THE ECOLOGY OF THE WATER VOLE (*ARVICOLA TERRESTRIS* L.) IN SOUTHERN ENGLAND

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ABSTRACT

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THE ECOLOGY OF THE WATER VOLE (*ARVICOLA TERRESTRIS* L.) IN SOUTHERN ENGLAND

By Jonathan Mark Benge

In the UK, the water vole is usually found associated with water; in rivers, canals, ditches, streams, lakes and ponds. Now listed as a UK Biodiversity Action Plan priority species for conservation it receives partial protection under UK legislation. The current study used various techniques to investigate aspects of the ecology of water voles at five sites in the southern England.

Live-trapping techniques examined aspects of social organisation, such as population size, structure, distribution and Observed Range Lengths. Capture rates, weight differences and survival were also examined. Water voles became extinct from two study sites most likely due to American mink predation. Densities of water voles at three sites were generally higher than those recorded elsewhere, suggesting density may be dependent on type of habitat or other variables. Water voles were distributed along almost the entire length of these study sites. All populations peaked in size (as a result of juveniles entering the populations) and adult weights peaked in the spring and summer, declining in the autumn. Adult weights were generally lower than found in previous studies with no difference between adult male and female weights at any site. High rate of ear tag loss meant individuals could not be reliably followed between months, therefore the population estimates based on Minimum Number Alive (MNA) may have been significantly underestimated. The highest period of activity was between 22:00hrs and 06:00hrs corresponding with published studies.

The relationship between water vole numbers and latrines was examined and compared with published literature. Seasonal patterns in the production of latrines were examined to gain further information on their function and the bearing that this may have upon any relationship between latrines and water vole numbers. Further examination considered the number of latrines per individual water vole and compared these with the published literature. Rainfall rendered many counts invalid as rising water levels or the act of the rain itself washed latrines away. Numbers of latrines per water vole were generally lower than published attributable to differences in the physical character of sites. Three sites showed a broadly similar trend in the numbers of latrine counts across months. Latrine numbers generally fell over winter which is likely to correspond with low water vole numbers and above ground activity. Peaks in latrine numbers in March and April were attributed to the onset of the breeding season whilst peaks seen in August were attributed to large population sizes. Relationships were found between latrines and the total number of water voles captured, MNA, adult females and all adults; latrines and adult females; all adults during the breeding season at two of the sites. The resultant predictive equation for the number of water voles from the number of latrines was not significantly different from the published relationship.

Water voles were radio-tracked at one study site to examine overwinter behaviour. Home range sizes, movements, activity patterns and interactions were investigated. Due to time constraints and difficulty of intensive radio-tracking during cold conditions some sessions were done in August and September and some continued into March and April. Three of the tracked voles died during the study, two assumed to be through predation, probably by foxes, and one due to unknown causes. There was no difference between the area of male and female home ranges, however, male home ranges appeared to be longer than female ones. Increases in mean range length were seen in January, February and April likely to correspond to the onset of the breeding season. In many cases the majority of activity was centred on one or two points, identified as nest sites. A number of male water voles, and one female, dispersed to 'new' home ranges. Activity occurred within discrete blocks of time, 1.5hrs to 4hrs with rest periods of 0.5hrs to 4.5hrs. Home ranges of a number of males and females overlapped and positive associations only occurred towards the end of the breeding season.

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CHAPTER 1 INTRODUCTION

1.1 THE WATER VOLE

The water vole (*Arvicola terrestris* L. Rodentia: Muridae) is the largest of the British microtine rodents. It is found throughout most of Europe, although it is absent from Ireland and most of the Iberian Peninsula, where the smaller Southern water vole (*Arvicola sapidus* L.) is found (Macdonald and Barrett, 1993). In the UK, the water vole is usually found associated with water; in rivers, canals, ditches, streams, lakes and ponds. This contrasts with smaller fossorial water voles, of the same species, which are often found in continental Europe living in meadows, pastures and orchards, where they can become a serious pest.

An adult UK water vole can weigh between 200-350g. Different colour forms exist within the UK population, although the most common colouration is chestnut brown dorsally, grading into a lighter grey ventrally. Other colour forms range from melanic, in the north and north-west of Scotland, to black and tan (Strachan and Jefferies, 1993). Albinism is rare but partial albinism is common in most populations, usually appearing as a white tail tip or white patches on the forehead (Stoddart, 1970b; Leuze, 1976).

1.1.1 Habitat

In the UK, the water vole is usually found within close proximity to water, with only a few records of voles living away from water (Southern and Crowcroft, 1956; Strachan, pers. comm.). Almost any type of water source is acceptable, including rivers, canals, ditches and even ponds. A number of studies have looked at the habitat of the water vole, two of the most comprehensive being a study of water vole habitat preferences in the Czech Republic (Zejda and Zapetal, 1969) and that done as part of the UK National Water Vole Survey (Strachan and Jefferies, 1993). Earth banks over 0.5m in height with an angle of greater than 35°, allow water voles to construct their extensive burrow systems. Water depth is also important, with water voles showing a preference for water less than 2m in depth. Still or slow flowing water is also favoured, whilst no preference is shown for water quality (Strachan and Jefferies, 1993). Perhaps more important to the water vole is the vegetation found at the water's edge, providing both food and cover. The type of vegetation present will be influenced by physical characteristics of banks. Watercourses with a dense cover of grasses and ruderals are preferred to dense cover from trees or shrubs. Emergent vegetation, such as sedges and rushes, and aquatic vegetation are also important for food. Sites bordering woodlands are often discriminated against (Strachan and Jefferies, 1993) as are those adjacent to parks and gardens (Jones and Molloy, 1997). Water voles do not appear to show a particular dislike to any level of disturbance, being found in both rural and suburban areas.

1.1.2 Diet

Water voles are primarily herbivorous, having a wide range of potential food plants. Some 227 different species of food plant have been identified through examination of water vole feeding remains (Strachan and Jefferies, 1993). A large part of the diet is made up of grasses (Ashby and Vincent, 1976; Holisova, 1965), although some dicotyledons, in particular common nettle (*Urtica dioica* L.), also appear to be important. A study in the Czech Republic found aerial parts of plants to make up over 70% of the water vole's diet (Pelikan, 1974), although roots and rhizomes may be more important in the winter (Strachan and Jefferies, 1993). Water voles may also eat flowers, fruit and seeds (Strachan, 1997), and have occasionally been observed eating molluscs, and dead fish (Ryder, 1962; Howes, 1979).

Vegetation is often taken to feeding platforms at the water's edge where it is eaten. These platforms are identifiable from the neat piles of chewed vegetation left behind after feeding. When a female is nursing young, time spent away from the nest is kept to a minimum so vegetation around burrow entrances is eaten, creating characteristic lawns.

1.1.3 Current status

The results of the two national water vole surveys undertaken in 1989-1990 (Strachan and Jefferies, 1993) and 1996-1998 (Strachan *et al.*, 2000) indicate that since the 1900's there has been a long-term gradual decline in the British water vole population (Strachan and Jefferies, 1993). The rate of this decline has increased in recent years with high losses of populations reported between the two surveys. The loss of populations has been highest in the north and southwest of England, to the extent that water voles are currently believed extinct in Cornwall (Cornwall Wildlife Trust, pers. comm.). The loss of water vole populations is generally blamed on habitat loss or degradation and predation from the introduced American mink (*Mustela vison*). The water vole is now listed as a UK Biodiversity Action Plan priority species for conservation, and receives partial protection in UK legislation under the Wildlife and Countryside Act 1981 (as amended).

With the rapid decline of water voles in the UK, survey to identify remaining populations and monitoring of these populations are essential aspects of the Species Action Plan for water voles at both the national and local levels.

1.2 MONITORING MAMMALS

The importance of monitoring mammals is widely recognised for species where there is a direct application to conservation or management. In the UK, the Tracking Mammals Partnership has been established to provide a central point for the many groups involved in surveying mammals. The Partnership was established to assist the UK government in fulfilling their international obligations in relation to monitoring of UK mammals.

A range of survey techniques are available for monitoring mammals, depending on the species concerned and the objectives of the monitoring. For species with a limited distribution, the primary objective is often to monitor changes in range as opposed to numbers of individuals (Harris and Yalden, 2004). Equally, for some more common species, monitoring techniques do not provide accurate data on numbers, and it is therefore more appropriate to monitor distribution. On a local basis, it is often possible to use techniques that allow monitoring of numbers of individuals, although these can often be time consuming.

1.2.1 Survey techniques

Survey techniques for monitoring mammals range from direct counts, using observation of live trapping, to indirect counts based on signs of mammal presence.

1.2.1.1 Direct counts

There are a number of methods for obtaining direct counts of individuals in a population. The simplest is through direct observation either of a whole population (*e.g.* counts of red deer *Cervus elaphus* on hill sides; Clutton-Brock and Albon, 1989) or counts along a transect line (*e.g.* brown hare *Lepus europaeus*; Hutchings and Harris, 1996). However, for some species, live trapping provides a usual means of estimating population size. Live trapping is commonly used for the monitoring of small mammal populations (*e.g.* yellow-necked mouse *Apodemus falvicollis*; Marsh *et al* 2001), although is time consuming and only possible to undertaken at a limited number of sites.

1.2.1.2 Indirect counts

Indirect counts provide a useful method of monitoring mammals where it is either not practical to undertake direct counts or not possible due to the cryptic nature of the species. Many mammal species leave signs of their presence which can be counted and either provide evidence of the presence of the species or be used to estimate population size. Faeces often provide the best means of identifying species and for some species through the use of counts, the population size can estimated (*e.g.* Dung counts to estimate deer population size; Ratcliffe, 1987). Faecal counts work when it is possible to predict the approximate area where the species may be found and hence the area of search. However, for other species, the use of footprint tubes (*e.g.* hedgehogs *Erinaceus europaeus*), hair tubes (*e.g.* stoats *Mustela erminea*) or bait tubes (water shrews *Neomys fodiens*), provides a more effective means of monitoring.

1.3 DEMOGRAPHY AND SOCIAL ORGANISATION

The numbers of animals present in a population relates to births, deaths, immigration and emigration, carrying capacity, food availability, nest site availability, predators, parasites and diseases. When monitoring mammals it is therefore important to understand the demography and social organisation of the target species.

The demography and social organisation of a wide range of small mammals has been well studied and provides a basis for the understanding of water vole ecology.

1.3.1 Dispersion

The dispersion of animals throughout an area is often driven by factors such as habitat suitability, distribution of food sources and geographical barriers. Brown rats (*Rattus norvegicus*) tend to live in colonies (Fenn and Macdonald, 1987) whose range is dependent upon the availability of food (Taylor, 1978). There is also some evidence to suggest that the house mouse (*Mus domesticus*) live in distinct inbred family groups although this may vary in different habitats (Berry, 1991).

Water voles, in the UK, are thought form discrete local populations or breeding colonies along a watercourse (Lawton and Woodroffe, 1991). These breeding colonies occupy 'core' sites, whereas adjacent areas where water voles may visit but not breed are known as 'peripheral' sites (Lawton and Woodroffe, 1991). Within a core site, each adult female has her own territory containing her burrow system (Leuze, 1976). Telfer *et al* (2001) described populations on a tributary of the River Ythan, Scotland, as "patchy and discrete", however this distribution was not static between years. Local extinctions occurred, whilst other sites were colonised. This occurred even with the presence of American mink, suggesting that these metapopulation processed allowed water voles to survive the presence of such a vociferous introduced predator. However, isolation was determined to be a factor in recolonisation of sites. The increased extinction rates caused by mink predation have increased the isolation of sites, rendering it less like that sites will be recolonised.

1.3.2 Reproductive behaviour and life history

Both monogamous and polygamous mating systems have been recorded in small mammal populations. Male bank voles (*Clethrionomys galreolus*) have home ranges that overlap several females, suggesting that they are polgynous (Wolton and Flowerdew, 1985). Both monogamous (Garson, 1975) and polygnous (Brown, 1969) mating systems have been recorded in the wood mouse (*Apodemus sylvaticus*). There is also some evidence of a monogamous mating system in the dormouse (*Mus avellanarius*; Bright and Morris, 1989).

Adult female water voles are thought to be usually monogamous, whereas males, whose territories may encompass those of several females, attempt to be polygynous; bonds between males and females may begin as juveniles (Leuze, 1976). Breeding starts in March or April and will continue until September (Strachan and Jefferies, 1993). Courtship may be initiated by the male drumming with his hind legs, accompanied by vocalisations (Blake, 1982). Mating takes place on land or in the water (Strachan, 1997). Gestation lasts for 20 to 30 days during which time the female may move to a new home range and in the case of a population of Swedish water voles may mate again (Jeppsson, 1987). Each female may produce up to five litters per breeding season, each of about six young (Boyce, 1991). The young are born naked with closed eyes weighing 3.5-7.5 g. Lactation lasts for approximately 22 days, when the young will leave the nest to make way for the next litter (Boyce, 1991). The growth rate of young water voles is highly variable, although young from the first litters of the year may reach 110g at 30 days of age (Vincent, 1974). Young of later litters may grow more slowly (Vincent, 1974). In an Oxfordshire study, the earliest sexual maturity of females was at 77 g, although the mean weight was 110 g (Efford, 1985). Juveniles from these early litters may reproduce in the year of their birth (Stoddart, 1968) and begin to disperse as early as June (Woodall, 1977).

1.3.3 Territorial behaviour

Many small mammal species exhibit territorial behaviour, often reflecting their mating strategy. For example, bank voles (*Clethrionomys glareolus*; Wolton and Flowerdew, 1985) and field voles (*Microtus agrestis*; Viitala, 1977) both maintain territories during the breeding season. The males of both species have home ranges that overlap several female territories. In brown rats each clan defends a territory, usually around a burrow system (Timmermans, 1978).

In March, female water voles establish individual territories in preparation for breeding and these are fiercely defended. However, territories of related females may overlap (Leuze, 1976). Female territories may extend up to 150m, although this will vary dependent upon water vole density (Strachan, 1997). Male territories may be up to 300 m in length (Strachan, 1997), and will often overlap each other (Leuze, 1976; Jeppsson, 1987) encompassing up to five female territories (Sharul *et al*, 1997).

Small mammals commonly use faeces or urine as a means of communication (Corbett and Harris, 1991). Water vole territories are marked by latrine sites where large amounts of faeces are deposited. There is also evidence that water voles scent mark these latrines by scratching sebaceous flank glands (Frank, 1957; Stoddart, 1968; Leuze, 1976) although this behaviour is rarely seen. Male water voles will establish latrines at the ends of their mates' territories, which are reported to inhibit extension of the female range into another's territory (Leuze, 1976).

1.3.4 Dispersal

Dispersal of small mammals is essential to the colonisation of new areas and the movement of individuals between populations. Dispersal often occurs at the end of the breeding season and predominately comprises sub-adults (*e.g.* field voles; Gipps and Alibhai, 1991). In other small mammals, such as the wood mouse, adult males and females are seen to disperse in autumn and winter (Wolton and Flowerdew, 1985).

Two types of dispersal are recognised in water voles, long distance movements and short distance movements (Stoddart, 1970a). Short distance movements are when an individual moves its home range to a new site whilst still within the boundaries of the core site. Long distance movements are when an individual moves away from the core site. Adult water voles may undergo dispersal (Stoddart, 1970a; Woodall, 1977), but it is perhaps more commonly thought of as a juvenile behaviour. Juvenile dispersal may take place at the end of the breeding season (Leuze 1976), but there is evidence to suggest that it also occurs at the start of the breeding season. The appearance of new adults into a population is a common occurrence in the spring (Woodall, 1977). Saucy and Schneiter (1997), studying fossorial water voles in Switzerland, found large numbers of juveniles dispersing between March and June. Notably, dispersal predominately occurred on rainy nights. Unfortunately, similar intensive studies have not yet been conducted on UK water voles.

1.3.5 Activity patterns

Activity patterns in small mammals are vary depending upon the food source of the species and predator avoidance behaviour. Many small mammals are more active at night or during dawn and dusk. Bank voles are active throughout the day and night but have peaks in activity at dawn and dusk (Ashby, 1972). Field vole tend to be nocturnal during the summer, as are wood mice (Montgomery and Gurnell, 1985), but also show peaks in activity at dawn and dusk (Brown, 1956).

There is some uncertainty about the activity patterns of water voles. Following extensive field observations, Ashby *et al.* (1969) found that water voles are equally as active during the day as during the night. Leuze (1976) found water voles to be active every two to four hours, being active for longer during the day than the night. Based on live trapping results, Stoddart (1969) also found water voles to be active during the day and night, although they were more active during the day. An observational study on captive voles, in Denmark, found that in summer there was little difference between day and night activity, whilst in the winter most activity occurred during the day (Lund, 1970). In the same study, a correlation between sunrise and sunset and peaks of activity was found. In addition, Knight (1975) confirmed that when brown rats occurred at the same site, water voles were not active during the night when the rats were foraging, but exhibited increased activity at dusk and dawn to compensate.

1.3.6 Communication

Olfaction is important in communication for many mammals. In field voles, odours are found in faeces, urine and flank glands (Stoddart, 1982). Sounds may also be used, such brown rats infants that communicate ultrasonically (Turkell *et al*, 1979). Adults also communicate by sound, particularly during aggressive encounters. For example, bank voles may squeak or make sounds like teeth chattering during such encounters (Alibhai and Gipps, 1991; Stoddart and Sales, 1985).

Water voles begin communicating with their parents at an early age. When cold, pups as young as one or two days old will produce ultrasonic calls to attract their parents' attention (Blake, 1992). In antagonistic encounters, the water vole, utters a rhythmic series of short calls. These calls are thought to inhibit further approach by conspecifics (Volker, 1974). As with many mammals, scent also plays a major role in communication. Water voles have a large lateral sebaceous gland that produces a secretion that has a unique molecular structure, possibly allowing voles to recognise each other (Tomkins, 1985). This gland is functional even before pups leave the nest. The gland continues to develop throughout the life of the vole, showing bursts of activity during the breeding season. By the end of the season the gland has become redundant (Stoddart, 1968). Frank (1957) described the use of the lateral scent gland in communication, with the hind feet being drawn over the glands, then stamping the feet on the ground or latrine, presumably to distribute the scent. Adult male water voles will react differently to urine from females in oestrus, which may lead to antagonistic encounters between males (Leuze, 1976).

1.3.7 Mortality

Small mammals have many predators, for example 14 have been recorded for the bank vole in the UK (Goszczynski, 1983). Predation can account for the mortality of a larger number of individuals, which will be particularly vulnerable during dispersal.

Foxes, stoats, weasels, barn owls, heron, cats and pike are all known to eat water voles (Weber and Aubry, 1993; Leuze, 1976; Jefferies *et al*, 1989). Otters may also occasionally take water voles as prey (Jenkins *et al*, 1979). Young water voles may be killed by brown rats (*Rattus norvegicus* L.; Ryder, 1962; Leuze, 1976). A more recent addition to the water vole's list of predators is the American mink, which has been observed to exterminate whole colonies of water voles (Woodroffe *et al*, 1990a). In areas where water voles were present, they were found to be a major component in the diet of the mink, particularly in the first half of the year (Strachan and Jefferies, 1993). The maximum recorded life span, for a water vole in captivity, is 31.5 months (van Wijngaarden, 1954). However, in the wild, Stoddart (1971) found two years to be the longest life span. Dispersing juveniles are exposed to a higher predation risk (Leuze, 1976) and overall winter mortality is particularly high, at around 70% (Jordan pers.com.).

1.4 AIMS OF THE CURRENT STUDY

Current understanding of water vole ecology is based on a relatively small number of studies. There is evidence to suggest that the ecology of water voles may vary depending on the type of habitat that they inhabit. The majority of work has concentrated on water voles using rivers and streams, with few studies in the UK examining water voles in grazing marsh systems. The current study explores some of these aspects of water vole ecology in greater detail using live-trapping and radio-tracking techniques, and field sign surveys to study five populations in southern England. The aim of this part of the study was to:

Compare and contrast the ecology of water voles in different habitats in Southern England

Various signs of animal activity, or field signs, have previously been used to assess population size. Indices based on signs of activity are usually much quicker to collect than those based on trapping. A previous study (Woodroffe, 1988) identified a relationship between water vole numbers and water vole latrines at three sites in the north of England. Using a combination of latrine counts and live trapping the current study aimed to:

Assess the effectiveness of latrine counts as a means of estimating population size and understand water vole social organisation.

Little is known about the overwintering behaviour of water voles. However, current evidence suggests that overwinter mortality is high. The current study used radio-tracking techniques to examine aspects of social and individual behaviour, such as home range size and interactions between water voles, in a grazing marsh system with a particular emphasis on over-wintering animals. The aim of this part of the study being to:

Use radio-tracking techniques to study overwintering behaviour of water voles in a grazing marsh system.

CHAPTER 2 POPULATION DYNAMICS

2.1 INTRODUCTION

Trapping is commonly used to study small mammal populations. Data obtained from such experiments can provide information on their ecology and behaviour such as population size, population composition, population cycles, distribution, home range size, activity patterns, immigration/birth rate and emigration/death rate. There are two fundamentally different types of trapping; the first being live trapping where animals are captured, marked and returned to the population (*e.g.* Gaisler and Zejda, 1973) and secondly removal trapping, where captured animals are removed from the population (*e.g.* Village and Myhill, 1990). Whilst removal trapping, using snap traps, has previously been used for studying water voles (*e.g.* Pelikan, 1974), is not an appropriate technique for a species rapidly declining in numbers, as is the water vole in the UK. Many previous studies have used live trapping to study aspects of water vole (*Arvicola terrestris*) ecology and behaviour in the UK (*e.g.* Stoddart, 1968; Leuze 1976; Woodall, 1977) and other European countries (*e.g.* Pelikan and Holisova, 1969; Gaisler and Zejda, 1974). A range of live traps have been used for water voles including bespoke wooden traps (*e.g.* Woodroffe, 1988), aluminium traps (Elliot traps – *e.g.* Barreto and Macdonald, 2000; Sherman traps – *e.g.* Jeppsson, 1987) and wire mesh traps (*e.g.* Wells, pers. comm.).

In the current study, live trapping was primarily conducted to look at the relationship between population size and numbers of latrines (Chapter 3). However, the data obtained from an intensive live trapping study such as this are likely to be of interest and importance in their own right. Much of the current knowledge of water vole ecology in the UK is based on a small number of studies (*e.g.* Stoddart, 1968; Leuze 1976; Woodall, 1977; Woodroffe, 1988). This chapter therefore addresses this important area and adds to the knowledge of water vole ecology in the UK, in addition to providing estimates of population size for later analysis with latrine data.

This chapter considers a range of aspects of water vole ecology and behaviour which can be examined using live trapping data namely; Population size (Section 2.1.1), Population composition (Section 2.1.2), Capture rate (Section 2.1.3), Distribution (Section 2.1.4), Activity (Section 2.1.5), Weight (Section 2.1.6), Survival (Section 2.1.7) and Movements (Section 2.1.8).

2.1.1 Population size

Studies using live or removal trapping of water voles often involve obtaining a measure of population size, either for further analysis or as a basis for comparison with other populations. Woodroffe (1988) used the actual numbers of water voles captured as an index of the population size during different trapping sessions at sites in the North York Moors National Park, UK. Green (1998) used a similar method on a population of water voles on the River Mimram in Hertfordshire, UK, as did Singleton (1984) for a population in West Lancashire, UK. However, estimation techniques are available to enable population estimates to be calculated from Capture-Mark-Recapture data. Methods are available for "open" populations (assumes that the population is open to emigration, immigration, births and deaths), such as the Jolly-Seber method and "closed" populations (assumes that no emigration, immigration, births or deaths occur), such as the Lincoln Index (Montgomery, 1987). These methods rely on a number of assumptions. The Lincoln Index assumes the following:

- the population is closed;
- all individuals have the same chance of being captured in the initial trapping session;
- capture in the first trapping session does not affect the probability of an individual being captured in a subsequent session;
- marked animals must mix evenly with unmarked ones;
- the marks applied in the first trapping session must last until the second;
- there is no ambiguity in identifying marks in the second session.

Assumptions of the Jolly-Seber model include:

- each animal (marked and unmarked) in the population has the same probability of being captured in any session provided it survives and is in the population during the session;

- following release, each marked animal has the same probability of surviving and remaining in the population.
- all captured animals are equally likely to be returned to the population;
- marks are not lost;
- the time required for sampling the population is short and animals are released immediately after the sample is taken.

Woodall (1977) used the Lincoln Index, to estimate the population size of water voles on a river in Uxbridge, UK. Jeppsson (1987) also used a mathematical estimator to estimate population size of water voles in Southern Sweden. In contrast, Woodall (1977) and Barreto and Macdonald (2000) used an enumeration technique, Minimum Number Alive (MNA), to estimate population size on the River Thames and the River Windrush respectively, both in Oxfordshire, UK. Enumeration techniques known as MNA methods are widely used in estimating small mammal populations (Krebs, 1999). The basis of this method is that if an individual misses being caught during one trapping session but is known to be present in both the previous and subsequent session it is assumed that they were present, although not captured, during the intervening session. It should be noted that MNA will usually give an estimate less than or equal to the true population size. Where mark loss is high, an underestimate will always occur.

2.1.2 Population composition

During trapping experiments, the sex and reproductive status of individuals is usually recorded, often enabling further comparisons between the sexes. Gaisler and Zejda (1974) looked at changes in the composition (proportions of males and females) of a water vole population in southern Moravia, Czech Republic, over a 3 year study. Another study in the Czech Republic looked at sex ratios based on removal trapping experiments (Pelikan and Holisova, 1969). Stoddart (1971) and Singleton (1984) looked at the reproductive status of females and the appearance of juveniles in a population in the UK to evaluate reproductive performance.

2.1.3 Capture rate

In any trapping study it is useful to have some measure of the trappability of animals to ensure that trapping has taken place for an appropriate length of time. The most comprehensive study of this kind on water voles was undertaken by Pelikan *et al.* (1971), who looked at the percentage of the water vole population captured during successive days over trapping sessions of up to four days in length in a population in southern Moravia, Czech Republic. Other studies have generally concluded that prebaiting of traps is unnecessary for water voles and that the majority of the population can be captured within three to five days (*e.g.* Zejda and Zapetal, 1969; Singleton, 1984)

The current study looked at the percentage catch size over the trapping sessions to validate the methods chosen (see Section 2.2.7.4).

2.1.4 Distribution of water voles

In a study in the North York Moors National Park, UK, Lawton and Woodroffe (1991) looked at the distribution of water voles in relation to habitat suitability and mink predation. Stoddart (1968) also looked at the distribution voles within stream system in Aberdeenshire, UK. Other authors have looked at the capture success of individual traps (*e.g.* Woodall, 1977; Barreto and Macdonald, 2000) which may influence the perceived distribution of water voles.

In this study the capture success of individual traps was examined and related to environmental features where possible, in order to provide site specific information on the distribution of water voles.

2.1.5 Activity

The activity patterns of water voles have been well studied in both the UK and other European countries. Knight (1975) and, Ashby and Vincent (1976) used field and laboratory observations to study daily activity patterns of water voles. More commonly, daily activity patterns have been inferred from trapping data (*e.g.*Stoddart, 1969; Gaisler and Zejda, 1973; Singleton, 1984; Green, 1998).

In this study data obtained from trap captures have been used to infer information on daily activity patterns.

2.1.6 Weight

Individual weights are commonly recorded during live trapping experiments. Changes in an animal's weight can be caused by a number of factors including natural growth, pregnancy or disease. By following the weight changes of individuals or groups (*e.g.* males, females and juveniles) it is possible to gain a greater understanding of the dynamics of a population. Comparisons can be made between different times of year, gender and sites. Numerous authors have recorded weights of individual water voles as part of trapping experiments (*e.g.* Gaisler and Zejda, 1973; Woodall 1977; Singleton, 1984; Barreto and Macdonald, 2000). Stoddart (1971) studied weight changes in more detail to look at the growth and survival of juvenile water voles, whilst Zejda (1992) looked at the overwintering weight of adults as well as juvenile growth.

The current study considered changes in adult, female and juvenile weights. Weights between study sites are also considered to give an understanding of geographical differences.

2.1.7 Residency

The residency of individual water voles can be estimated from trapping data. A weakness of this approach is that the disappearance of an individual from a population does not necessarily imply its death, but may be due to emigration or the animal being present but not captured or the individual mark being lost. However, this approach always gives an estimate equal to or less than the actual survival rate and is the most efficient method of determining residency rate in the natural environment. Stoddart (1971) looked at the survival rates of individuals whose birth dates had been calculated using an estimation technique based upon body weight. Woodall (1977) also investigated survival rates of a population of water voles in the UK, whilst Singleton (1984) concentrated on over winter survival.

Despite the weaknesses of estimating residency or survival rates, this study investigated redsidency in an attempt to compare these data with the published survival rates.

2.1.8 Movements

Water vole home ranges have previously been estimated from live trapping data (*e.g.* Woodall, 1977; Singleton, 1984). Pelikan and Holisova (1969) also looked at the distance between the two remotest capture points for water voles to calculate the Observed Range Lengths (ORL) or trap-based home ranges. This method is far less accurate that using radio tracking techniques (*e.g.* Saucy, 1987; Barreto and Macdonald, 2000) (see Chapter 4) and will always give an underestimate of home range size, as the apparent home range is limited by the location of available traps and the number of captures of an individual (Pelikan and Holisova, 1969). In addition, the presence of traps within the home range may alter the behaviour and space utilisation of individuals (pers. obs.).

This study investigated movements by individuals between traps, looking at ORL, to give a general understanding of space use by different sexes and between sites over different times of year.

2.2 METHODOLOGY

2.2.1 Study Sites

Five study sites, where water voles had previously been recorded, were chosen. Sites were chosen to represent a range of different habitat types and on the basis of accessibility. The size of the study sites, *i.e.* the length of watercourse varied depending on accessibility and the number of traps available. All five sites were located in southern England (Figure 2.1).

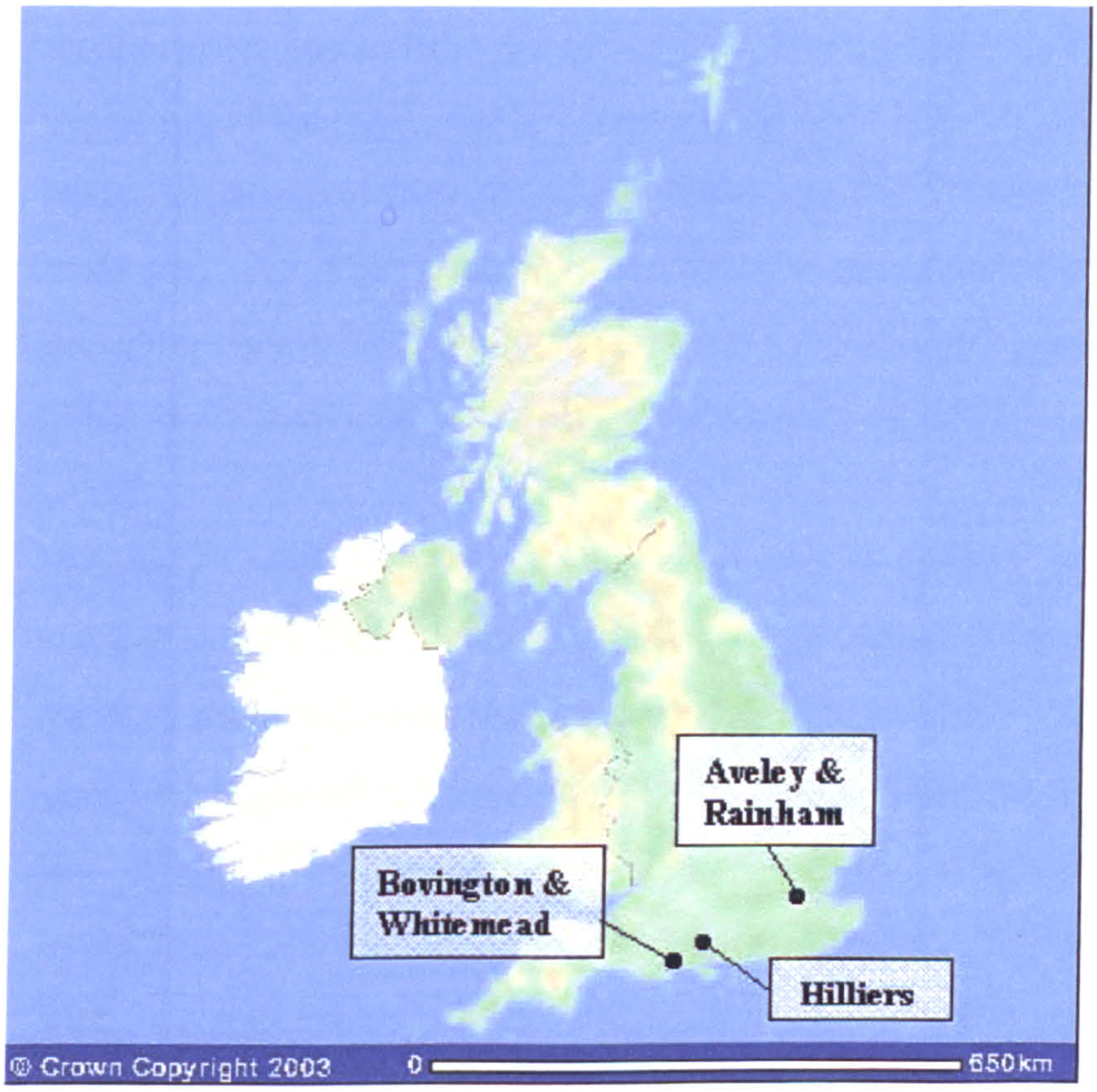

Figure 2.1 Location of study sites within the UK
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2.2.1.1 Aveley study site (TQ 543792; Figure 2.2; Plates 2.1 & 2.2)

This study site was a 200m length of drainage ditch within Aveley Marsh, part of the Inner Thames Marshes Site of Special Scientific Interest (SSSI) (Figure 2.2) in Essex. The entire area contained an extensive network of inter-connecting ditches (ranging from brackish to fresh water) taking water off the site via a pump situated at the end of the ditch on which this study site was situated. The presence of water voles was suspected in most of these ditches and a survey undertaken for English Nature during this study found over 50% of the total ditch length to be inhabited by water voles (Benge 1999). The area is part of a traditional coastal grazing marsh, although cattle were only reintroduced to the site in 1996 after an absence of several years. At the beginning of the study, cattle were confined to an area covering the northern end of the study site, however from September 1998 they were allowed access to the whole of the study site. The grazing marsh is dominated by grasses common of neutral soils, including cock's-foot (*Dactylis glomerata*), red fescue (*Festuca rubra*) and Timothy (*Phleum pratense*), with an open, short tussocky structure.

The study site was divided into two 100m lengths of ditch, one to the north of the road and one to the south. However, as water voles regularly passed through a culvert under the road, these two sections were treated as a single 200m length. The section of ditch in this study site was approximately 3m in width with a depth varying between 1m and 2m. Banks varied in steepness from 35° to 65° and the top of the bank above water level varied from between approximately 20cm and 100cm. Vegetation within the section of ditch was dominated by dense stands of common reed (*Phragmites communis*). The banks were dominated by common grasses. No management activities had been undertaken on the study site for at least 10 years.

Figure 2.2 Aveley study site within the Inner Thames Marshes SSSI, Essex
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Plate 2.1 Section of Aveley study site (photograph taken May 1999)

Plate 2.2 Section of Aveley study site (photograph taken January 1999)

2.2.1.2 Rainham study site (TQ 530810; Figure 2.3; Plates 2.3 & 2.4))

This study site was a 100m length of drainage ditch within Rainham Marsh, part of the Inner Thames Marshes (SSSI) in Essex. As with Aveley Marsh, the area contains an extensive network of inter-connecting ditches. Water voles were suspected to be present in most of these ditches and a survey undertaken during this study found over 85% of the total ditch length to be inhabited by water voles (Benge, 1999). The area had not been grazed for over 10 years and consisted of areas of rank tussocky grassland and ruderal herbs.

The study site was chosen as it was the most accessible section of ditch in the area. The section of ditch was approximately 4m wide and between 1-2m in depth. The banks varied in steepness from 35° to 45° with a height to the top of the bank of between 5cm and 20cm. It was dominated by very dense stands of common reed within the channel and on the banks. No management activities had been undertaken on the study site for at least 10 years.

Figure 2.3 Rainham study site within the Inner Thames Marshes, London
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Plate 2.3 Section of Rainham study site (Photograph taken June 1999)

Plate 2.4 Rainham study site (photograph taken January 1999)

2.2.1.3 Hilliers study site (SU 395255; Figure 2.4; Plates 2.5 & 2.6)

This study site was a 320m length of chalk stream within the Sir Harold Hillier Gardens and Arboretum, near Romsey in Hampshire. The stream flowed through an area of lowland hay meadow on neutral soils, which was cut for hay each year. A mown grass path bordered one bank of the stream approximately 1m from the water's edge. The other bank was bordered by the hay meadow.

The study site was bounded at one end by a road with a culvert underneath taking the stream into arable fields and the other by a wooded area in which no signs of water vole activity had been found. It was therefore assumed that the entire population was confined within the 320m long study site. The stream varied in width from 1m to 1.5m, with a depth of between 5cm and 50cm. However the depth would increase rapidly following rainfall to a maximum depth of 1m. The banks varied in steepness from 45° to 90°, however mud banks were commonly exposed along the bottom of the banks during times of moderate or low flows. The bank height varied from 50cm to 100cm. Whilst not prolific, the in-channel vegetation consisted of areas of floating sweet-grass (*Glyceria fluitans*). The banks of the stream were dominated almost exclusively by rosebay willowherb (*Chamerion angustifolium*) and meadowsweet (*Filipendula ulmaria*). Four exotic trees, all *Crategus* spp, were situated on the bank side. Management of the stream consisted of an annual cut of the vegetation on both banks in late October. Cut vegetation was usually left on site. However, no cut took place in October 1998.

Figure 2.4 Hilliers study site within Sir Harold Hillier Arboretum, Romsey, Hampshire
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Plate 2.5 Section of Hilliers study site (photograph taken August 1998)

Plate 2.6 Section of Hilliers study site (photograph taken February 2000)

2.2.1.4 Bovington study site (SY 839874; Figure 2.5; Plate 2.7)

This study site was a 200m stretch of the River Frome, a chalk stream river, passing through the Bovington wàter meadows, adjacent to a Ministry of Defence vehicle training area in Dorset. The north bank of the river lies within land owned by the Ministry of Defence adjacent to an unmanaged lowland hay meadow. The south bank was grazed by sheep.

A 200m stretch of the river was chosen as a study site on the basis of the number of traps available. The width of the river in the study site was approximately 5-6m, with a depth of 40cm to 100cm rising to120cm in the winter. The banks were mostly at 90°, however mud banks and stands of floating vegetation were frequent along the base of the bank. Bank height varied from 50cm to 150cm.

In-channel vegetation consisted primarily of *Ranunculus* spp. communities and stands of floating sweet-grass. Bankside vegetation was dominated by common grasses at the top of the banks with stands of reed sweet-grass (*Glyceria maxima*) at the water's edge. Five trees, including oak (*Quercus* spp.) and hawthorn (*Cratageus* spp), were located on the southern bank overhanging the river. Management was limited to sheep grazing on the southern bank. American mink and otter were known to use the study site (Pers. obs.).

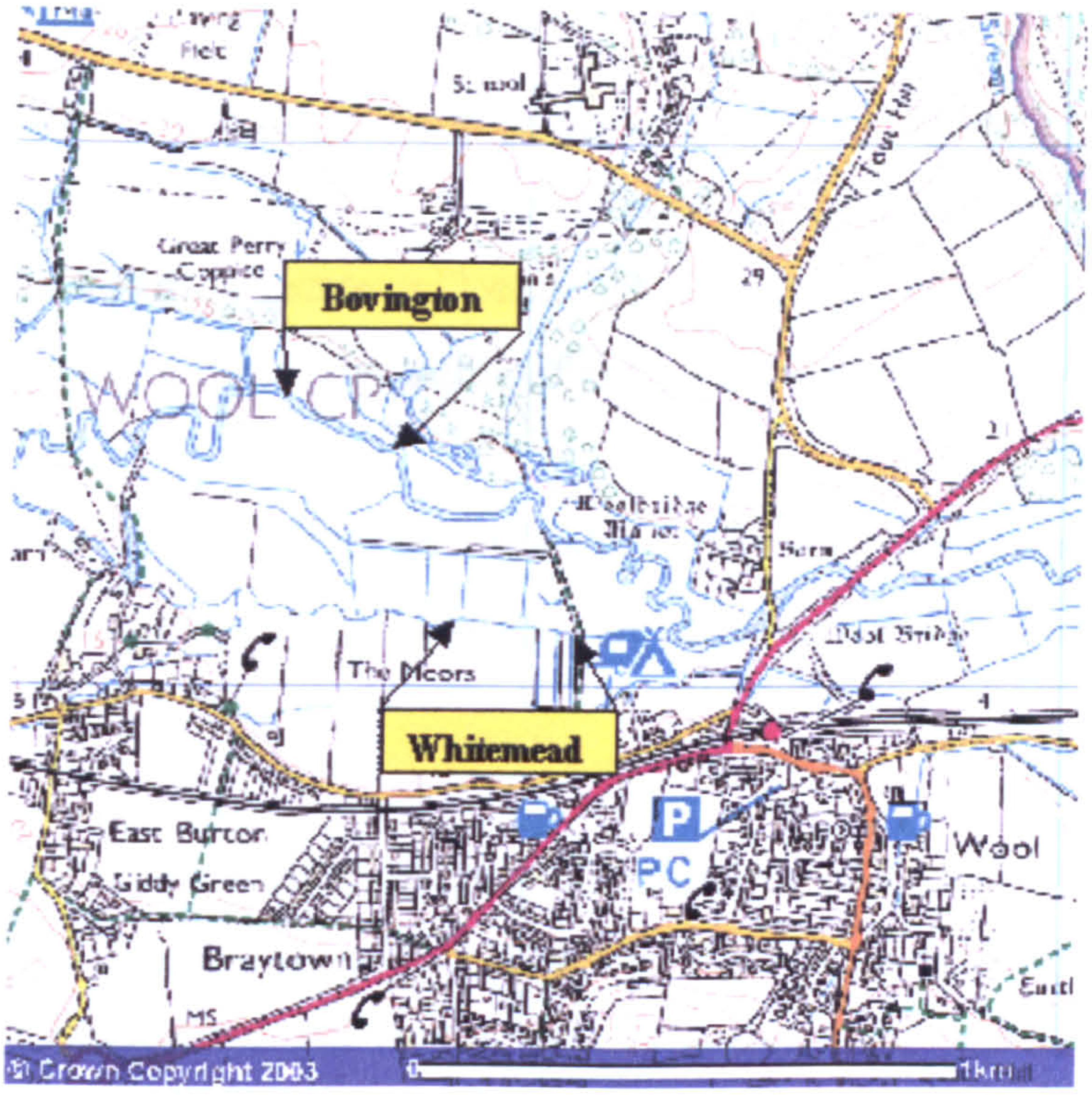

Figure 2.5 Bovington and Whitemead study sites at Wool, Dorset
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Plate 2.7 Bovington study site (photograph taken August 1999)

2.2.1.5 Whitemead study site (SY 840872; Figure 2.5)

This study site was a 200m stretch of a carrier channel of the River Frome within the East Burton Estate in Dorset. The channel flowed through an area of sheep grazed water meadow, consisting of common grasses and rushes.

The channel within the 200m study site was approximately 4m wide with a depth of 70cm to 150cm. The banks were approximately 90°, however the height varied from 10cm to 50cm.

In-channel vegetation consisted primarily of *Ranunculus* spp. communities and stands of floating sweet-grass. Bankside vegetation was dominated by common grasses. The northern bank was heavily grazed by sheep and therefore the vegetation had little structure. The southern bank was not grazed as heavily and had stands of floating sweet-grass and reed sweet-grass. American mink and otter were known to use the study site (pers. obs.).

