can then be performed and the coefficient of determination (r^2 - the proportion of the total variance explained by the regression line) calculated. This procedure was followed for transition periods of 3, 4, 5, 7, 10, 15, 20, 25, 30, 40, 60, 120 and 180 mins. for both flight-tested water fed groups and also for 240 and 300 mins. for the N0-N1 group (Table 5.3).

It may be expected that as the "assumed" expensive period approaches the "real" expensive period r^2 would increase. Increasing the expensive period beyond its real value would incorporate more cheap flight into the regression so decreasing

Fig. 5.13

Diagrammatic representation of the transition from an energetically expensive early phase of flight to a cheaper later phase. In this simple model the transition is represented as occurring instantly at a particular flight duration for all flights (for further explanation, see text).

Expensive period
Transition
Cheaper period



↑
Take-off
Flight duration →

Table 5.3.

The coefficients of determination (r^2) for regressions of weight related fecundity (number of eggs per 100mg pharate adult weight) on the sum of expensive flight for each moth and for different periods of expensive flight.

Expensive Period/mins.	N0 - N1		N0 - N2	
	r^2	P <	r^2	P <
3	0.245	0.01	0.422	0.02
4	0.244	0.01	0.458	0.02
5	0.245	0.01	0.490	0.01
7	0.255	0.01	0.539	0.005
10	0.269	0.005	0.572	0.002
15	0.286	0.005	0.598	0.002
20	0.297	0.005	0.618	0.002
25	0.311	0.002	0.630	0.001
30	0.323	0.002	0.635	0.001
40	0.342	0.001	0.637	0.001
60	0.382	0.001	0.607	0.002
120	0.402	0.001	0.555	0.005
180	0.392	0.001	0.551	0.005
240	0.381	0.001	-	-
300	0.372	0.001	-	-
1440	0.379	0.001	0.593	0.002

r^2 . A maximum r^2 would therefore indicate the end of the "real" expensive period.

The regressions for both flight-tested groups are significant for the three min. transition period and all longer periods. Significance values for the three min transition period are : N0-N1, $F=9.75$, $P<0.01$; N0-N2, $F=9.50$, $P<0.01$.

Fig. 5.14 shows the relationship between r^2 and the expensive period. Both samples of moths show a maximum r^2 : N0-N1 at c.120 mins. and N0-N2 at c.40 mins. The shape of these curves will be determined by the distribution of flight durations in the two samples i.e. by the amount of flight included with each increment of flight time. Therefore r^2 was also plotted against the sum of expensive flight included in each regression expressed as a percentage of the total flight produced by that sample of moths (Fig. 5.15). The maxima in these two curves coincide at c.70% of the total flight produced. It is possible that this reflects a relationship between the length of flight and the length of the expensive period.

The maxima in Figs 5.14 and 5.15 confirm the existence of an early phase of expensive flight followed by cheaper flight. That the maxima are broad humps may be explained by relaxing the assumptions made initially that the expensive period is a constant for all moths and flights and that the transition to cheap flight is instantaneous.

From considerations of the behaviour of moths in the field it was anticipated that a short period of expensive flight would be found, reflecting pre-flight warm-up and the climbing phase of flight of the order of 10 mins. (Riley et al., 1983) before less

Fig. 5.14

A regression of weight-related fecundity against the duration of a postulated energetically expensive period at the beginning of every flight may be performed for moths flight-tested and subsequently fed water (see text). The coefficients of determination (r^2) of such regressions have been plotted here against various values of periods of expensive flight. A maximum in the resulting curve is assumed to confirm the existence of such an expensive period.

Curves were plotted for moths flight-tested for N0-N1 and for those flight-tested N0-N2.