Plate 2.8 Section of Whitemead study site (photograph taken August 1999)

2.2.2 Trap design

The live-traps used in the present study were XLK folding traps (H.B. Sherman, Tallahassee, USA). During August 1998 to November 1998 traps were used with a minimal amount of hay as a bedding material as this was found to impair the trigger mechanism. In March 1999 the traps were modified to include a wooden nest box (designed and built by Dr Edward Eastwood, University of Hertfordshire), in which bedding could be provided, allowing trapping to continue through the winter. The five sided nest boxes were made from 9mm marine ply wood treated with a wood varnish (Outdoor Varnish, Ronseal, Sheffield, UK). The rear door of the traps was removed and a section of ply wood attached around the end of the trap, which then slotted into a groove on the nestbox (see Figure 2.6 and Plate 2.9)

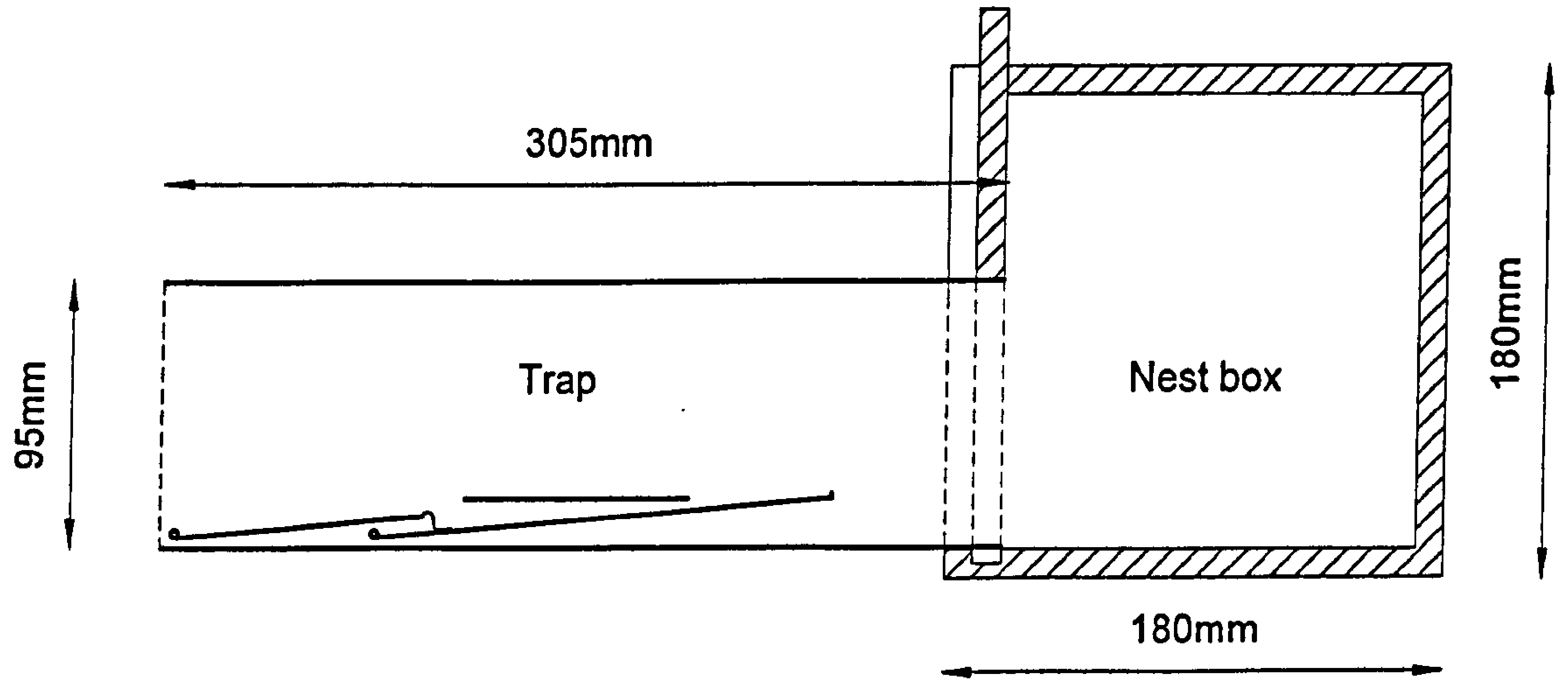


Figure 2.6 Longitudinal section of XLK trap (H.B. Sherman, Tallahassee, USA) with 9mm marine ply nestbox attached as used at all sites in the current study.

Plate 2.9 XLK trap (H.B. Sherman, Tallahassee, USA) with 9mm marine ply nestbox attached

2.2.3 Trapping methods

At each site, traps were baited with approximately 100g of grated carrot and hay within the nest box for bedding. The traps were placed at 10m intervals along both banks. As in previous studies, 10m spacing was considered the optimum distance to obtain most captures (Stoddart, 1970a; Singleton, 1984; Woodroffe, 1988). The traps on opposite banks were staggered by five metres, so that along the water course there was a trap every 5m on one of the banks (see Figure 2.7 for example of trap positions). The traps were placed parallel or at right angles to the water's edge, as close to the waterline as possible if there was no risk of flooding and were not prebaited (*i.e.* placing bait in the trap with the door locked in the open position) as Woodall (1993) found this unnecessary. Traps remained in position for three days, constituting one trap session. Stoddart (1968), with comparable trap spacing (12.5m), used trapping sessions of up to three days and after one day of trapping had captured in excess of 70% of the population. In another study, in the Czech Republic, 62% of the population had been captured after the first day of trapping (Zejda and Zapetal, 1969). Three days was therefore considered sufficient for the current study.

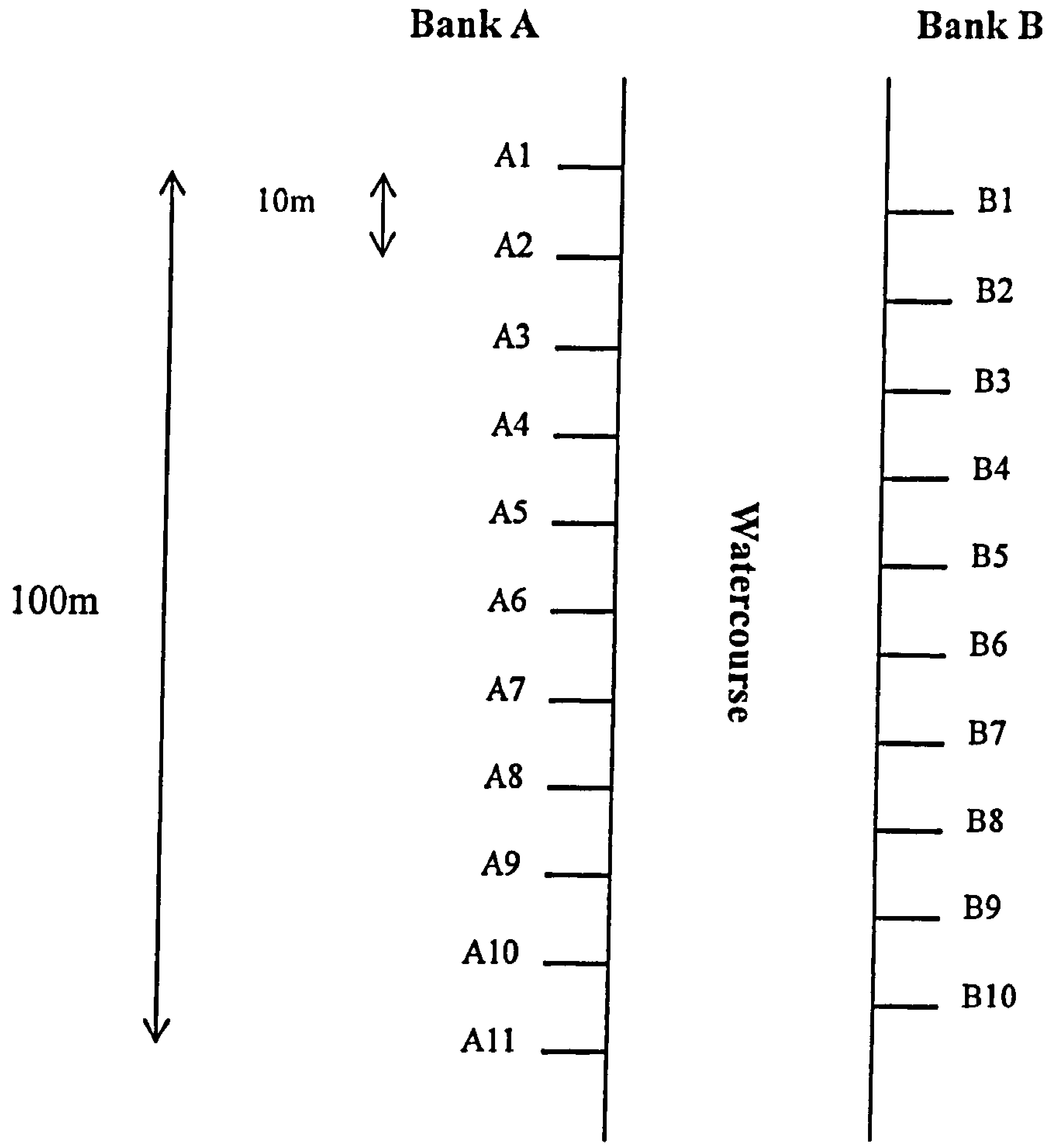


Figure 2.7 Schematic showing trap positions (A1–A11 & B1–B10) and spacing for a 100m length of watercourse.

During each session, traps were checked initially by a trap round every 12 h (06:00h and 18:00h), in August 1998 and September 1998, however it was subsequently decided to check the traps at 8 hourly intervals to reduce the stress on captured animals. Therefore trap rounds were made at 06:00h, 14:00h and 22:00h.

Field measurements (Section 2.2.4) were taken of captured voles which were subsequently released at the point of capture. Traps were rebaited with fresh grated carrot and hay, then returned to their original position.

All traps were rebaited daily, during one of the trap rounds, whether or not any animals had been captured. During the summer months the traps were often rebaited twice per day (06:00h and 22:00h) to ensure that fresh carrot was available throughout the trapping session.

Each trap position remained constant, to the nearest metre, throughout the study. Slight variations in trap position were allowed to accommodate changes in the bank structure and changing water levels between months. Trapping took place at Aveley each month between August 1998 and July 2000 inclusive, with the exception of December 1998 to February 1999. No trapping took place during this period as it was considered that there was a high mortality risk to animals being caught in traps with little bedding. Subsequently, nest boxes were added to the traps enabling trapping to take place throughout the following winter. As with Aveley, trapping took place at Hilliers each month between August 1998 and July 2000 inclusive, with the exception of November 1998 to February 1999 for the reasons explained above. Trapping at Rainham took place between August 1998 and June 2000, with the exception of November 1998 to February 1999. Trapping was terminated in June 2000 at Rainham due to vandalism of traps associated unauthorised people accessing the site. Trapping at Bovington and Whitemead took place between August 1998 and November 1998.

2.2.4 Field measurements

Captured water voles were placed into a nylon net bag (mesh size 10mm) and weighed using a 500g spring balance (Model 12, Salter Brecknell Weighing Products, Minneapolis, USA). The bag was weighed immediately after each vole had been weighed and the mass of the bag subtracted to obtain the vole's true mass, which was measured to the nearest 5g.

Captured voles were then removed from the bag using thick cotton and leather gloves (Superior Industrial Gloves, Draper Tools, Hampshire, UK) and were sexed using a combination of techniques. When external signs, such as swollen nipples in females and descended testicles in males, were not obvious, animals were sexed based on the observed distance between the anus and the urinary papilla (Stoddart, 1968). For males the distance often exceeds 10mm, whereas for females the distance is usually less. In addition in males the penis can often be everted.

Where possible, the reproductive status of the voles was recorded, as were any distinguishing characteristics. The reproductive categories used for females were imperforate, perforate, pregnant and lactating. Imperforate animals are immature females in which the vagina is covered in a membrane. This membrane perforates prior to the first oestrus and these animals were termed perforate. The vagina may also temporarily close up during pregnancy or outside the breeding season making it difficult to distinguish from imperforate. Pregnancy was recognised by weight and abdominal swelling. In lactating females the nipples are large and visible, indicating that the animal is suckling young. In immature or non-breeding males the testes are held within the body, descending at the start of the breeding season. The reproductive status of male voles was therefore characterised by testes size, large, medium or small.

2.2.5 Marking

A variety of techniques are available for marking small mammals in Capture-Mark-Recapture studies. In water vole studies, toe-clipping (*e.g.* Woodall, 1977; Moffatt, 1984), ear tagging (*e.g.* Stoddart, 1971; Singleton, 1984), implanted transponders (Baretta and Macdonald, 2000) and fur clipping (Singleton, 1984) have been used to identify individuals. For this study, toe clipping was rejected on the basis that it would cause unnecessary harm to voles. Fur clipping and fur dying techniques were not used as these marks have limited life expectancy. Implanted transponders were too expensive to use in such an intensive study. Woodall (1977) reported ear tag loss to be a serious problem, however other studies have not suffered to such a degree (e.g. Singleton 1984). Therefore, in the current study, captured voles were tagged using numbered monel metal small animal ear tags (model 1005-1, National Band and Tag Company, Kentucky, USA). The tags were inserted into either ear using an applicator (model 1005s1, National Band and Tag Company, Kentucky, USA). The ears of animals under 40g in weight were often difficult to locate and very easily damaged. In most instances these animals were marked using a simple adhoc fur clip instead of an ear tag. The point of capture, time and date were noted along with the tag number (or fur clip position). Any identifying characteristics, such as scars, abnormal pelage colours and white patches of fur were noted to aid identification of animals in the event of ear tag loss. The voles were then released at the point of capture and the trap rebaited with fresh grated carrot and hay.

2.2.6 Data preparation

For analysis of the data, it was necessary to define age class (Section 2.2.6.2) and also season (2.2.6.2).

2.2.6.1 Age classes

Before data analysis it was necessary to categorise animals as either adult or juvenile. For the purposes of the current study juveniles were taken to be young animals that had not reached reproductive condition. In reality, unless the history of an animal is known, it is not possible to determine this. It was therefore necessary to establish a working definition of a juvenile water vole. Working with captive water voles, Stoddart (1971) concluded that it is possible to determine the age of individuals weighing less that 110g as being not more that 49 days. He also found that no water voles bred during the year of their birth and overwintered at approximately 130g. In another study, voles were found to overwinter at approximately 150g and by the following March no animal weighed less than 140g, therefore a juvenile was classed as an individual weighing less that 170g between May and December (Singleton, 1984). In the current study no individuals weighing less than 140g were found to be in breeding condition. Therefore, juveniles were categorised as those animals weighing less than 140g.

2.2.6.2 Seasons

For some statistical analyses it was necessary to condense the data. The simplest method was to group monthly trapping data into seasons. The groupings were chosen on the basis of known (Strachan and Jefferies, 1993) and observed water vole seasonal activity. Strachan and Jefferies' (1993) description of the water vole calendar can be summarised as follows:

January – February: Few signs of activity as the population density is low and the majority of time is spent underground.

March – April: Females determine onset of breeding. Latrines begin to be established and immigration makes up the full complement of females.

April – May: Peak in birth rate.

June: Peak in newly weaned juveniles.

July – September: Second and third litters produced. Juveniles begin to disperse.

September: Peak in population size.

October – November: Dispersal, sexual activity ceases and voles store food for the winter.

December: Home ranges contract and more time is spent underground.

Based on the above description months were grouped to best reflect changes in water vole seasonal behaviour as shown in Table 2.1.

Table 2.1 Water vole seasons, as used in analysis of live-trapping data. Based on data from Strachan and Jefferies (1996) and personal observations.

Month	**Season**
March/April/May	Spring
June/July/August	Summer
September/October/November	Autumn
December/January/February	Winter

2.2.7 Data analysis

2.2.7.1 Population estimation

In order to compare the data between study sites and published data it was necessary to obtain population estimates, using a consistent method. Absolute counts are the ideal way of measuring the size of a population, however it is unlikely that all animals will be captured in any one trapping session due to factors such as dispersal, differences in trappability and the presence of lactating females. It is therefore more useful to use some form of index, using the animals captured as a sample of the population.

The populations in the current study are not closed, as they are in fact samples of a larger population on the watercourses, with the potential for emigration and immigration at either end. Additionally, immigration and emigration are known to have occurred in the form of births and deaths. Already, one of the assumptions of the

Lincoln Index is not met. The populations in the current study were open and therefore the Jolly-Seber method was examined. One of the assumptions of this method is that marks are not lost. In the current study, the frequency of ear tag loss was high (Section 2.3.7) with few individuals being recognised as having been captured in more than one trapping session. The loss of marks will lead to an overestimation of the population size (Begon, 1979 cited in Montgomery, 1987). Mark or tag loss can be taken into account in the estimation of population size, however, an estimate of the rate of tag loss is first required (Montgomery, 1987).

For estimating water vole populations either the total number captured (*e.g.* Woodroffe, 1988; Barreto and Macdonald, 2000) or MNA (*e.g.* Woodall, 1977) have been used. Whilst it is noted that it is likely to be an underestimate of the actual population size, total number captured and MNA were used for population estimates in the current study, over the Jolly-Seber method which, given the high frequency of tag loss, would have provided an overestimate of the actual population size.

In addition the density of water voles was calculated for each month at each site by calculating the number of water voles per 100m of watercourse.

2.2.7.2 Population structure

The data were explored to look at trends in population size, number of adult females, number of adult males and number of juveniles between months. See Section 2.2.6.1 above for an explanation of the criteria used to categorise juveniles and adult. The data were explored for trends in the onset of breeding using the reproductive characteristic of individuals determined as described in Section 2.2.4.

2.2.7.3 Capture rate

To examine the distribution of captures over the three trap days in each trapping session, the mean percentage of the population captured on each of the three trap days was calculated. Only data from Aveley, Rainham and Hilliers were analysed in this way as there were too few captures at Bovington and Whitemead for any meaningful analysis.

2.2.7.4 Distribution of water voles

In order to determine the use of each study site by water voles the data were explored to look for patterns in their distribution. The total number of captures at individual trap positions was used to examine the distribution of voles.

2.2.7.5 Activity

The data were examined to explore the daily activity patterns of water voles at Aveley, Rainham and Hilliers. Data from Bovington and Whitemead were too few to analyse. With the exception of August 1998 at all sites and September 1998 at Hilliers, trap rounds took place at the same times every month. Therefore the data can be used to examine any effects of the time of day on the numbers of water voles captured (*i.e.* water vole activity). The percentage contribution of each trap round to the total number of catches during each session was calculated. Data from trapping sessions were then pooled into each of the seasons.

2.2.7.6 Weight

Data collected on weights of captured water voles were explored to investigate changes in the mean weight of adult males and females between months and sites (Aveley, Rainham and Hilliers only). The data were also explored to look at changes in the distribution of weight classes between months and sites. In this case the weight on first capture only was used to avoid increases or decreases in weight caused by repeated capture (Vincent, 1974; pers. obs.).

2.2.7.7 Residency

The residency of individuals was examined based upon appearances of individual tag numbers between monthly trapping sessions (tag life) for Aveley, Hilliers and Rainham.

2.2.7.8 Observed Range Length

The movements of individuals at Aveley, Rainham and Hilliers were analysed to determine the home range, or Observed Range Length (ORL) based on trap captures. ORLs were calculated for male, female and juvenile water voles at each site during each month by determining the distance between the two remotest trap positions that an individual was captured at. This analysis only used records from animals that were captured more than once in a trap session. Mean ORLs for males, females and juveniles for each month at each site were calculated.

2.2.8 Statistical methods

The statistical analysis used both parametric and non-parametric tests. In order to use parametric tests the data must be normally distributed (Siegel and Castellan, 1988). The distribution of the variables in each case was examined to ensure that it was normal by displaying the data as a histogram. If it was not normal then the variables were either transformed (see individual results sections) to normalise the data or non-parametric tests were used. Non-parametric statistics require little or no knowledge of the distribution of the data.

All hypotheses were tested using a critical probability (P) value of 0.05, unless otherwise stated. The following descriptions of each analysis is based on SPSS Base 7.0 for Windows, User's Guide (1996), Fowler *et al* (1998) and Dytham (1999).

Analysis of Variance (ANOVA): Parametric test used to examine the effect of independent variables (in the case of two-way ANOVA two independent variables) upon a single dependant variable. The independent variables divide the population into groups. ANOVA tests null hypotheses about the main effects of independent variables by comparing means. It can also be used to investigate interactions between the independent variables.

After determining that differences do exist among the means, **post hoc range tests** are used to determine which means differ. Range tests identify homogenous subsets of means that are not different from each other. **Duncan's multiple range test** was used throughout because of all the possible post hoc tests, this is the most conservative (Steel & Torrie, 1980).

Spearman's rank-order correlation: Non-parametric test describing the range of associations between two variables. This test is appropriate provided that there are two observations for each individual and that the observations are measured on a scale that can be put into a meaningful rank order.

Kruskal Wallis test: Non-parametric rank test, the data are converted to ranks before the test is performed, so can be interval or scale measurements, frequencies, derived variables (*e.g.* proportions) or ordinal ranks. This test compares three or more independent samples with a null hypothesis that all samples are taken from populations with the same median. In this way it is considered to be the non-parametric equivalent of the one-way ANOVA. $P<0.05$ indicates that the samples are from different populations.

Chi-Square test: Non-parametric test that tabulates a variable into categories and computes a chi-square statistic. This test compares the observed and expected frequencies in each category to either test that all categories contain the same proportion of values or that each category contains a specified proportion of values. The null hypothesis will be that the observed and expected frequencies are not different from each other.

Morisita's Standardised Index of Dispersion: Based on Morisita's Index of Dispersion that produces an index of dispersion ranging from -1 to +1, with 95% confidence limits at -0.5 and +0.5 (Krebs , 1999). Random patterns give a value of zero, clumped patterns above zero and uniform patterns below zero. The test is independent of population density and size.

2.3 RESULTS

2.3.1 Population estimation

The population size during each month at each site was estimated from the trapping data using the Minimum Number Alive (MNA) method (Table 2.2). The number estimated differed only slightly (not more than three individuals in any one month for any site) from the actual number of individuals captured and for Bovington and Whitemead the figures were the same (see Figure 2.8 d and e). Density of water voles per 100m was also calculated for Aveley, Hilliers and Rainham (Table 2.2), but not for Bovington and Whitemead as the populations were so small and both became extinct four months into the study.

Table 2.2 A comparison of the number of individuals captured each month at Aveley, Hilliers and Rainham, and the population size estimated using the Minimum Number Alive (MNA) method and the density of water voles per 100m of watercourse. Grey shading indicates where MNA differs to the number of captures. Diagonal lines indicate months when no trapping took place.

	Aveley			**Hilliers**			**Rainham**		
Month	**Captures**	**MNA**	**Density**	**Captures**	**MNA**	**Density**	**Captures**	**MNA**	**Density**
Aug-98	49	49	24.50	55	55	17.19	6	6	6.00
Sep-98	52	54	26.00	22	22	6.88	21	21	21.00
Oct-98	19	20	9.50	12	12	3.75	12	12	12.00
Nov-98	7	7	3.50	0	0	0	0	0	0
Dec-98									
Jan-99									
Feb-99									
Mar-99	12	12	6.00	10	10	3.13	8	8	8.00
Apr-99	10	10	5.00	17	18	5.31	14	14	14.00
May-99	13	13	6.50	37	37	11.56	15	16	15.00
Jun-99	7	7	3.50	46	48	14.38	12	12	12.00
Jul-99	4	4	2.00	51	54	15.94			
Aug-99	15	15	7.50	30	32	9.38			
Sep-99	15	15	7.50	18	18	5.63			
Oct-99	8	8	4.00	3	3	0.94			
Nov-99	0	1	0	0	0	0			
Dec-99	2	2	1.00	0	0	0			
Jan-00	5	5	2.50	0	0	0			
Feb-00	3	4	1.50	0	0	0			
Mar-00	5	5	2.50	2	2	0.63			
Apr-00	4	5	2.00	7	7	2.19			
May-00	6	6	3.00	6	6	1.88			
Jun-00	6	6	3.00	13	13	4.06			
Jul-00	14	14	7.00	17	17	5.31			

In order to illustrate changes in population size over the duration of the study, Figures 2.8a–e were plotted showing the estimated population size for each of the five study sites for each month that trapping took place. It should be noted that no trapping took place during December 1998 to February 1999 at any site.

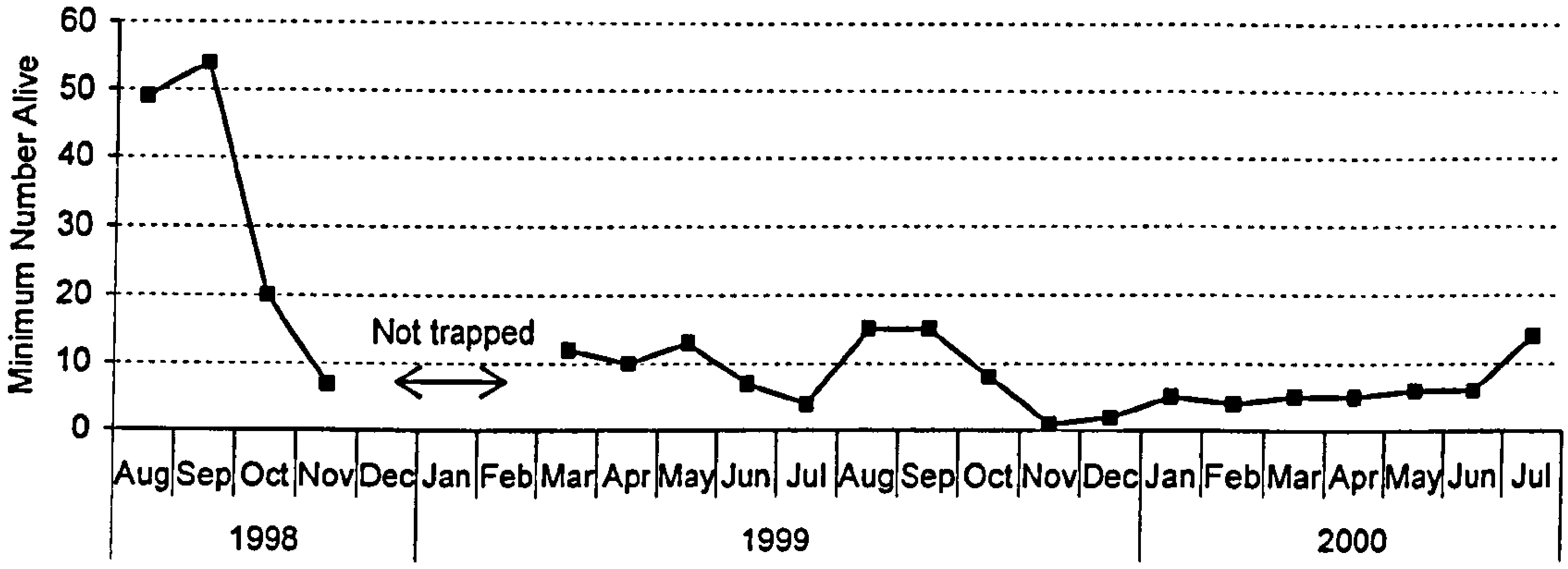
A peak was seen in the population at Aveley in September 1998 (54 individuals) with the population rapidly decreasing in size by November 1998 (7 individuals). A second smaller peak was then seen in September 1999 (15 individuals).

At Hilliers the population dropped dramatically from August 1998 (55 individuals) to November 1998 when no individuals were captured. A peak was then seen in July 1999 (54 individuals) again decreasing rapidly to November 1999 when no individuals were captured. No further animals were captured until March 2000 when the population was seen to slowly increase to 17 individuals in July 2000 at the end of the study period.

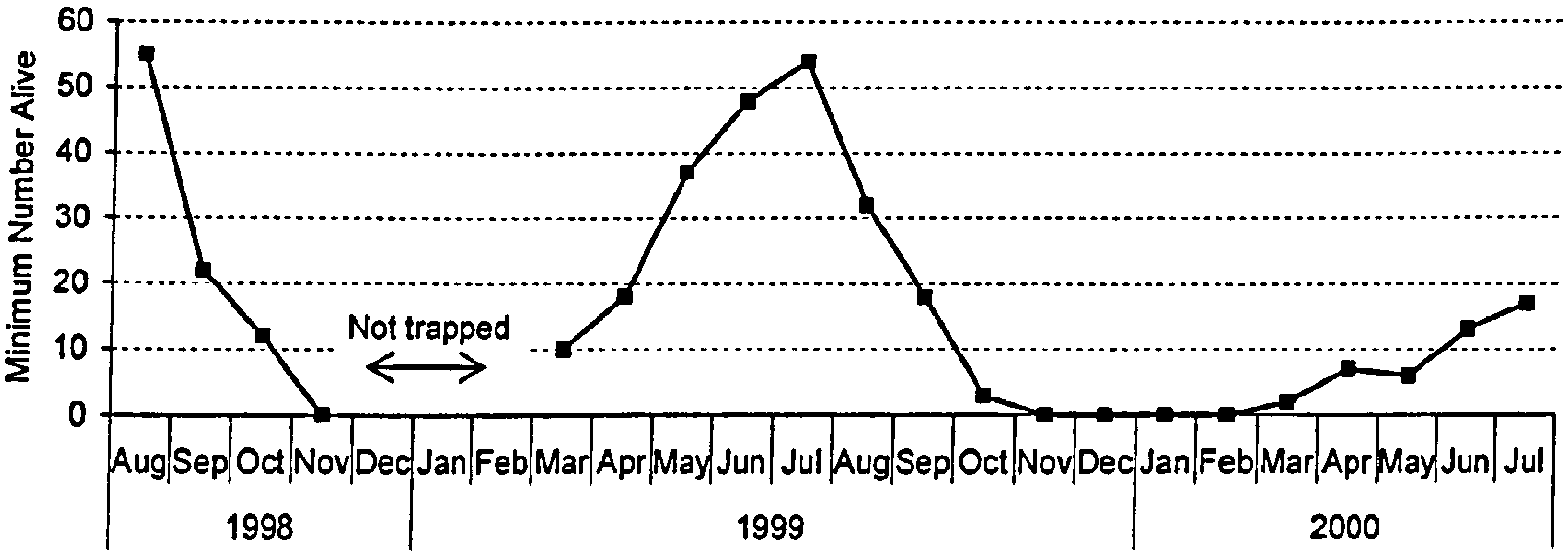
The population at Rainham showed a peak in population size in September 1998 (21 individuals) dropping to no animals being captured in November 1998. Upon the resumption of trapping in 1999, a second smaller peak in population size was seen in May 1999 (16 individuals).

The populations at both Bovington and Whitemead were particularly small with maxima of 3 and 5 individuals respectively. No water voles were found at either of these two sites after October 1998.

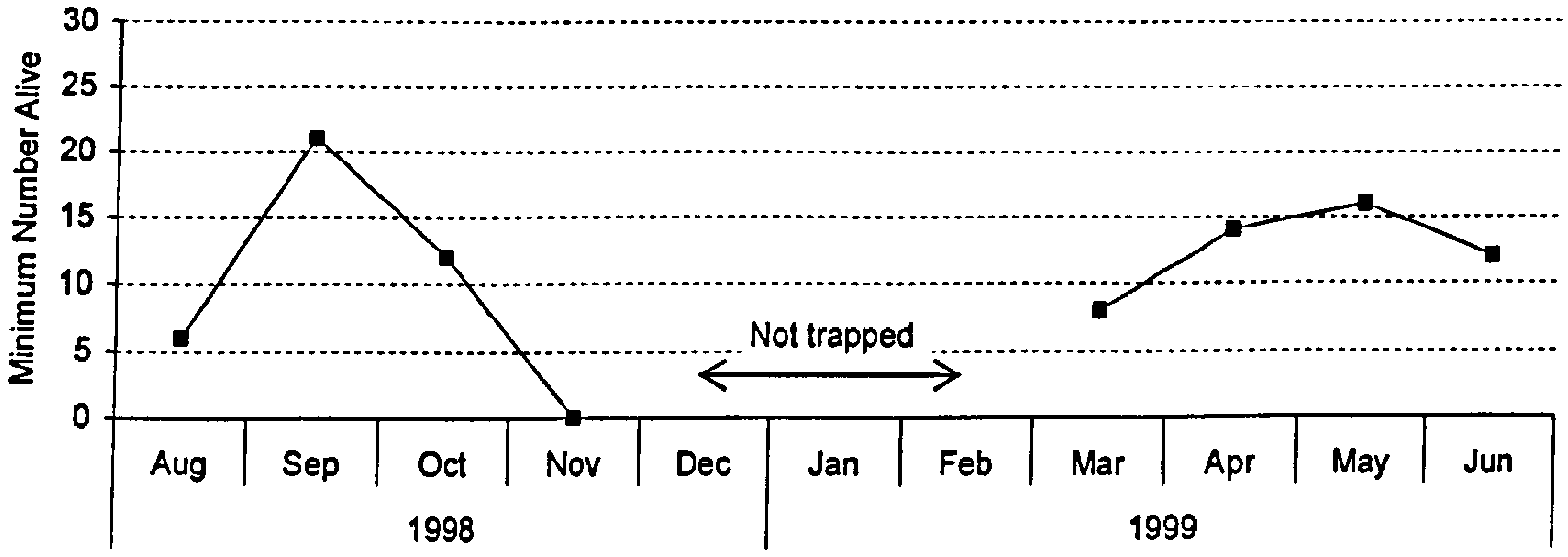
a) Aveley



b) Hilliers

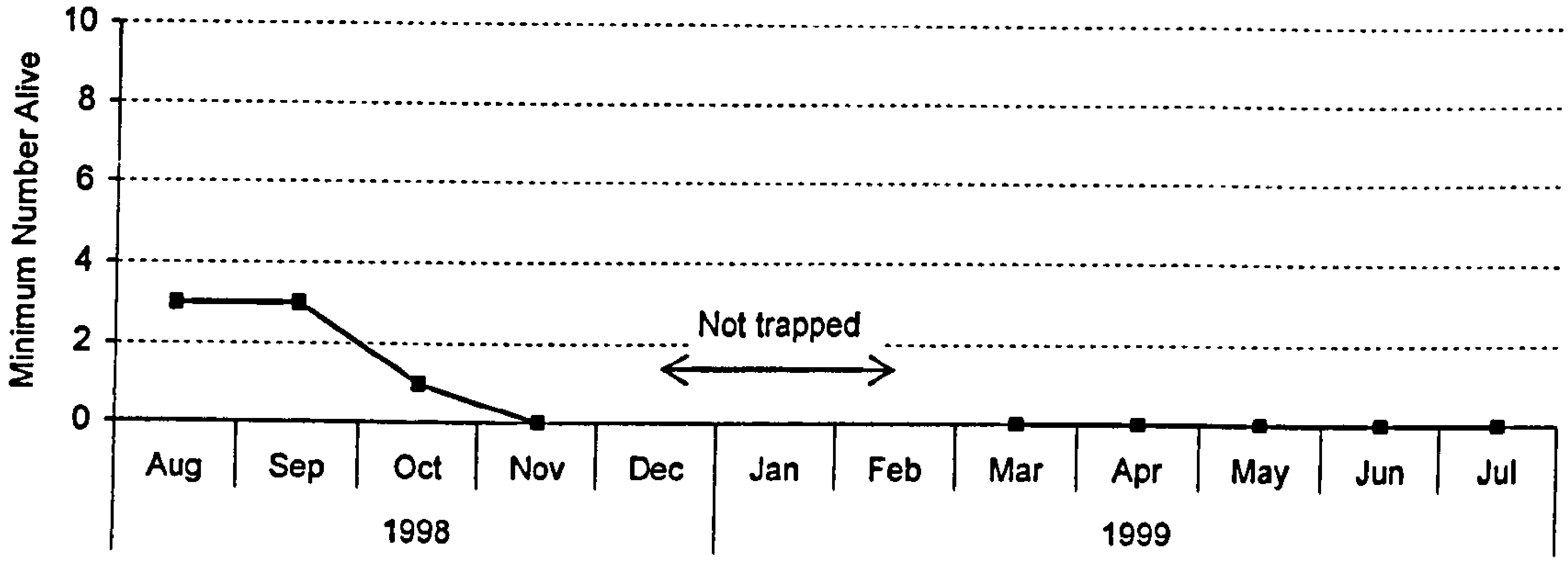


c) Rainham

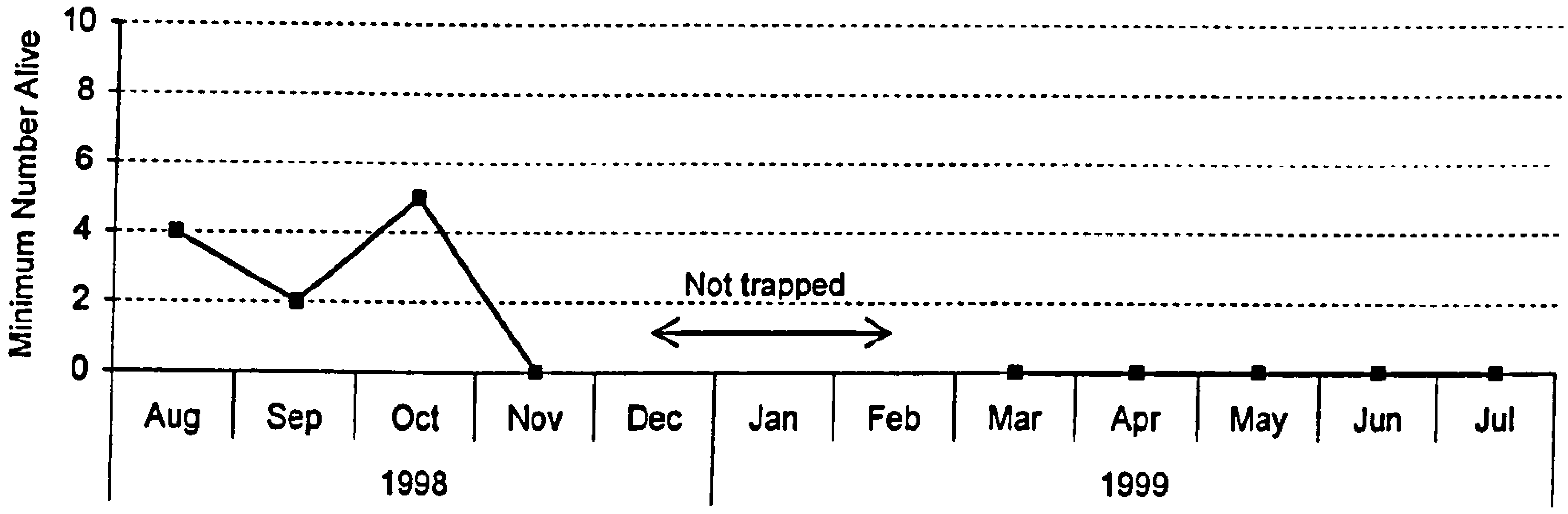


Figures 2.8 a-c Monthly population estimate using Minimum Number Alive based on trapping data.

d) Bovington



e) Whitemead



Figures 2.8 d and e Monthly population estimate using Minimum Number Alive based on trapping data.

2.3.2 Population structure

The composition of each population was examined by grouping the individuals into males, females and juveniles. Figures 2.9 a–e show the composition of the populations at each of the five study sites for each month that trapping took place. The numbers of males, females and juveniles, at all sites, decreased to very low levels over the winter months (December to January).

Aveley (Figure 2.9a)

Juveniles constituted a large proportion of the population at Aveley in August 1998 (25 individuals) gradually declining to no juveniles by March 1999. After the first winter at Aveley, juveniles appeared in the population in August 1999 (seven individuals) and had disappeared by November 1999. The following year, juveniles first appeared in May 2000 (one individual) and peaked in June 2000 (three individuals). The number of males varied throughout the study making up the majority of the population from January 2000 to April 2000 (three to four individuals). The number of females also varied considerably peaking in September 1998 (18 individuals) falling by October 1998 (six individuals) and rising slightly by March 1999 (eight individuals). Numbers then declined into July 1999 (one individual) before briefly rising in August 1999 (six individuals) then falling until no females were seen in November 1999. By March 2000, one female was present increasing to four in July 2000 at the end of the study.

Hilliers (Figure 2.9b)

At Hilliers, juveniles were present at the start of the study (11 individuals), disappearing from the population by October 1999. The following year they first appeared in April (eight individuals), peaking in May (26 individuals) and disappearing by October 1999. In 2000 juveniles appeared much later, in June (eight individuals). The number of males varied throughout the study peaking in July 1999 (15 individuals). The number of females started high in August 1998 (34 individuals) declining to six individuals in October 1998 and then peaking again in August 1999 (15 individuals). A third smaller peak in numbers was seen in July 2000 (seven individuals).

Rainham (Figure 2.9c)

Juveniles were present at the start of the study (two individuals), peaked in September 1998 (17 individuals) until October 1998 (six individuals), with none in March 1999. They next appeared in the population in April 1999 (eight individuals), peaking in numbers again in May 1999 (nine individuals). Males were present throughout the study, except September 1998. Females were present throughout the study peaking in March 1999 (five individuals).

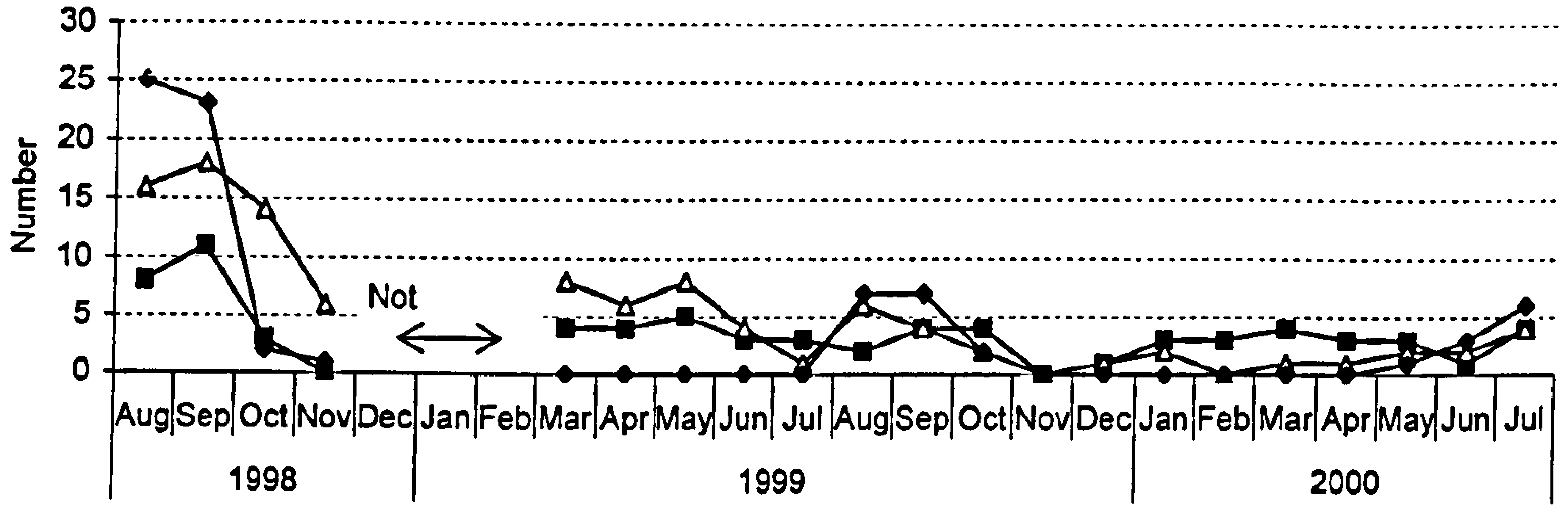
Bovington (Figure 2.9d)

In August 1998 the population consisted entirely of males (3 individuals). In September 1998 the population consisted of two juveniles and one female, and in October 1998 one juvenile.

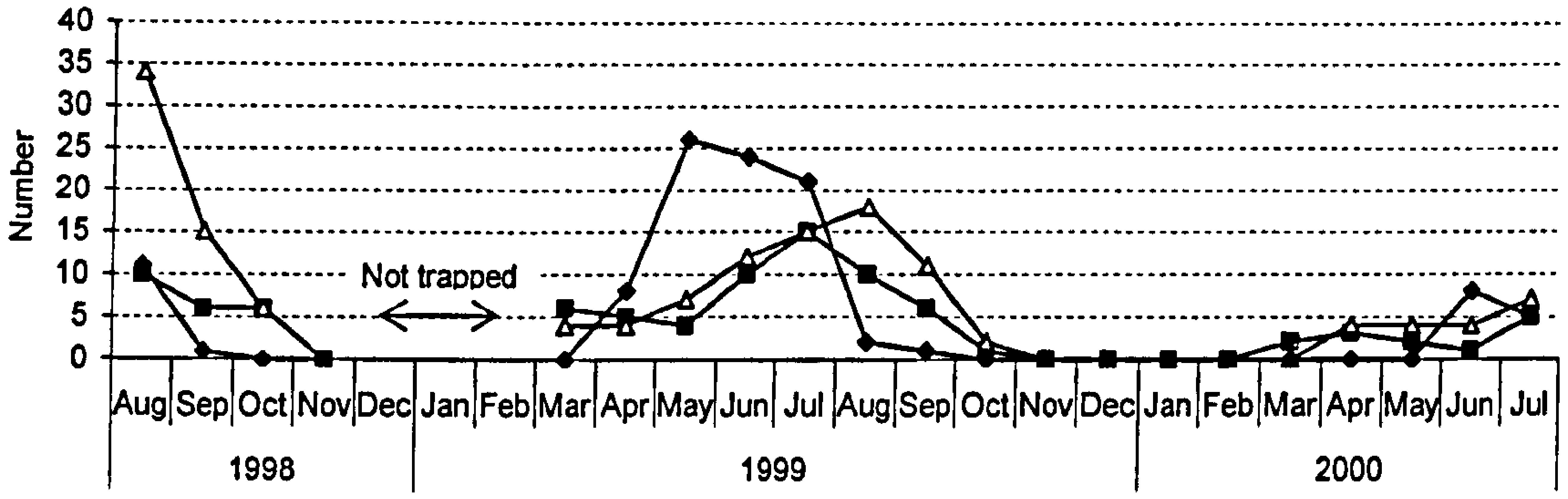
Whitemead (Figure 2.9e)

In August 1998 the population consisted of one juvenile, two males and one female. In September 1998 the population consisted of one male and in October 1998, there were three females with one male and one juvenile.

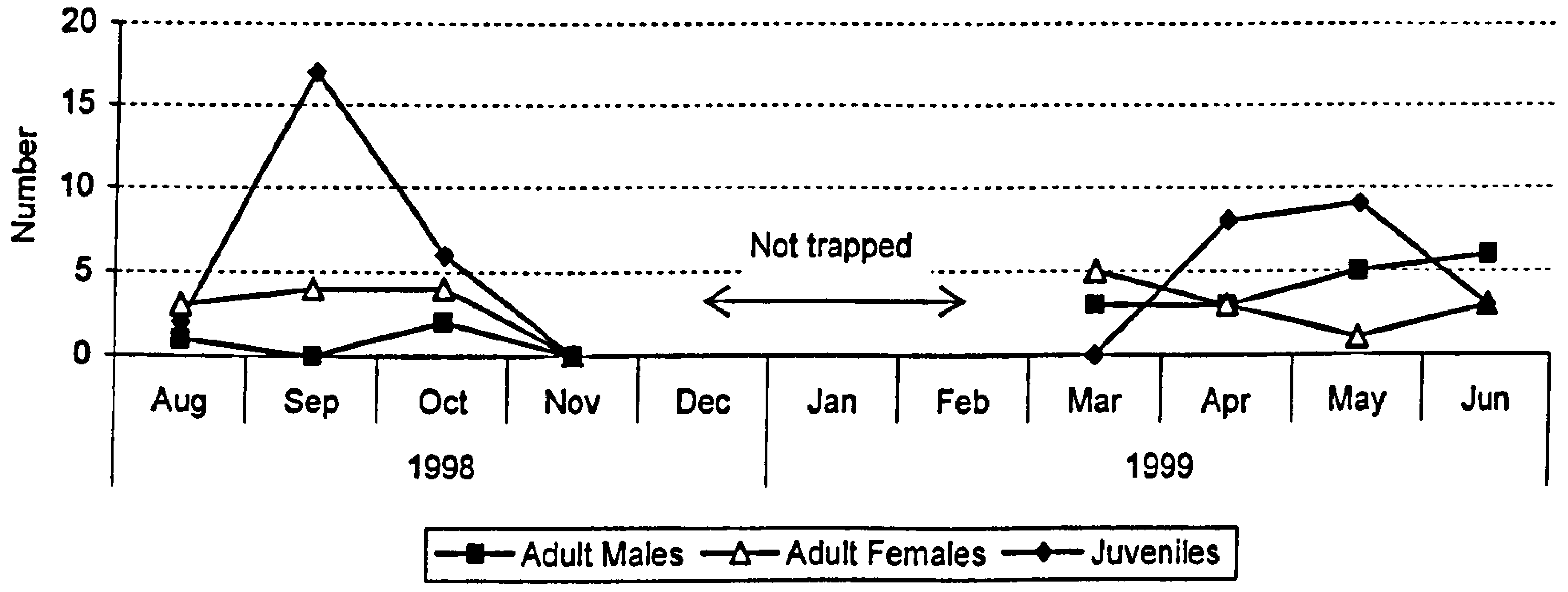
a) Aveley



b) Hilliers

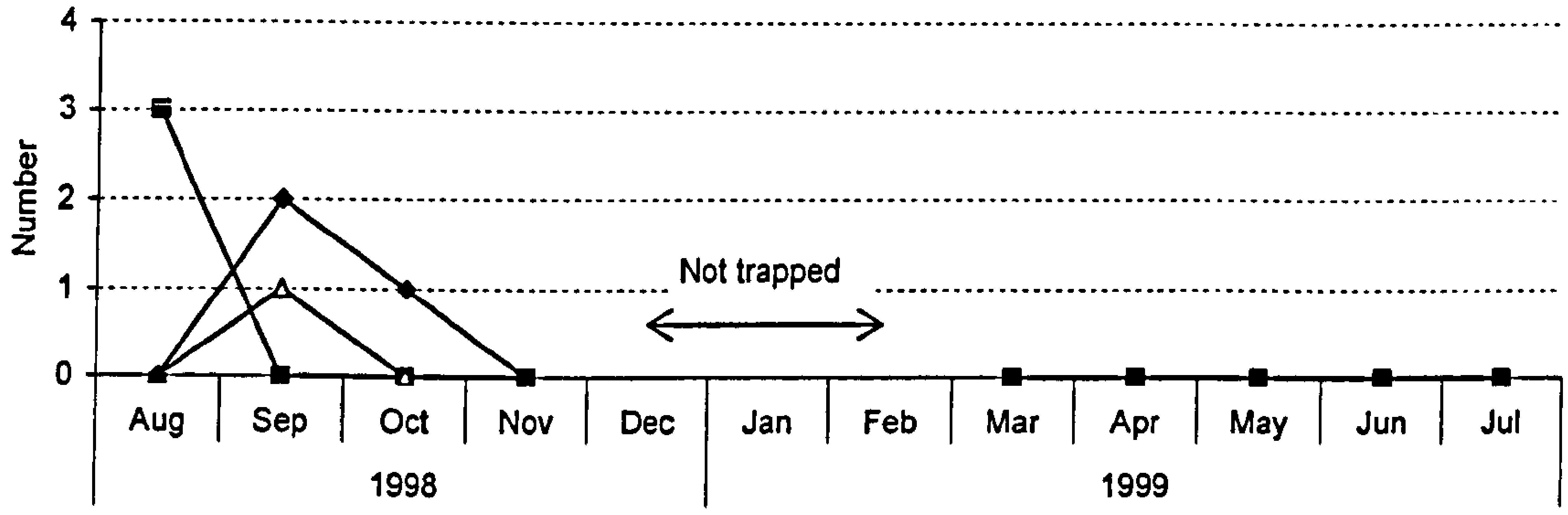


c) Rainham

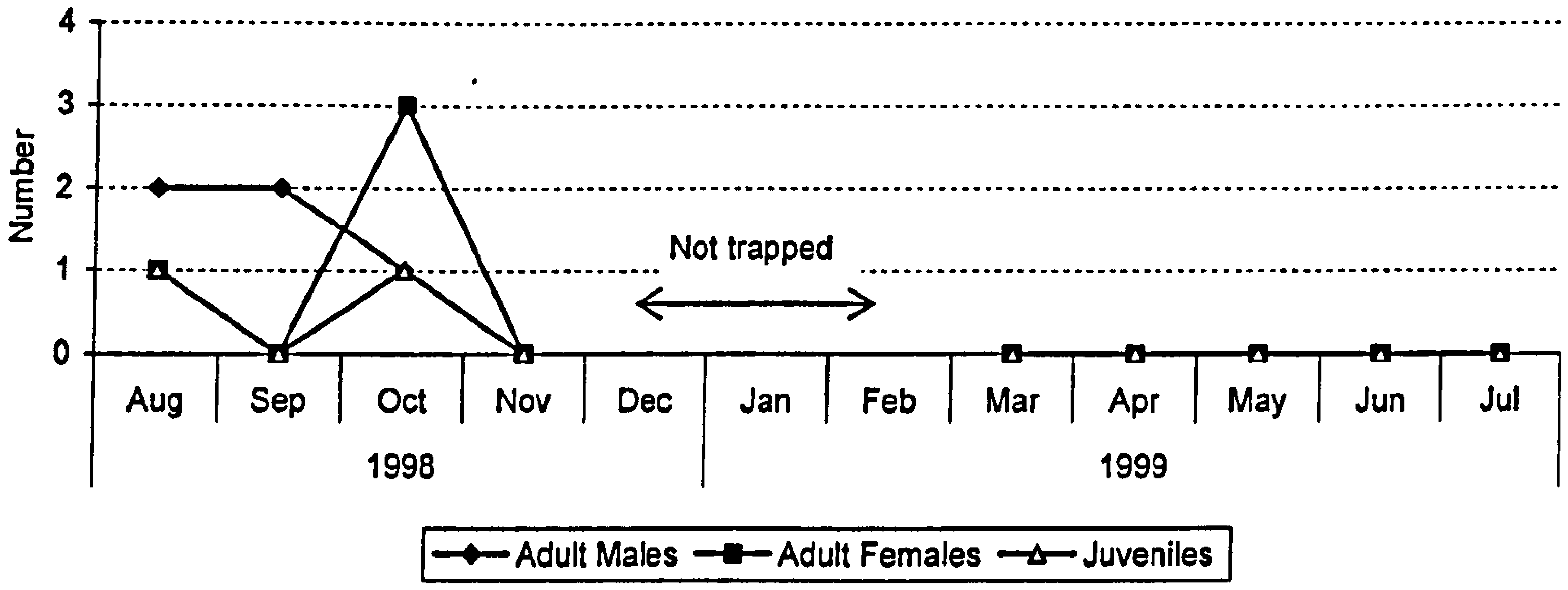


Figures 2.9a-c Numbers of males, females and juveniles in the population for each month that trapping took place. Note that no trapping took place during December 1998 to February 1999 at any site.

d) Bovington



e) Whitemead



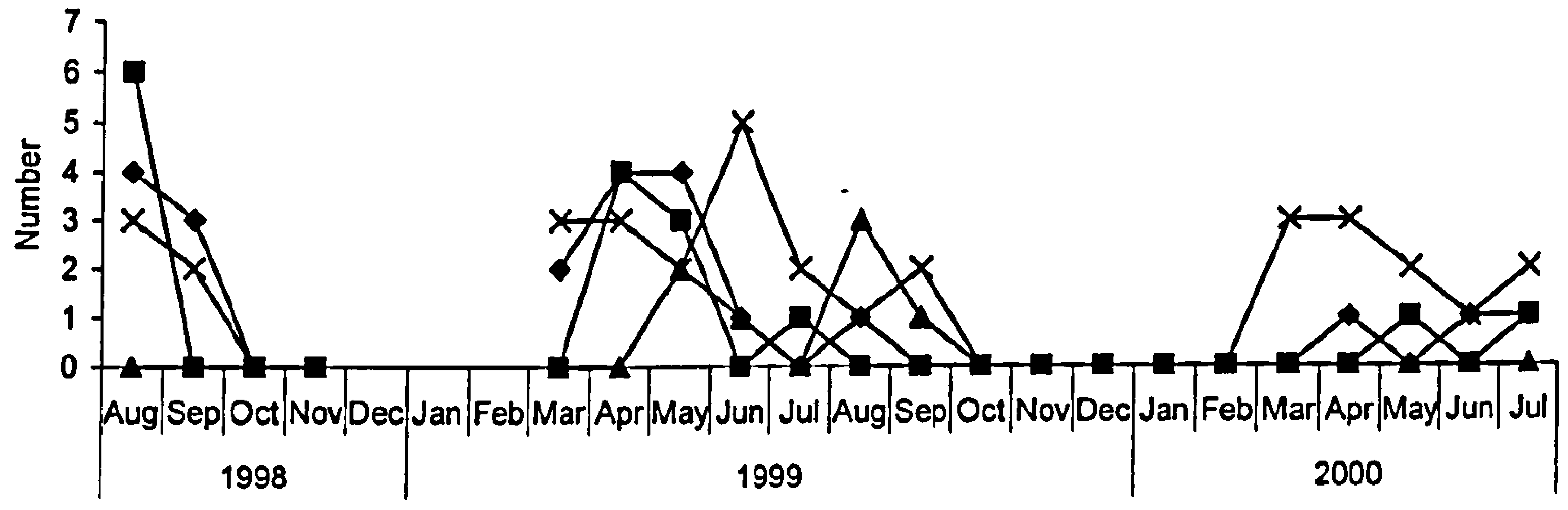
Figures 2.9d and e Numbers of males, females and juveniles in the population for each month that trapping took place. Note that no trapping took place during December 1998 to February 1999 at any site.

Breeding

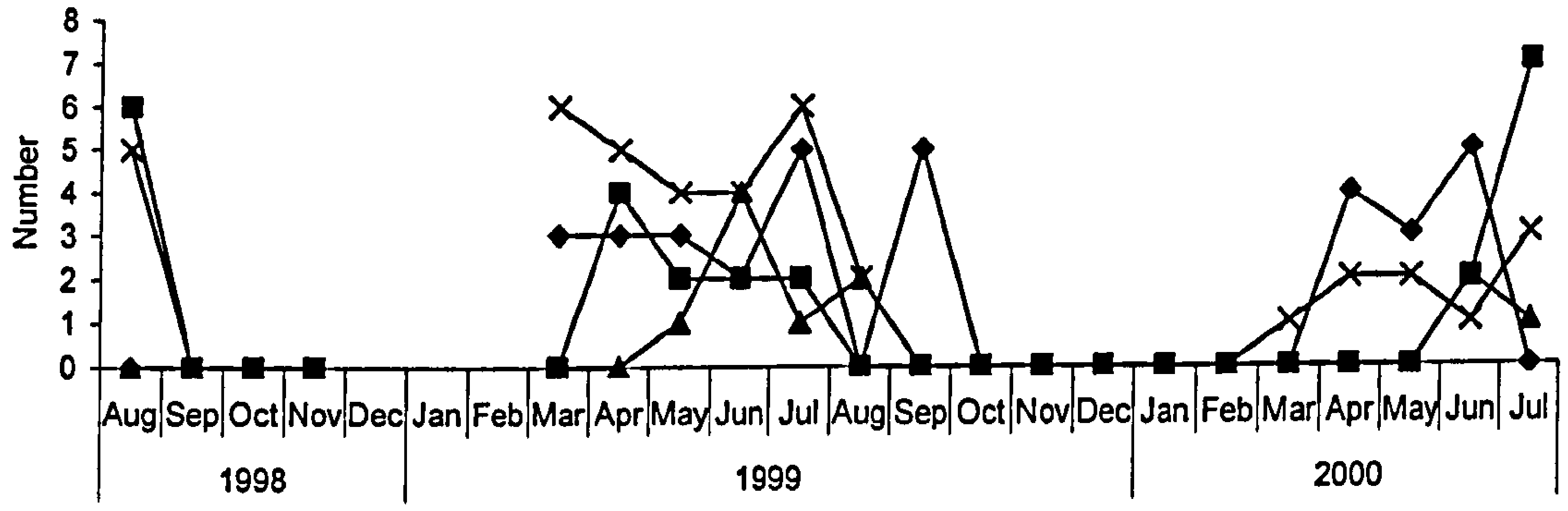
Perforate females first appeared at all Aveley, Hilliers and Rainham in March 1999. Trapping at Rainham did not continue into 2000, however, at Aveley and Hilliers, they appeared again in April 2000. The minimum weight of any peforate female was 140g. Males in reproductive condition (Testes Large) appeared at all three sites in March 1999. At Aveley, they appeared in April 2000 and March 2000 at Hilliers. The minimum weight of a male in reproductive condition was 140g.

Figure 2.10 a-c shows the number of individuals recorded as perforate (females), pregnant (females), lactating (females) and testes large (males) over each month of trapping for Aveley, Hilliers and Rainham.

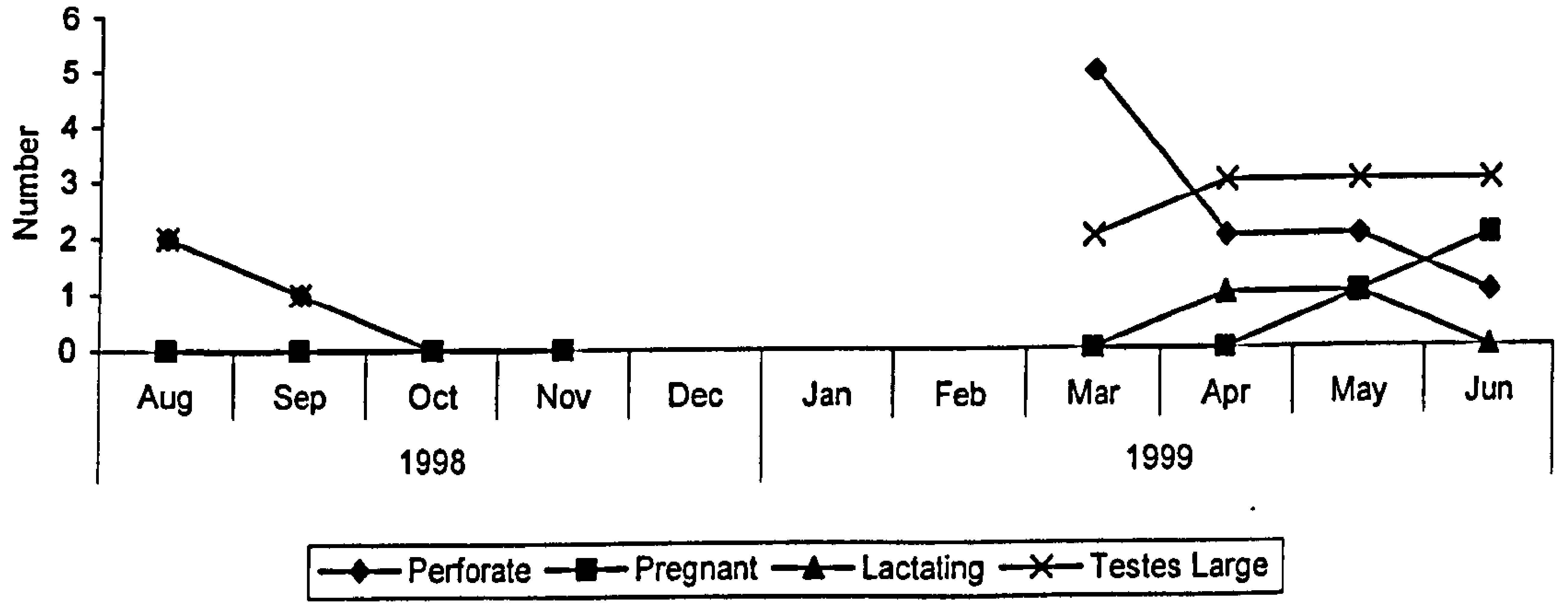
a) Aveley



b) Hilliers



c) Rainham



Figures 2.10a-c Numbers of males and females in reproductive condition for each month that trapping took place. Note that no trapping took place during December 1998 to February 1999 at any site.

2.3.3 Capture rate

Data from Bovington and Whitemead were excluded from this section as the total number of captures during any month was too small for any meaningful analysis.

Figure 2.11 shows the overall mean percentage of the total number of captures on each of the three trap days in each trapping session for Aveley, Hilliers and Rainham.

Months where no water voles were captured were not included in the means. The overall means suggested that there may be a difference in the number of captures between trap days within each site, this was tested statistically using a ANOVA test.

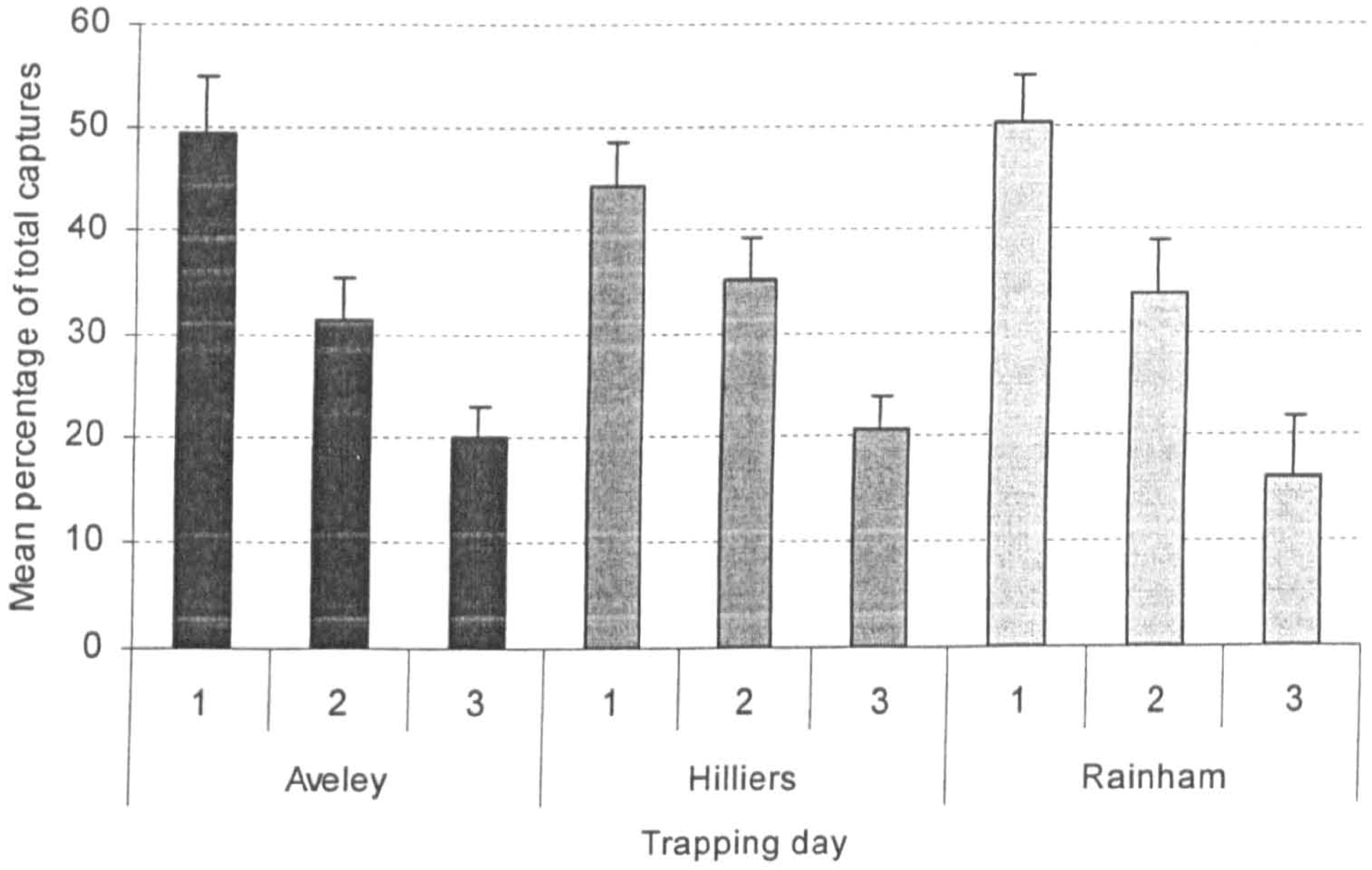


Figure 2.11 Mean percentage (+ standard error) of the population caught on each of the three trap days in each trapping session for Aveley, Hilliers and Rainham.

The percentages of the total captures were converted in to proportions and transformed using the arcsine square-root transformation, which is appropriate for observations that are proportions (Fowler *et al*, 1998). The data for the three sites were then analysed using ANOVA.

In this case a one-way ANOVA was used to test for significant differences between the days within each site.

For Aveley, the ANOVA showed that the proportion was significantly affected by trap day ($F_{2,57} = 6.45$, $P<0.005$). The multiple range test (Duncan) performed on the transformed means showed that trap day 1 had a significantly higher mean proportion (backtransformed mean = 0.49) than trap day 2 (backtransformed mean = 0.31) or trap day 3 (backtransformed mean = 0.21).

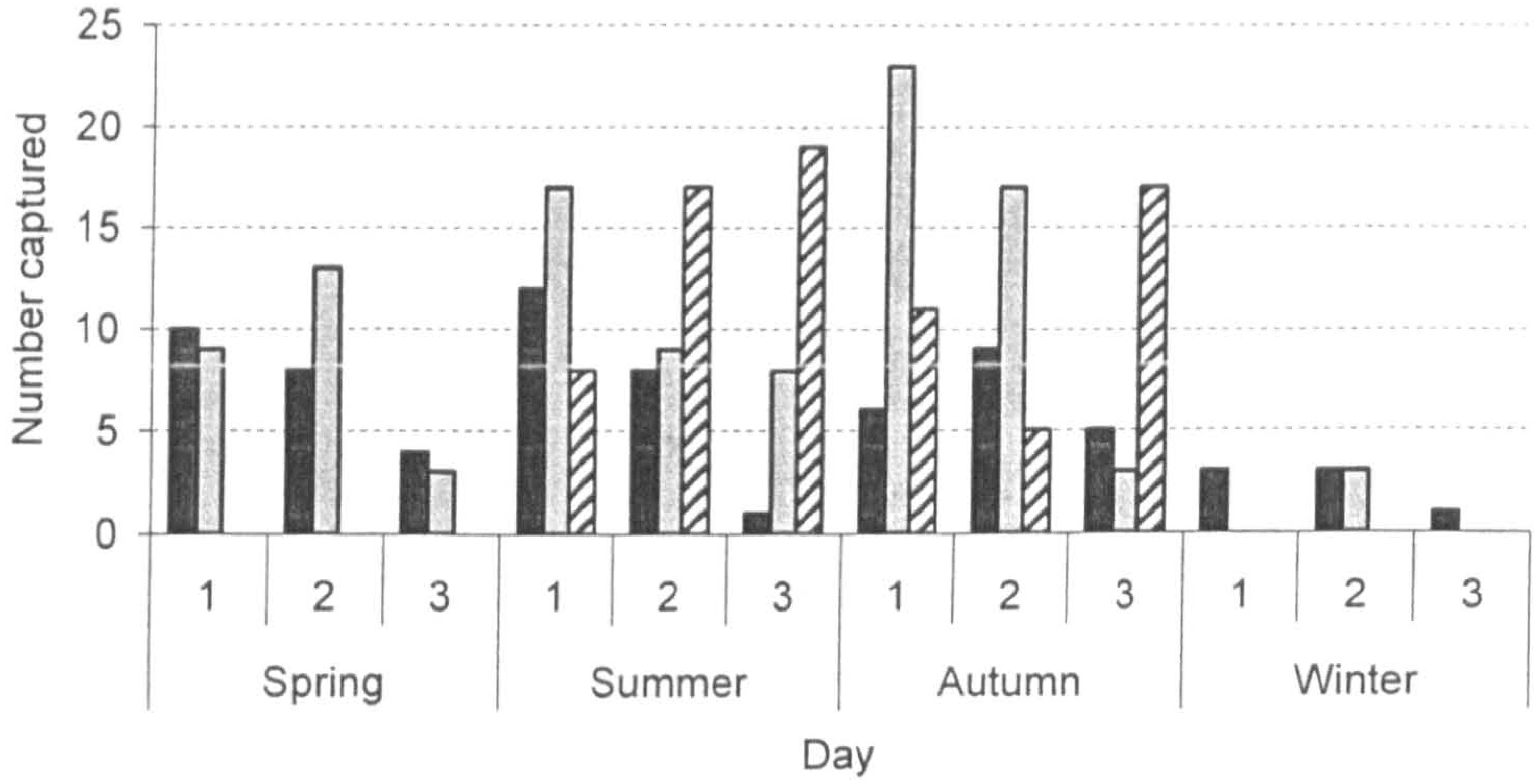
For Hilliers, the ANOVA showed that the proportion was also significantly affected by trap day ($F_{2,45} = 9.52$, $P<0.001$). The multiple range test (Duncan) showed that trap days 1 (backtransformed mean = 0.44) and 2 (backtransformed mean = 0.35) had significantly higher mean proportions than trap day 3 (backtransformed mean = 0.21).

For Rainham, the ANOVA showed that the proportion was significantly affected by trap day ($F_{2,18} = 11.23$, $P<0.001$). The multiple range test (Duncan) showed that all trap days were significantly different from each other. Trap day 1 (backtransformed mean = 0.50) had a significantly higher mean proportion that trap day 2 (backtransformed mean = 0.34) or 3 (backtransformed mean = 0.16) and trap day 2 had a significantly higher mean proportion than trap day 3.

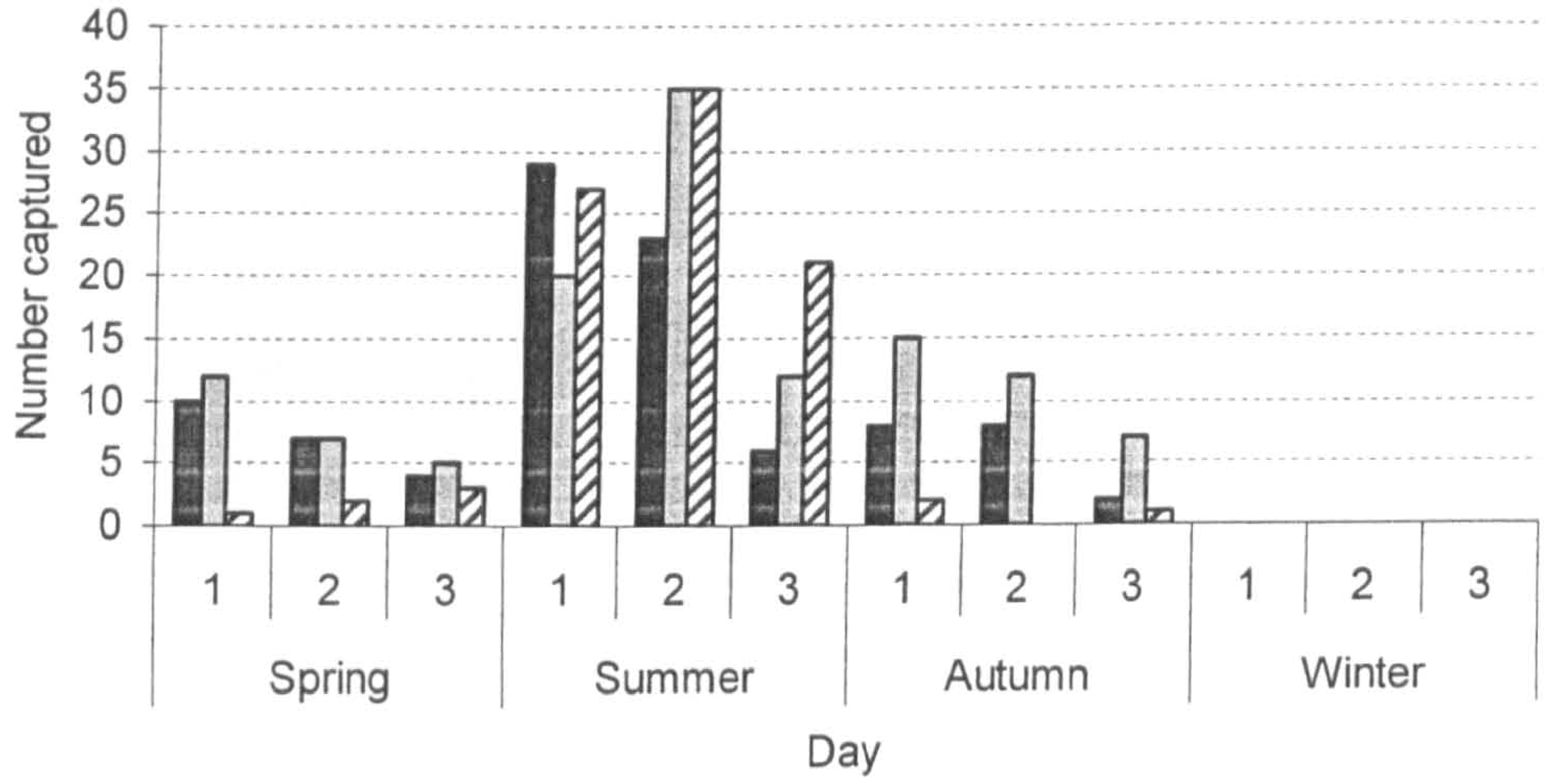
The data were additionally examined for differences in the day of first capture for males, females and juveniles. Figures 2.12 a-c illustrate the day for first capture for males, females and juveniles during each season at Aveley, Hilliers and Rainham. At all three sites, it appears that most males and females were generally captured on trap day 1. The data for Aveley suggest that most juveniles were captured on trap day 3, however, this trend is not apparent for either Hilliers or Rainham.

The frequency of recaptures was also examined with respect to sex. Figures 2.13 a-c illustrate the frequency of zero to five recaptures (five being the most recaptures recorded) for Aveley, Hilliers and Rainham. The majority of individuals were only captured once in a session. There does not appear to be any relationship between the type of individual (male, female or juvenile) and the number of times it was recaptured in a session.

a) Aveley



b) Hilliers



c) Rainham

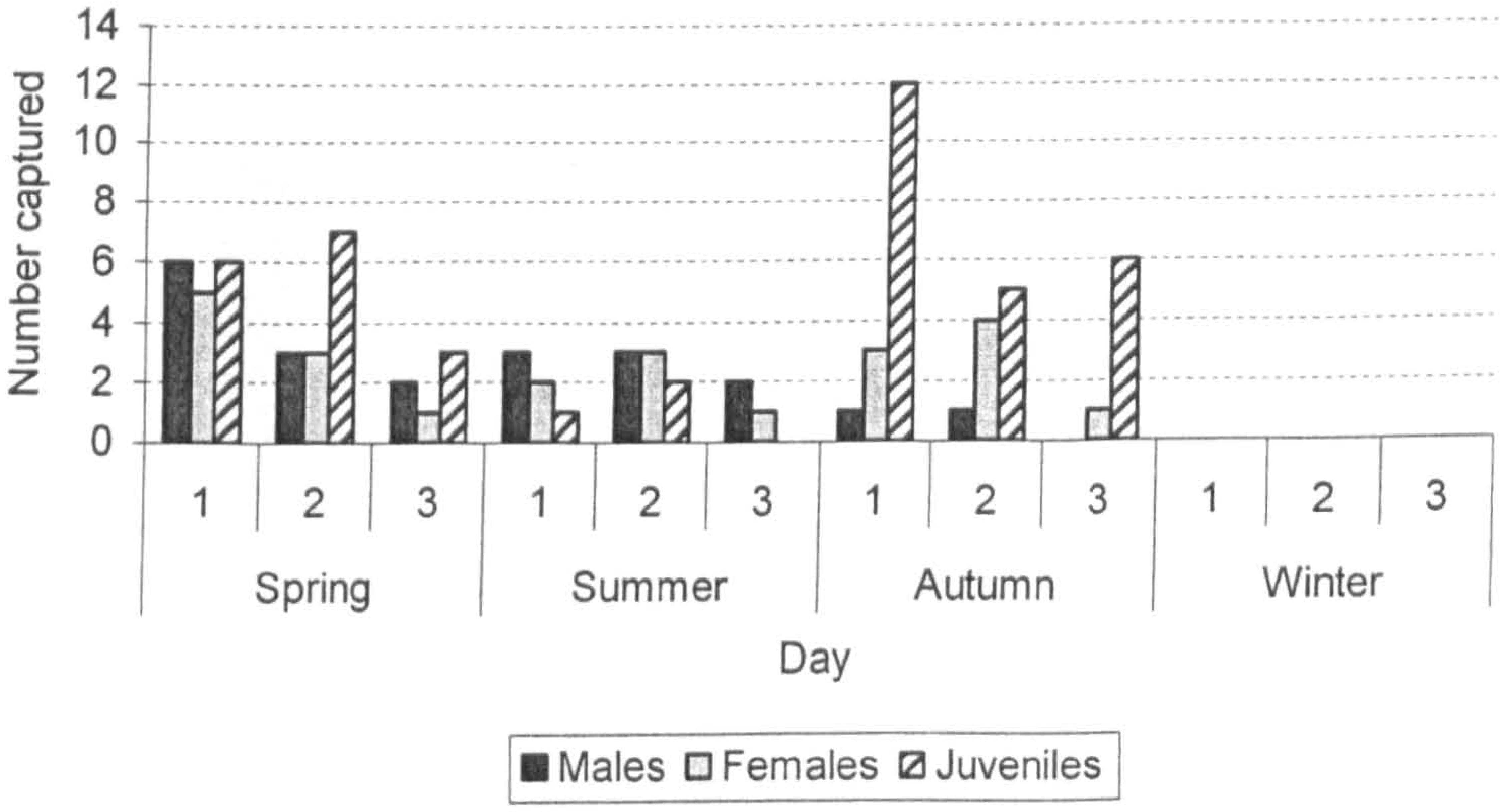
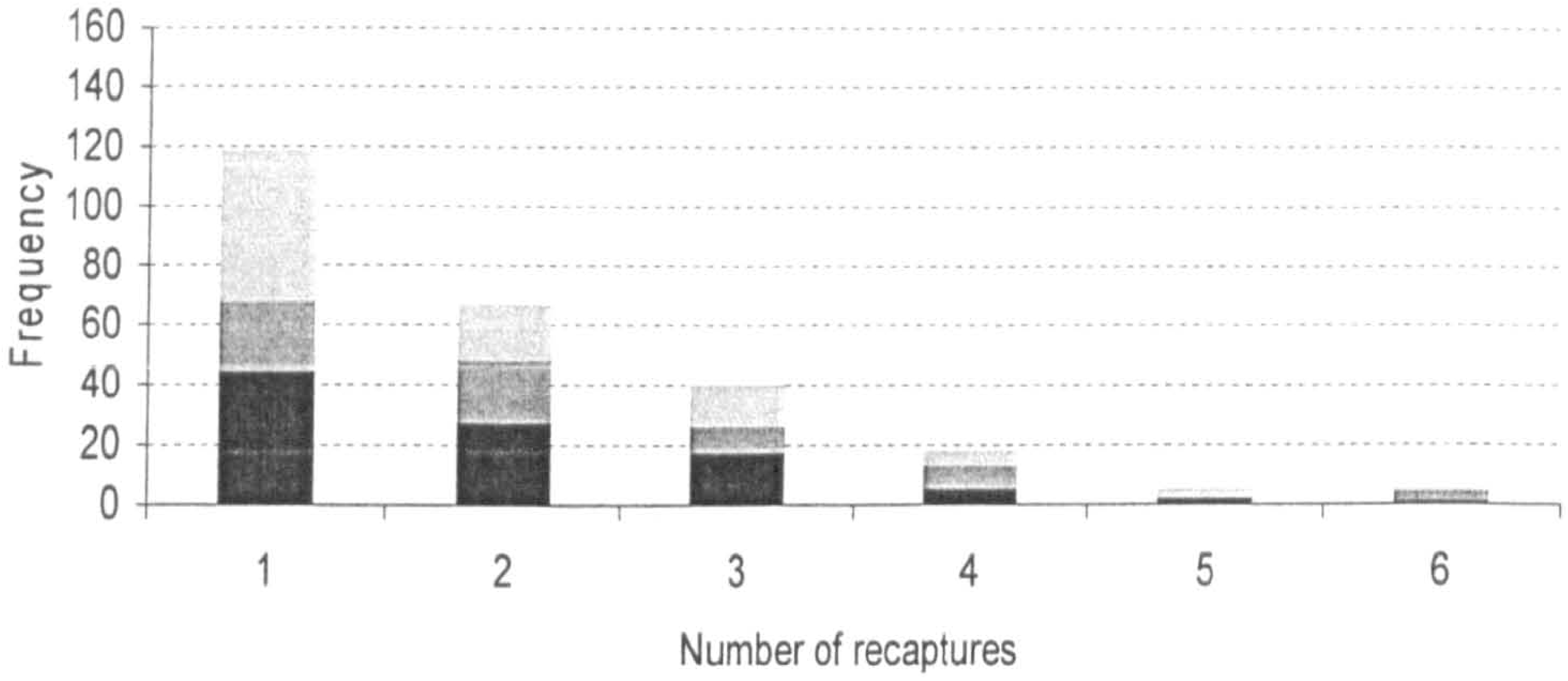
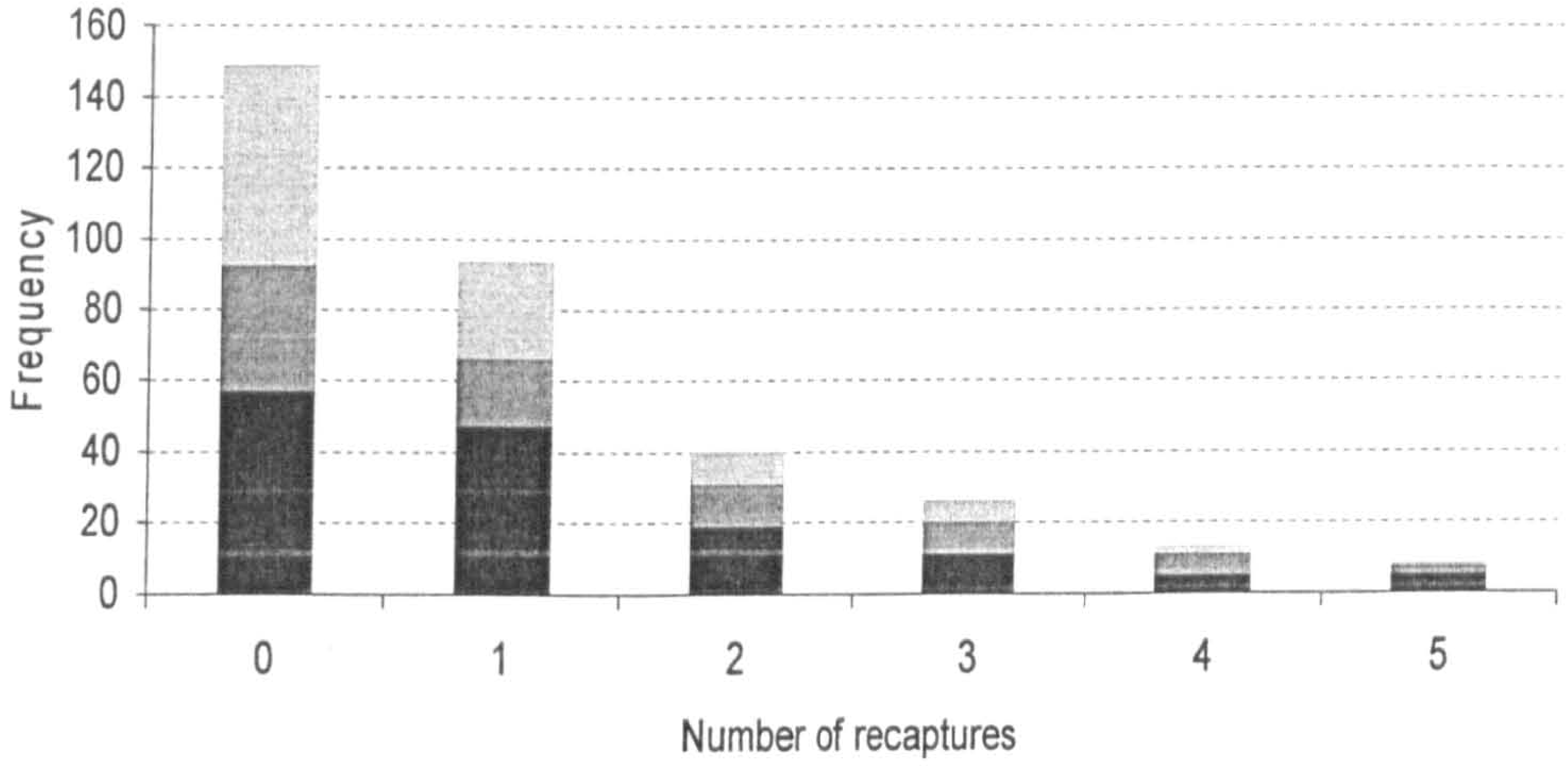


Figure 2.12 a-c The number of first captures of males, females and juveniles on each trap day in each season for Aveley, Hilliers and Rainham

a) Aveley



b) Hilliers



c) Rainham

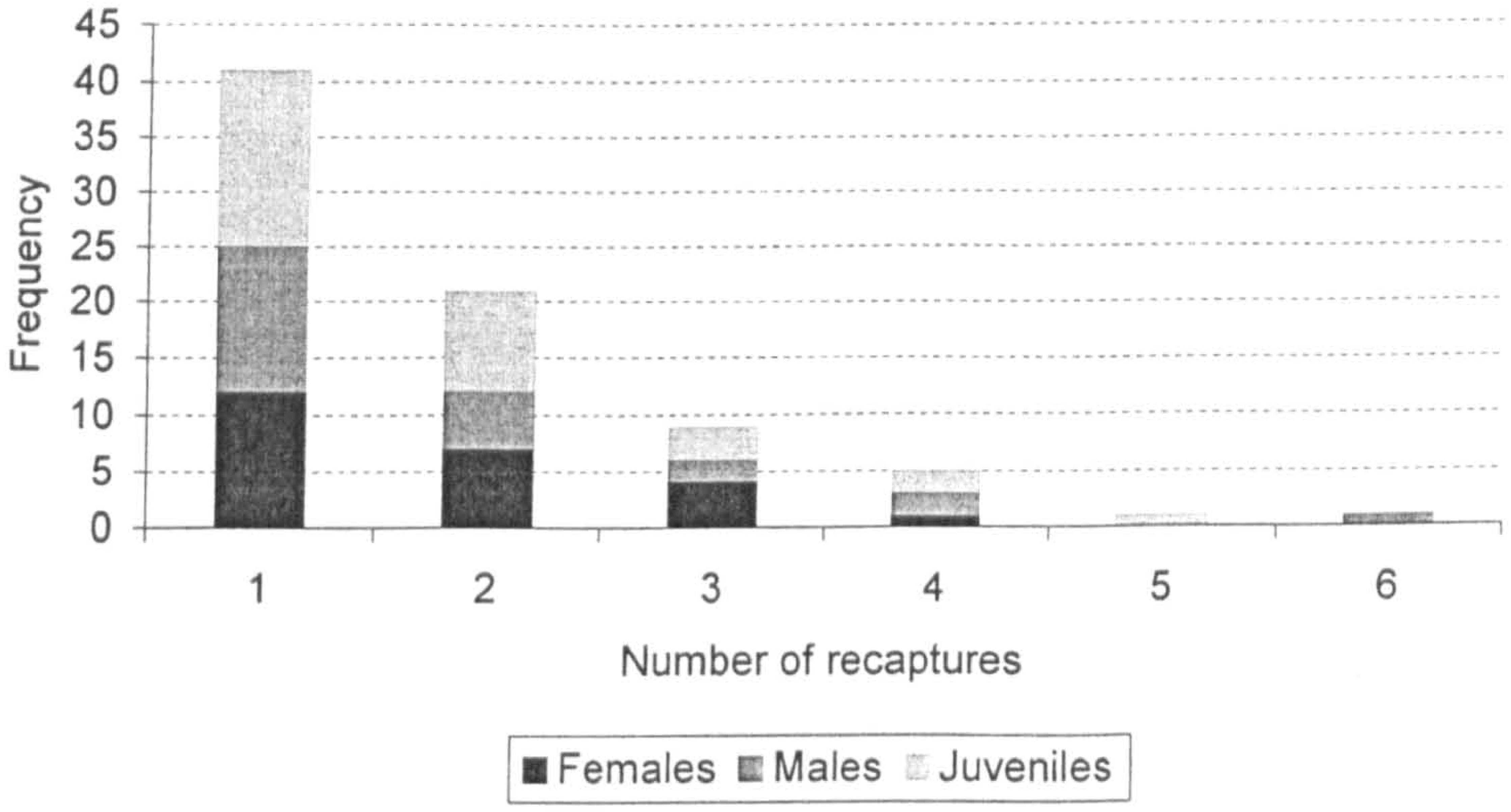


Figure 2.13 a-c Frequency of recaptures with respect to sex (female, male, juvenile) for Aveley, Hilliers and Rainham.