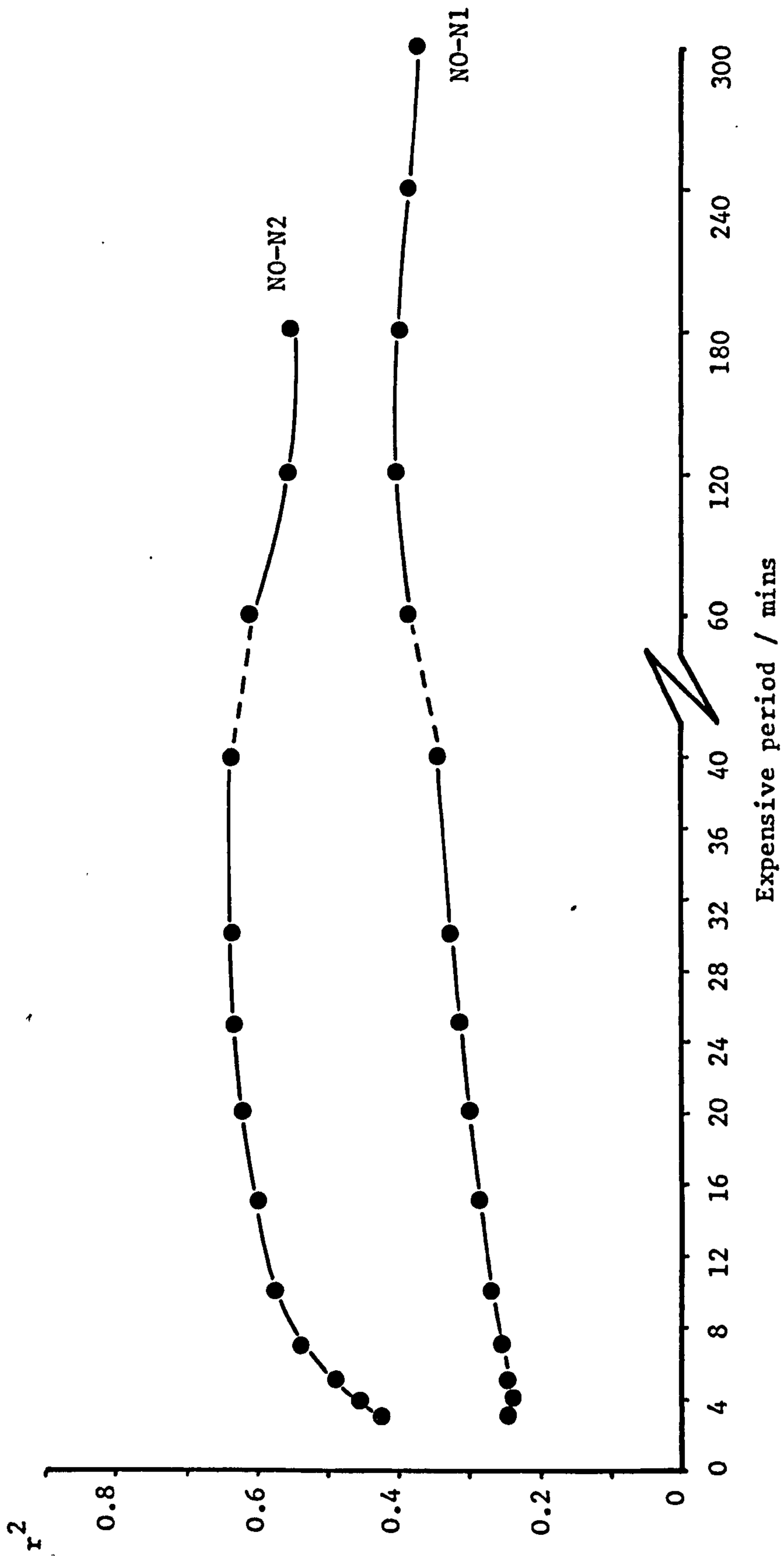
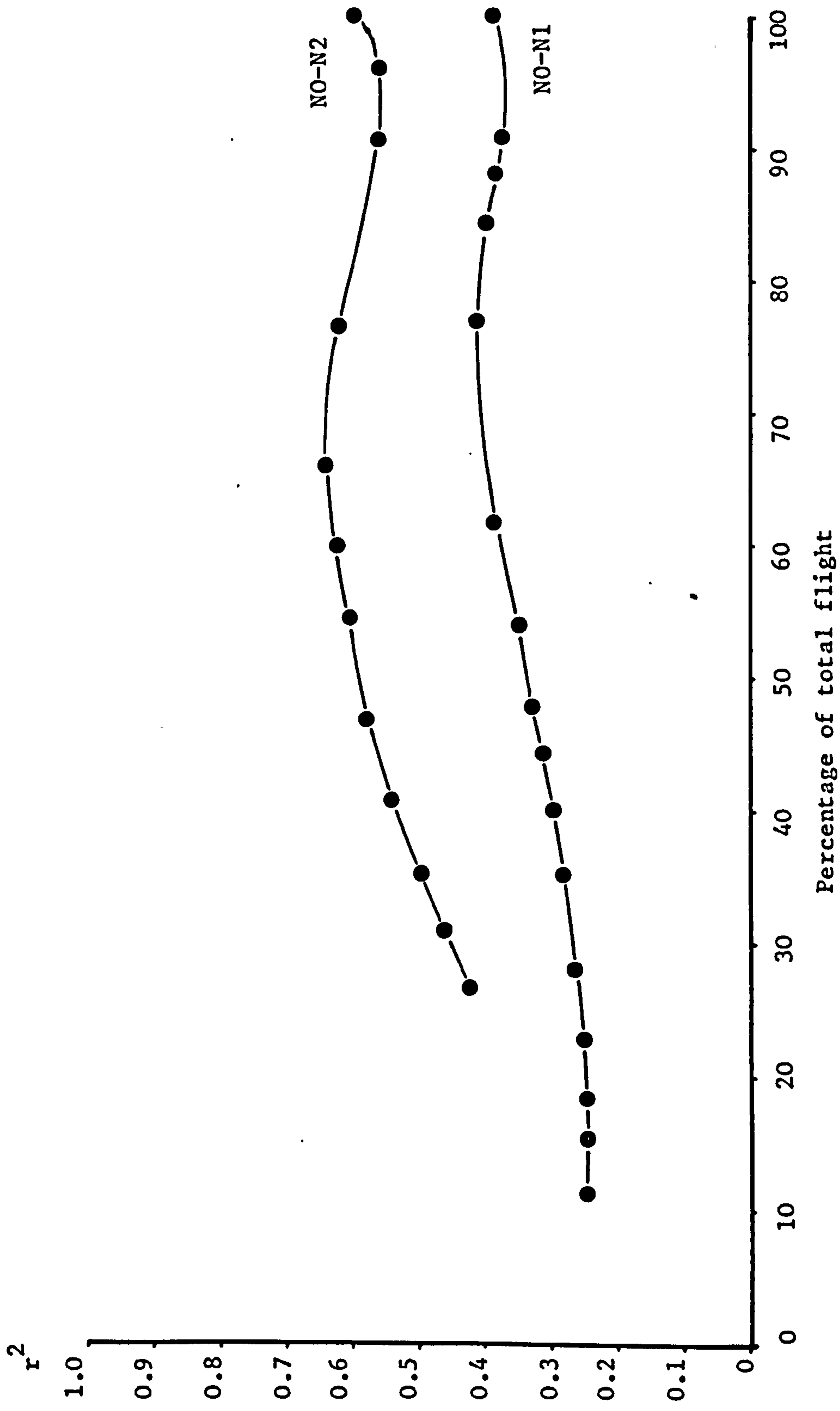