2.3.4 Activity

Data from Bovington and Whitemead were excluded from this section as the total number of captures during any month was too small for any further analysis.

Figures 2.14a–c show the distribution of the total number of captures over the different trap rounds at the different times of day for each season at each site. It should be noted that no trapping took place during December 1998 to February 1999 at any site.

The data suggested that there may be differences between the percentages of captures at different times of day within each site. This was analysed statistically, however, data from all sites in August 1998 and Hilliers in September 1998 were excluded from the analysis as the times of trap rounds were different (see Section 2.2.3.)

The percentages of the total captures were converted into proportions and transformed using the arcsine square-root transformation. The data for the three sites were then analysed using ANOVA.

In this case a two-way ANOVA was used, for each site, to test for significant differences between the times of trap rounds and seasons

For Aveley, the ANOVA showed that the proportion was significantly affected by the time of trap round ($F_{2,42} = 4.50$, $P<0.05$). The ANOVA also showed that there was no significant interaction between the time of a trap round and season. The multiple range test (Duncan) for site showed the mean proportion of the total number of captures was significantly higher at 06:00 (mean = 0.41) than at 22:00 (mean = 0.36), but that neither 06:00 nor 22:00 were significantly different from 14:00 (mean = 0.26).

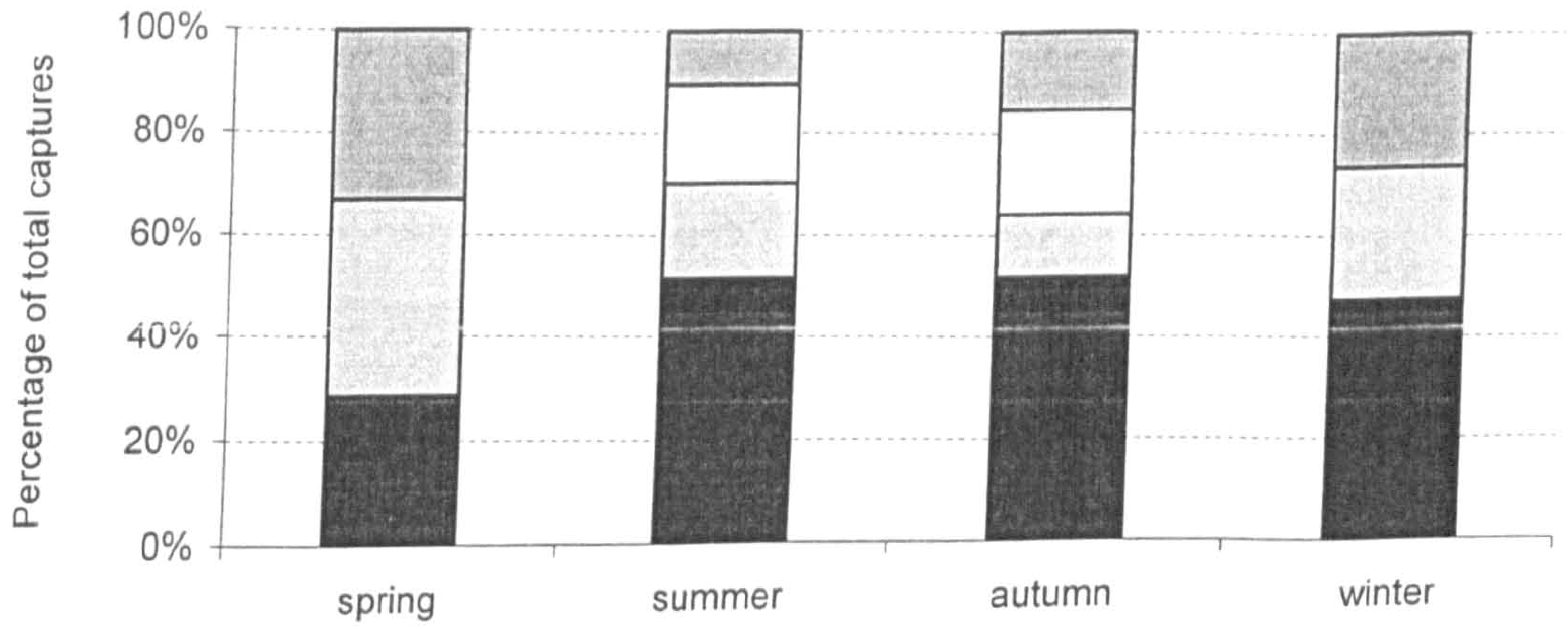
For Hilliers, the ANOVA showed that the proportion was significantly affected by the time of trap round ($F_{2,36} = 6.22$, $P<0.05$) and that there was a significant interaction between the time of a trap round and season. The multiple range test (Duncan) for site showed the mean proportion of the total number of captures was significantly higher at 06:00 (backtransformed mean = 0.40) than at 14:00

(backtransformed mean = 0.28), but that neither 06:00 nor 14:00 were significantly different from 22:00 (backtransformed mean = 0.31). To examine the significant interaction between time and season the mean proportions for each season were plotted (Figure 2.15). This shows that the significant difference was probably driven by the 06:00 data, particularly in autumn., suggesting that the proportion of captures at 06:00 differs with season.

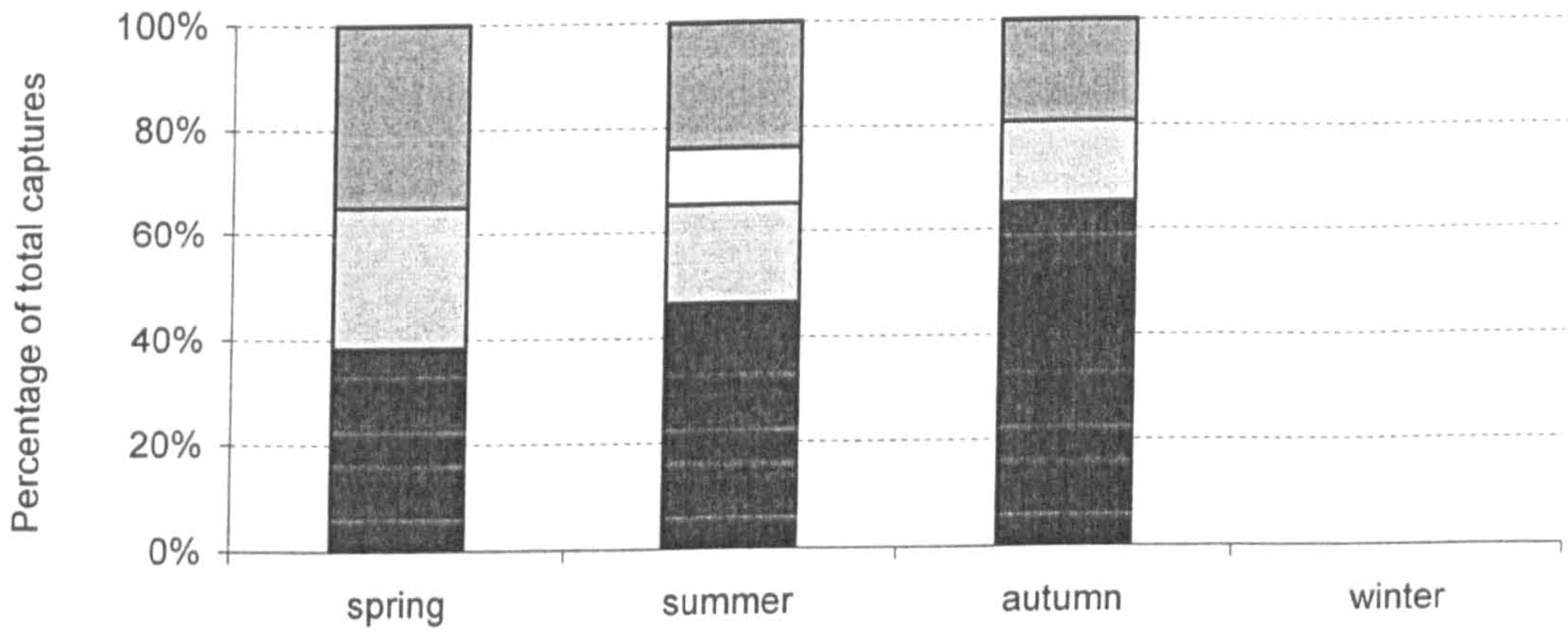
For Rainham, the ANOVA showed no significant effect of the time of trap round on the proportion of the total number of captures. The ANOVA also showed that there was no significant interaction between the time of a trap round and season.

Although not recorded, weather did not appear to affect the activity of water voles.

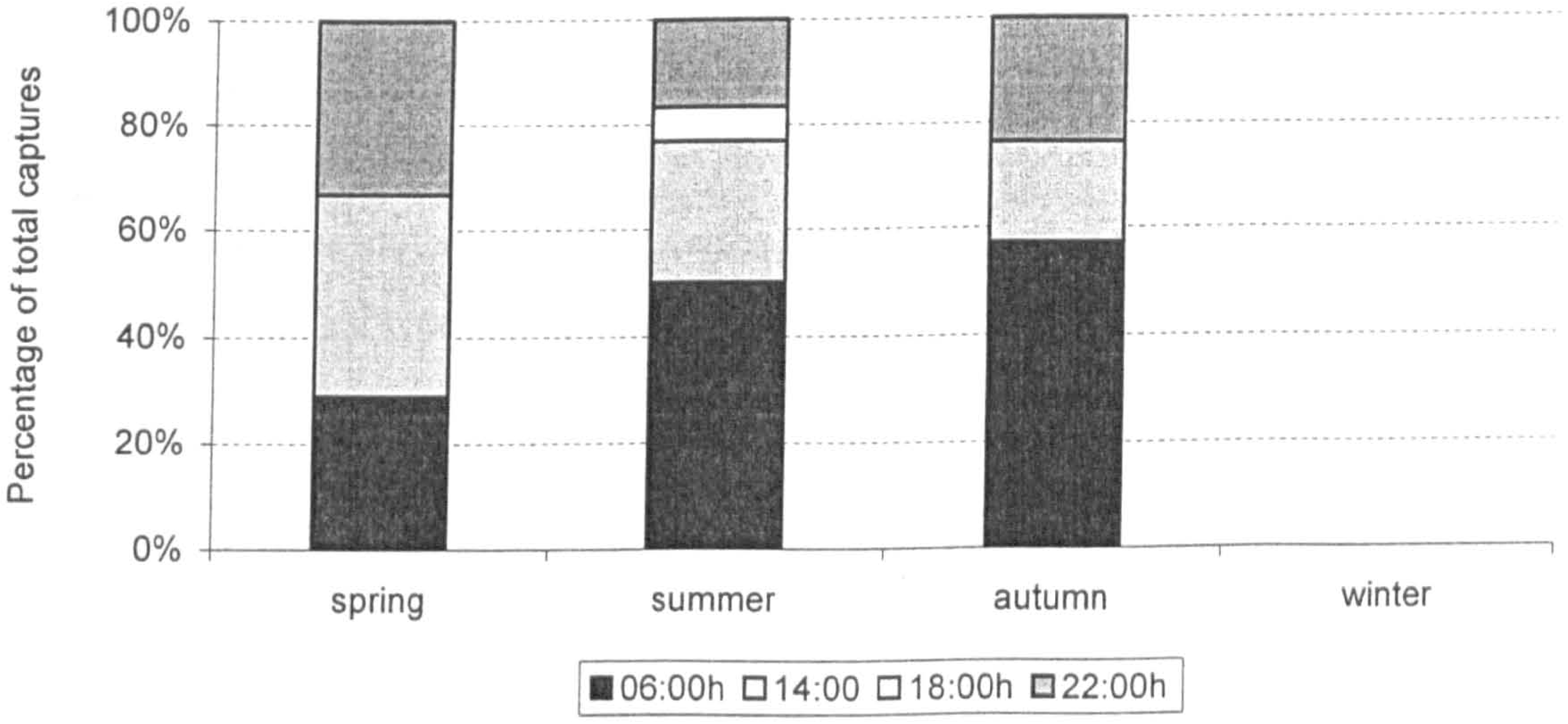
a) Aveley



b) Hilliers



c) Rainham



Figures 2.14a-c Percentage of captures over the different trap rounds (times) for each season at Aveley, Hilliers and Rainham.

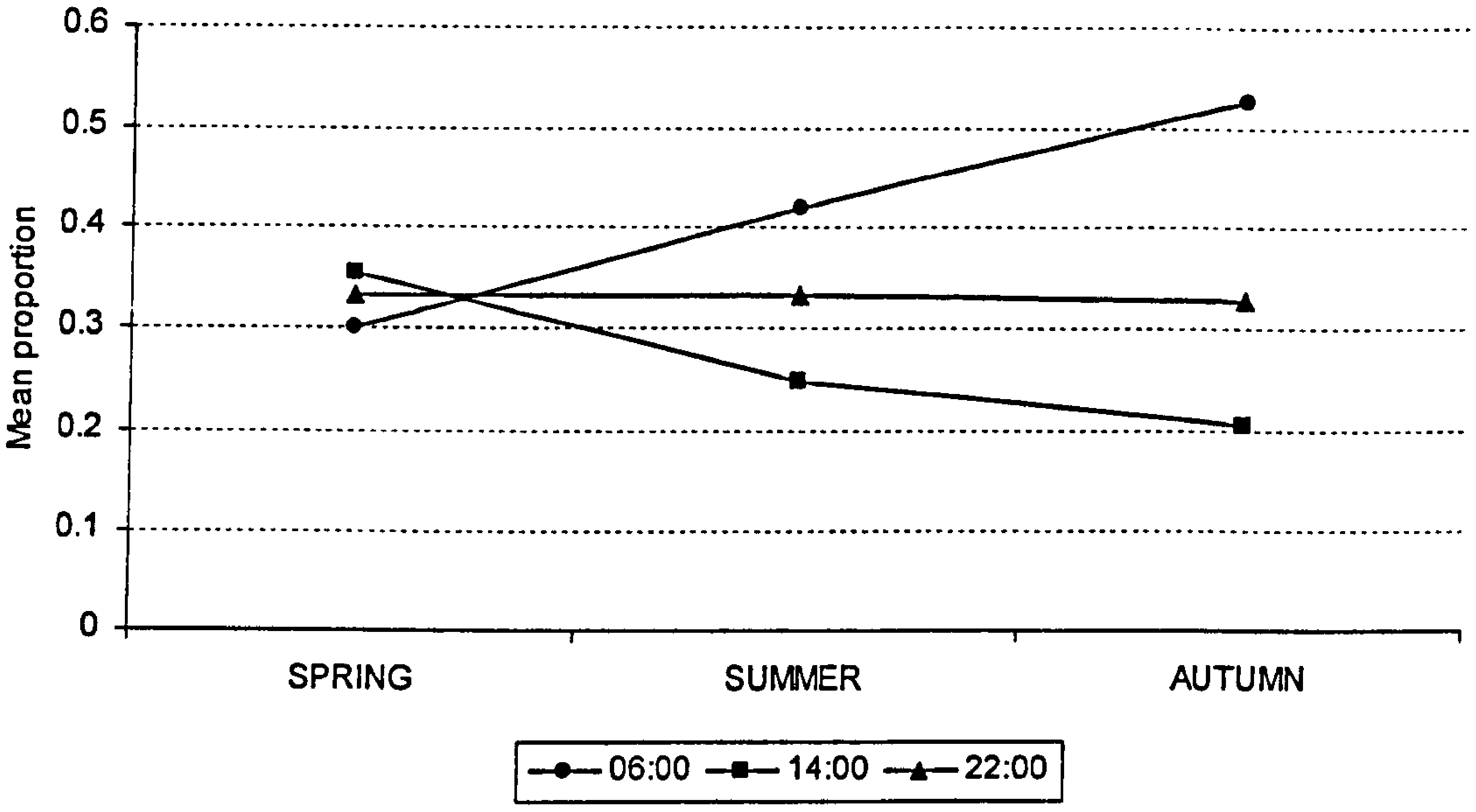


Figure 2.15 Mean proportions of total captures for each trap round time (06:00, 14:00 and 22:00h) at Hilliers grouped by season.

2.3.5 Distribution

The distribution of water vole captures between trap positions and the number of individuals captured in each trap position for each study site over the period of this study was examined (Figures 2.16a–e).

The data suggest that the total numbers of captures were not evenly distributed amongst the trap positions at Aveley, Hilliers and Rainham. This was analysed statistically. Whilst the numbers captured at Bovington and Whitemead are very small a similar trend was suggested. Due to the small numbers of captures it was not possible to use statistical analysis for the data from these two sites.

A Chi-square test was used to analyse the distribution of total numbers of captures.

For Aveley, there was a significant difference between the total number of captures at each trap position ($\chi^2_{41} = 75.83$, $P<0.001$) indicating that each trap position was not equally used by water voles.

For Hilliers, there was also a significant difference between the total number of captures at each trap position ($\chi^2_{60} = 129.19$, $P<0.001$) indicating that each trap position was not equally used by water voles at Hilliers.

For Rainham there was a significant difference between the total number of captures at each trap position ($\chi^2_{20} = 32.16$, $p<0.05$) indicating that each trap position was also not equally used by water voles at Rainham.

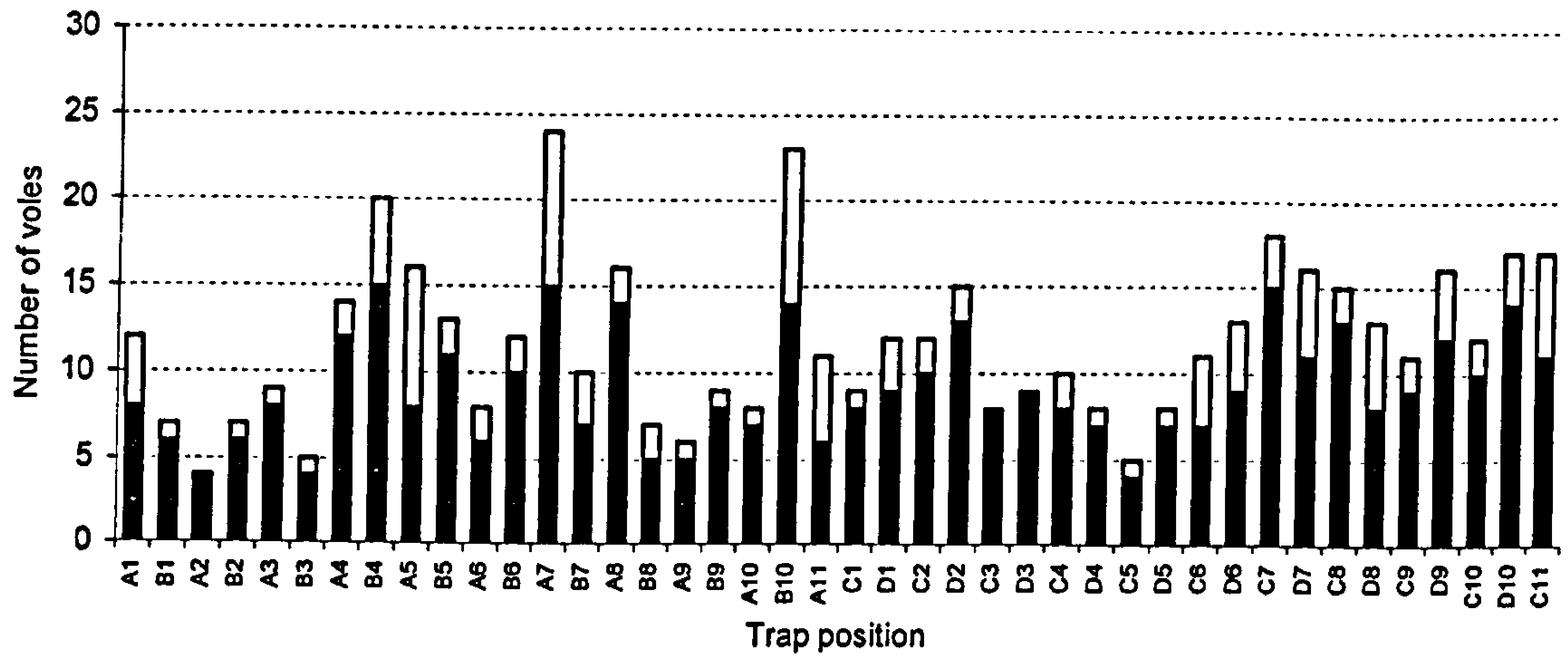
Morisita's Standardised Index of dispersion (I_p) was used to further examine the distribution of water voles captured for Aveley, Hilliers and Rainham. For Aveley and Hilliers, the data were examined with respect to season, although winter was not included as too few captures rendered the test unreliable. For Rainham, due to the short duration of trapping, the data from all seasons were combined.

For the summer season at Aveley, $I_p = -0.124$ which is not significant at the 95% confidence limits, indicating that the population was randomly distributed. For autumn $I_p = 0.015$ and for spring $I_p = 0.072$, both of which indicate a random distribution.

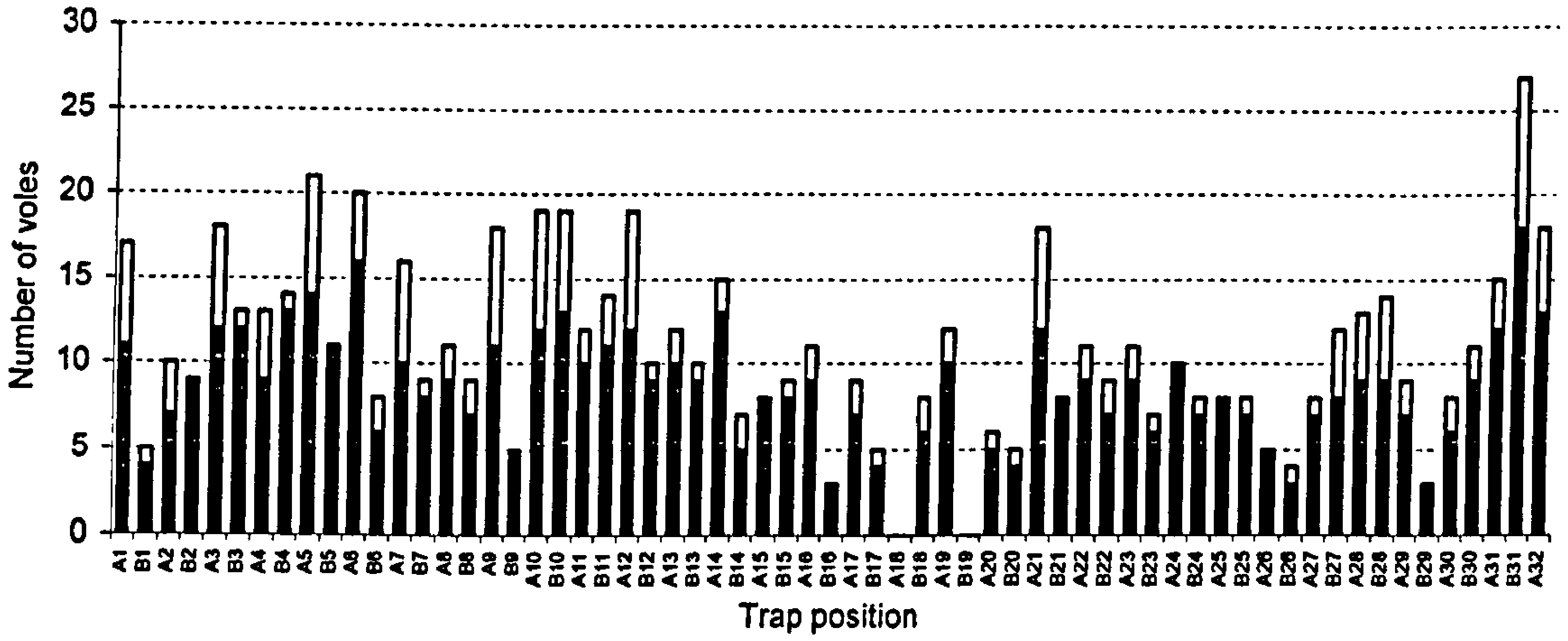
For Hilliers, summer $I_p = 0.510$, autumn $I_p = 0.500$ and spring $I_p = 0.503$. These indicate that the water vole population at Hilliers showed a significantly clumped distribution during summer, autumn and spring.

At Rainham, the combined data gave $I_p = -0.297$, suggesting a random distribution of the water vole population.

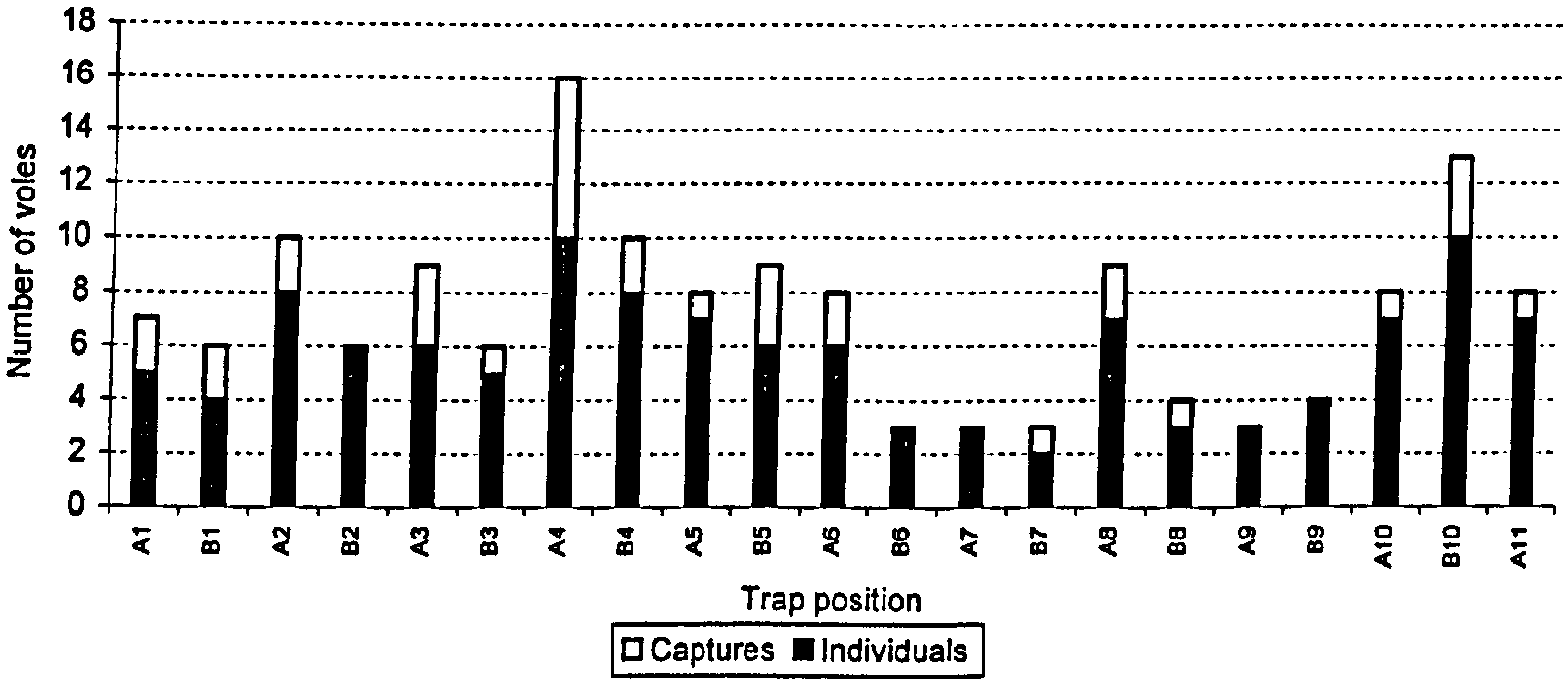
a) Aveley



b) Hilliers

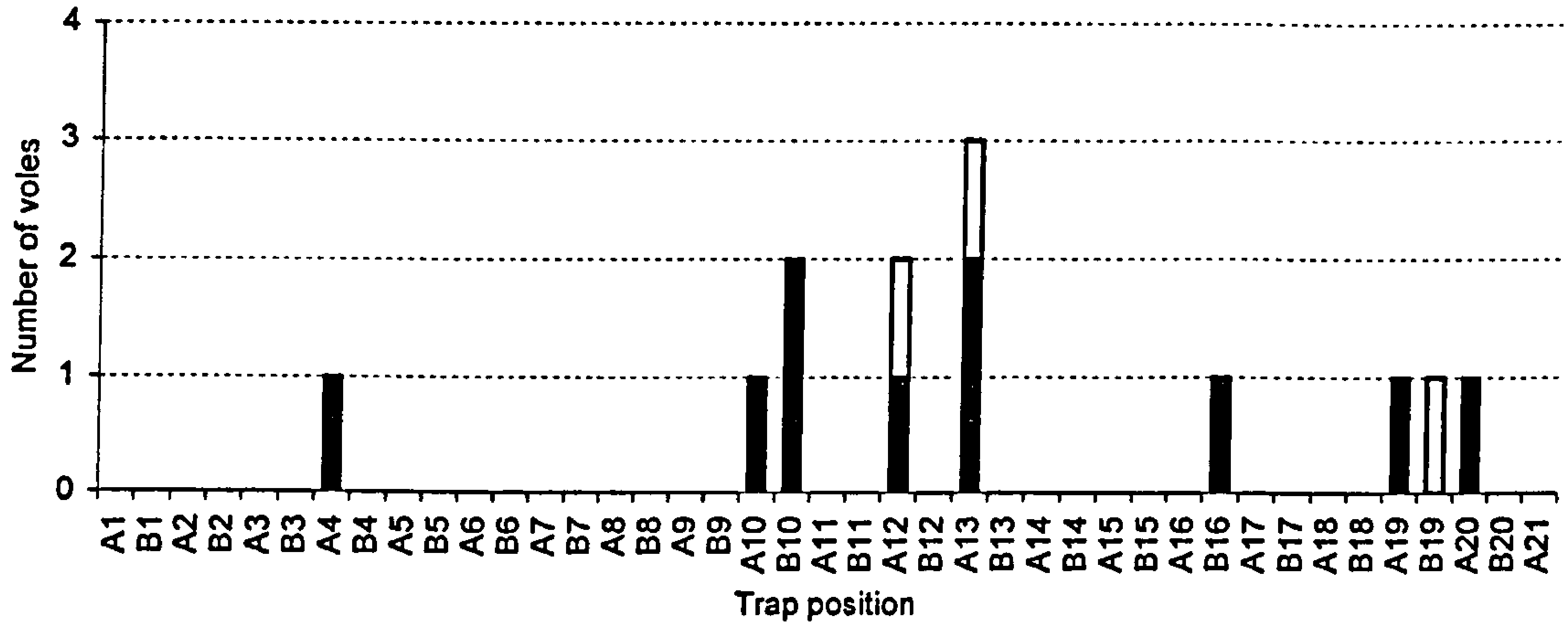


c) Rainham

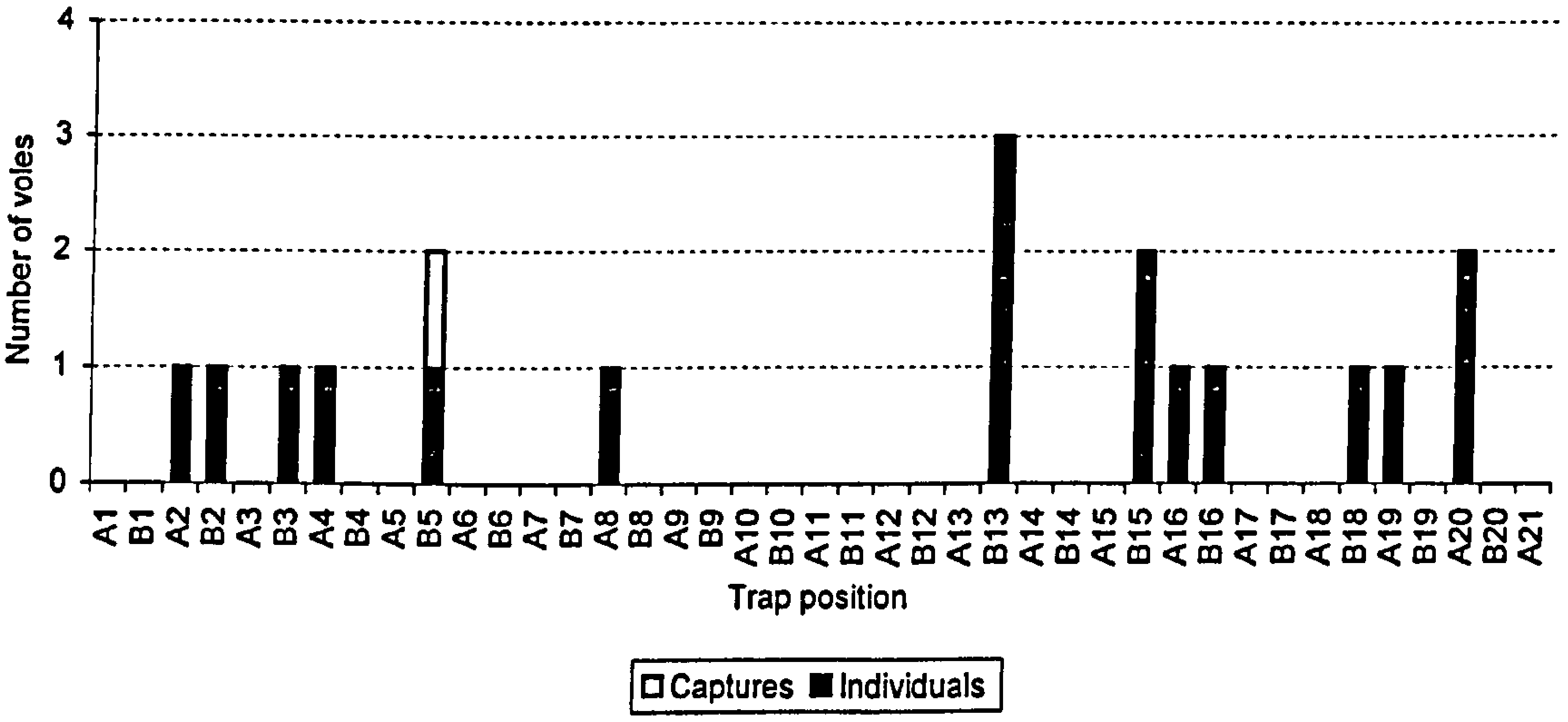


Figures 2.16a-c Distribution of total captures and individuals over trap positions for Aveley, Hilliers and Rainham

d) Bovington



e) Whitemead



Figures 2.16d and e Distribution of total captures and individuals over trap positions for Bovington and Whitemead.

2.3.6 Weights

The mean adult male, adult female and juvenile weights for each month at Aveley, Hilliers and Rainham were calculated. Mean weights for Bovington and Whitemead were not examined due to the small numbers of individuals.

Figures 2.17 a-c show the variation in mean weights (± standard error) of males, females and juveniles between months at Aveley, Hilliers and Rainham.

At Aveley (Figure 2.17a) male mean weight peaked in both May 1999 (229g ± 9.8, N=5) and May 2000 (258g ±6.7, N=3), whereas female mean weight peaked in both July 1999 (225g, N=4) and July 2000 (229g ±20.0, N=4). The lowest male weight was seen in December 1999 (150g, N=1) and June 2000 (145g, N=1), whilst the lowest female weight was in December 1999 (150g, N=1) and March 2000 (150g, N=1). During the winter of 1998/1999 males began, in October 1998, at a mean weight of 193g (±6.7, N=3) rising to 217g (±1.4, N=4) by March 1999. Males began the winter of 1999/2000, in October 1999, at 198g (±13.3, N=4), falling as low as 150g (N=1) in December and rising to 203g (±10.5, N=4) by March 2000. Females began the winter of 1998/1999, in November 1998, at a mean weight of 178g (±16.8, N=5) remaining at a similar figure in March 1999 (176g ±10.0, N=8) before rising in April 1999 (213g ±22.1, N=6). In the winter of 1999/2000, female mean weight started at 175g (±35, N=2) in October 1999 to March 2000 at 150g (N=1) and 190g (N=1) by April 2000. No trend could be seen in juvenile mean weights which could not be analysed due to the small number of data points.

For Hilliers (Figure 2.17b) mean male weight peaked in March 1999 (283g ±23.9, N=6) and again in June 2000 (300g, N=1). The lowest mean male weight occurred in July 1999 (176g ±11.5, N=15). Mean female weight peaked in April 1999 (249g ±12.0, N=4) and June 2000 (245g ±32.8, N=4) coinciding with the first appearances of juveniles. Both males and females entered the winter of 1998/1999 with similar mean weights in October 1998 (males: 190g ±16.2 N=6; females: 190g ±21.5 N=6). By March 1999 mean weights of both sexes had increased (males: 283g ±23.9 N=6; females: 244 ±11.3 N=4). Both sexes started the winter of 1999/2000 with similar mean weights in October 1999 (males: 200g, N=1; females: 193g ±17.5, N=2). By March 2000 the mean male weights had increased to 245g (±5 N=2) and in April 2000 female mean weight was 185g (±6.1 N=4). As with Aveley, due to the small number of data points, no trend can be seen in juvenile mean weights.

At Rainham (Figure 2.17c) mean male weight peaked in May 1999 (253g ±5.8, N=5) and mean female weight in June 1999 (277g ±8.8, N=3). Both sexes entered the winter of 1998/1999 with similar mean weights (males: 173g ±27.5, N=2; females: 178g ±13.6, N=4). By March 1999 males mean weight had increased (240g ±10, N=3) whilst female mean weight had remained similar to that before the winter (187g ±7.8, N=5).

Adult male and female weights between sites were compared using ANOVA. No significant difference was found between any of the sites with respect to either male weight ($F2,_{184} = 2.58$, NS) or female weight ($F_{2,272} = 0.37$, NS).

Adult male and female weights from all sites were combined to examine the data for differences between male and female weight. However, as changes in female weight occur during the spring and summer due to pregnancy, the data were analysed with respect to season (as described in Table 2.1) using ANOVA.

A significant difference between male and female weights with respect to season was shown ($F_{5,38} = 4.08$, $P<0.01$

The data were further examined for males and females at each site to investigate differences in weights between seasons using ANOVA. A Muliple Range Test (Duncan) was used to further examine any significant differences.