Fig. 5.15

A regression of weight-related fecundity against the duration of a postulated energetically expensive period at the beginning of every flight may be performed for moths flight-tested and subsequently fed water (see text). The coefficients of determination (r^2) of such regressions have been plotted here against various values of periods of expensive flight expressed as a percentage of the total flight activity of the sample of moths. A maximum in the resulting curve is assumed to confirm the existence of such an expensive period.

Curves were plotted for moths flight-tested for N0-N1 and for those flight-tested N0-N2.



energy expensive "cruising" flight at constant altitude would occur. The periods of expensive flight estimated in this study were much greater than this estimate from the field. Riley et al. observed insects flying in the latter half of the night at less than their expected height after climbing at their recorded rate of 0.5ms^{-1} . They attributed this to the insects restricting their flight altitude to avoid the cold air above the isothermal layer. No decrease in temperature (or other environmental cues to height) would be experienced by moths flown in the laboratory so that the regulation of altitude and climbing time by temperature would not occur. This has the implication that expensive flight in the field would be restricted in duration which, along with wind assistance, might reduce the cost per unit time of flight well below that observed in the laboratory.

One additional possible source of a transition from expensive to cheaper flight in the laboratory is the counterweighting system of the tethered-flight technique. As the moth loses weight through the night its counterweight will become a greater proportion of its body weight. Therefore the proportion of its body weight which the moth will have to support to sustain flight will decrease. This factor may contribute to the decreasing expense of flight but is unlikely to explain it fully.

This investigation has focused on the fecundity of S. exempta females as a major component of fitness. Further components related to both larval and adult nutrition are the growth and survival of progeny (Gordon, 1968), subjects which are

seldom explored and which certainly merit investigation for S.
exempta.

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CHAPTER SIX

General discussion and conclusions.

This investigation of the regulation of flight capacity in Spodoptera exempta has confirmed the conclusion by Parker and Gatehouse (1985), that variation in flight performance has a high additive genetic component (Ch. 4). This study has extended their findings by suggesting that flights beginning at different times of night are qualitatively different, with variance in the durations of flights beginning before midnight exhibiting a large genetic component and variance in those beginning after midnight having a very small or no genetic component.

Perhaps the most interesting of the results obtained in this work have been those revealing a bimodality in the distribution of log-transformed tethered-flight durations of samples of moths which had been selected for increased flight capacity for one generation. No such discontinuity was apparent in unselected samples, samples selected for decreased flight durations or later generations selected for prolonged flight. This bimodality has been suggested to be due to the presence of a major gene (Ch. 4).

Moths may, therefore, be divided into two categories, long- and short-fliers, with only a small degree of overlap between their flight performance. If the bimodality in the distribution of flight performance is a phenomenon which is found in flights expressed in the field then the long-flier category may be interpreted as representing potential long-distance migrants, which have been seen on radar to emigrate from their emergence site early in the night, while the short-flier category may represent moths undertaking localised dispersal, possibly those moths observed at intervals through the night forming plumes whose displacements seem to be more limited (Riley, et al.,

1983). The timing of take-off of long-distance migrants and pluming moths, with the difference in heritability of the duration of flights in the laboratory which begin at different times of the night, has led to the suggestion that migratory flight is under genetic regulation but that pluming flight is not (Ch. 4).

An analysis which has not been performed here is the examination of the take-off times of moths in each category of the bimodal distribution. If moths in the short-flier category are adapted to achieve no more than limited local displacements, it is possible that their flight activity is concentrated in the latter part of the night when low level winds in East Africa are generally lighter and more variable in direction (Riley, et al., 1983; Tucker, 1983). Moths in the long-flier category take-off into stronger, more consistent winds before midnight and it is their flight durations which are determined genetically, the frequency of the flight genotypes being adjusted by the spatial and temporal distribution of suitable habitat (Ch. 4). This analysis could be the starting point for a rewarding investigation of the bimodality.

It is very interesting that Rose (1972) also found a bimodality in the distribution of transformed tethered-flight durations of samples of Cicadulina spp. in Zimbabwe (Rhodesia). Many individuals in these samples were the result of selection for flight over one generation. No selection and flight-testing were applied in subsequent generations so it is not known whether the bimodality would have persisted. He also found that flight

ability was correlated with body length for individuals with similar wing lengths, shorter body length being associated with more prolonged flight. No correlation of flight ability with moth weight (Parker, 1983; Ch. 4) or wing-loading (Parker, 1983) has been found for S. exempta.

Field evidence had previously indicated that Cicadulina leafhoppers disperse from a breeding source in two different ways (Rose, 1978). Some fly for only a few metres as shown by the sharp decrease in numbers caught on trap plants placed at increasing distances away from the source. Others were captured in suction traps 20m above the ground during the main flight season. Field results also demonstrated that long-bodied forms were found in permanent breeding populations in green Kikuyu grass during the summer and short-bodied forms on green oats and wheat invaded during the winter flight season. Rose, therefore, postulated that cycling selection was acting to change the proportions of the forms in a population, with long-bodied poor-fliers adapted for reproduction in favourable grass habitats which are widespread during the summer, and short-bodied strong-fliers suited to dispersal from the drying habitats present in winter.

While the scale of flight durations is very different for Cicadulina spp. and S. exempta (the detransformed means of the two modal categories being only 8-15s and 500s for the former) the similarity between the shapes of the flight duration distributions is striking and suggests that the strategy of two flight types may be characteristic of a number of species of migratory insects. Investigation of the distributions of flight

durations in other species is therefore likely to prove rewarding.

The investigation of the effect of larval phase on adult flight behaviour reported in this thesis is the first of a Noctuid moth which has revealed a significant effect (Woodrow et al., 1987; Ch. 3). Females reared in the gregaria phase flew significantly more than those reared as solitaria but with no effect of phase detected in males. The relationship of this effect to the situation in the field has been discussed in Ch. 3. This experiment was performed using moths which had been selected for two or three generations and hence were presumably from the higher flight duration category of the bimodal distribution present in the F1 generation. This raises the question of the role of phase in regulating the flight capacity of moths belonging to the lower modal category.

The female moths used for the investigation of the effect of flight on fecundity were unselected. A trade-off of reserves was found between flight and fecundity. There were also some indications that there was an early expensive period of each tethered-flight in terms of the reserves used, with later flight being energetically cheaper (Ch. 5). Moths in the field might be expected to undergo an expensive period at the beginning of an emigration or dispersal flight because the initial climbing phase must demand more power consumption than horizontal "cruising" flight. The early minutes of flight recorded in the laboratory may be equivalent to climbing flight in the field (i.e. the tethered moth is attempting to climb) but little can be deduced

from the laboratory data about the duration of the climbing period in the field, or its cost in terms of reserves, because of the artificial conditions experienced by the moth in the laboratory. In particular the constraint imposed by the apparatus, the lack of visual inputs associated with climbing, and the lack of any change in environmental conditions e.g. temperature, relative humidity and anisotropic wind movements (Riley and Reynolds, 1986) experienced by a moth in the field as it reaches the altitude for horizontal flight will not be experienced by a moth in the laboratory. It is possible, therefore, that the energetically expensive, climbing phase of flight may be extended in the laboratory. A further problem is that the period of relatively expensive flight detected in this investigation may be a laboratory artefact. The loss of weight by the moth during prolonged flight must result in an increase in the effective counterweight on the flight arm and a decrease in the power output required to remain in flight on the apparatus.

The existence of genetic variance in a character so closely related to fitness as is flight in this species (particularly in achieving successful dispersal and tracking of available habitats) must be maintained by variance in the direction of selection in time and/or space. During the dry season in East Africa only a very small proportion of the range of S. exempta is suitable to support even low density populations and patches which are suitable e.g. highlands, river valleys and coastal areas are generally separated by large distances of unsuitable terrain (Rose, 1979). Selection under these conditions must be expected to act against moths emigrating from their patches.

However, loss of long-flight genotypes will be limited by the fact that populations at this time are developing in the solitaria phase (meteorological systems capable of concentrating flying moths are extremely infrequent) in which the expression of flight potential is reduced (Ch. 3).