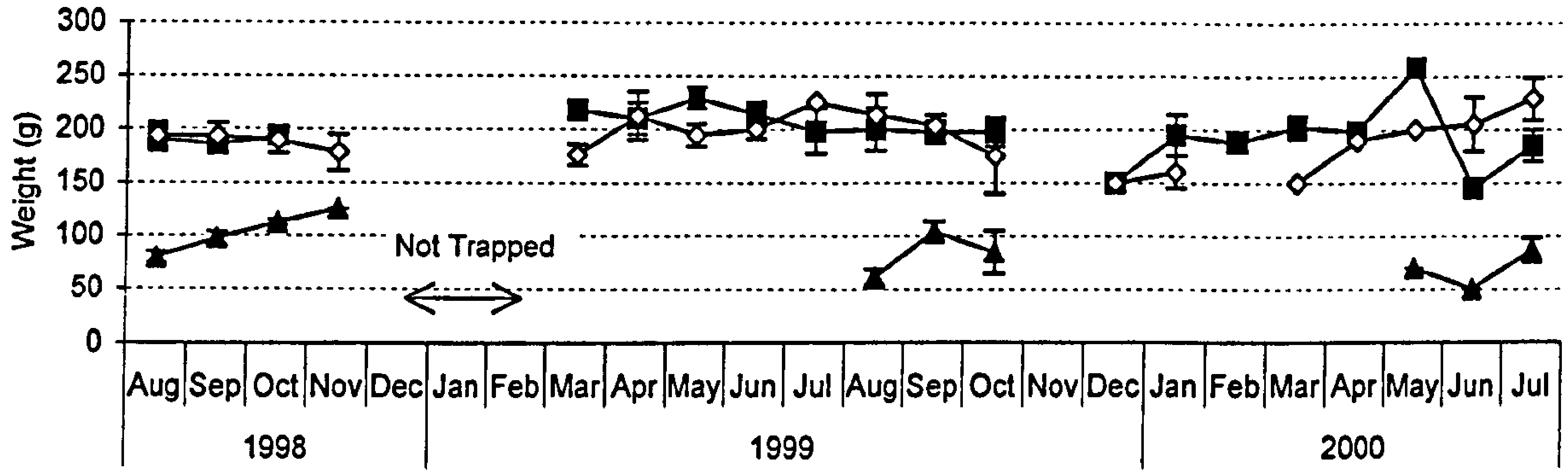
For Aveley the ANOVA showed that there was a significant difference in adult male weights between seasons ($F_{3,70} = 6.10$, $P<0.01$). The Multiple Range Test (Duncan) showed that mean male weight in spring (mean = 219) was significant higher than in summer (mean = 194), autumn (mean = 190) or winter (mean =

186). No significant difference in adult female weights between seasons was found at Aveley ($F_{3,101} = 1.85$, NS).

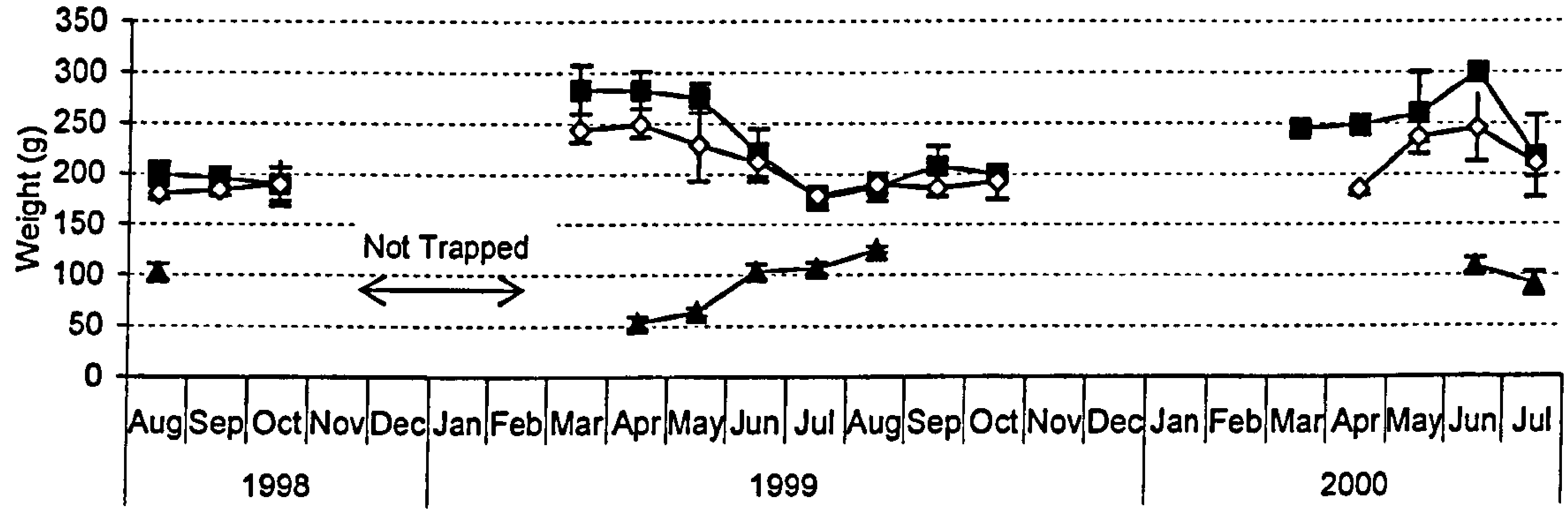
At Hilliers a significant difference was found in adult male weights between seasons ($F_{2,89} = 17.84$, $P<0.001$). In this case the Multiple Range Test (Duncan) showed that mean male weight in spring (mean = 271) was significantly higher than in summer (mean = 198) or autumn (mean = 198). Adult female weights at Hilliers were also significant different between seasons ($F_{2,144} = 7.63$, $P<0.01$). The Multiple Range Test (Duncan) showed that mean adult female weight in spring (mean = 229) was significant higher than summer (mean = 192) or autumn (mean = 186).

At Rainham there was a significant difference in male weights between seasons ($F_{2,18} = 5.08$, $P<0.05$). The Multiple Range Test (Duncan) showed that mean adult male weights in spring (mean = 241) were significant higher than in autumn (mean = 173), but that neither were significantly different from summer (mean = 195). A significant difference in mean adult female weights was found between seasons ($F_{2,20} = 4.02$, $P<0.05$). The Multiple Range Test (Duncan) showed that mean adult female weight in the summer (mean = 237) was significantly higher than in autumn (mean = 179), but that neither were significantly different to spring (mean = 199).

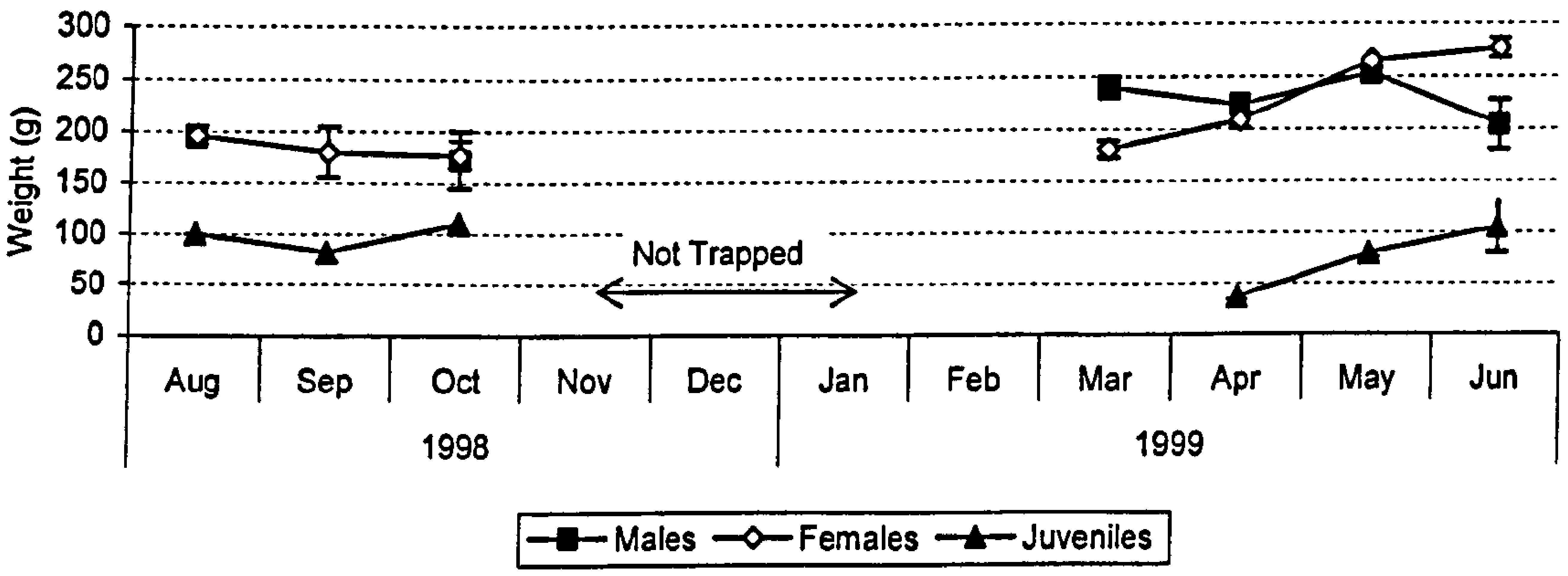
a) Aveley



b) Hilliers



c) Rainham



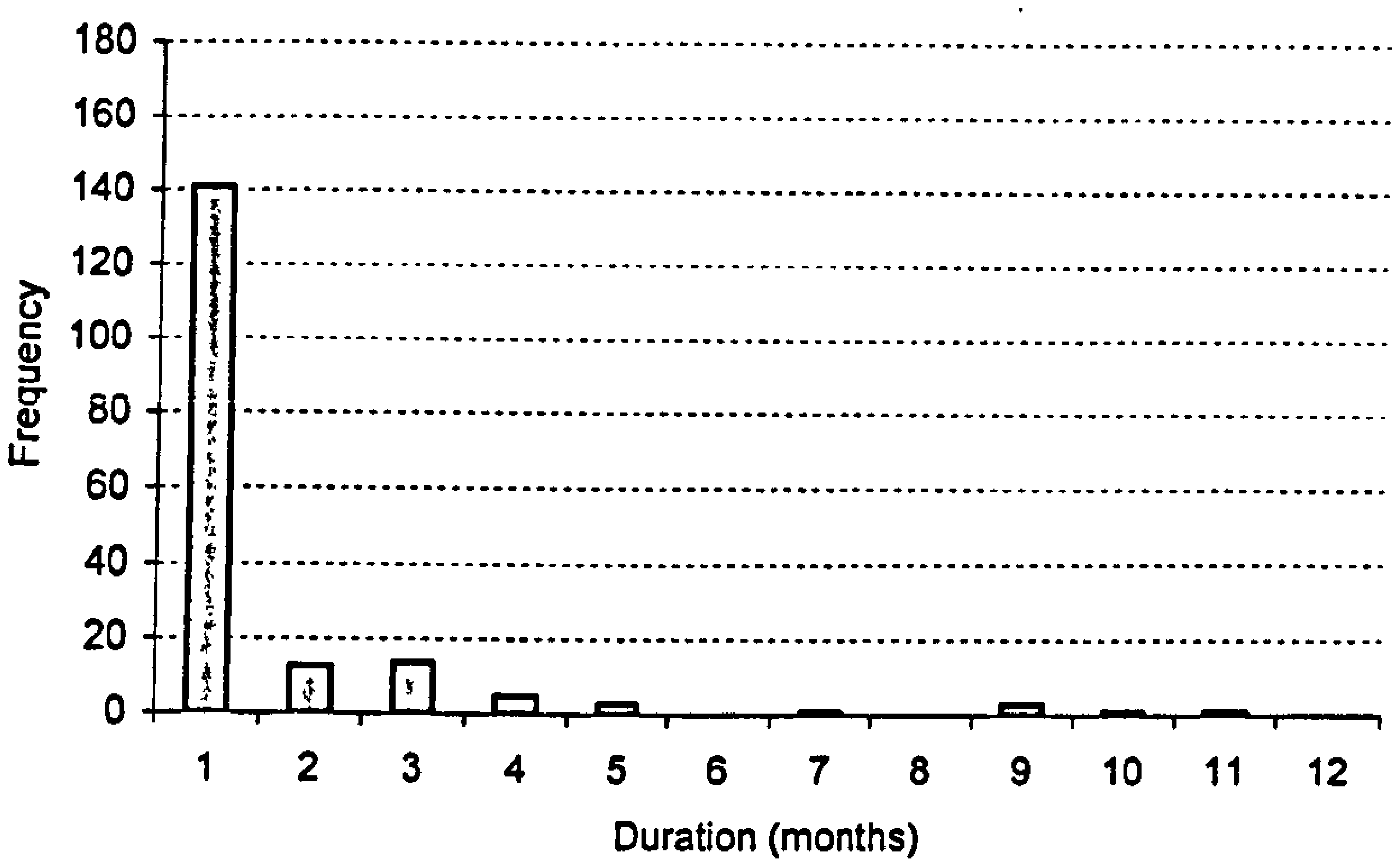
Figures 2.17a-c Mean adult male, adult female and juvenile weights (± standard error) for each month at Aveley, Hilliers and Rainham (refer to Table A1.1, Appendix 1 for number of individuals *N* in each month)

2.3.7 Residency

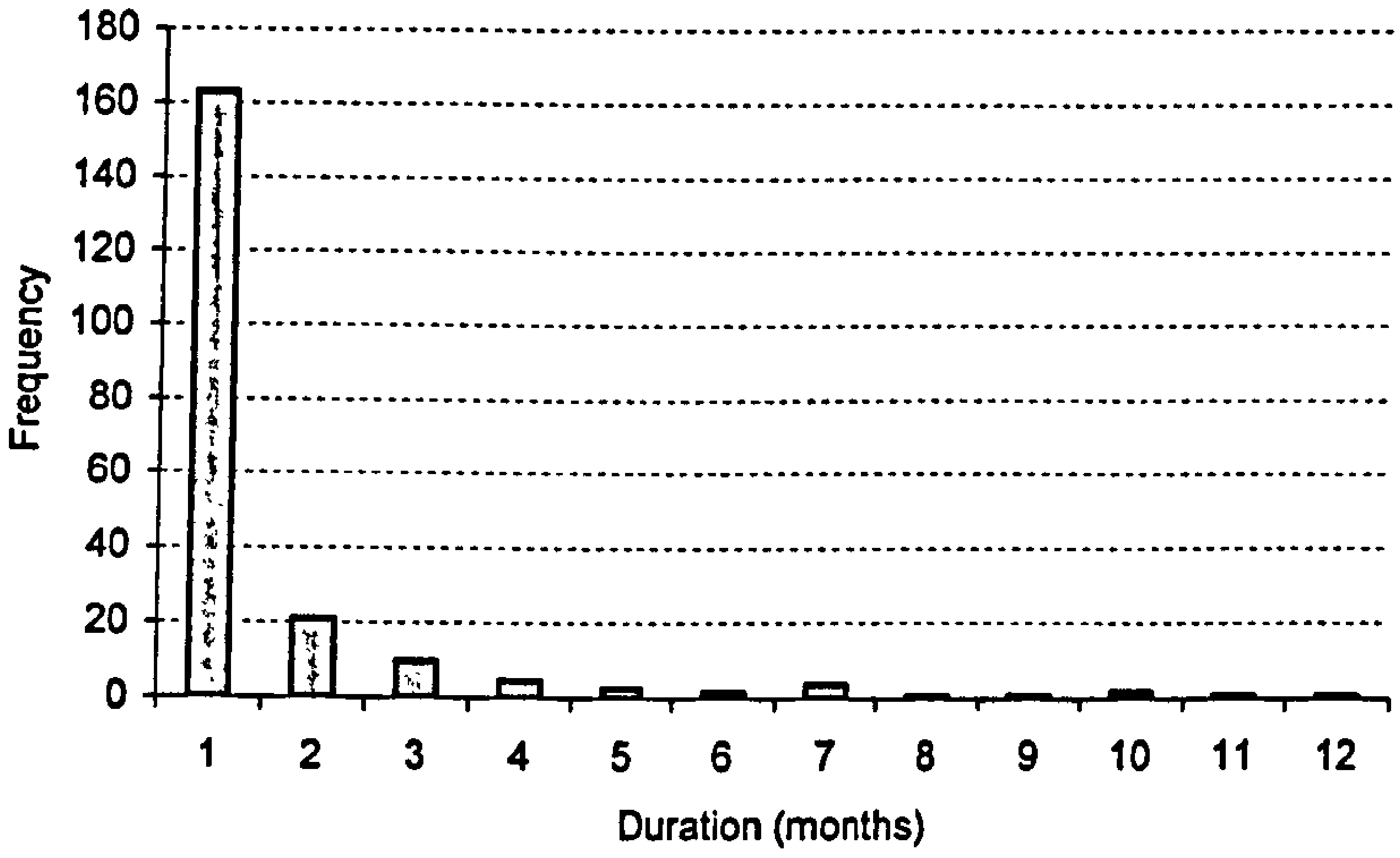
The residency of individuals was examined based upon appearances of individual tag numbers between monthly trapping sessions (tag life) for Aveley, Hilliers and Rainham. Data from Bovington and Whitemead were not examined as too few individuals were captured.

Figures 2.18a-c show frequency histograms of tag life, in months, for each of the three sites. The histograms suggest there is a significant difference in the frequency of occurrences between months. This was not tested statistically as the data are not independent.

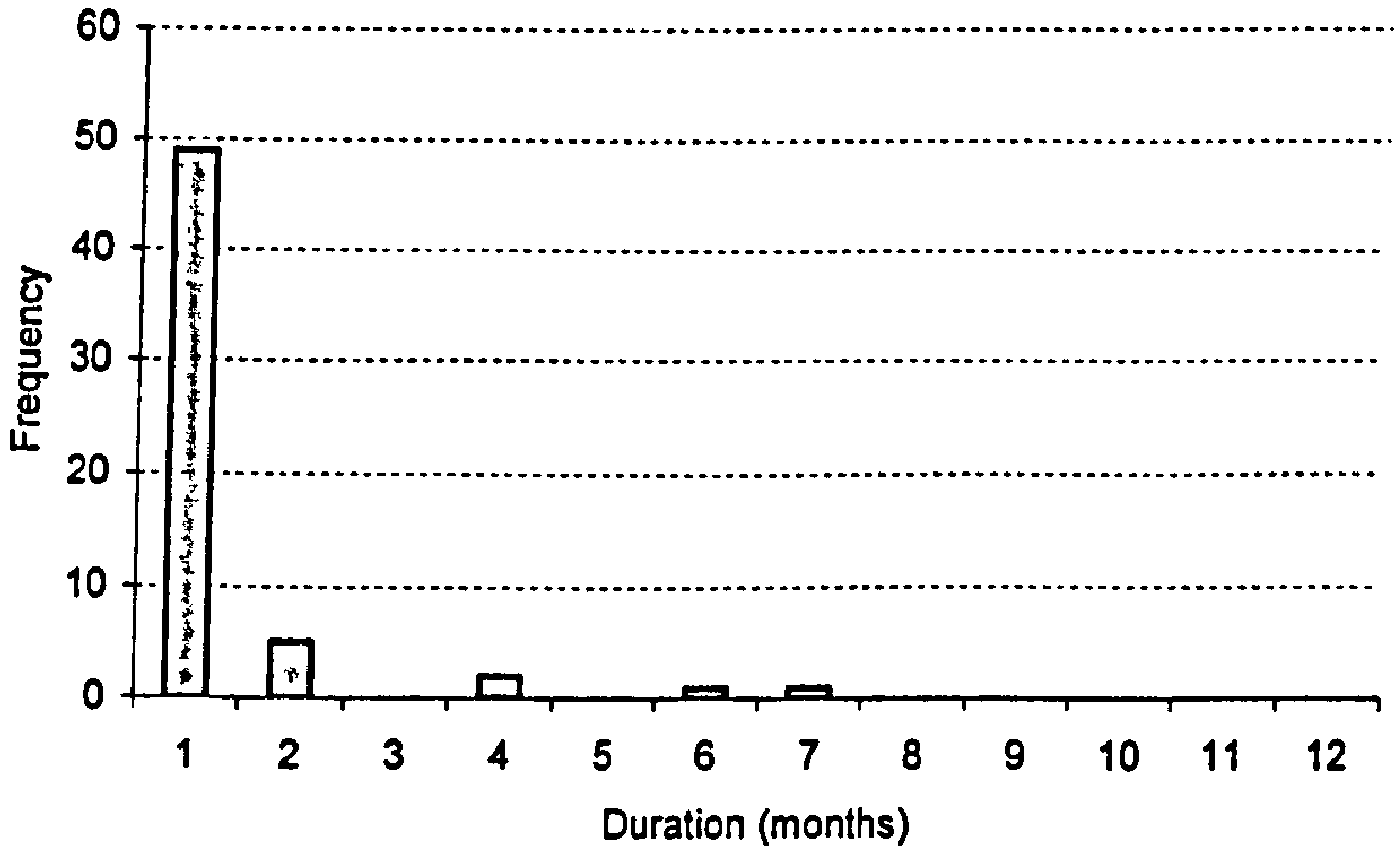
a) Aveley



b) Hilliers



c) Rainham



Figures 2.18 a-c Frequency histograms of ear tag life (in months) for Aveley, Hilliers and Rainham

2.3.8 Observed range length

The Observed Range Length (ORL) of individuals at each site was examined, based on the distance between the two remotest capture points. Individuals that were only captured once in any one month were excluded from the analysis. The mean ORL (± standard error) was calculated for males, females and juveniles for each month at each site (Tables 2.3a-c)

The data were statistically analysed for differences in the mean ORL of males, females and juveniles at each site using a Kruskal-Wallis test

There was no significant difference in ORL between males ($N = 47$), females ($N= 60$) and juveniles ($N = 25$) at Aveley ($K=4.597$, NS), Hilliers ($K=4.153$, NS) or Rainham ($K=3.637$, NS: males $N = 11$; females $N = 13$, juveniles $N = 14$), suggesting that male, females and juveniles had similar mean ORLs.

The data were then statistically analysed for differences in mean ORL between months and season within each site using the same test.

The Kruskal-Wallis test showed that there were no significant differences for the different months [Aveley ($K=19.00$, NS); Hilliers ($K=15.00$, NS); Rainham ($K=7.00$, NS)] or seasons [Aveley ($K=3.95$, NS); Hilliers ($K=0.56$, NS); Rainham ($K=0.28$, NS)], indicating that the mean water vole ORLs were not affected by time of year.

The data were then analysed for any correlation between ORL and the monthly population size at each site.

In this case a Spearman's rank-order correlation was used. No correlation was found between mean ORL and monthly population size at Aveley ($r_s = 0.145$, $N = 21$, NS) or Hilliers ($r_s = -0.342$, $N = 21$, NS). A significant, but fairly weak, correlation ($r_s = 0.731$, $p<0.05$, $N=8$) was found at Rainham. This means that there is a just over 50% chance of the variation in mean ORL being explained by variation in the population size at Rainham. However, there could easily be some other factor involved.

Table 2.3a Monthly mean Observed Range Length (ORL) based on the distance between the two remotest capture points for Aveley.

	Mean ORL (m)		
	Female	**Male**	**Juvenile**
Aug	16 ±3.9 (N=7)	19 ±4.3 (N=5)	11 ±3.4 (N=9)
Sep	26 ±11.9 (N=11)	27 ±19.0 (N=6)	13 ±9.6 (N=6)
Oct	8 ±2.0 (N=9)	10 (N=1)	10 (N=1)
Nov	5 (N=1)	N=0	5 (N=1)
Dec	Not trapped	Not trapped	Not trapped
Jan	Not trapped	Not trapped	Not trapped
Feb	Not trapped	Not trapped	Not trapped
Mar	16 ±7.3 (N=5)	43 ±18.9 (N=4)	N=0
Apr	18 ±6.6 (N=4)	30 ±7.6 (N=3)	N=0
May	13 ±5.6 (N=6)	40 (N=1)	N=0
Jun	20 (N=2)	57 ±44.8 (N=3)	N=0
Jul	25 (N=1)	43 ±37.5 (N=2)	N=0
Aug	28 ±14.5 (N=4)	28 ±2.5 (N=2)	0 (N=1)
Sep	18 ±6.3 (N=4)	3 ±2.5 (N=2)	15 ±7.9 (N=4)
Oct	5 (N=1)	30 (N=1)	N=0
Nov	N=0	N=0	N=0
Dec	N=0	13 ±2.5 (N=2)	N=0
Jan	N=0	28 ±17.5 (N=2)	N=0
Feb	N=0	3 ±3.3 (N=3)	N=0
Mar	N=0	16 ±5.5 (N=4)	N=0
Apr	N=0	10 (N=1)	N=0
May	88 ±57.5 (N=2)	0 (N=1)	N=0
Jun	5 (N=1)	N=0	N=0
Jul	30 ±5.0 (N=2)	70 ±25.6 (N=4)	37 ±14.5 (N=3)

Table 2.3b Monthly mean Observed Range Length (ORL) based on the distance between the two remotest capture points for Hilliers.

	Mean ORL (m)		
	Female	**Male**	**Juvenile**
Aug	27 ±11.4 (N=21)	23 ±8.2 (N=6)	40 ±14.2 (N=5)
Sep	9 ±3.0 (N=7)	65 ±49.4 (N=4)	N=0
Oct	5 (N=1)	25 ±10.0 (N=2)	N=0
Nov	Not trapped	Not trapped	Not trapped
Dec	Not trapped	Not trapped	Not trapped
Jan	Not trapped	Not trapped	Not trapped
Feb	Not trapped	Not trapped	Not trapped
Mar	33 ±20.8 (N=3)	41 ±19.8 (N=4)	N=0
Apr	23 ±6.0 (N=3)	125 (N=1)	N=0
May	58 ±39.9 (N=6)	20 (N=1)	14 ±4.3 (N=5)
Jun	46 ±28.0 (N=6)	39 ±17.8 (N=7)	37 ±18.0 (N=10)
Jul	16 ±6.9 (N=7)	61 ±24.1 (N=7)	14 ±4.5 (N=10)
Aug	15 ±2.0 (N=16)	17 ±5.8 (N=9)	0.00 (N=1)
Sep	13 ±7.5 (N=4)	8 ±3.0 (N=5)	N=0
Oct	40 (N=1)	110 (N=1)	N=0
Nov	N=0	N=0	N=0
Dec	N=0	N=0	N=0
Jan	N=0	N=0	N=0
Feb	N=0	N=0	N=0
Mar	N=0	40 (N=1)	N=0
Apr	0 (N=3)	10 ±10.0 (N=2)	N=0
May	25 ±15.0 (N=2)	100 ±25.0 (N=2)	N=0
Jun	43 ±6.6 (N=4)	105 (N=1)	43 ±10.6 (N=6)
Jul	24 ±9.9 (N=5)	145 ±70.6 (N=3)	105 ±100.0 (N=2)

Table 2.3c Monthly mean Observed Range Length (ORL) based on the distance between the two remotest capture points for Rainham.

	Mean ORL (m)		
	Female	**Male**	**Juvenile**
Aug	0 (N=1)	8 ±2.5 (N=2)	0 (N=1)
Sep	15 ±2.9 (N=3)	N=0	28 ±3.4 (N=5)
Oct	13 ±3.3 (N=3)	30.0 (N=1)	N=0
Nov	Not trapped	Not trapped	Not trapped
Dec	Not trapped	Not trapped	Not trapped
Jan	Not trapped	Not trapped	Not trapped
Feb	Not trapped	Not trapped	Not trapped
Mar	0 (N=2)	10.0 (N=1)	N=0
Apr	25 (N=2)	40 ±35.0 (N=2)	25 (N=1)
May	0 (N=1)	30 ±5.0 (N=2)	11 ±4.4 (N=6)
Jun	15 (N=1)	25 ±7.6 (N=3)	0.00 (N=1)

2.3.9 Other observations

2.3.9.1 Partial albinism

Throughout the study physical characteristics of individual water voles were noted. Partial albinisms occurred within the populations at Aveley, Hilliers and Rainham. White tail tips and white crowns occurred separately and individually.

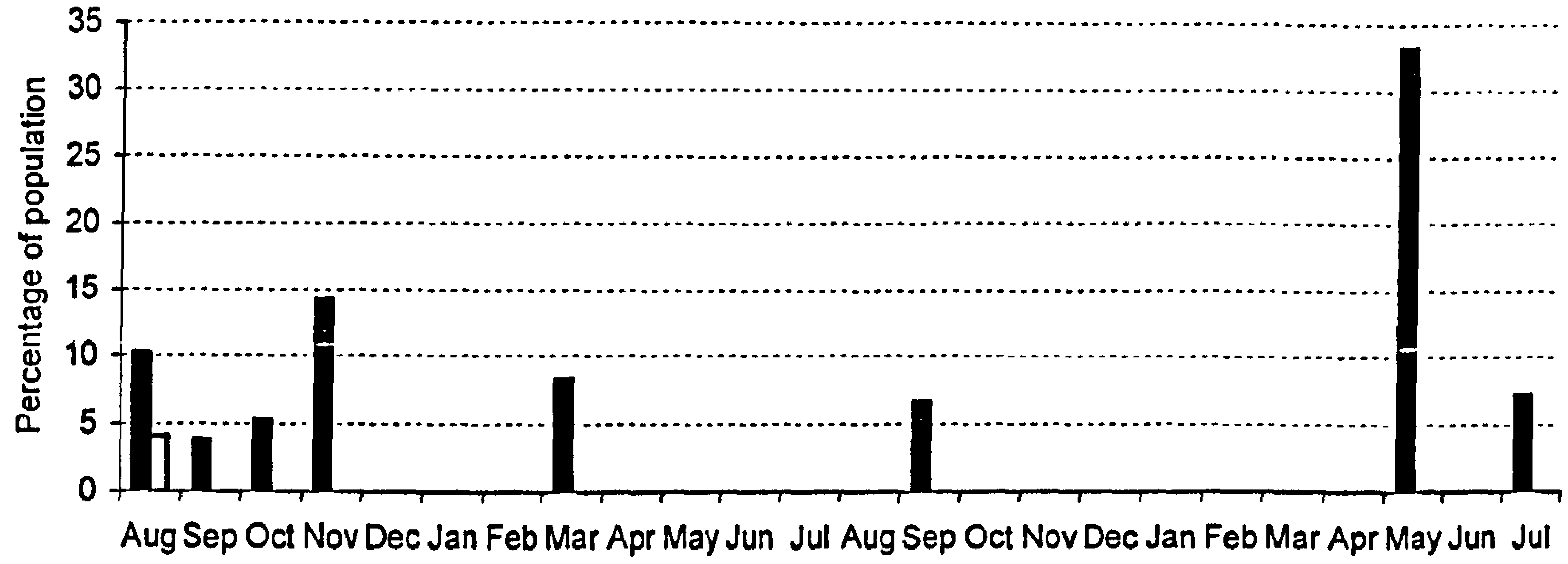
In all cases these partial albinisms occurred more frequently from April to September in young animals (Figure 2.19a-c).

At Aveley, the percentage of individuals in the population each month with white tails tips varied from 0 to 10% (N=5, August 1998) and 33% (N=2, May 1999). White crowns were only seen twice giving a percentage of 5% (N=2, August 1998).

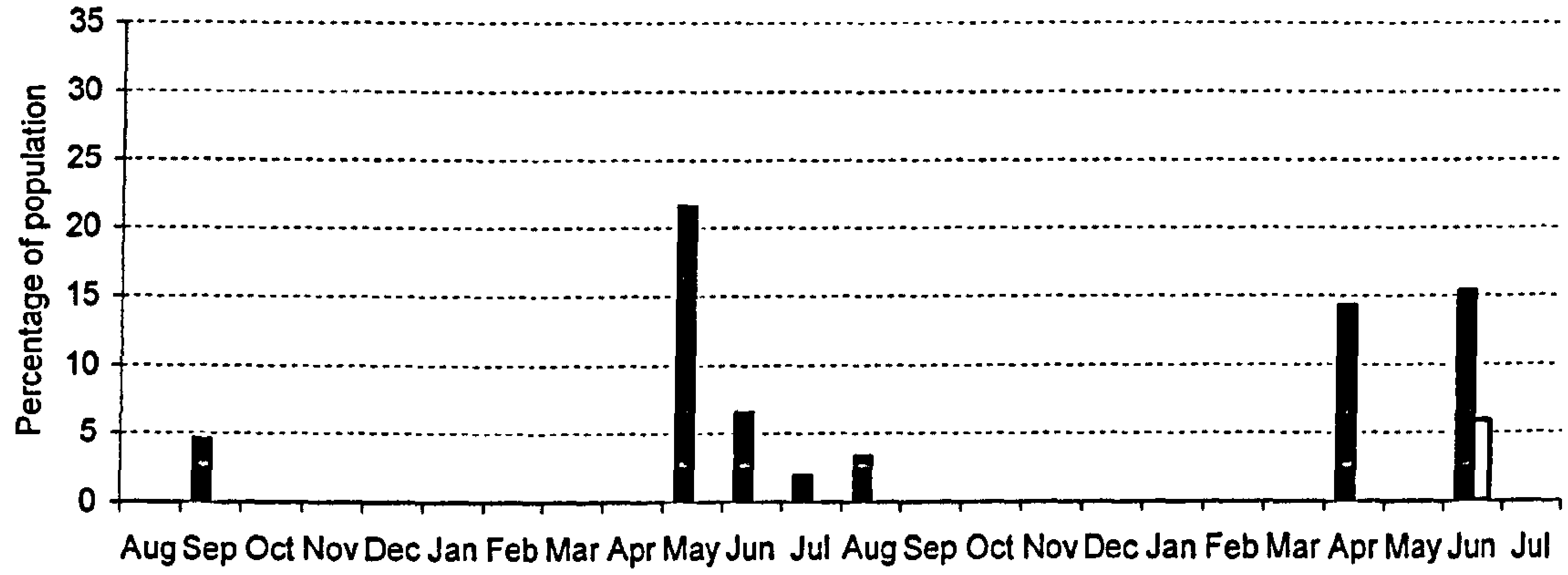
At Hilliers, white tails tips varied from 0 to 22% (N=8, May 1999) of the population. Only one individual with a white crown was seen (5.88%, July 2000).

At Rainham, the percentage of individuals in the population each month with white tails tips varied from 0 to 60% (N=9, May 1999) and white crowns varied from 0 to 24% (N=5, September 1998).

a) Aveley



b) Hilliers



c) Rainham

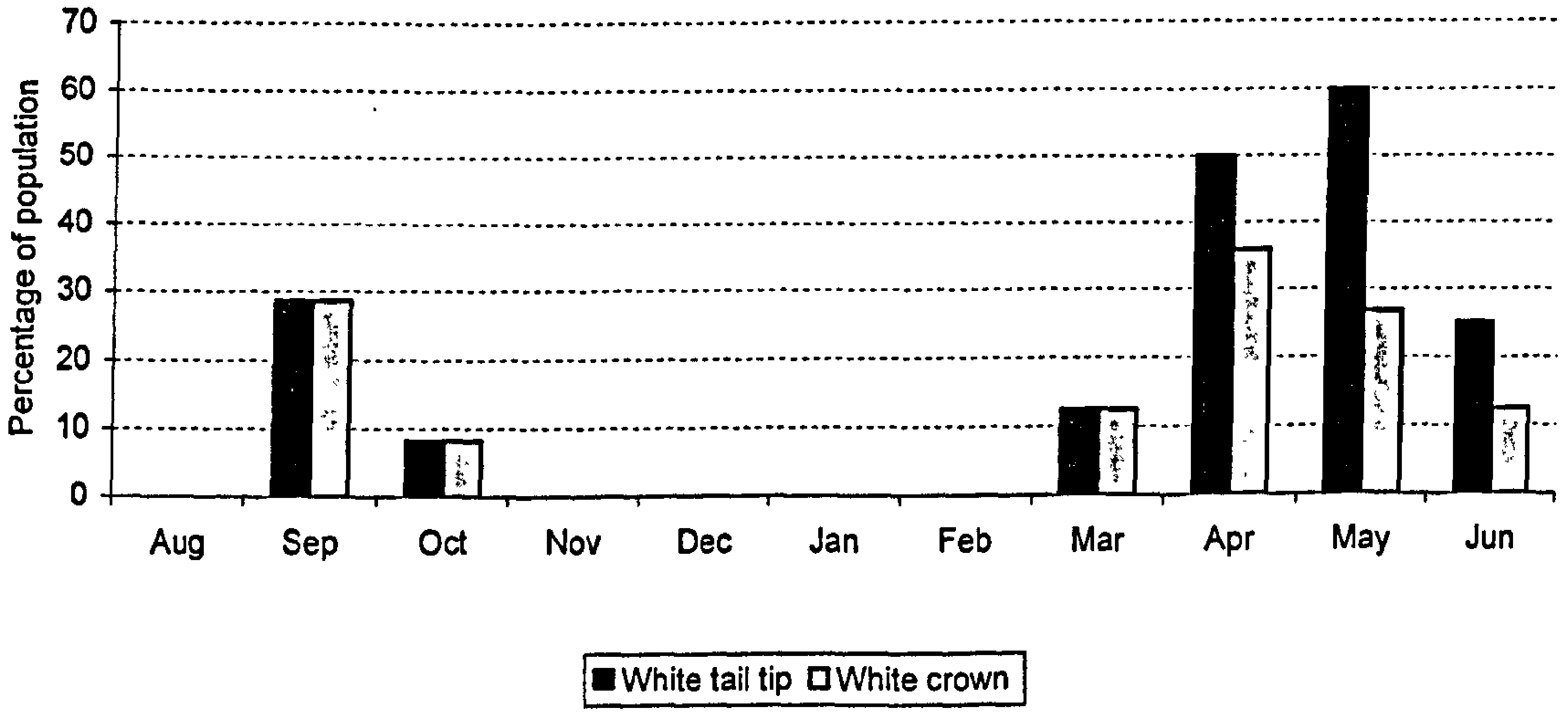


Figure 2.19a-c Percentage of populations showing signs of partial albinisms (white tail tips and white crowns) at Aveley, Hilliers and Rainham

2.4 DISCUSSION

This section discusses the results of the trapping data analysis individually: Population size (Section 2.4.1); Population composition (Section 2.4.2); Capture rate (Section 2.4.3); Activity (Section 2.4.4); Distribution (Section 2.4.5); Weights (Section 2.4.6); Residency (Section 2.4.7); Inter trap movements (Section 2.4.8); Partial albinism (Section 2.4.9). The results are also compared with published accounts. In addition the final section (Section 2.4.10) considers the relationships between the different aspects previously discussed.

2.4.1 Population size

The population sizes at all five sites varied considerably throughout the study. Using the Minimum Number Alive (MNA) method to estimate the populations; the population at Aveley varied from one individual (November 1999) to 54 (September 1998); at Hilliers the population varied from no individuals (November 1999 to February 2000) to 55 (August 1998); at Rainham the population varied from six individuals (August 1998) to 21 (September 1998). Bovington and Whitemead populations were both small at the start of the study in August 1998, with three and four individuals respectively, and then declined rapidly until in November 1998 no water voles were present at either of these sites for the duration of the study. The other three sites appeared to suffer a decline in population size over the course of the study. However, the Rainham population was only studied for 11 months (see Section 2.2.3) and therefore this apparent decline may simply have been due to seasonal fluctuations in numbers.

In order to compare sites it is necessary to consider the density of voles as opposed to the population size. The density at Aveley varied from no water voles per 100m (November 1999) to 26 (September 1998); at Hilliers the density varied from no voles per 100m (November 1999 to February 2000) to 17.19 (August 1998); at Rainham the density varied from 6 voles per 100m (August 1998) to 21 (September 1998). These densities were generally higher than those reported elsewhere. Pelikan and Holisova (1969) reported densities from 4 to 9.3 water voles per 100m on a brook in the Czech Republic. The maximum density recorded by Barreto and Macdonald (2000) was 1.25

voles per 100m of river and Leuze (1976) estimated densities of 4 to 16 voles per 100m of river. For fossorial water voles densities of approximately 10 voles per $100m^2$ of grassland in western Switzerland have been reported (Weber *et al*, 2002), whilst in a reed bed in the Czech Republic a maximum density of 1.5 voles per $100m^2$ was recorded (Pelikan, 1974).

The high densities at Aveley and Rainham could be explained by the site characteristics. Both of these sites were situated within a grazing marsh system with extensive drainage ditch networks, many of which were occupied by water voles (Benge, 1999). The design of the drainage ditches, a trapezoidal shape, appeared to provide good burrowing substrate. At the start of this study neither site had been disturbed for several years, allowing the ditches to become dominated by dense stands of common reed (*P. communis*) thus providing sufficient food and protection to support the high densities recorded. The high density at Hilliers cannot be as easily explained as for the other two sites, however it may again be a product of the habitat being of sufficient quality to support such high densities.

In 1998 and 1999 the populations at Hilliers clearly showed a summer peak (June/July/August) in size and this trend seemed to be occurring again towards the end of the study in July 2000, albeit at lower numbers. This peak has been reported in many other studies, often occurring between May and September (Woodall, 1977; Green, 1998; Barreto and Macdonald, 2000) and is associated with a peak in the number of juveniles in the population (see Section 2.4.2). At Aveley the peak occurred later than at Hilliers in August to September and Rainham showed a peak in September similar to that reported by Woodall (1977).

All of the populations were at their lowest over winter. The Aveley population declined rapidly to seven individuals in November 1998 increasing slightly to 12 by March 1999. In November 1999 only one individual was known to be alive, this subsequently increased to five individuals by January 2000. A subsequent substantial increase was not seen until July 2000 (14 individuals). In October 1998 the population fell to 12 individuals, this subsequently crashed until no individuals were known to be alive in November 1998 and by March 1999 ten individuals were present. Similarly, in October 1999 the Hilliers population fell to three individuals then to zero in November 1999, recovering to two voles by March 2000. This suggests that, at Hilliers, at least some animals overwintered and that water voles probably were present during the winter but did not enter any traps. The Rainham population declined to 12 individuals in October 1998 falling to zero in November 1998 with 8 individuals caught in March 1999. This further supports the hypothesis that water voles were present but not trapped during the winter months. Previous studies have reported a decrease in the activity of water voles above ground during the winter (Leuze, 1976; Singleton, 1984) which may explain why none were captured over winter in the current study.

Barreto and Macdonald (2000) reported a similar decrease in population size over winter, as have many other authors (*e.g.* Stoddart, 1968; Vincent, 1974; Woodall, 1977; Green, 1998).

Due to the high frequency of tag loss (see Section 2.2.3) it was not possible to examine over winter mortality of individuals. However, the numbers of individuals captured in the October and in the following March each winter at Aveley, Hilliers and Rainham suggest that winter mortalities occurred (Aveley: 40% in 1998, 37.5% in 1999; Hilliers: 16.67% in 1998, 33.33% in 1999; Rainham: 33.33% in 1998). Jordan and Netherton (1999) reported losses 74% of the population between November and April, almost all of which were attributed to predation. Singleton (1984) also reported high winter mortality with the population in April consisting of only 12 to 33% of over winter survivors. In contrast, Woodall (1977) reported low adult winter mortalities. It is equally possible that the reduction in the size of the populations was due to emigration. However, whilst it is possible that juveniles may disperse during this time period there is little evidence to suggest that adults do so (Woodall, 1977).

The start of the decline in water vole numbers at Aveley coincided with the introduction of cattle on to the site in September 1998 until the end of the study. The grazing livestock had a marked, but not quantified, effect on the bankside and emergent vegetation. In addition, poaching of the banks of the ditch became severe, particularly following wet weather over the winter of 1998/1999.

Although no direct evidence was found, the decline and ultimate extinction of water voles at Bovington and Whitemead is thought to be attributed in part to predation from

American mink. However, in the absence of data on the water vole population sizes prior to the start of this study this conclusion cannot be definitive.

2.4.2 Population composition

The numbers of males, females and juveniles in the populations at all sites varied throughout the duration of the study. Numbers of females peaked at Aveley in September 1998, May 1999 and August 1999 and were seen to have begun rising in July 2000. Similarly, female numbers at Hilliers peaked in August 1998 and August 1999 and at Rainham in September and October 1998. Singleton (1984) also noted a preponderance of females in August and September. It seems likely that this increase in females was due in part to juveniles born early in the year reaching a weight at which they became classed as an adult. It could also be as a result of the breeding season ending and previously nursing females spending more time foraging above ground, hence being more trappable. Perforate females were first seen in the populations in March or April and were no longer present after September, which is comparable with other studies (*e.g.* Woodall, 1977).

A peak was seen in male numbers at Aveley in September 1998, however no comparable peak was seen in 1999. At Hilliers, male numbers were highest in August 1998 and July 1999. It seems likely that, as with females, this was due in part to juveniles born early in the year reaching a weight at which they became classed as an adult. At Rainham, no obvious peaks in male numbers were seen. Other studies have reported higher numbers of males in the spring and early summer, which is generally attributed to the greater activity of males during this time (Pelikan, 1974; Gaisler and Zejda, 1973; Woodall, 1977). Such an increase at this time of year was not noticed in any of the current study sites. Sexually active males first appeared in the populations in March or April, which corresponds to the recording of perforate females at the same time and other published studies (*e.g.* Leuze, 1976).