In East Africa the dry season comes to an end with the onset of the early rains as the Inter-Tropical Convergence Zone passes south. The correlation between the quality of the short rains and the severity of the following armyworm season during the long rains is well established (Tucker, 1984). Poor, scattered early rains usually result in a severe armyworm season during the subsequent long rains. It has been suggested that the build-up of armyworm populations during the short rains is related principally to larval survival and especially to the incidence of viral disease. Poor early rains will be associated with clear skies, high levels of ultra-violet radiation and hence low levels of viral disease (Rose et al., 1987). Larval survival and growth may also be related to changing food plant quality and quantity with rainfall after periods of drought (D.J.W. Rose, personal communication.). One possible way in which genetic determination of flight capacity could influence population build-up leading to the formation of outbreaks depends on the patchiness of the habitat during the early rains (Gatehouse, 198-). Good early rains result in a rapid and extensive flush of new growth of grasses over much of the area subject to invasion from the off-season habitats. Emigrants from a source area are, therefore, increasingly likely to find favourable habitats as the early

rains develop, irrespective of their flight capacity, because these habitats rapidly become generally distributed. Hence selection must act to increase flight capacity to some extent, simply because emigrants now survive, but not very strongly. In this scenario, all individuals have a high probability of reproducing and the new habitat is likely to be invaded progressively on a broad front. Furthermore, moths will encounter favourable habitat whether they are concentrated in flight or not. Many populations will, therefore, be developing in the solitaria phase and the subsequent emergence of moths will tend not to be highly synchronised.

In poor early rains, however, the storms are infrequent and widely separated producing a very patchy distribution of favourable habitat outside the off-season areas. Moths which reach these patches are likely to be only those which fly for a long period and hence, not only travel for the long distances between patches, but are available in flight to be caught up in and concentrated by the converging wind systems associated with storms. When favourable habitat is confined to the scattered patches watered by those storms, this process must play a crucial role in drawing insects into habitat patches in which the populations will generally be at high densities. Those moths with low or intermediate flight capacities are less unlikely to reach a suitable patch and selection will strongly favour very long flight in the population. If poor rainfall persists through the three or four months of the short rains, similar selection for prolonged flight can be expected over three or more generations. In this situation the resulting moths emerging at

the beginning of the main rains in the New Year in East Africa will be composed of a high proportion of long-flier genotypes (the population having responded rapidly to the selection imposed during the short rains). These moths will, therefore, spend more time in flight, and take-off early in the night when winds are stronger and more constant (Riley et al., 1983), and so they are more likely to be concentrated to cause high density outbreaks. A further factor contributing to a high probability of outbreaks is that these populations have developed largely in the gregaria phase in which development, and therefore the emergence of moths, is generally synchronous. It is clear that the capacity for prolonged flight has its main impact on survival during, and particularly early in, the rains. Moths which fly for long periods have been shown to experience a decrease in their expressed fecundity (Ch. 5), however, access to sucrose solution (or nectar) allows females to recover their full potential fecundity so it is interesting that it is precisely at the times of year that migratory flight is most important for survival, that nectar is most easily available in the field.

The control strategy employed in the field in recent years in East Africa has been to concentrate resources on effective control of early season outbreaks, particularly the first, or primary, outbreaks. The reduction in numbers of the population and, in particular, the numbers of moths which are developing synchronously, will be flying at the same time and so will be available to be concentrated in the same wind systems to form further outbreaks, will be reduced. In addition the genetic

basis for the regulation of flight, as just discussed, suggests that the reduction in numbers of moths emerging from primary outbreaks will contain the build-up of long-fliers in those years in which outbreaks are likely to be serious, so further reducing the numbers available to be concentrated in subsequent generations.

The key to the migratory strategy of Spodoptera exempta is the large scale dispersal of the population throughout its range during each rainy season. Since green areas which can support the survival of low density populations over the dry season vary in position and extent from year to year, this annual redispersal must be a major factor in promoting survival whenever favourable habitat persists.

There is now substantial evidence that, in years in which the African armyworm is a serious pest, those elements of the population whose future development is to make the major contribution to damage are largely confined in identifiable primary outbreaks. This vulnerability in the annual cycle of the insect offers real prospects for the success of a regional approach to control.

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ACKNOWLEDGEMENTS.

Prof. E. Naylor, Lloyd Roberts Professor of Zoology and Head of the School of Animal Biology for the use of departmental facilities.

Dr A.G. Gatehouse for initiating my involvement in the project, and for his supervision and encouragement throughout the study and especially in times of adversity.