Juveniles were present at Aveley, Hilliers and Rainham at the start of the study in August 1998. In the Aveley and Hilliers populations, the numbers of juveniles rapidly decreased until none were present in November 1998. At Rainham the numbers of juveniles first peaked in September before declining. A similar pattern was seen in

1999 at Aveley and Hilliers. In 1999 juveniles first appeared at Hilliers in April and in August at Aveley. In 2000, they first appeared in the Aveley population in May and at Hilliers in June. Other authors have reported juveniles being present in April, including Pelikan (1974). The differences in the time of year that juveniles appeared in the populations may be attributed to weather conditions or possibly predation. Juvenile numbers peaked at Aveley from August to September in 1998 and 1999 and at Hilliers in April 1999 to July 1999. These peaks in numbers are consistent with the published accounts of juvenile numbers (Woodall, 1977: August to September; Singleton, 1984: June to October) and young being born between April and September (Boyce, 1991).

2.4.3 Capture rate

As expected the percentage of new captures decreased over the three day trapping period. Combining the data for different months, the difference in the percentage of new captures was statistically significant at Aveley, Hilliers and Rainham, as would be expected if the trapping programme was efficient. More adult males and females were first captured on day one than on days two or three. Further analysis showed that at all three sites, the mean percentage of new captures was higher on day one than on day three. Stoddart (1968) and Zejda and Zapetal (1969) reported captures of 70% of the population in the first day of a three day trapping session. In contrast, Singleton (1984) took three days of trapping to obtain 60 to 70% of the population. In this study the mean captures on the first day were around 50% of the total number of captured animals (Aveley: 49.44%; Hilliers: 44.28%; Rainham: 50.25%). Given this it seems likely that during the three day trapping sessions in this study the majority, if not all, of the trappable animals within populations were captured.

The majority of individuals were only captured once in each trapping session, although some individuals were captured up to five times in a trapping session. Water voles have not generally been reported in the literature as being trap-shy, however there is likely to be individual variation. Incidence of once only captures may be increased during dispersal phases when transient animals are captured. In addition, many of the once only captures were noted as juveniles, many only a few weeks old. In the current study, a few water voles re-entered the trap as soon as it was replaced, indicating trap-proneness.

2.4.4 Activity

Statistical analysis of the activity data showed that there was a significant difference between the proportion of captures at 06:00 hrs, 14:00 hrs and 22:00 hrs at Aveley and Hilliers. There was no significant difference at Rainham. Further analysis showed that at Aveley the proportion of captures was significantly higher at 06:00 hrs than at 22:00 hrs which was in turn higher that at 14:00 hrs. At Hilliers the proportion at 06:00 hrs was significantly higher that at 14:00 hrs which was significantly higher than at 22:00. The analysis also highlighted that at Hilliers the proportion of captures at 06:00 hrs varied with season. Gaisler and Zejda (1973) reported the highest capture rate in the morning (06:00 hrs to 08:00 hrs), a lower rate in the night (20:00 hrs to 22:00 hrs) and the lowest capture rate in the afternoon (14:00 hrs), corresponding with that found at Aveley. This suggests that water voles may be more active between 22:00 and 06:00 and also between 14:00 and 22:00, which corresponds with the summer peaks in activity at dawn and dusk reported by Knight (1975) and Lund (1970). In addition, Ashby *et al* (1969), using direct observation, suggested that a lull in activity existed around midday (12:00). Gaisler and Zejda (1973) suggested that activity could be affected by the presence of human recreational activities and even grazing of livestock. It is interesting to compare the relative disturbance levels at the three sites in the current study. Aveley was grazed by cattle, Hilliers was subject to disturbance from people walking along the path adjacent to the bank and Rainham was completely undisturbed. It is possible that water vole activity at Aveley was affected by the presence of cattle, certainly they have been known to have a deleterious effect on population size (see Section 2.4.1). It is therefore likely that the absence of human or livestock disturbance at Rainham provided water voles with the opportunity to remain active throughout the day and night without an enforced lull in activity.

2.4.5 Distribution

Analysis of the distribution of water vole captures over the duration of the study showed that there was a significant difference between the total number of captures at each trap position at Aveley, Hilliers and Rainham. Only nine of the 41 traps at Bovington and

13 of the 41 at Whitemead were used, however, the total number of captures was very low at both sites (≤3 individuals). At Aveley and Rainham, none of the trap positions had no captures and only two positions, in the middle of the study site, had no captures at Hilliers. These two trap positions were both located high on a steep bank (90°) of the study site and were therefore possibly not found by water voles. It is likely that this is the reason that the standardised Morisita's Index for Hilliers indicated a clumped distribution during spring, summer and autumn, whilst Aveley and Rainham both showed random distributions.

In a study in the North York Moors National Park, UK, Lawton and Woodroffe (1991) showed that water voles were not evenly distributed along a watercourse, but occupied discrete colonies. They concluded that gaps in the distribution of voles were due to unsuitable habitat or because some areas were too isolated or had suffered high levels of mink predation. Woodall (1977) also found the distribution of water voles to be significantly clumped. On the other hand, Stoddart (1970a) found no clumping of water voles and no sizeable stretches of bank to be uninhabited. Barreto and Macdonald (2000) found that water vole captures were not evenly distributed along a section of the River Windrush, Oxfordshire, UK. Bonesi *et* al (2002) reported that the distribution of water voles was determined by the presence of freshwater, food and cover. In the current study, some trap sites captured more individuals whereas no captures were made at other trap sites, coinciding with areas of river bank poached by livestock, where both a lack of food and cover was present. At Aveley, poaching was seen along the majority of the study site and many of the other ditches in close proximity. Therefore water voles would not have the option of avoiding these poached areas as occurred in the much longer site studied by Barreto and Macdonald (2000).

2.4.6 Weights

The mean weights of adult males, adult females and juveniles over each month for each site were analysed. The maximum mean male weights were 258.33g at Aveley, 283.33g at Hilliers and 223.33g at Rainham. No significant difference was found between the mean adult male weights at these three sites. At Bovington and Whitemead the maximum individual male weights were 200g and 260g respectively. Ashby *et al* (1969) reported weights of between 250 and 320g for sexually mature males, and

Woodall (1977) reported many males weighing over 300g. This suggests that the male water voles in the current study were slightly smaller than in previous studies. The maximum mean female weights were 229 (±20.0, N=4) at Aveley, 236 (±5.5, N=4) at Hilliers and 277 (±8.8, N=3) at Rainham. No significant difference was found between the mean adult female weights at these three sites. At Bovington the maximum individual female weight was 200g and 230g at Whitemead. In a study in Oxfordshire, UK, female weights ranged from 255 to 310g (Efford 1985). As with males, this suggests that the female water voles in the current study were generally smaller than previously reported.

No significant difference was found between male and female weights at any site, which is consistent with that reported in other studies (Woodroffe, 1988; Barreto and MacDonald, 2000). However, when the data were pooled significant difference was found between male and female weights with respect to season.

Both males and females started both winters with similar mean weights in October at Aveley, Hillier and Rainham (all ≤200g). By the following March of both years, male mean weight had increased and was higher than female mean weight which was similar to the October mean weight. This has also been reported in a population of water voles in the Czech Republic (Zejda, 1992). Woodall (1977) reported juveniles to overwinter at below 200g which is consistent with the current study. However, Woodroffe (1988) noted slightly lower mean overwinter weights of 145g to 175g. At Aveley, Rainham (1999/2001) and at Hilliers (2000) mean male weight peaked in May or June, before declining to the overwinter mean weight. When analysed seasonally for Aveley, Hilliers and Rainham, the mean adult male weight was significant higher in spring than in autumn. Female mean weights increased from March to peak in June or July at Aveley, Rainham and Hilliers (2000) before declining to the overwinter mean weight. At Hilliers, the mean female weight was significantly higher in spring than summer or autumn. Whilst at Rainham, mean female weight was significantly higher in summer than autumn. In 1999 at Hilliers, both male and female mean weights declined from April. It is also interesting to note that juveniles first appeared in April of 1999 indicating that breeding had begun in March. This indicates that both males and females reached peak mean weights earlier in the year than usually seen because the population began breeding earlier. In the Czech Republic, Gaisler and Zejda (1973) found that most individual's body weight increased between April and May, followed by a drop between May and June with an occasional increase in June, July or August. Woodroffe (1988) also found that mean male and female weights peaked in May and June. The mean weights in the current study indicate that this was also the case at Aveley and Hilliers and probably at Rainham. Zejda (1992) demonstrated that sexual activity had a considerable influence on the weights of individuals; male weight increasing due to the growth of testes and accessory glands and female weight increasing due to the growth of embryos, foetuses and milk glands.

2.4.7 Residency

The data for ear tags showed that the majority of tags only lasted for one month (Aveley: 84%; Hilliers: 76%; Rainham: 77%). It cannot be ascertained whether this relates to residency of water voles or to the loss of ear tags. However, a number of water voles were noted to have ripped ears strongly suggesting that they had previously been tagged. Many previous studies have utilised ear tags for marking water voles with varying degrees of success. Woodall (1977) found a high rate of ear tag loss and Woodroffe (1988) also noted that a number of tags were lost between trapping sessions. In contrast Singleton (1984) using two tags per animal found only 5% of animals lost both tags. This suggests that if ear tagging is to be used, both ears of each individual should be tagged.

2.4.8 Observed Range Length

The maximum mean ORL for females at Aveley was 88m in May 2000, 70m for males in July 2000 and 37m for juveniles also in July 2000. At Hilliers the maximum mean female ORL was 46m in June 1999, 145m for males in July 2000 and 105m for juveniles in July 2000. At Rainham the maximum mean female ORL was 25m in April 1999, 40m for males in April 1999 and 28m for juveniles in September 1998. The largest ORLs were 145m for females at Aveley and Hilliers and 75m for females at Rainham; 145m for males at Aveley and Hilliers and 25m for females at Rainham; 60m for juveniles at Aveley and Hilliers and 40m for juveniles at Rainham. Stoddart (1970) reported a maximum mean ORL, estimated using live trapping, to be 119m (±66). Singleton (1984) showed the mean ORL, based on trapping, to be 74.6m for males, 30.7m for females, 44m for juvenile males and 23m for juvenile females. Barreto and Macdonald (2000) reported a male's range to be as much as 220m, whilst the movements of four juveniles never exceeded 30m. In the Czech Republic, Pelikan and Holisova (1969) recorded mean ORLs of 42m and 32m for males and females respectively. Clearly there is a great deal of variation in the ORL recorded for water voles as the current study has also demonstrated.

In the current study, no significant difference was found between the ORL of males, females and juveniles at any site. Woorall (1964) also found no significant difference between male and female ranges, whilst in contrast, Singleton (1984) found that males had significantly larger ranges than females. Pelikan and Holisova (1969) reported that ranges based on live-trapping increased with the number of recaptures of an individual. This suggests that the ORLs obtained in the current study may have been limited by the length of the trapping sessions.

No significant differences were found between ORL of different months or seasons at any site, however, at Rainham a significant but weak correlation was found with population size. Singleton (1984) found a correlation between movements of adults and the size of the female population and Woodall (1977) found a correlation between female home range, based on trapping, and estimated population size (MNA).

ORLs based on live trapping should not be taken as equivalent to home range size in the water vole. As Pelikan and Holisova (1969) found, ORL can increase as the number of times an animal is captured increases, although it should begin to plateau. The ORL may also be influenced by trap spacing (*e.g.* Hayne, 1949). Trap proneness may result in a prevalence of ORLs of zero (pers. obs.). In addition, many individuals were only captured once, as found by other researchers (*e.g.* Barreto and Macdonald, 2000), and therefore no range estimation can be made for these individuals. Home ranges estimated by radio tracking are considered in Chapter 4, where a comparison of the two methods is discussed.

2.4.9 Partial albinism

Partial albinisms occurred in the study populations at Aveley, Hilliers and Rainham. These consisted of white tail tips and white crowns. Stoddart (1970b) estimated mean occurrence of white tail tips in Britain to be 39.8% and white crowns 20.9%. In the current study, Rainham exhibited the highest percentage of partial albinisms with up to 60% of the population having white tail tips and 23% having white crowns. 21% of a population of water voles in Western Siberia have been reported as having partial albinisms, mainly white crowns (Bragin *et al*, 2000). During years of population decline, when environmental stressors are severe, Popatov *et al* (1998, cited in Bragin *et al*, 2000) reported the proportion of partial albinisms to increase in the young of that year. This could indicate that the population at Rainham was undergoing a population decline. However, no obvious environmental stressors were noted, and further evidence would be required to substantiate such an argument. Other trapping studies undertaken in watercourses adjacent to the Rainham study site revealed two 100m stretches with 9% and 38% of the population having white crowns (Benge, 1999). In the same study, in a 100m stretch adjacent to the Aveley study site 60% individuals had white tail tips. Also in this study, three 100m sections of ditch between Aveley and Rainham on the Inner Thames Marshes yielded high captures of individuals with partial albinisms (Ditch 1- 36% with white tail tips and 9% with white crowns; Ditch 2 - 67% with white tail tips; Ditch 3 - 50% with white tail tips). Interestingly Bragin *et al* (2000) found that males with partial albinisms had a lower frequency of agonistic behaviours at the ages of 5 and 10 months. These individuals remained subordinate to males without any white marks throughout the "stressful" year. This suggested that females must have been choosing to mate with these subordinates in order for the observed increase in partial albinisms to occur.

2.4.10 General discussion

The densities of water voles at Aveley, Hilliers and Rainham were all generally higher than those recorded elsewhere, suggesting that density may be dependent on the type of habitat or other variables. Water voles were distributed along almost the entire length of these study sites. The introduction of grazing by cattle, and associated poaching of the ditch banks at Aveley, seemed to have a deleterious effect on the population size, whilst mink predation was the likely cause of the extinction of populations at Bovington and Whitemead. All populations peaked in size, as a result of juveniles entering the populations, and adult weight in the spring and summer, declining in the autumn. Adult weights were generally lower than those found in previous studies and there was no difference between adult male and adult female weights at any site. Captures were rare during the winter, as the populations were at their smallest. A high rate of ear tag loss meant that individuals could not be reliably be followed between months and therefore the population estimates based on MNA may be significantly underestimated.

The highest period of activity at Aveley, Hilliers and Rainham was between 22:00 hours and 06:00 hrs corresponding with that found in previous studies.

Partial albinisms were found in voles from Aveley, Hillers and Rainham suggesting the populations may have been under some kind of environmental stress.

CHAPTER 3 LATRINES

3.1 INTRODUCTION

The use of live-trapping to estimate populations is often a time consuming, expensive and difficult method particularly when dealing with larger mammals. Therefore other methods of population estimation may be used, such as observation counts of individuals (*e.g.* Palomares, 2003) or indices based on counts of field signs (*e.g.* Redpath *et al*, 1995). Most mammals leave some form of field sign indicating their presence. These have been exploited by researchers to provide both evidence of presence or absence of a species and in many cases to provide an estimate of the population size. Trackway counts have been used to estimate deer population size in the south and east of England (Mayle *et al*, 2000). Village & Myhill (1990) and Redpath *et al* (1995) looked at the use of a range of field signs to estimate the size of small mammal populations. House, or nest, counts have also been used to estimate populations of small mammals including dusky-footed woodrats (*Neotoma fuscipes*; Vreeland and Tietje, 1999) and muskrat (*Ondatra zibethicus*; Proulx and Gilbert, 1984).

The most commonly used field sign for estimating population size is faeces. Krebs *et al* (1986) found the density of faecal pellets to be related to average snowshoe hare (*Lepus americanus*) density. Faecal pellet group counts are commonly used in estimating deer populations (*e.g.* Dasmann and Taber, 1955; Ratcliffe, 1987). Tuyttens *et al* (2001) demonstrated that the number badger (*Meles meles*) latrines correlated with the number of adults of a social group. By recording faeces deposited on wooden boards placed in the habitat, Emlen *et al* (1957) were able to observe fluctuations in small mammal populations.

Various field sign indices have been examined for relationships with water vole populations size. Giraudoux *et al* (1995) developed a method to estimate the abundance of the fossorial form of the water vole based on surface indices, primarily earth tumuli, similar to the molehills of the European mole (*Talpa europaea*). The study reported a high correlation between the numbers of water voles estimated from surface indices and the numbers estimated from live-trapping. Moffatt (1992) used the numbers of water vole burrows, footprints and droppings as indices of water vole activity, but did not relate them to water vole numbers. Another study found no relationship between footprints and numbers of water voles caught during live-trapping (Woodroffe, 1988). However, this same study, based on three sites in the North York Moors National Park, UK, also compared numbers of water vole latrines with numbers of animals caught from live-trapping and found a positive correlation. This relationship has since been used in local and national water vole surveys, to estimate water vole numbers from latrine counts (*e.g.* Strachan and Jefferies, 1993).

The current study aimed to further examine the relationship between water vole numbers, as ascertained from Chapter 2, and latrines at five sites in the south of England and compare the results with published literature. Seasonal patterns in the production of latrines were examined to gain further information on their function and the bearing that this may have upon any relationship between latrines and water vole numbers. Further examination considered the number of latrines per individual water vole and compared these with results from the published literature.

3.2 METHODOLOGY

3.2.1 Study Sites

Five study sites were used, (for detailed descriptions of the sites see Section 2.2.1) and the entire length of each study site was examined for latrines. Searches for latrines concentrated on the area between the water's edge and the bank top, although latrines seen within the watercourses were also recorded.

3.2.2 Latrine counts

3.2.2.1 Definition of a latrine

A water vole latrine has often been described as flattened masses of droppings topped with fresh ones (*e.g.* Strachan & Jefferies, 1993). Woodroffe (1988) states that whilst latrines were observed as described above, some were not of this type. During the current study flattened masses of droppings were observed, although during many months, often following rainfall, no such latrines were observed having been washed away. It was therefore necessary to define a latrine for the purpose of this study. It was decided that for a pile of faeces to constitute a latrine it must have been visited on more than one occasion. *Ad hoc* observations of water vole defecations revealed that the most common number of faecal pellets deposited in one sitting was five. This corresponds with other workers findings (five pellets: Woodroffe, personal communication; six pellets: Strachan, personal communication). Therefore any pile of faeces with six or more pellets was assumed to have been visited more than once and could be described as a latrine (see Plate 3.1 for example of typical latrine).

3.2.2.2 Count methods

At each site, a careful search of both banks was made for latrines as defined in Section 3.2.2.1. The position of each latrine relative to a fixed point at each site was recorded. The age of faecal pellets in each latrine was estimated as fresh, old or fresh and old, based on the level of decomposition of pellets. In addition, any comments on colour of faecal pellets, size, or position of latrines and weather conditions were noted. Latrine counts were undertaken at Aveley, each month between August 1998 and July 2000; Hilliers between August 1998 and July 2000; Rainham between August 1998 and June

1999; Bovington and Whitemead between August 1998 and November 1998. Each month the latrine counts took place prior to the start of the live trapping studies, to avoid changes in latrine behaviour caused by the presence and use of traps.

Plate 3.1 Typical water vole latrine (photograph taken at Hillers study site)

3.2.3 Data preparation

For analysis of the data, those latrines recorded as comprising only old faecal pellets were removed as these may have been redundant and no longer used.

When considering the relationship between water vole numbers and latrines, those latrine counts that took place when no trapping occurred (*i.e.* December 1998 to February 1999) were removed from the dataset. Those latrine counts that had taken place during or immediately following heavy rainfall were also removed for the purpose of this analysis along with the corresponding trapping data. This was due to the fact that heavy rainfall and/or rising water levels resulted in many latrines being washed away and therefore these counts could not be considered reliable.

For the analysis of relationships between latrine numbers and water vole numbers it was necessary to look at the data in terms of 'breeding season' and throughout the year. Breeding season was defined as the period between March and September inclusive based on the description of the water vole calendar provided in Section 2.2.6.2.

3.3.4 Data analysis

3.3.4.1 Latrine counts

The latrine count data for each site were explored for seasonal patterns in number of latrines. The latrine count data were considered in relation to Minimum Number Alive (MNA) as previously calculated (Section 2.3).

3.3.4.2 Relationship between latrines and water vole numbers

The relationship between latrine numbers and the numbers of water voles was examined. The number of latrines per water vole was calculated (using MNA obtained in Chapter 2) as was the number of latrines per adult water vole, for each month at each site.

Further analysis considered the relationship between latrines during the breeding season and throughout the year and the following categories of water vole numbers:

- Adults;
- Adult males;
- Adult females;
- Total number of water voles captured;
- MNA.

The findings of the current study were compared with the findings of a similar study undertaken by Woodroffe (1988).

3.3.4.3 Relationship between latrines and water vole captures

The relationship between the latrines and captures of water vole was analysed. For each month at each site the presence of latrines in the vicinity of each trap point (within 5m) was determined. For each month at each site the percentage of trap points with associated latrines that captured at least one water vole was then calculated.

3.2.8 Statistical methods

All hypotheses were tested using a critical probability (P) value of 0.05, unless otherwise stated. The following description of each analysis is based on SPSS Base 7.0 for Windows, User's Guide (1996), Fowler *et al* (1998) and Dytham (1999).

Linear Regression Analysis: Determines the form and strength of a relationship between two variables. Produces a **regression line** that can be used to predict a value for *y* (dependent variable) from a given value of *x* (independent variable). The slope of the line (*b*) indicates the increase or decrease in *y* with increasing *x*. The intercept (*c*) indicates the value of *y* when *x* equals zero. $P<0.05$ indicates that the slope is significantly different from zero.

Comparing two Regression Lines: Used to determine whether there is a significant difference between the slopes of two regression lines (see Fowler *et al* (1998). Uses the following equation:

$$t = \frac{b_1 - b_2}{\sqrt{(S.E._{b1}^2 - S.E._{b2}^2)}} \qquad df = (n_1 - 2) + (n_2 - 2)$$

3.3 RESULTS

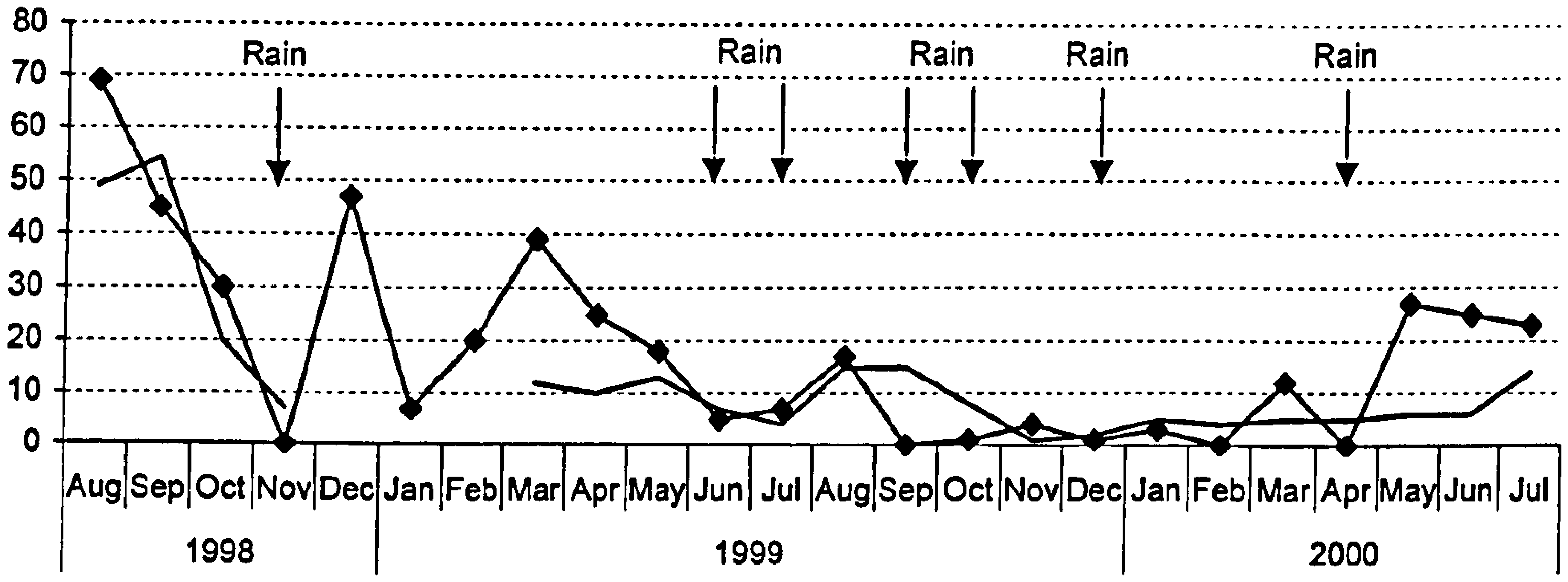
3.3.1 Latrine counts

Latrines were counted each month at all of the study sites. No latrines were observed at either Bovington or Whitemead.

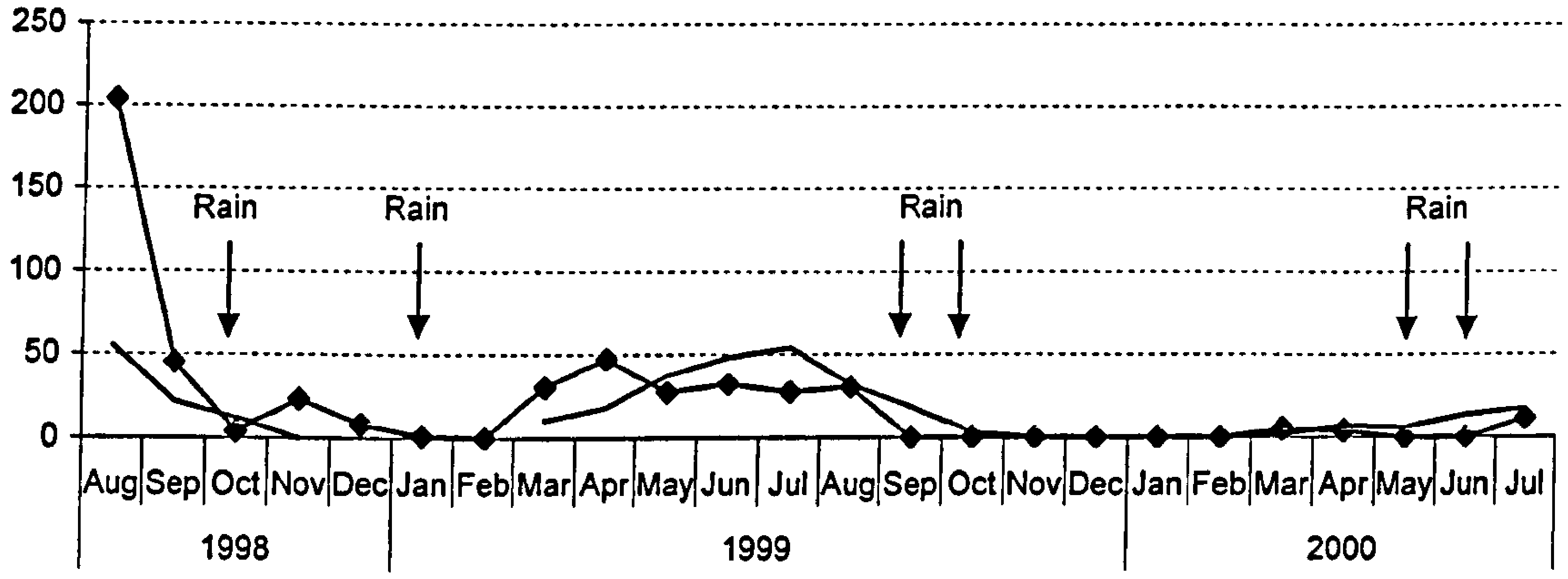
Figures 3.1a-c show the monthly variation in numbers of latrines counted at Aveley, Hilliers and Rainham. The MNA for each month at each site, as calculated in Section 2.3.1, is also shown in these figures. Those months were rain occurred either during or immediately before the latrine count are indicated.

At all three sites the highest number of latrines was recorded at the start of the study in August 1998 (Aveley and Hilliers) or September 1998 (Rainham), coinciding with peaks in the MNA. The numbers of latrines then fell over the winter months to reach their lowest in either January 1999 (Aveley and Rainham) or February 1999 (Hilliers), although a peak was seen at Aveley in December 1998. A peak was then seen at all three sites in March and/or April 1999, with a subsequent fall in numbers of latrines. This pattern was repeated at Aveley and Hilliers in 2000.

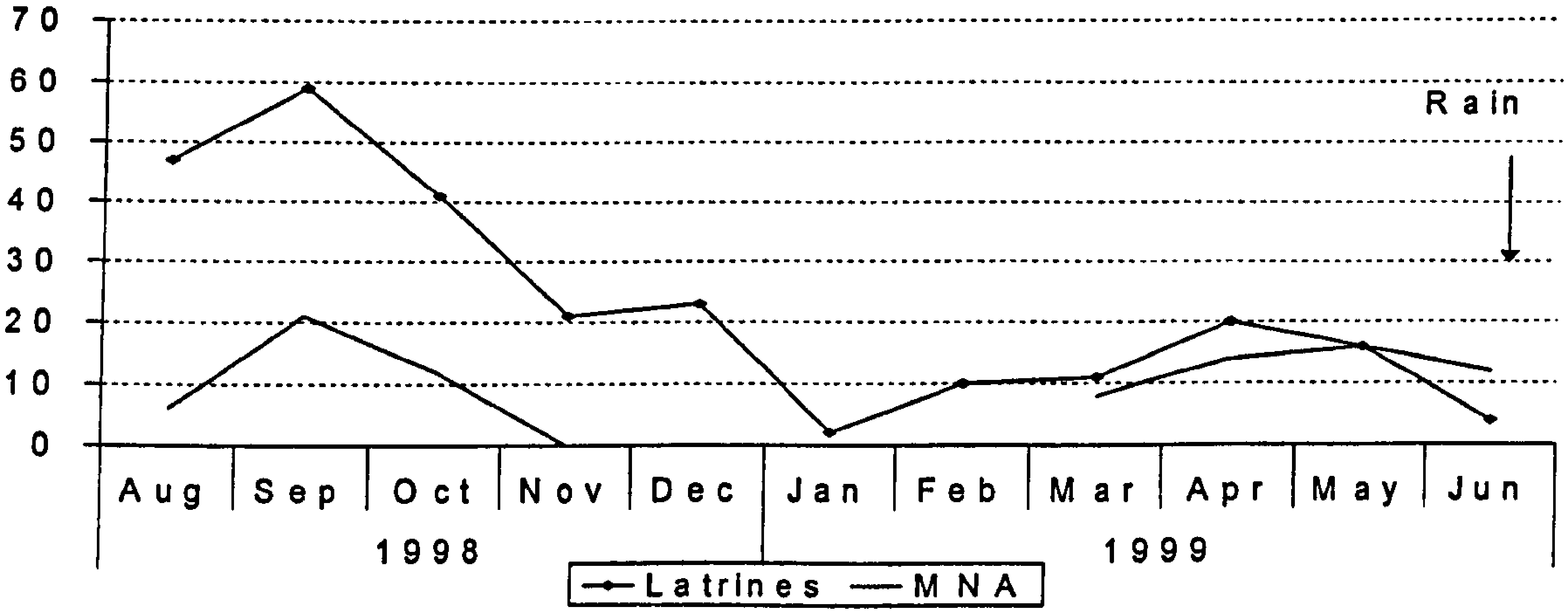
a) Aveley



b) Hilliers



c) Rainham



Figures 3.1 a-c Numbers of latrines counted each month at Aveley, Hilliers and Rainham. Black arrows indicate months when rain occurred either during or immediately prior to the latrine count. MNA as calculated in Section 2.3.1 is also shown for each month.

3.2.3 Relationship between latrines and water vole numbers

The numbers of latrines per water vole and per adult water vole were calculated for each month at each site, based on MNA as obtained from live-trapping data (Chapter 2). The results are present in Table 3.1.

Table 3.1 Numbers of latrines per water vole for each month at Aveley, Hilliers and Rainham

	Aveley		**Hilliers**		**Rainham**	
	Latrines / water vole	**Latrines / adult water vole**	**Latrines / water vole**	**Latrines / adult water vole**	**Latrines / water vole**	**Latrines / adult water vole**
Aug-98	1.41	2.88	3.71	4.64	7.83	11.75
Sep-98	0.83	1.55	2.05	2.14	2.81	14.75
Oct-98	1.50	1.76	Rain		3.42	6.83
Nov-98	Rain		0	0	0	0
Dec-98	No trapping					
Jan-99						
Feb-99						
Mar-99	3.25	3.25	3.00	3.00	1.38	1.38
Apr-99	2.50	2.50	2.61	5.22	1.43	3.33
May-99	1.38	1.38	0.73	2.45	1.00	2.67
Jun-99	Rain		0.67	1.45	Rain	
Jul-99			0.50	0.90		
Aug-99	1.13	2.13	0.94	1.07		
Sep-99	Rain					
Oct-99						
Nov-99	4.00	0	0	0		
Dec-99	Rain		0	0		
Jan-00	0.60	0.60	0	0		
Feb-00	0	0	0	0		
Mar-00	2.40	2.40	2.50	2.50		
Apr-00	Rain		0.57	0.57		
May-00	4.50	5.40	Rain			
Jun-00	4.17	8.33				
Jul-00	1.64	2.88	0.65	0.92		

The highest number of latrines per vole (7.83) and latrines per adult vole (11.75) were seen at Rainham in August 1998. The highest number of latrines per vole at Aveley occurred in May 2000 (4.50) and latrines per adult vole in June 2000 (8.33). At Hilliers the highest number of latrines per vole occurred in August 1998 (3.71) and latrines per adult vole in April 1999 (5.22).

Linear regression analysis was used to determine the presence and nature of any relationship between the numbers of latrines counted and numbers of water voles as shown in Section 2.3.1 and Section 2.3.2. The following categories of water vole numbers were used: number captured; MNA; adult males; adult females; all adults and juveniles. Two categories of latrine numbers were used; all months and breeding season. Breeding season only included data from months between March and September. Data from months where rain occurred immediately prior or during the latrine count were excluded from the analysis.

Consideration was given to the regression line passing through the origin, however, during the study latrines were found when no water voles were captured (*e.g.* winter at Hilliers) and water voles were captured when no latrines were found (*e.g.* Bovington and Whitemead). As this analysis examines the relationship between water voles captured and latrines, artificially placing the regression line through the origin would not reflect the observed situation.

Table 3.2 shows the results of the regression analysis for all of the categories mentioned above.

At Aveley all regressions were significant except for adult males during the breeding season. At Hilliers during the breeding season only adult males and all adults were significant. For all months, number captured, MNA, adult females and all adults gave significant correlations. The only regressions which were significant at Rainham were adult males and all adults during the breeding season.

Table 3.2 Results of linear regression analysis for categories of number of water voles and numbers of latrines for Aveley, Hilliers and Rainham. Shaded boxes indicate a significant relationship.

		Number Captured	**MNA**	**Adult males**	**Adult females**	**All adults**	**Juveniles**
Aveley	**Mar-Sep**	$r^2 = 0.67$, $F_{1,8} = 16.04$, $P<0.01$	$r^2 = 0.65$, $F_{1,8} = 15.03$, $P<0.01$	$r^2 = 0.44$, $F_{1,8} = 6.21$, NS	$r^2 = 0.63$, $F_{1,8} = 13.81$, $P<0.01$	$r^2 = 0.66$, $F_{1,8} = 22.98$, $P<0.001$	$r^2 = 0.64$, $F_{1,8} = 14.40$, $P<0.01$
	All	$r^2 = 0.70$, $F_{1,12} = 27.32$, $P<0.001$	$r^2 = 0.67$, $F_{1,12} = 24.86$, $P<0.001$	$r^2 = 0.46$, $F_{1,12} = 10.34$, $P<0.01$	$r^2 = 0.67$, $F_{1,12} = 23.60$, $P<0.001$	$r^2 = 0.59$, $F_{1,12} = 11.59$, $P<0.01$	$r^2 = 0.60$, $F_{1,12} = 18.00$, $P<0.001$
Hilliers	**Mar-Sep**	$r^2 = 0.34$, $F_{1,9} = 4.60$, NS	$r^2 = 0.31$, $F_{1,9} = 4.01$, NS	$r^2 = 0.12$, $F_{1,9} = 1.21$, NS	$r^2 = 0.72$, $F_{1,9} = 22.74$, $P<0.001$	$r^2 = 0.59$, $F_{1,9} = 20.39$, $P<0.001$	$r^2 = 0.02$, $F_{1,9} = 0.14$, NS
	All	$r^2 = 0.42$, $F_{1,14} = 10.03$, $P< 0.01$	$r^2 = 0.39$, $F_{1,14} = 9.09$, $P< 0.01$	$r^2 = 0.23$, $F_{1149} = 4.27$, NS	$r^2 = 0.73$, $F_{1,14} = 37.51$, $P<0.001$	$r^2 = 0.57$, $F_{1,14} = 12.00$, $P<0.01$	$r^2 = 0.07$, $F_{1,14} = 1.09$, NS
Rainham	**Mar-Sep**	$r^2 = 0.09$, $F_{1,3} = 0.30$, NS	$r^2 = 0.09$, $F_{1,3} = 0.30$, NS	$r^2 = 0.80$, $F_{1,3} = 11.09$, $P<0.05$	$r^2 = 0.02$, $F_{1,3} = 0.07$, NS	$r^2 = 0.83$, $F_{1,5} = 14.62$, $P<0.05$	$r^2 = 0.04$, $F_{1,3} = 1.17$, NS
	All	$r^2 = 0.13$, $F_{1,5} = 0.74$, NS	$r^2 = 0.13$, $F_{1,5} = 0.74$, NS	$r^2 = 0.41$, $F_{1,5} = 3.51$, NS	$r^2 = 0.10$, $F_{1,5} = 0.49$, NS	$r^2 = 0.06$, $F_{1,5} = 0.34$, NS	$r^2 = 0.29$, $F_{1,5} = 2.03$, NS

Each significant regression was compared with its equivalent for the other two sites, if also significant, by comparing the slopes of the regression lines (see Section 3.2.8).

Significant differences were found between the regression lines for all adults with latrines from the breeding season for Hilliers and Rainham ($t_{15} = 4.59$, $P<0.01$) and Aveley and Rainham ($t_9 = 4.00$, $P<0.01$). Significant differences were also found between adult females with latrines from all months at Aveley and Hilliers ($t_{24} = 2.20$, $P<0.05$) and also for latrines during the breeding season ($t_{14} = 2.23$, $P<0.05$).

No significant difference was found between regression lines for all adults with all latrines at Aveley and Hilliers ($t_{24} = 0.21$, NS) and also all adults with latrines during the breeding season ($t_{15} = 1.76$, NS). The data for Aveley and Hilliers all latrines were therefore combined (Figure 3.2a). The data for Aveley and Hilliers during the breeding season were also combined (Figure 3.2b).

No significant difference was found between regression lines for the total number of individuals captured with all latrines at Aveley and Hilliers ($t_{24} = 1.20$, NS) and also MNA with all latrines ($t_{24} = 1.09$, NS). The data for MNA at Aveley and Hilliers with all latrines (Figure 3.2c) were therefore combined as were the data for the total number captured with all latrines at Aveley and Hilliers (Figure 3.2d).