Mr D.A Davies for designing and building much of the apparatus used in this study, in particular the datalogging electronics, and for writing the datacollection and much of the analysis software. Without his many practical skills this project would not have been possible in its present form.

All the technical staff of the School of Animal Biology, and in particular Mrs Pamela Bower for her unfailing care of the stock culture and helping hand when needed, and Mr H.O. Pritchard and Mr N. Brown for growing the maize.

Dr Alan Gunn for counting the eggs of the water fed moths in the investigation of the effect of flight on fecundity, for vigorous discussions and for his ever present (black) humour.

Thanks also to Pam and Alan for sharing the weekend feeding rota of the stock cultures and for sometimes relieving me of the care of my experimental lines for a whole weekend.

Dr Derek Rose, Bill Page, Charles Dewhurst and Lincoln Fishpool for their welcome and kindness shown to me on a visit to Kenya in 1985. A special thanks to Bill Page for his wonderful hospitality and for regular, securely packaged, consignments of pupae.

The project was funded by a Science and Engineering Research Council CASE award with the Tropical Development and Research Institute (now the Overseas Development Natural Resources Institute). My thanks to my cooperating body supervisor Dr David Pedgley. Experiments were carried out in Bangor under MAFF licences PHF 66/99, 116 and 125.

Finally my thanks to my wife, Sarah, for marrying me during the period of this study despite my large number of ever hungry dependents.

APPENDIX.

1. Life-history data for moths flight-tested for N0-N1 and subsequently fed water as part of the investigation of the effect of flight on fecundity.

Moth code	Longevity (days)	Fecundity	Pharate adult weight (mg)	Weight related fecundity (/100mg)	Sum of all flights (hours)	Sum of long flights (hours)	Pre-oviposition period (days)
495	6	124	102	121.6	*	*	3
498	5	285	92	309.8	*	*	3
501	5	370	120	308.3	5.8167	4.8167	3
503	4	86	98	87.8	6.3500	3.9833	3
504	6	500	117	427.4	3.6167	0.8333	4
506	5	111	113	98.2	10.5667	4.4667	3
508	5	493	132	373.5	12.2833	11.5333	3
509	5	306	111	275.7	11.9500	10.9667	3
510	5	416	121	343.8	8.7000	7.7000	3
511	7	835	123	678.9	2.8667	2.0167	3
512	5	374	130	287.7	5.8000	4.2000	3
517	8	824	157	524.8	8.2000	5.1500	3
519	8	495	128	386.7	1.7333	1.3500	4
520	6	510	126	404.8	3.1667	3.1333	4
522	8	715	160	446.9	6.4167	5.7833	3
523	7	245	162	151.2	11.2500	9.4167	6
524	7	269	109	246.8	4.4167	3.4333	3
525	7	791	121	653.7	2.7000	0.6333	3
528	4	615	171	359.6	5.2833	4.8167	3
529	8	474	108	438.9	2.0333	0.5333	3
531	6	622	107	581.3	1.2000	0.7000	3
532	6	286	94	304.3	4.4667	3.0667	3
534	6	848	132	642.4	1.6667	1.3833	3
535	5	705	113	623.9	0.4667	0.0000	3
537	5	589	137	429.9	9.3500	8.4333	3
538	5	36	101	35.6	3.7333	2.4333	4
539	6	440	119	369.7	3.5500	2.1500	3
540	6	724	169	428.4	4.0167	2.1833	4
543	9	736	154	477.9	2.1500	0.5833	4
544	6	7	154	4.5	13.1500	7.6500	6
545	6	930	136	683.8	1.6000	0.0000	3
546	6	900	130	692.3	0.2000	0.0000	3
547	6	884	139	636.0	2.8833	0.0000	3
548	8	504	139	362.6	0.4833	0.0000	4

2. Life-history data for moths flight-tested for N0-N2 and subsequently fed water as part of the investigation of the effect of flight on fecundity.