Regression lines for the combined data were plotted using latrines as the independent variable in each case, providing descriptive equations for the relationship between voles and latrines. In addition, regression lines using voles as the independent variable were plotted to obtain predictive equations to enable the calculation of number of voles from latrines.

a) Adults with all latrines

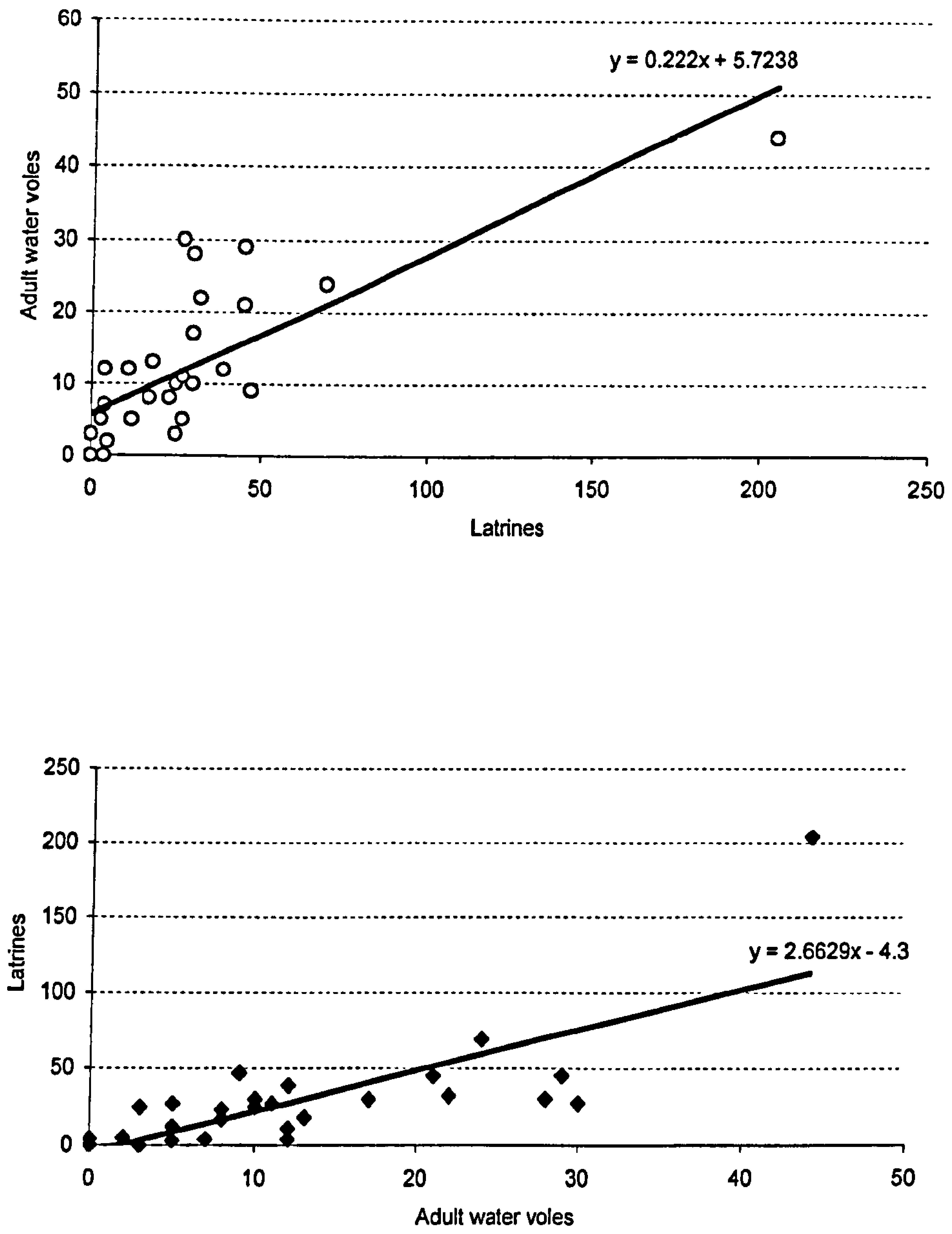
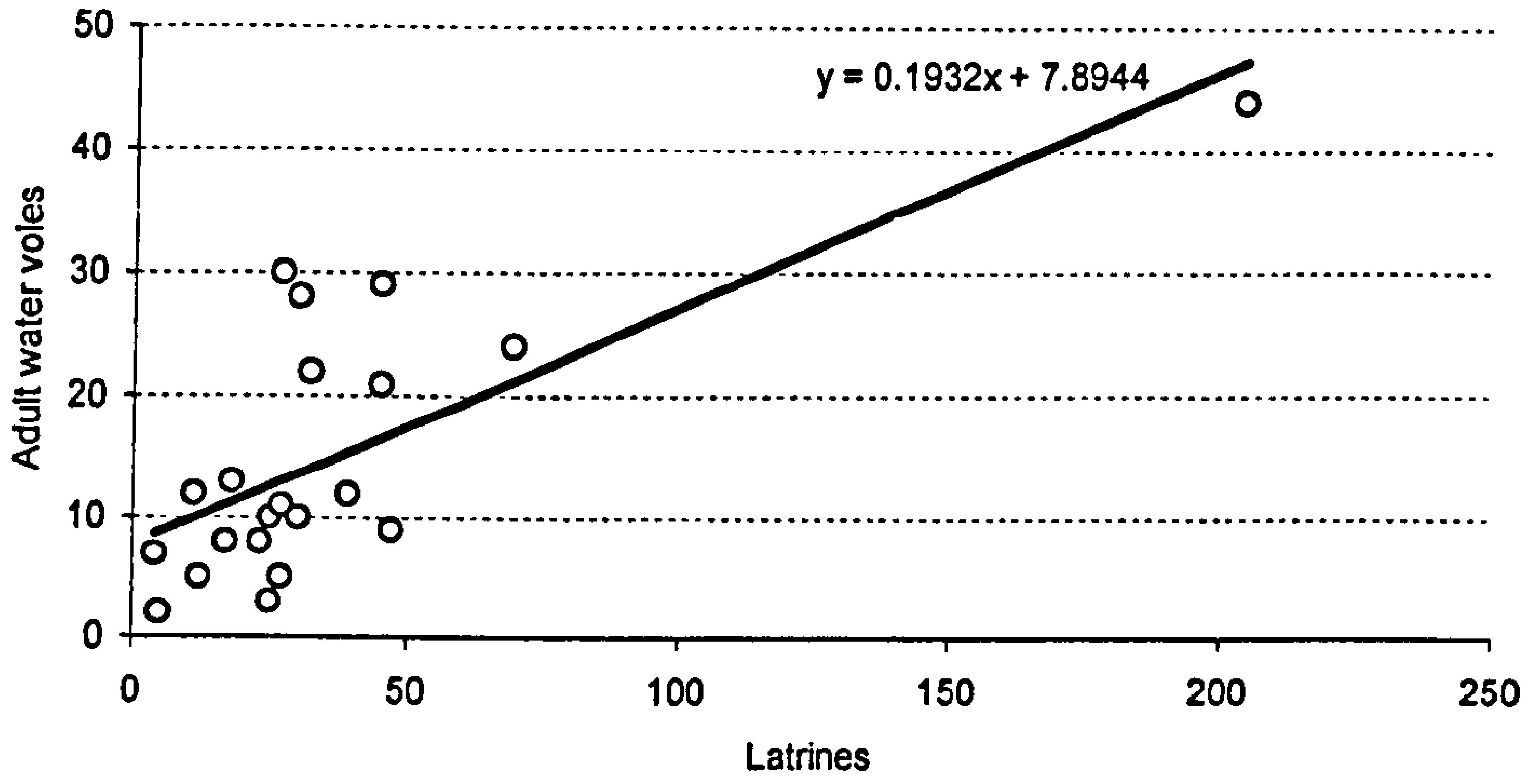


Figure 3.2a Regression lines showing the relationships between numbers of adult water voles and numbers of latrines for Aveley and Hilliers combined

b) Adults with latrines during the breeding season



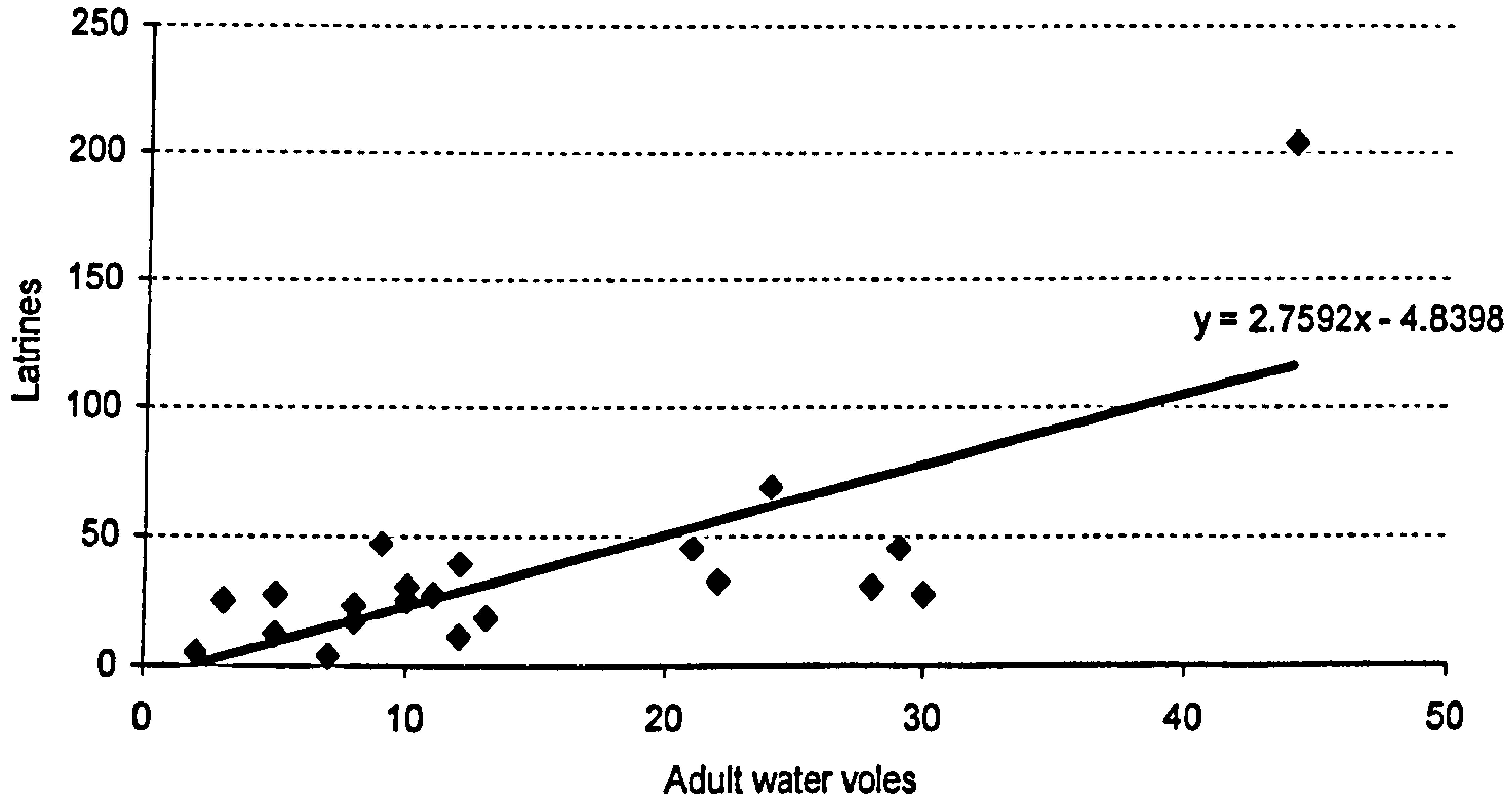
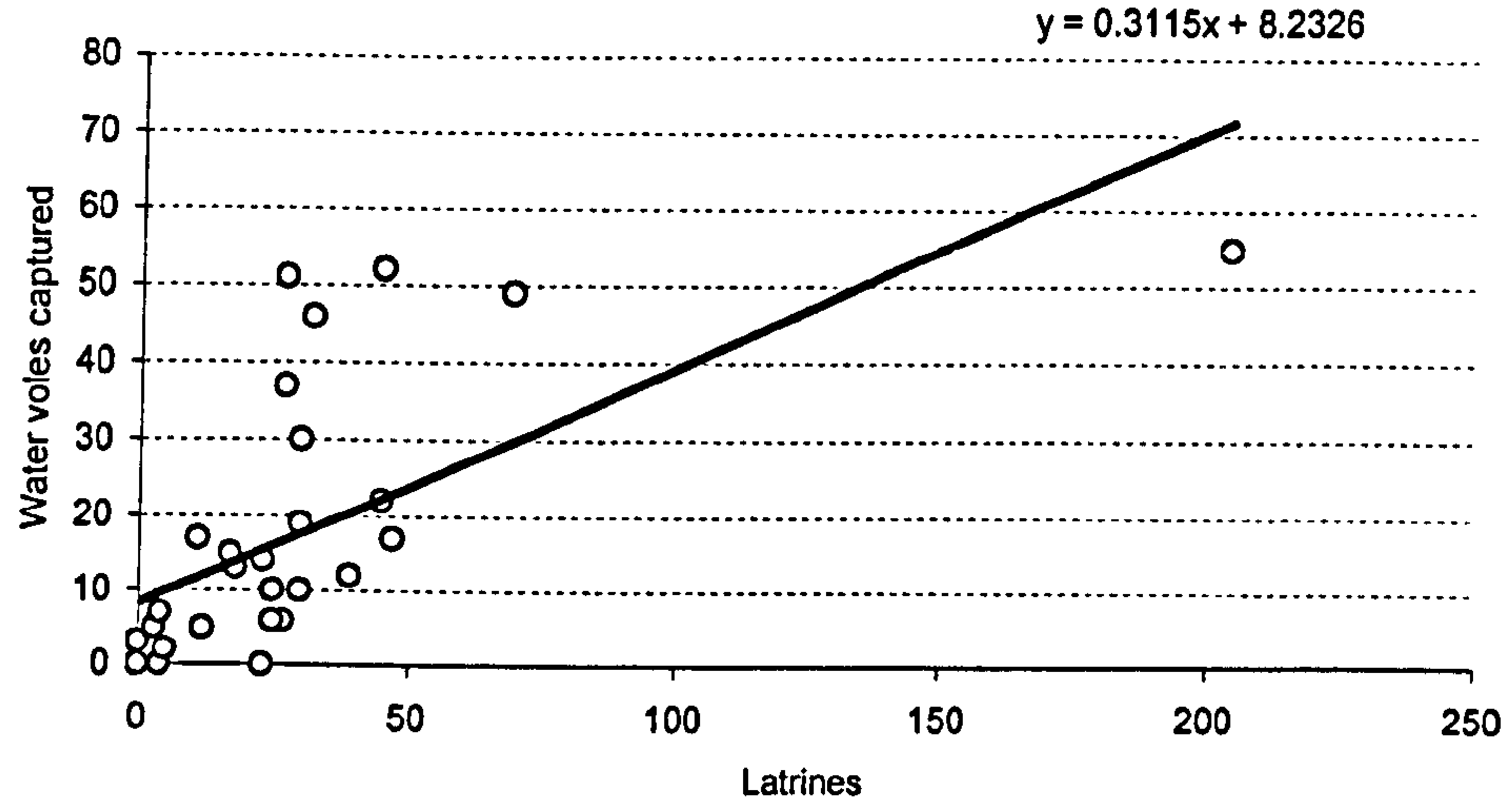


Figure 3.2b Regression lines showing the relationships between numbers of adult water voles and numbers of latrines for Aveley and Hilliers combined

c) Total number captured with all latrines



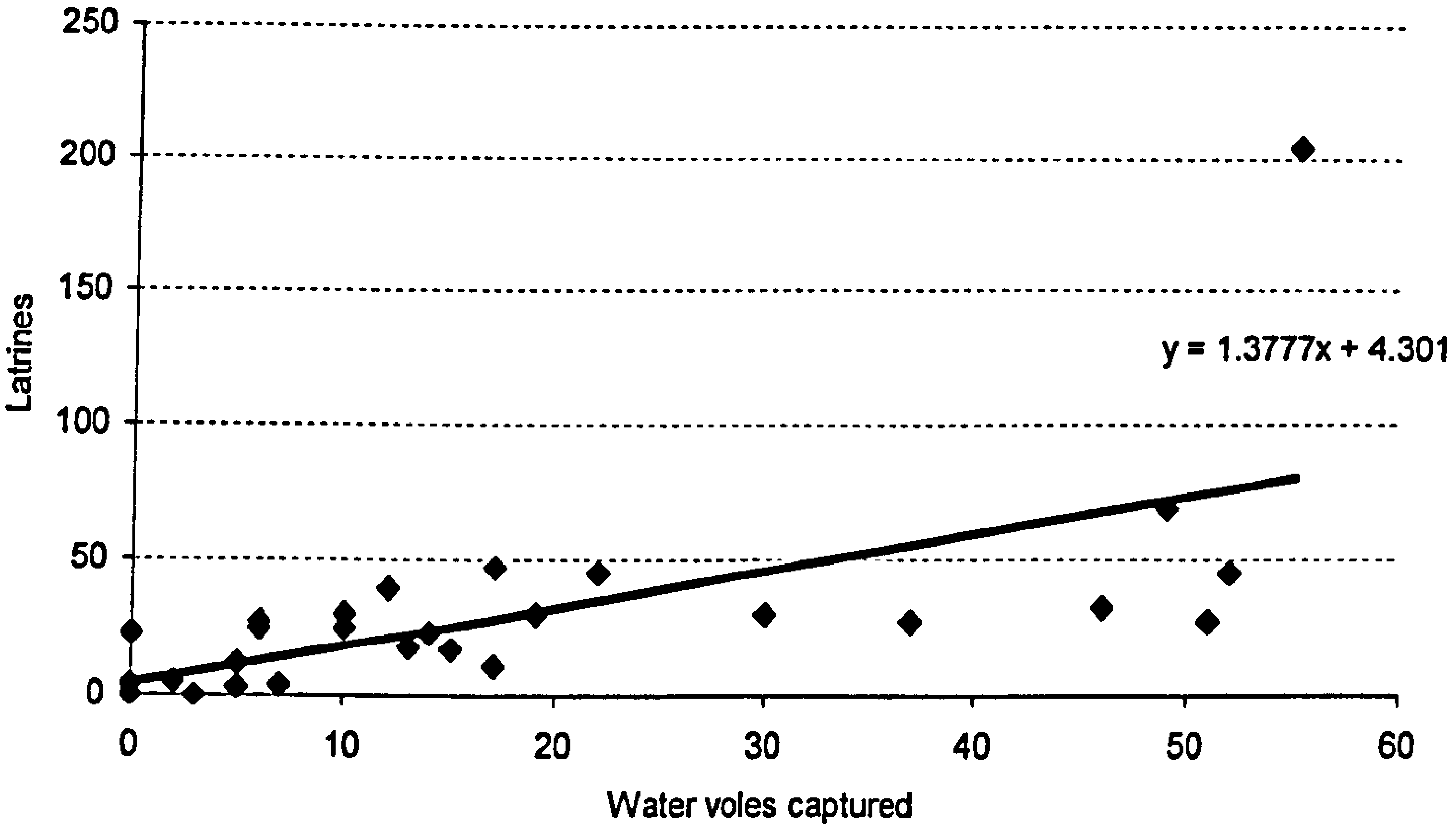
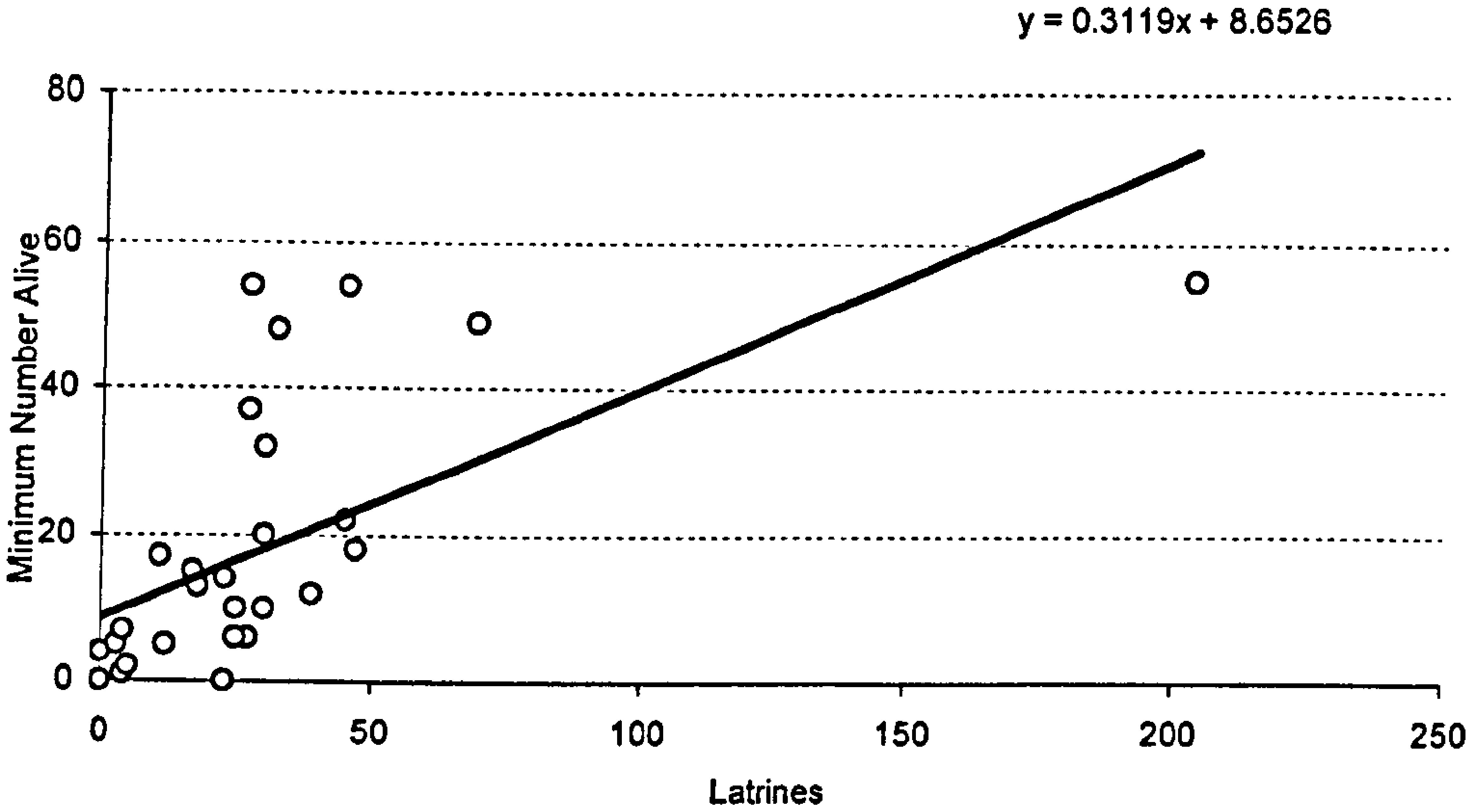


Figure 3.2c Regression lines showing the relationships between numbers of water voles and numbers of latrines for Aveley and Hilliers combined

d) MNA with all latrines



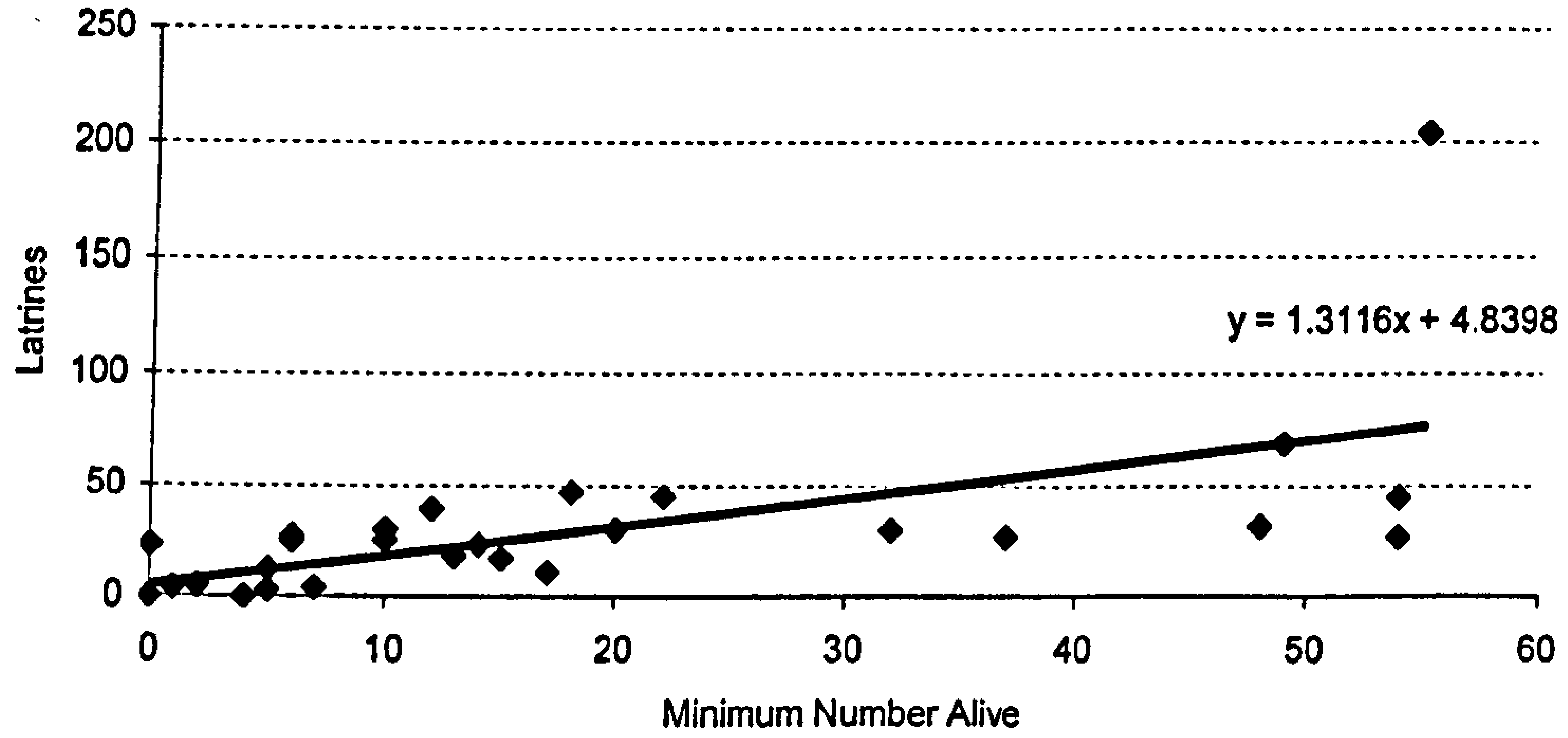


Figure 3.2d Regression lines showing the relationships between Minimum Number Alive (MNA) and numbers of latrines for Aveley and Hilliers combined

Linear regression analysis was used the determine the presence of any relationships between latrines and water voles in the combined Aveley and Hilliers data as shown in Figure 3.2. All of the regressions were significant indicating the presence of a relationship between water voles and latrines in the combined Aveley and Hilliers data for adults with all latrines ($r^2 = 0.59$, $F_{1,28} = 41.00$, $P<0.001$); adults with latrines during the breeding season ($r^2 = 0.53$, $F_{1,19} = 21.69$, $P<0.001$); total number captured with all latrines ($r^2 = 0.67$, $F_{1,28} = 22.47$, $P<0.001$) and MNA with all latrines ($r^2 = 0.65$, $F_{1,28} = 20.70$, $P<0.001$).

The four equations below describe the relationship between water vole numbers and latrines based on the combined data from Aveley and Hilliers:

$y = 2.66x - 4.30$
All latrines; where y = latrines and x = number of adults

$y = 2.76x - 4.84$
During the breeding season; where y = latrines and x = number of adults

$y = 1.38x + 4.30$
All latrines; where y = latrines and x = total number captured

$y = 1.31x + 4.84$
All latrines; where y = latrines and x = MNA

To obtain predictive equations allowing water vole numbers to be estimated from the number of latrines a second regression was calculated where y = water voles and x = latrines to provide the following equations.

$y = 0.22x + 5.72$
All latrines; where y = number of adults and x = latrines

$y = 0.19x + 7.89$

During the breeding season; where y = number of adults and x = latrines

$y = 0.31x + 8.23$
All latrines; where y = total number captured and x = latrines

$y = 0.31x + 8.65$
All latrines; where y = MNA and x = latrines

3.3.2 Comparison with published data

Morris *et al* (1998) produced the following predictive equation to estimate the number of water voles from the number of latrines:

$y = 0.683x + 1.48$
where y = water voles and x = latrines

The equation was based on the total number of water voles captured and latrine counts from throughout the year as obtained by Woodroffe (1988). In this section the corresponding predictive equation below, as obtained in the current study (i.e. Total number captured with all latrines for Aveley and Hilliers combined [Section 3.3.2]) was considered against that obtained by Morris *et al* (1998):

$y = 0.31x + 8.23$
where y = total number captured and x = latrines

The original data on which the Morris *et al* equation was based was not available for use in this comparison, therefore the equations could not be compared.

The data were examined further. It was noticed that one data point was very different from the others, this being at Hilliers in August 1998 where the number of latrines counted was 204. Whilst the total number of captures was highest at this time (55), 204 latrines was still substantially more than counted at any of the sites at any time. Consideration was given to log transforming the data however, the confidence in this point in question. This latrine count was the first to be undertaken at Hilliers, and a number of factors could have resulted in the high count: The period prior to the latrine count had been very dry and therefore many older latrines would have been present; the unusually dense vegetation would have shaded old latrines rendering them less susceptible to desiccation and making them appear 'fresher'; and the observer was not as experienced in recognising differences between old and fresh latrines, therefore some old latrines are likely to have been included in the count. This data point was therefore removed and the data reanalysed.

Linear regression analysis was used to determine the presence and nature of any relationship between the numbers of latrines counted and numbers of water voles.

Table 3.3 shows the results of the regression analysis for all Hilliers with the spurious data point removed.

Table 3.3 Results of linear regression analysis for categories of number of water voles and numbers of latrines for Hilliers. Shaded boxes indicate a significant relationship.

		Number Captured	**MNA**	**Adult males**	**Adult females**	**All adults**	**Juveniles**
Hilliers	**Mar-Sep**	$r^2 = 0.40$, $F_{1,8} = 1.52$, NS	$r^2 = 0.40$, $F_{1,8} = 1.51$, NS	$r^2 = 0.13$, $F_{1,8} = 1.20$, NS	$r^2 = 0.46$, $F_{1,8} = 2.19$, NS	$r^2 = 0.45$, $F_{1,8} = 2.00$, NS	$r^2 = 0.23$, $F_{1,8} = 0.44$, NS
	All	$r^2 = 0.30$, $F_{1,13} = 5.64$, $P < 0.05$	$r^2 = 0.30$, $F_{1,13} = 5.64$, $P < 0.05$	$r^2 = 0.27$, $F_{1,13} = 4.90$, $P<0.05$	$r^2 = 0.26$, $F_{1,13} = 4.54$, NS	$r^2 = 0.28$, $F_{1,13} = 5.15$, $P<0.05$	$r^2 = 0.17$, $F_{1,13} = 2.67$, NS

The regressions for latrines with the total number captured, MNA, adult males and all adults with all latrines were significant. None of the regressions for data during the breeding season or adult females and juveniles with all latrines were significant.

Each significant regression was compared with its equivalent for the other two sites (Table 3.2), if significant, by comparing the slopes of the regression lines.

No significant differences were found between the regression lines for:
The total number captured with all latrines for Aveley and Hilliers ($t_{21} = 1.41$, NS); MNA with all latrines for Aveley and Hilliers ($t_{21} = 1.41$, NS); adult males with all latrines for Aveley and Hilliers ($t_{21} = 1.47$, NS); and adults with all latrines for Aveley and Hilliers ($t_{21} = 1.23$, NS).

These data were therefore combined in Figure 3.3.

a) Total number captured with all latrines

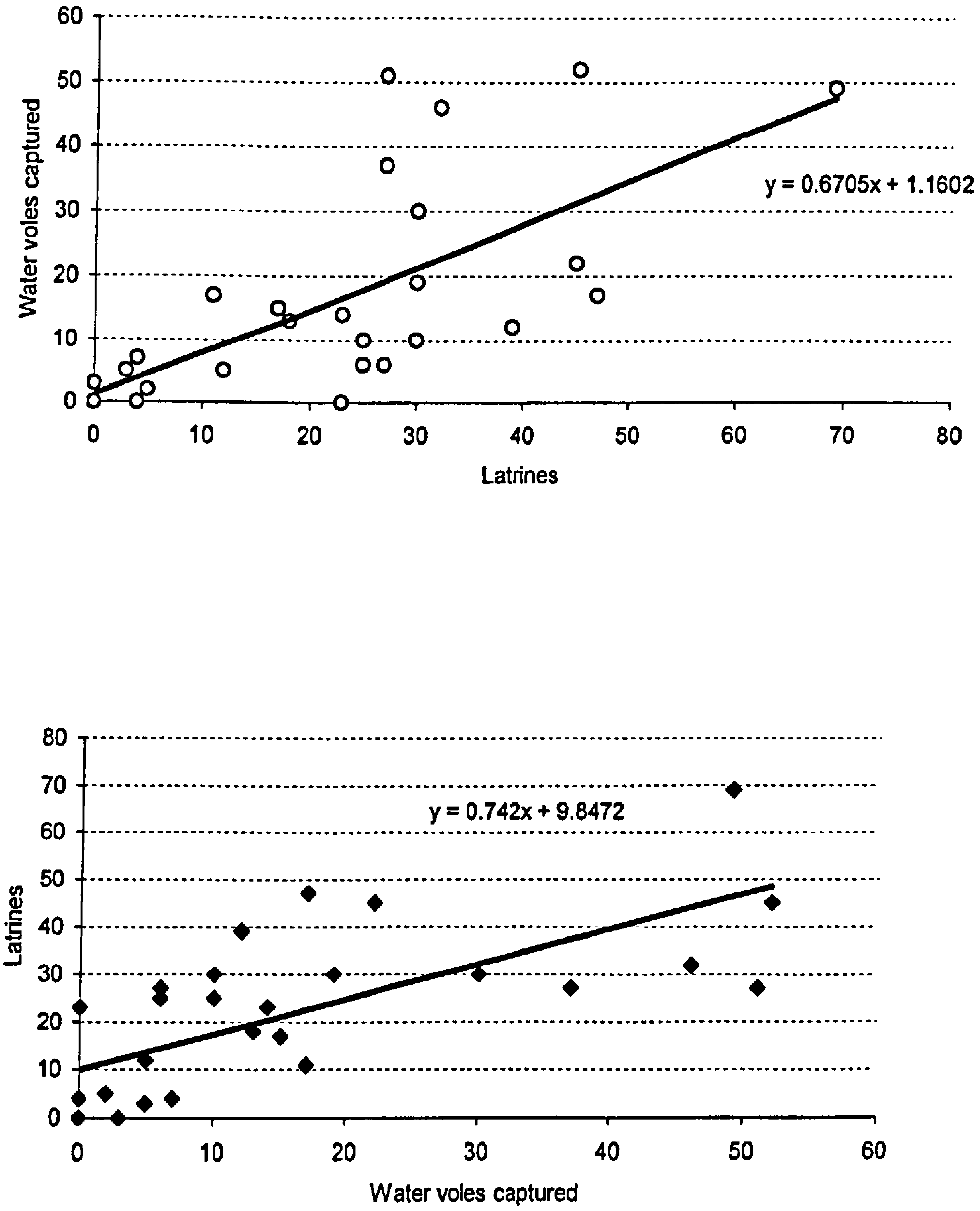
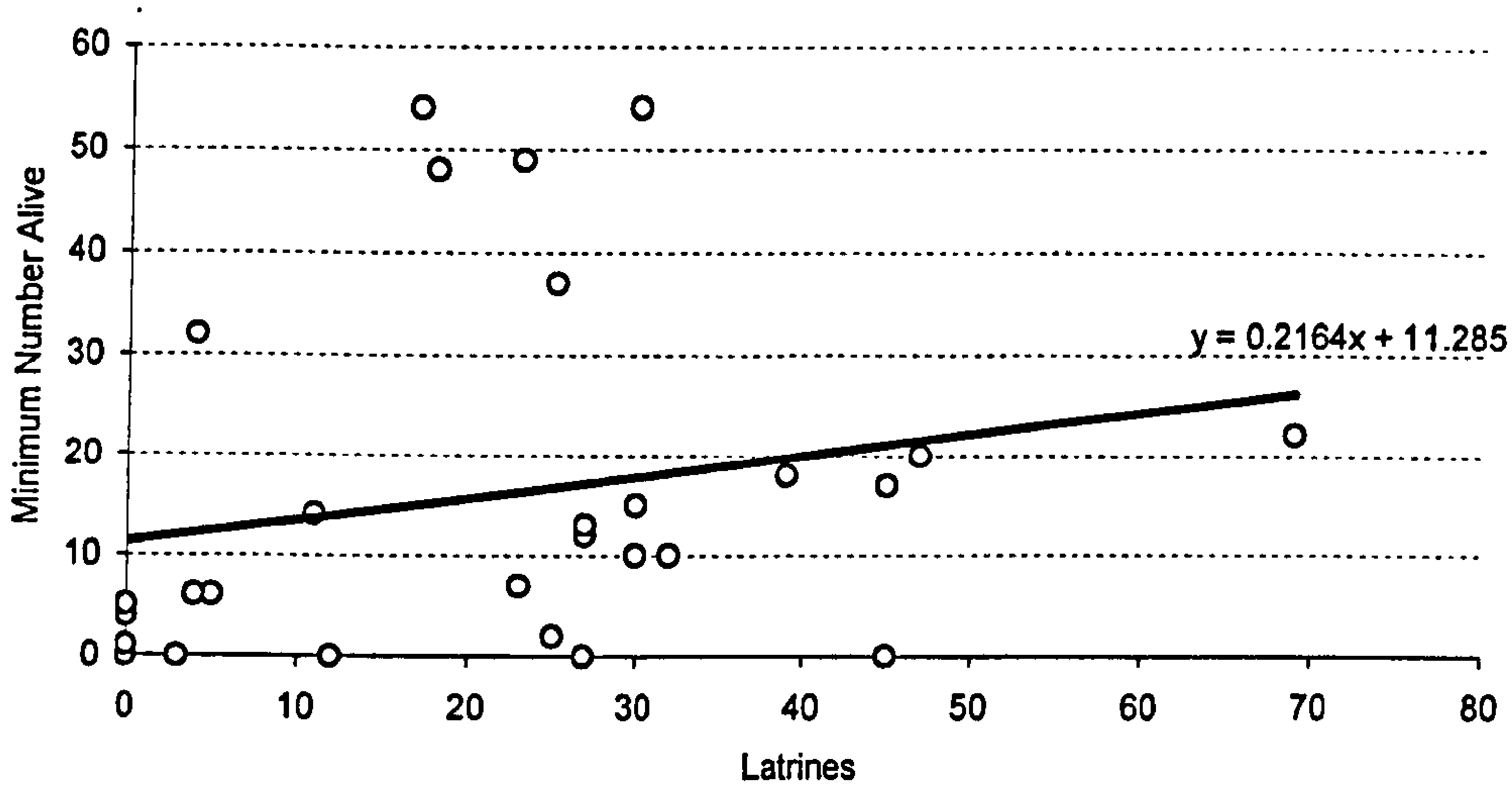


Figure 3.3a Corrected regression lines showing the relationships between numbers of water voles and numbers of latrines for Aveley and Hilliers combined

b) MNA with all latrines



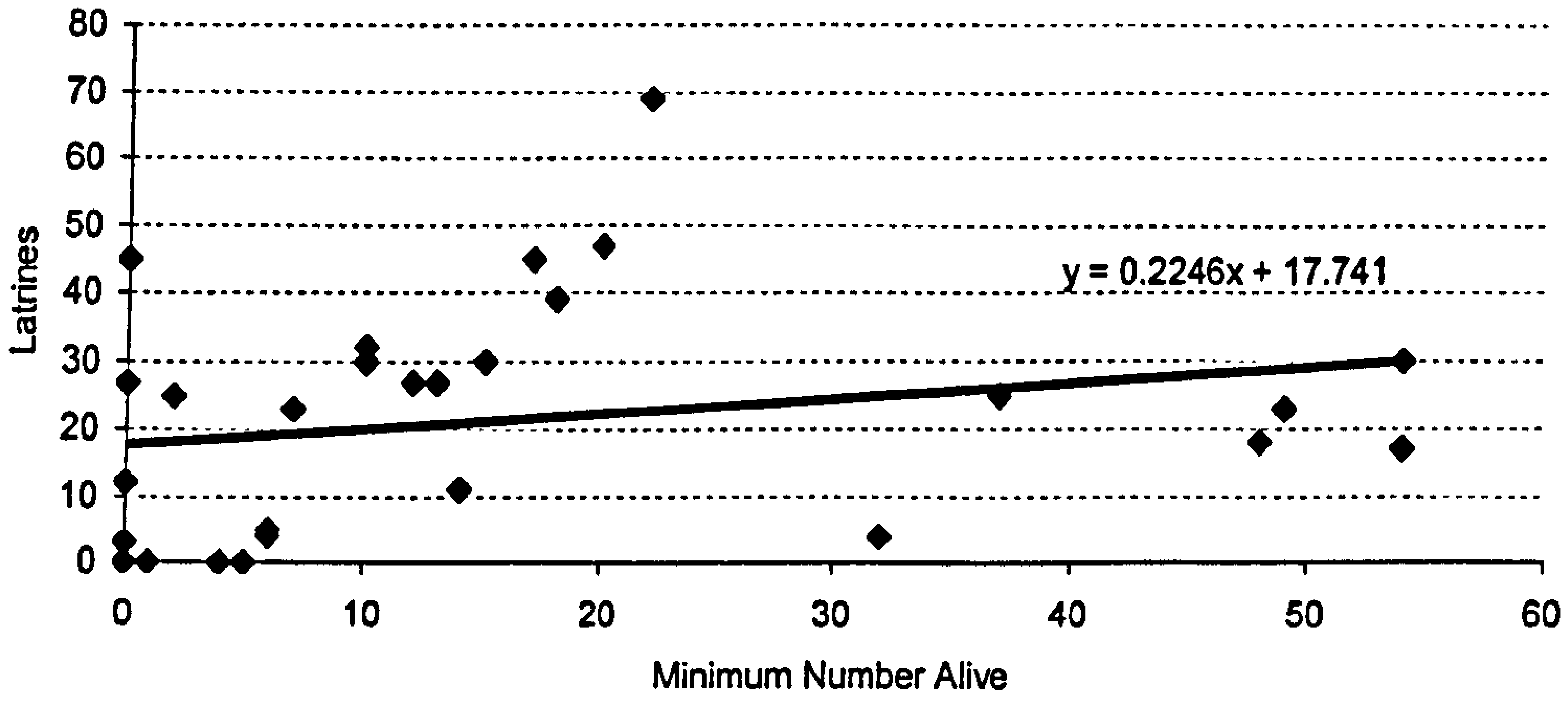
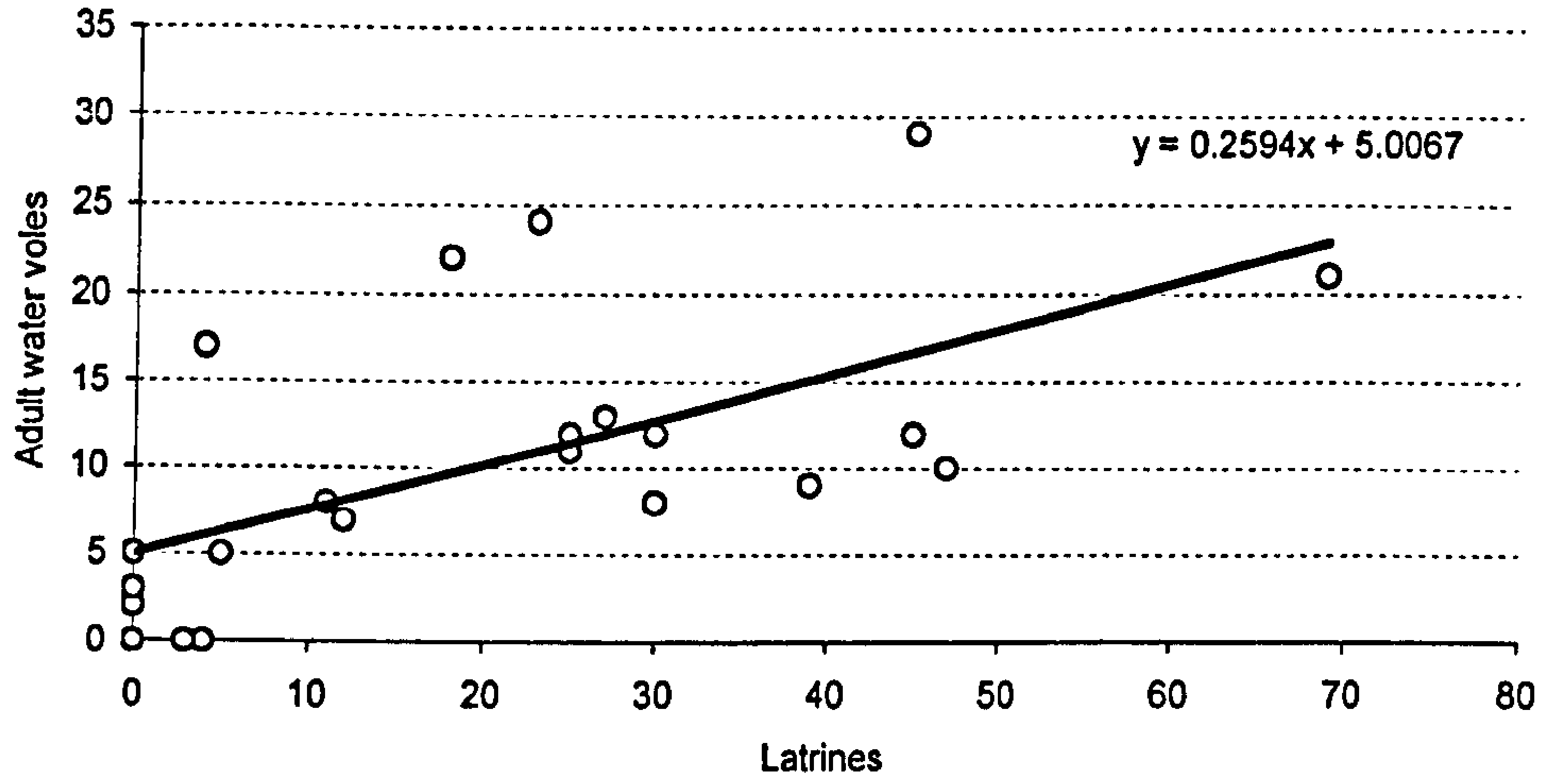