Moth code	Longevity (days)	Fecundity	Pharate adult weight (mg)	Weight related fecundity (/100mg)	Sum of all flights (hours)	Sum of long flights (hours)	Pre-oviposition period (days)
550	5	88	140	62.9	14.9333	10.7000	4
551	8	1012	140	722.9	0.2333	0.0000	4
552	5	234	145	161.4	11.8833	8.7000	4
565	8	490	133	368.4	2.6000	0.0000	4
567	6	23	128	18.0	7.2000	3.0667	5
568	5	3	141	2.1	7.7667	6.6167	4
575	6	386	142	271.8	3.9333	2.1833	3
576	6	97	135	71.9	9.7167	5.1333	5
585	7	573	116	494.0	1.4000	0.0000	4
586	6	140	106	132.1	2.6667	0.0000	4
589	8	962	141	682.3	0.8833	0.0000	4
590	7	756	140	540.0	1.3000	0.0000	4
593	6	343	117	293.2	3.6000	0.0000	4
594	6	122	118	103.4	7.9667	1.7833	4
595	6	348	130	267.7	4.6500	2.1333	4

3. Life-history data for moths flight-tested for N0-N2 and subsequently fed 10% sucrose w/v as part of the investigation of the effect of flight on fecundity.

Moth code	Longevity (days)	Fecundity	Pharate adult weight (mg)	Weight related fecundity (/100mg)	Sum of all flights (hours)	Sum of long flights (hours)	Pre-oviposition period (days)
1	8	705	107	658.9	0.7803	0.0000	5
2	9	910	126	722.2	0.2325	0.0000	5
3	10	826	108	764.8	0.1556	0.0000	5
4	11	825	142	581.0	4.9781	2.1017	5
5	9	923	148	623.6	6.7583	5.4189	5
6	8	789	115	686.1	0.0936	0.0000	5
7	11	1207	156	773.7	0.7489	0.0000	5
8	10	1295	175	740.0	6.8817	4.6247	5
9	8	1060	168	630.9	3.2636	0.0000	5
10	8	1343	187	718.2	2.6717	0.0000	5
11	8	765	112	683.0	0.2781	0.0000	5
12	14	628	169	371.6	2.3294	1.4025	5
13	10	1050	137	766.4	0.4956	0.0000	5
14	11	727	142	512.0	10.4903	9.2506	6
15	12	555	156	355.8	1.9606	0.0000	9
16	10	753	178	423.0	11.8414	3.5156	6
17	11	633	88	719.3	2.0708	0.0000	5
18	9	855	121	706.6	7.7544	6.2528	5
19	9	788	103	765.0	0.7944	0.0000	5
20	8	1053	155	679.4	0.2778	0.0000	5
21	9	592	104	569.2	1.7572	0.0000	5
22	8	720	108	666.7	6.1078	1.4264	5
23	8	860	122	704.9	0.4033	0.0000	5
24	12	752	100	752.0	0.0442	0.0000	5
25	8	742	107	693.5	2.1811	0.0000	5
26	9	911	133	745.1	3.6581	2.6189	5
27	10	908	134	677.6	10.2708	4.2119	5
28	12	1057	161	656.5	10.3889	6.9272	5
29	12	502	121	414.9	5.4336	1.5089	6
30	11	821	113	726.5	0.6692	0.0000	5
31	11	838	149	562.4	0.3431	0.0000	5
32	10	843	108	780.6	0.5431	0.0000	5
33	10	955	144	663.2	0.0722	0.0000	5
34	10	555	102	544.1	1.9264	0.0000	5
35	9	934	144	648.6	4.4839	0.0000	5
36	9	403	104	387.5	1.1686	0.0000	6
37	10	1138	137	830.7	3.7286	1.5892	5
38	10	912	142	642.3	0.9361	0.6411	5
39	10	1245	162	768.5	3.0411	0.0000	5
40	9	1224	166	737.3	0.6489	0.0000	5
41	10	826	130	635.4	5.2117	1.7617	5
42	11	1028	153	671.9	0.4536	0.0000	5
43	11	1028	153	671.9	0.9694	0.0000	5