Figure 3.3b Corrected regression lines showing the relationships between numbers of water voles and numbers of latrines for Aveley and Hilliers combined

c) **Adults with all latrines**



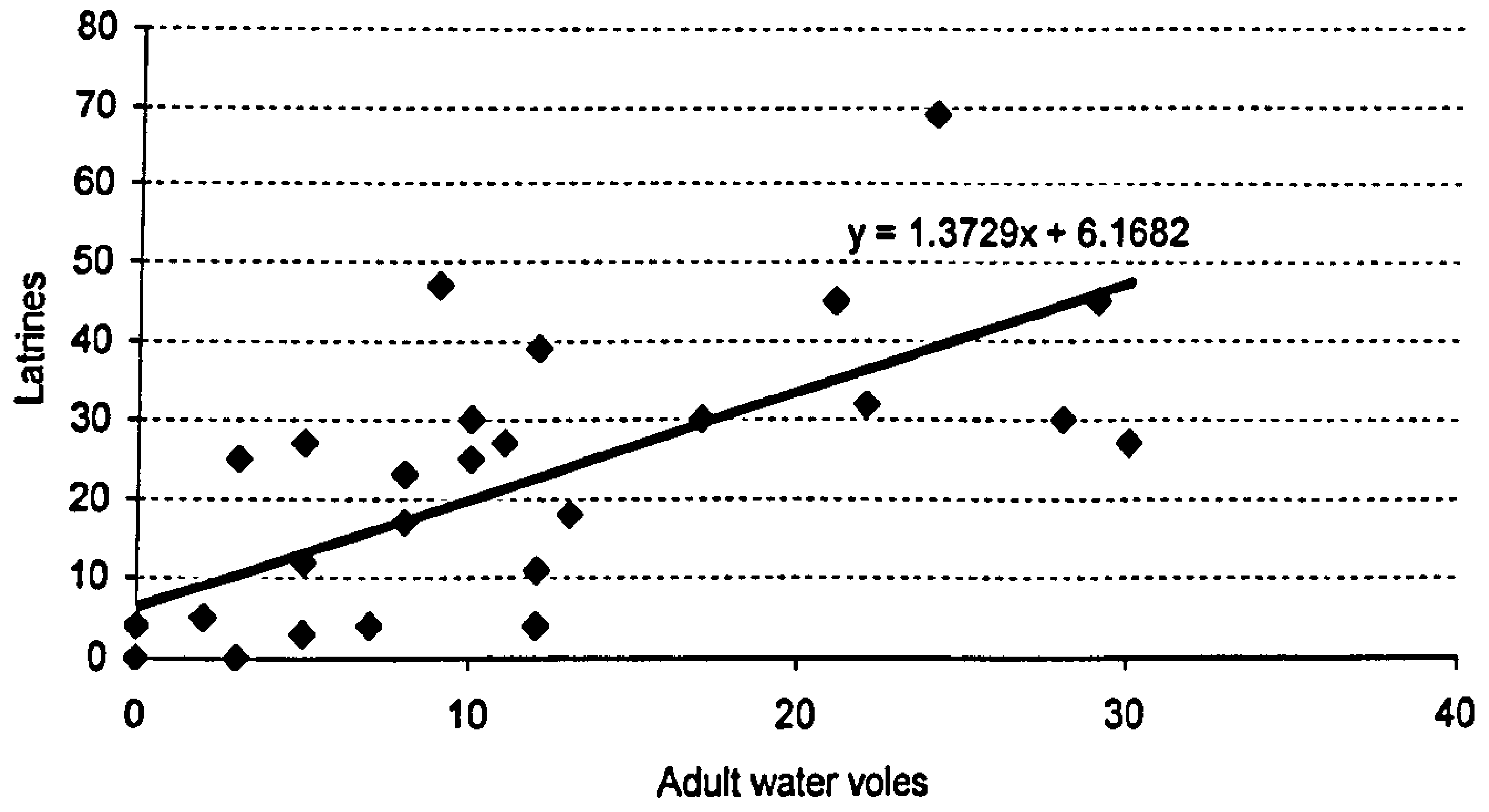
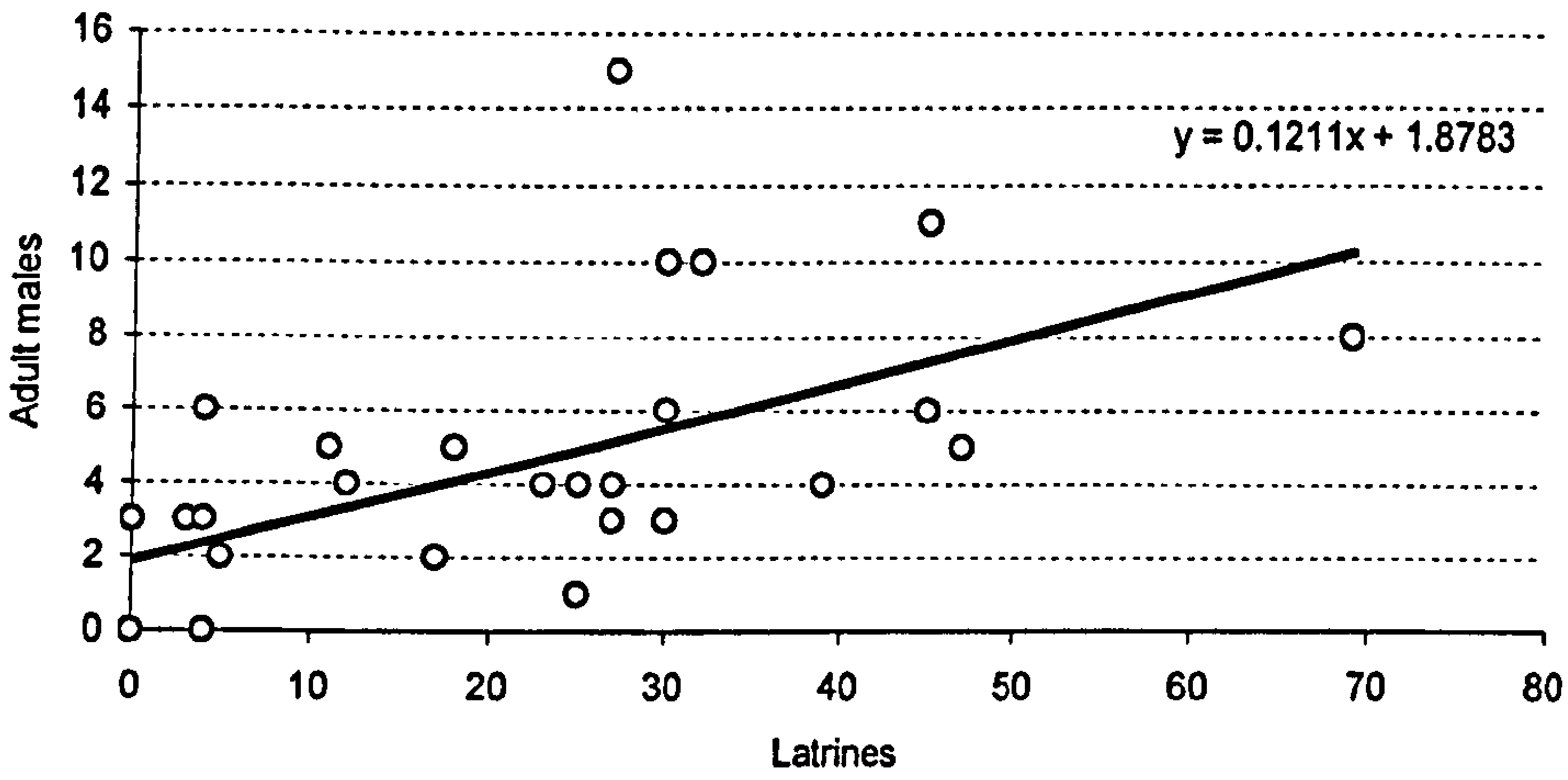


Figure 3.3c Corrected regression lines showing the relationships between numbers of water voles and numbers of latrines for Aveley and Hilliers combined

d) Males with all latrines



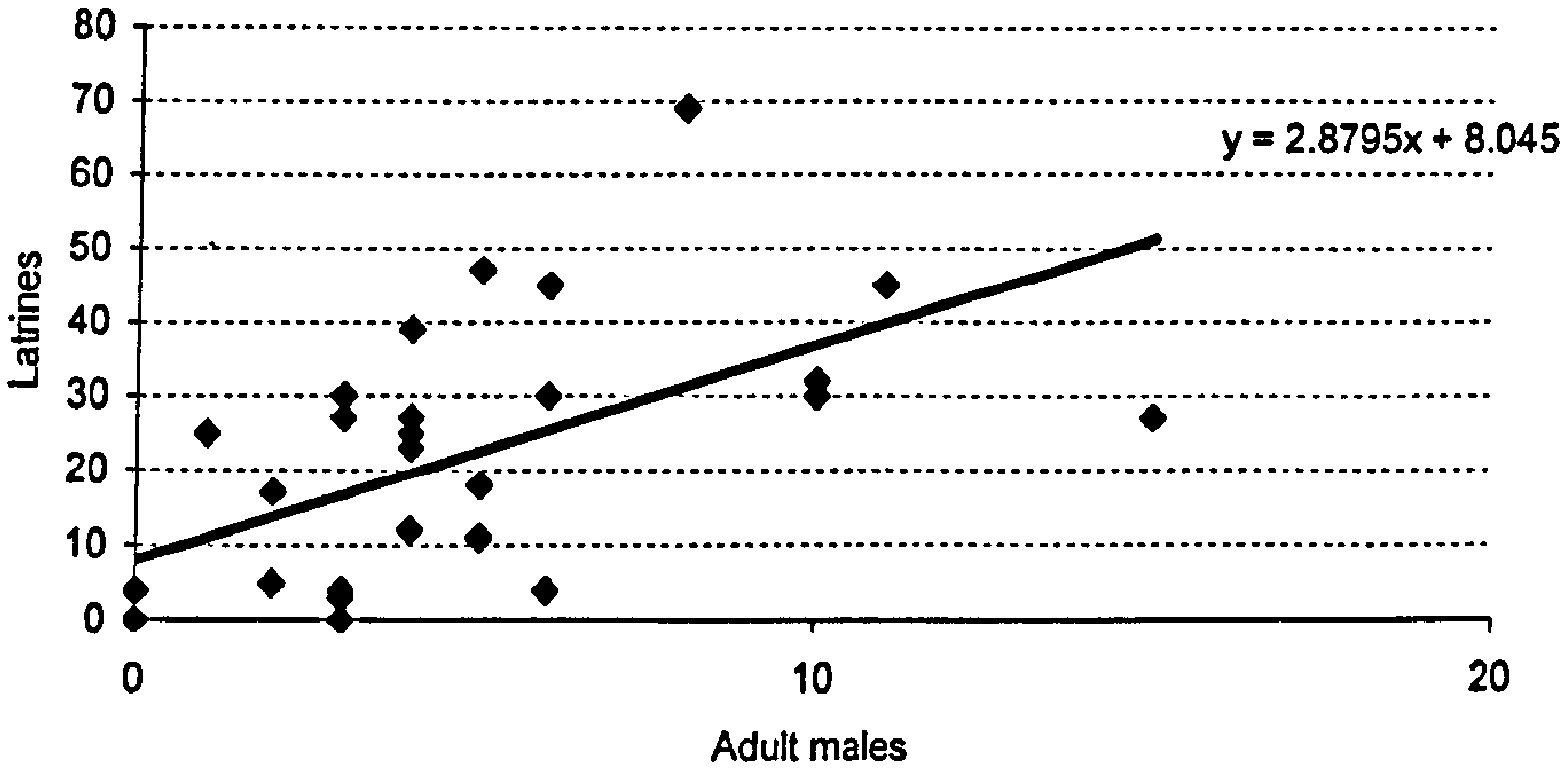


Figure 3.3d Corrected regression lines showing the relationships between numbers of water voles and numbers of latrines for Aveley and Hilliers combined

Linear regression analysis was used to determine the presence of any relationships between latrines and water voles in the combined Aveley and Hilliers data (with the data point removed) as shown in Figures 3.3. All of the regressions were significant indicating the presence of a relationship between water voles and latrines in the combined Aveley and Hilliers data, with the anomalous data point removed, for the total number captured with all latrines ($r^2 = 0.50$, $F_{1,27} = 26.73$, $P<0.001$); MNA throughout the year ($r^2 = 0.48$, $F_{1,27} = 25.20$, $P<0.001$); adults with all latrines ($r^2 = 0.53$, $F_{1,27} = 30.55$, $P<0.001$) and adult males with all latrines ($r^2 = 0.34$, $F_{1,27} = 13.63$, $P<0.001$).

The four equations below describe the relationship between water vole numbers and latrines based on the combined data from Aveley and Hilliers:

$y = 0.74x + 9.85$
All latrines; where y = latrines and x = total number captured

$y = 0.22x + 17.74$
All latrines; where y = latrines and x = MNA

$y = 1.37x + 6.17$
All latrines; where y = latrines and x = number of adults

$y = 2.88x + 8.05$
All latrines; where y = latrines and x = number of adult males

To obtain predictive equations allowing water vole numbers to be estimated from the number of latrines a second regression was calculated where y = water voles and x = latrines to provide the following equations.

$y = 0.67x + 1.16$
Throughout the year; where y = total number capture and x = latrines

$y = 0.22x + 11.29$
All latrines; where y = MNA and x = latrines

$y = 0.26x + 5.01$
All latrines; where y = adults and x = latrines

$y = 0.12x + 1.88$
All latrines; where y = adult males and x = latrines

Analysis of the significance of constants for all predictive equations showed that in all cases the constant was significant (total number captured $t = 2.639$, $P<0.05$, $N = 30$; MNA $t = 2.659$, $P<0.05$, $N = 30$; adults $t = 3.217$, $P<0.05$, $N = 13$; adult males $t = 2.302$, $P<0.05$, $N = 13$). It was therefore not considered appropriate to remove the constant for these predictive equations. In addition, diagnostics of the predictive equations, looking at the residuals, were used to determine whether, in each case, the model was a good fit. If the model is a good fit, then the residuals will show a normal distribution. This is demonstrated by the standardised residuals showing mean of zero and a standard deviation of one. In all cases, the model proved to be a good fit (total number captured standardised residual mean = 0, SD = 0.983, N = 30; MNA standardised residual mean = 0, SD = 0.983, N = 30; adults standardised residual mean = 0, SD = 0.968; N = 13; males standardised residual mean = 0, SD = 0.966, N = 13).

The new predictive equation for total number captured ($y = 0.67x + 1.16$) appears to be very similar to the equation obtained by Morris *et al* 1998 ($y = 0.68x + 1.48$), although statistical analysis was not possible in the absence of the original data collected by Woodroffe (1988) and used by Morris *et al* (1998).

If this predictive equation were to be used to predict the number of water voles present as opposed the number of captures. Consideration was therefore given to putting the regression line through the origin. However, the constants for each equation were significant, as described above, therefore it is inappropriate to do so. In addition, it is conceivable that latrines may be recorded with no water voles resident or water vole present with no latrines recorded.

It is worth considering that one of the conditions for linear regression is that the x variable is independent. In the current study this condition is not strictly met. For such a sample, from a bivariate distribution with two random variables, Model 2 regression could be used, such as reduced major axis regression. The purpose of this study was to compare the data collected with the conclusions of Morris *et al* (1998) and to enable predictions to be made from the data. Simple linear regression is considered to be more reliable for making such predictions (Fowler *et al* 1998), and was the method used by Morris *et al* (1998), therefore it was considered appropriate to use this method in the current study.

3.3.4 Relationship between latrines and water vole captures

The relationship between the number of water voles captured and the number of latrines was examined further to explore the relationship between latrines and water vole captures for each site in each month by looking at the percentage of trapping sites that had associated latrines (*i.e.* within 5m) and captured at least one water vole. Those months during which no trapping took place or rainfall invalidated the latrine count were excluded from the analysis.

For each month, Tables 3.3a-c present the percentage of trapping points with associated latrines, the percentage of trapping points that captured at least one vole and the percentage of trapping points with an associated latrine that captured at least one vole for Aveley, Hilliers and Rainham respectively.

At all three sites, excluding the winter months, for the majority of months over 30% of trapping points with an associated latrine captured at least one vole. In many cases the percentage was notably higher than 30%. No seasonal trends in the percentage of trapping points was observed, however this may be in part due to a lack of data points owing to rain invalidating latrine counts and the absence of trapping during December 1998 to February 1999.

Table 3.3 Percentage trapping points with associated latrines, percentage of trapping points with at least one water vole captured and the percentage of trapping points with associated latrines that captured at least one water vole

a) Aveley

	Percentage of trapping points		
	Latrines	**Water voles**	**Latrines and water voles**
Aug-98	73.81	85.71	83.87
Sep-98	64.29	76.19	81.48
Oct-98	42.86	45.24	55.56
Nov-98	No trapping		
Dec-98			
Jan-99			
Feb-99			
Mar-99	64.29	35.71	73.33
Apr-99	50.00	45.24	71.43
May-99	33.33	42.86	35.71
Jun-99	rain		
Jul-99	rain		
Aug-99	19.05	42.86	37.50
Sep-99	rain		
Oct-99	rain		
Nov-99	0	7.14	0
Dec-99	rain		
Jan-00	0	21.43	0
Feb-00	0	9.52	0
Mar-00	19.05	26.19	25.00
Apr-00	rain		
May-00	52.38	21.43	22.73
Jun-00	35.71	16.67	13.33
Jul-00	47.62	54.76	50.00

b) Hilliers

	Percentage of trapping points		
	Latrines	Water voles	Latrines and water voles
Aug-98	100	73.02	73.02
Sep-98	44.44	33.33	32.14
Oct-98	rain		
Nov-98	0	0	0
Dec-98	No trapping		
Jan-99			
Feb-99			
Mar-99	30.16	22.22	42.11
Apr-99	44.44	25.40	17.86
May-99	31.75	58.73	60.00
Jun-99	36.51	69.84	60.87
Jul-99	25.40	76.19	68.75
Aug-99	41.27	46.03	42.31
Sep-99	rain		
Oct-99	rain		
Nov-99	0	0	0
Dec-99	0	0	0
Jan-00	0	0	0
Feb-00	0	0	0
Mar-00	7.94	4.76	0
Apr-00	4.76	9.52	33.33
May-00	rain		
Jun-00	rain		
Jul-00	9.52	41.27	55.56

c) Rainham

	Percentage of trapping points		
	Latrines	**Water voles**	**Latrines and water voles**
Aug-98	57.14	28.54	16.67
Sep-98	85.71	85.71	88.89
Oct-98	61.90	71.43	76.92
Nov-98	28.57	0	0
Dec-98	No trapping		
Jan-99			
Feb-99			
Mar-99	38.10	33.33	50.00
Apr-99	52.38	71.43	90.91
May-99	57.14	61.9	91.67
Jun-99	rain		

3.4 DISCUSSION

This section discusses the trends in latrine counts (Section 3.4.1), the relationship between latrines and water vole numbers (Section 3.4.2), a comparison with the published data (Section 3.4.3) and the relationship between latrines and water vole captures (Section 3.4.4).

3.4.1 Latrine counts

Aveley, Hilliers and Rainham all show a broadly similar trend in the numbers of latrine counts across months. All three sites show high numbers of latrines in August or September 1998 relating to a peak in the MNA. Woodroffe *et al* (1990b) found a similar peak in latrine production in mid to late summer. This is likely to correspond with a peak in the number of water voles present, as indicated by the MNA. With the exception of Aveley, latrine numbers dropped over winter. Again this was also experienced by Woodroffe *et al* (1990b) and is likely to correspond with low water vole numbers and little above ground activity (see Chapter 4). At Aveley a particular high latrine count was observed in December 1998 possibly associated with a short period of warmer weather. The counts at all three site rise to peak in March/April with a subsequent slight fall in June/July peaking again in the following August at Aveley and Hilliers. The peak in March and April is likely to be associated with the onset of the breeding season (*e.g.* Singleton, 1984) and potentially the establishment of territories. The August peak can again be attributed to high number of water voles as indicated by the MNA. At Aveley low numbers of latrines were recorded in the following winter then rising in March to peak in May. The MNA throughout this time remained low. At Hilliers the number of latrines remained very low until the end of the study. Again, the MNA was also low during this time. This infers that, whilst fluctuations may occur, MNA (or the number of water voles) dictates the general trend in latrine numbers.

Rainfall prior to or during the latrine counts rendered many count invalid as rising water levels or the act of the rain itself washed latrines away. Moffatt (1984) also highlighted rainfall as a confounding factor when using field signs.

No latrines were recorded at either Bovington or Whitemead even when water voles were known to be present (see Chapter 2). It is possible that the low number of water voles present meant that latrines production for territory marking was not necessary. Equally it is possible that the presence of mink in the area affected the behaviour of the remaining water voles. Barreto and Macdonald (1999) reported water voles to avoid the odour of American mink. Upon a mink entering the area water vole activity may increase in the short-term, although in the longer-term water vole activity will decrease (Woodroffe *et al,* 1990b). This decrease in activity is likely to result in less time spent maintaining territories and hence producing latrines. Subsequently water voles became extinct from the site.

One of the primary difficulties with latrine counts is in the definition of a latrine. Typically a water vole latrine has been defined as a pile of droppings on top of a mass of old droppings (*e.g.* Strachan and Jefferies, 1993). In the current study, these 'latrines' were rarely found probably due to fluctuating water levels and rainfall. Therefore a definition was devised whereby a latrine was any pile of faeces consisting of six or more pellets (Section 3.2.2.1). This differs from other typical definitions assumed to have been used by other researchers (*e.g.* Woodroffe, 1988; Barreto and Macdonald, 2000) and in national surveys (Strachan and Jefferies, 1993). In addition the purpose of latrines may vary, some being as territorial (Leuze, 1976) or simply accumulations of faeces at favoured feeding locations (pers. obs). In the current study water voles commonly left piles of faeces on top of live-traps, piles of chewed vegetation and in one case on the dead young of a female water vole. It seems likely that faeces at favoured feeding locations will vary between sites and within sites dependent upon the local distribution of favoured food plants or feeding platforms in addition to the number of water voles present.

3.4.2 Relationship between latrines and water vole numbers

The current study calculated the number of latrines per water vole and the number of latrines per adult vole for each month at each site. This varied a great deal between months and sites and no trends were observed. Baretto and Macdonald (2000) calculated a mean of approximately six latrines per water vole in July on a River in

Oxfordshire, UK. In the current study, the highest number of latrines per water vole in July was 1.64 (Aveley, July 2000). Overall the highest number of latrines per water vole was 7.83 (Rainham, August 1998), however this was unusual with the figure not exceeding five latrines per water vole in any month at any site. The differences between this and the current study may be a result of differences between the study sites. In the current study all the sites (with the exception of Bovington and Whitemead) were narrow well vegetated watercourses from 1m to 3m in width, whilst Baretto and Macdonald (2000) were studying an 8-10m wide river.

Linear regression showed relationships between numbers of latrines and a number of different categories of water vole at Aveley, Hilliers and Rainham. At Rainham relationships were only found between latrines and adults males and latrines and all adults in the breeding season. The absence of further relationships is likely to be due to the lack of data points for Rainham, due to the shorter trapping period (August 1998 to July 1999). Relationships common to both Aveley and Hillers were found between all latrines and the total number captured, MNA, Adult females and all adults; and latrines and adult females and all adults during the breeding season. Aveley and Hillers data were compared and no significant difference was found between the sites for all latrines with all adults, total number captured and MNA and latrines during the breeding season with all adults. These data were combined and predictive equations for the number of water voles from latrines were calculated.

It is expected that any linear relationship between water voles and latrines would occur during the breeding season, during which time latrines are maintained. In the current study a relationship between adults and latrines was found during the breeding season. Given that both males and female produce latrines (Leuze, 1976) this was not unexpected.

Surprisingly, relationships were found between latrines and the number of water vole captures, MNA and adults throughout the year. The data from Aveley and Hilliers suggest that whilst some latrines are maintained during the winter the number is very low. It is likely that these relationships seen occurring throughout the year are driven by low water vole and latrine numbers during the winter period.

The predictive equation for the total number of water voles capture from latrine throughout the year appeared different from thee predictive equation calculated by Morris *et al* (1998). It seems likely that any relationship between water voles and latrines will differ between sites due to the availability of latrine sites. Weather conditions and changes in water levels may also contribute to differences between the two relationships. In addition differences in the definition of a latrine may contribute to the differences between the two studies. Woodroffe (1988) states that some latrines are composed of a flattened mass of old droppings topped with fresh ones but that not all latrines in his study were of this type. It may therefore not be appropriate to compare the two studies. However, when the data from the current study were further examined one particularly high latrine count was noticed (Hillers, August 1998). This count was the first to be undertaken at Hilliers, and whilst the accuracy is not doubted it was decided to remove this point and reanalyse the data. Justification for this was based on the latrine count being significantly higher than any other latrine count at any site. It is likely that a combination of dry weather and the shade from uncut vegetation allowing faecal pellets to retain moisture led to this unusually high count.

When the data were reanalysed and the predictive equation for the total number of water voles capture from latrine throughout the year appeared very similar to with that obtained by Morris *et al* (1998), no significant difference was found. Whilst it could be argued that the data in the current study were altered to produce this result it is nonetheless interesting. Consideration was given to putting the regression line through the origin on the assumption that if no water voles were present no latrines would be recorded and *vice versa*, however for all predictive equations the constant was found to be significant. Additionally, the current study demonstrated that there will be cases where water voles will be present and no latrines recorded and *vice versa.*

This study demonstrates that it may be possible to estimate water vole population size from latrine numbers. However, as with any index of population size it must be used with care. At this stage, it is potentially more useful to use latrines to provide an indication of water vole density as opposed to an actual number of individuals in the population.

A major drawback of the technique is the potential low permanence of latrines due to rainfall and changes in water level. Another is the definition of a latrine.

3.4.3 Relationship between latrines and water vole captures

For each month at each site the data were analysed to determine any relationship between latrines associated with a trapping point and water vole captures. It might be expected that if a latrine was present within the vicinity of a trap then the likelihood of capturing a water vole might be higher. The data suggest that this may be the case, particularly during the breeding season with some exceptions. In many of the months during the breeding season over 50% of the trapping points with associated latrines subsequently resulted in a captured water vole. A greater degree of association may be seen on sites where a water vole only uses one bank of the watercourse. In the current study, at all the study sites, water voles were known to use both banks of the watercourses. As previously discussed the availability of latrine sites is likely to affect the distribution of latrines and therefore no latrine associated with a trapping point does not necessarily mean that no water vole is present. Similarly the position of traps would also affect the likelihood of capture of any individual water vole. Lawton and Woodroffe (1991) described gaps in the distribution of water vole field signs along rivers in the North York Moors National Park, UK. They classified sites into 'core' and 'peripheral' and other sites; core sites containing breeding colonies (and latrines) and peripheral sites containing transient voles but not breeding colonies (no latrines) and other sites with no water voles. Core sites were characterised by a high percentage of grass, steep bank angles and a high layering of vegetation all habitat characteristics which are favoured by water voles (*e.g.* Strachan and Jefferies, 1993). Whilst the habitat was not studied in depth in the current study, variations in the banks and vegetation structure along all of the study watercourses were noticed, for example, due to localised poaching by cattle. It may be that small areas of the habitat were unsuitable for breeding, resulting in their use only as peripheral sites, possibly for feeding. At high population densities (*i.e.* when young emerge into the population) voles may occupy less suitable habitat, however at times of low population density these gaps may become more prevalent. However, it should be noted that Woodroffe (1988) found no latrines at peripheral sites and failed to capture any water voles.

The results of this Chapter indicate that there is a relationship between water voles and latrines, which may be expressed as a linear relationship. The nature of the relationship may differ between sites and between seasons. Further work to identify the relationship between latrines and habitat features may serve to inform this relationship and identify the reasons for differences between sites. However, it is suggested that any such relationship can only be used as an indication of water vole density and not as an absolute index of water vole numbers. Should latrine counts be used for either purpose, it will be essential to define the definition of a latrine before field work commences. Field work should also only take place following a period of dry weather.

CHAPTER 4 OVERWINTERING MOVEMENT PATTERNS

4.1 INTRODUCTION

Radio-tracking provides a valuable technique for studying the behaviour and ecology of animals. Radio-tracking has been used to gain information about the behaviour of a wide range of mammals including deer, badgers (*Meles meles*) and a number of small mammal species (*e.g.* Banks *et al.*, 1975; Douglass, 1989). Radio-tracking can be used to measure home ranges, dispersal, habitat use, social interactions and activity patterns. The benefit of this technique over the use of live trapping is that the animals are not constrained by the position of traps.

A number of studies have employed radio-tracking to measure water vole behaviour in the UK (*e.g.* Leuze, 1976; Carter and Bright, 2003) and the behaviour of fossorial water voles in other parts of Europe (*e.g.* Jeppsson, 1987).

In the current study radio-tracking was used to examine overwintering behaviour of water voles. Of particular interest were home range sizes, movements, activity patterns and interactions.

4.1.1 Home range

For the purposes of the current study a home range is defined as the area an individual covers in its normal activities of feeding, mating and caring for its young (Burt, 1943 cited in Braun, 1985).

Live trapping has commonly been used to estimate the home ranges of water voles (*e.g.* Pelikan and Holisova, 1969; Singleton, 1984), but is constrained by the number and location of traps. Stoddart (1970a) used a radioisotope technique allowing recognition of faeces. This method relies on the assumption that water vole latrines are positioned at the outer limits of an animal's home range. Efford (1985) also employed faecal marking, using strands of polypropylene cord. Radio-tracking to measure water vole home ranges has been used by a number of researchers (*e.g.* Leuze, 1976; Efford, 1985; Woodroffe, 1988; Barreto and Macdonald, 2000).

The current study compared home range estimates with those published in the literature.

The utilisation of an animal's home range is of equal importance to the size of the home range. Tattersall *et al* (2001) used radio-tracking to examine habitat use by wood mice (*Apodemus sylvaticus*). In the current study home range utilisation is considered.

4.1.2 Dispersal

Stoddart (1970a) recognised two types of dispersal in water voles; long distance movements where the individual moves out of the geographical confines of the colony; and short distance movements where the individual moves to a new home range within the confines of the colony. Stoddart (1970a) used live trapping and faecal marking techniques, although radio-tracking provides a more accurate means of recording movements. Other studies of water voles using radio-tracking have considered the dispersal of individuals (*e.g.* Leuze, 1976; Barreto and Macdonald, 2000).

The current study considered dispersal movements and movements within an individuals' home range.

4.1.3 Activity patterns

A number of studies have used direct observations to study the activity patterns of water voles, either in the field (*e.*g. Ashby *et al,* 1969) or under experimental conditions (*e.g.* Lund, 1970). Different studies have conflicted in their descriptions of diel trends. Other studies (similar to this study; Chapter 2) have used live trapping to provide an indication of activity patterns (*e.g.* Stoddart; 1969; Gaisler and Zejda, 1973). Radio-tracking provides a useful technique for monitoring water vole activity and allows observations to continue even if the animals are not directly observed.

4.1.3 Social interactions

Accounts of social interactions between individual water voles based on observations occur frequently in the literature (*e.g.* Dean, 1947). However, radio-tracking provides an opportunity to study the spatial organisation and relationships of water voles in further detail. Leuze (1976) demonstrated through radio-tracking that male ranges overlapped and subsequently identified latrines as the mechanism for the spacing of male water voles. Barretto and Macdonald (2000) found male ranges overlap female ranges.

The current study utilises radio-tracking to determine any overlap in home ranges and also define any interaction between water voles.

4.2 METHODOLOGY

4.2.1 Study site

The study site was Aveley Marsh as described in Chapter 2. Two different habitats within Aveley Marsh were studied; the ditch that was used in the live-trapping studies and two brackish water ponds (see Figure 4.1). A description of the ditch is provided in Chapter 2. Pond 1 was approximately 3000m^2 and shallow with a maximum depth of approximately 1m in the centre. The maximum height of the bank above water level was 50cm. Emergent vegetation was predominately sea club-rush (*Scirpus maritimus*) around the shallow margins of the pond. Grasses dominated the banks. Pond 2 is approximately 1000m^2 with a maximum depth of 1.5m in the centre. The banks were a maximum of 50cm above water level. Marginal and emergent vegetation was dominated by common reed, leaving only a small area of open water in the centre of the pond.

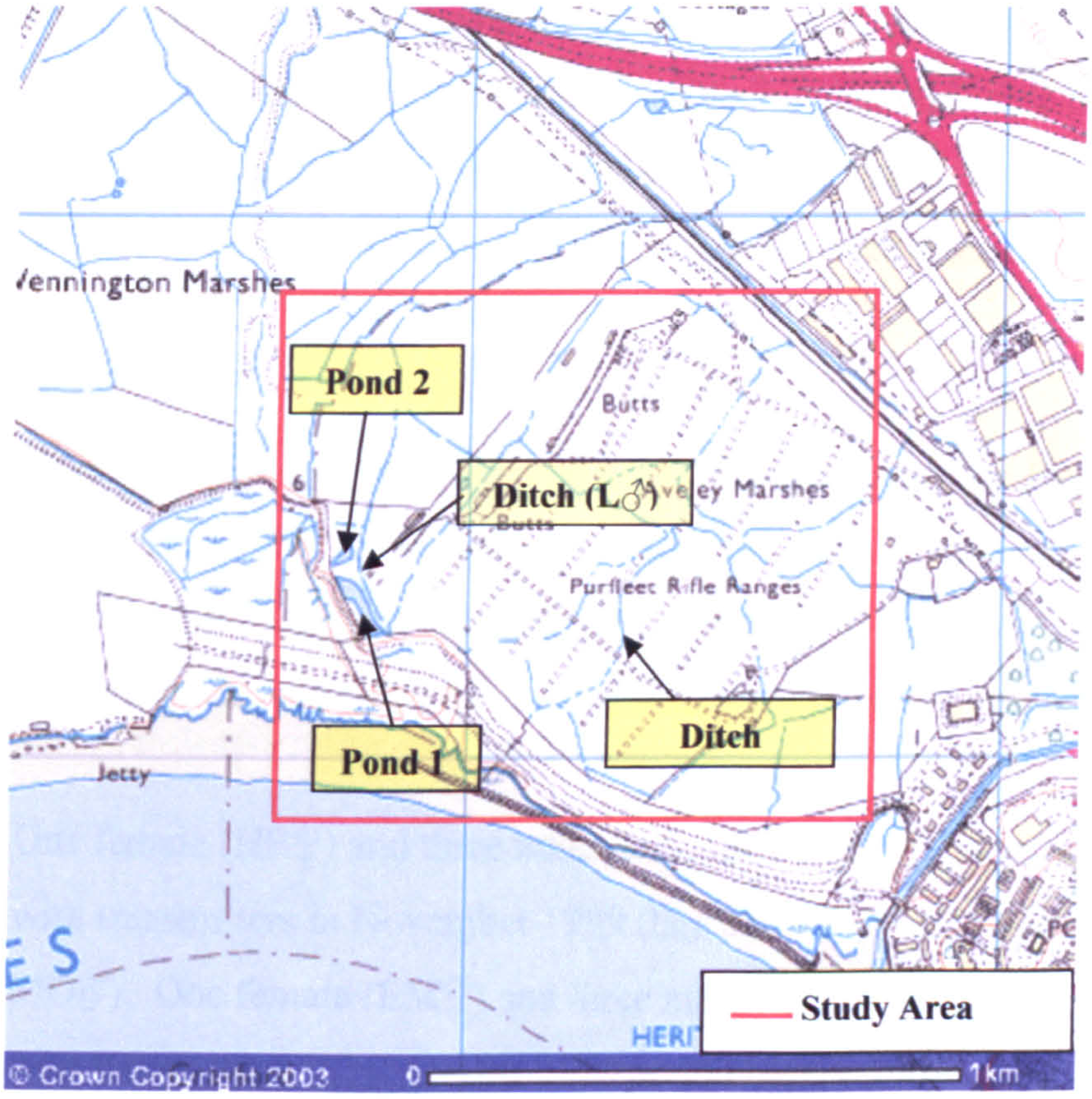


Figure 4.1 Radio-tracking study area.
(Reproduced from Ordnance Survey data by permission of Ordnance Survey, © Crown Copyright.)

4.2.2 Field methods

4.2.2.1 Live-trapping

Water voles were live-trapped using the methodology described in Chapter 2. Water voles used in the radio-tracking study were captured as part of the monthly live-trapping study. Trapping on Ponds 1 and 2 was undertaken between November 1999 and February 2000 on an *ad hoc* basis in order to capture water voles to be used in the radio-tracking study.

Captured water voles were sexed, weighed and marked with a numbered ear tag as described in Chapter 2. Only adult animals (*i.e.* weighing greater than 140g) were considered to be suitable for use in the radio-tracking study. Smaller animals were not used as these are likely to be juveniles whose movements and activity may have been different to adult animals.

4.2.2 Radio-tracking

Water voles were fitted with radio transmitters (TW-4SM-R tags, Biotrack Ltd, Wareham, Dorset, UK) attached to self-locking plastic cable tie collars (see Plate 4.1). Fitting was undertaken, without the use of anaesthetic, by manually restraining the animal and then attaching the collar. Animals were immediately released at the site of capture.

Three female voles (A♀, B♀ and C♀) from the ditch were fitted with transmitters in November 1998. Three male voles (E♂, F♂,and H♂) and one female vole (G♀) were fitted with transmitters in January and February 2000. Two female voles (O♀ and Q♀) and one male vole (N♂) were fitted with transmitters in August 2000.

One female (HE♀) and three male (D♂, FR♂ and MO♂) voles from pond 1 were fitted with transmitters in November 1999 (D♂ and FR♂) and February 2000 (HE♀ and MO♂). One female (EM♀) and three male (I♂, J♂ and K♂) from pond 2 were fitted with transmitters in November 1999 and February 2000 respectively. In addition a single male vole (L♂) from a ditch immediately adjacent to Ponds 1 and 2 was fitted with a transmitter in February 2000.

Plate 4.1 Water vole fitted with radio transmitter (TW-4SM-R tags, Biotrack Ltd, Wareham, Dorset, UK)

A Mariner receiver (Biotrack Ltd, Warham, UK) and handheld flexible 5-element Yagi aerial were used to track the transmitters.

Upon initial release, water voles generally moved rapidly to either a burrow or vegetation within the watercourse. Although above ground activity was usually observed within 1 hr of fitting, tracking was undertaken a minimum of 4 hrs after the fitting of the transmitter to the animal to allow it to become accustomed to the collar. Throughout the study, water voles quickly became accustomed to the observer, with little evidence of movement away from the observer recorded. In many cases fixes could be obtained at a distance of several metres from the animal as they could be easily heard or seen. Fixes on the animal's position were taken at 15 minute intervals over a 24 hr to 48 hr session.

The transmitters could be detected from approximately 100-150m, although this diminished rapidly if the animals were below ground. Triangulation was not considered necessary as animals were located to within 1m using signal strength and direction as a guide. Whilst animals were underground it was often possible to locate their position precisely. Above ground fixes were often confirmed by visual sightings of the animal or from feeding noises. Marker canes laid out in a grid formation with 10m intervals were used to assist in estimating the position of fixes. Fixes were related to an OS grid reference.

The activity of water voles at each fix, as indicated by fluctuations in signal strength was determined. A constant, steady signal indicated that the animal was stationary (activity code 0). A fluctuating signal originated from a single location indicated the animal was moving whilst remaining in the same location (*e.g.* feeding, grooming; activity code 1). A signal with rapidly diminishing or increasing signal strength indicted that the animal was moving to a different location (activity code 2)

Wherever possible, the location of nest sites (locations where voles were inactive for five successive fixes) was estimated. In the majority of cases these estimated nest sites remained consistent over the course of the radio-tracking session and with the exception of one animal (whose nest could be seen in emergent vegetation within Pond 1) all of the nest sites were underground.

The majority of transmitters had a lifetime of at least three months. However several transmitters ceased to function after one week. Wherever possible, at the end of the study water voles were recaptured and the transmitters removed.

4.2.3 Data analysis

A variety of analytical techniques were employed to analyse the extensive data obtained in this study. A number of the analyses described utilised computer software (Wildtrak; Todd, 1992) specifically designed for the analysis of radio-tracking data. A range of software packages area available, such as Ranges6 (Anatrack Ltd) which can be used to estimate home range sizes, overlap and animal interactions. Wildtrak is a suite of programmes for the analysis of radio-tracking data designed for use on Macintosh computers. Wildtrak can be used to plot home ranges, measure static and dynamic interactions between individuals and measure a range of movement parameters. It uses non-parametric analyses and makes no assumptions about the distribution of fixes.

Todd (1992) provides full details on the use of Wildtrak.

For the interpretation of the results, in some instances, the data from the winter period were extracted for analysis of overwintering behaviour. The winter period used was a defined in Chapter 2; from December to February inclusive.

4.2.3.1 Minimum Convex Polygon

This analysis is used to indicate the shape and size of an animal's home range. The polygon is constructed by joining the outer fixes to form a polygon from which an area can be calculated (White & Garrott, 1990). One of the major disadvantages with this technique is that the size of the home range estimate will increase with the number of fixes, as the probability of more outlying fixes increases (Jenrich and Turner, 1969 cited in White and Garrott, 1990). Additionally, if the animal's home range is not convex, the polygon will also encompass areas that are not really within the animal's home range (Kenward, 1987). To go some way to correcting this problem, in this study 95% Minimum Convex Polygons (MCP) were calculated, using 95% of the points lying most closely to the arithmetic mean centre of the range. This can eliminate some of the outlying points that contribute to inaccuracies in the home range estimate. A full description is provided in White and Garrott (1990). In the current study, Wildtrak was used to calculate 95% MCPs for each water vole during each session. The analysis used both active fixes (activity code 2) and inactive fixes (activity code 0 and 1). A home range estimate was calculated and the MCP presented graphically. Known nest sites, recorded during radio-tracking, were plotted on the MCPs.

Using the assumption that 95% MCPs represent a reasonable estimate of the size and shape of a water vole's home range, home range lengths for water voles radio-tracked on ditches were estimated by measuring the total length of watercourse between the two furthest points of the 95% MCP.

4.3.3.2 Grid Cell analysis

This technique focuses on the grid cell in which each fix occurs. The results can be displayed to represent the time that the animal spent in each grid cell, which can then be used to study habitat use (Kenward, 1987). Grid cells can also be used to estimated home range size. Wildtrak was used to perform the grid cell analysis for each vole in each session. In this case 1m grid squares were used. The analysis used both active and inactive fixes and the independence interval (the minimum time interval between fixes necessary for them to be included in the analysis) set at 0 mins allowing for the inclusion of all fixes.

4.3.3.3 Movement

Wildtrak was used to analyse the data, for each vole in each session, to obtain the minimum distance moved, the animal's speed of movement and the proportion of time spent moving. The minimum distance moved is calculated by the addition of all the straight-line distances between consecutive fixes in each tracking night (determined by calendar date). Whilst this is likely to provide an underestimate of the actual distance moved it provides a useful insight into the water vole movements. The speed of movement was calculated for all fixes and moving fixes. Moving fixes refers to fixes where the animal's location is different at successive time intervals.

In all calculations, fixes from all sessions were included, with the exception of those sessions with less that 20 fixes (J♂ and K♂ 16 February 2000).

4.3.3.4 Activity patterns

The data were analysed for patterns in the activity cycles of each vole. For each session for each vole the data were examined for trends in the daily activity using the activity codes recorded. For each session, the proportion of fixes that each vole spent on each of the activity codes was calculated and examined for trends over time and between voles. A Mann Whitney U test was used to examine the data for differences in the proportion of fixes during the day and night.

4.3.3.5 Static Interactions

The percentage of overlap between two home ranges can provide an estimation of static interaction (Macdonald *et al*, 1980). However this does not take into account the utilisation of each of the home ranges by the animals concerned (Doncaster, 1990). Wildtrak uses grid cells (refer to Section 4.3.3.2) to examine static interactions. In the current study static interaction analysis, using Wildtrak, was performed for those voles which had overlapping home ranges (based on 95% MCPs) and which were radio-tracked simultaneously. 1m grid cells were used. Active and inactive fixes with 0 min independence interval were used. The analysis identified the area and percentage overlap of the two ranges. A Spearman's Rank Correlation coefficient was calculated to show the concordance of utilisation of the grid cells.

4.4.3.6 Dynamic interactions

Analysis of the data for evidence of dynamic interactions was performed using Wildtrak. This examines the dependency in the movement of two animals within the limits of their home range (Doncaster, 1990). The analysis was undertaken for those voles that had overlapping or adjacent home ranges (as determined from the 95% MCPs) and which were radio-tracked simultaneously. The block width for simultaneous fixes was set at 0 min. The block width determines the maximum time interval between the fixes of the two individuals required for the pair of fixes to be 'simultaneous'. In the current study, fixes for all animals tracked simultaneously were recorded as a single time despite the fact in practice the fixes for two animals tracked simultaneously may have been 5 min apart. Active and inactive fixes were used and the independence interval was set at 0 min. The results were presented to show the proportions of observed and expected separations for discrete separation intervals (*e.g.* 20-30m). Wildtrak uses the two-tailed binomial distribution to obtain the probabilities that any excess or deficit of the paired fixes may be a result of random variation.

4.4.3.7 Autocorrelation

Autocorrelation analysis was undertaken using Wildtrak to calculate the minimum time interval between fixes where independence is found.

4.3 RESULTS

4.3.1 Minimum Convex Polygon

95% Minimum Convex Polygons (MCPs) were calculated and plotted for all water voles for each session that they were tracked. An example of one of these MCPs is presented in Figure 4.2. Appendix 2 presents MCPs for all water voles. MCPs for each vole over different session were overlain to indicate any changes in range over time. Figure 4.3 provides an example of one of these plots (refer to Appendix 2 for other plots). For different water voles tracked in the same session, MCPs were overlain to indicate potential overlaps in range. Figure 4.4 presents an example of this type of plot (refer to Appendix 2 for other plots).

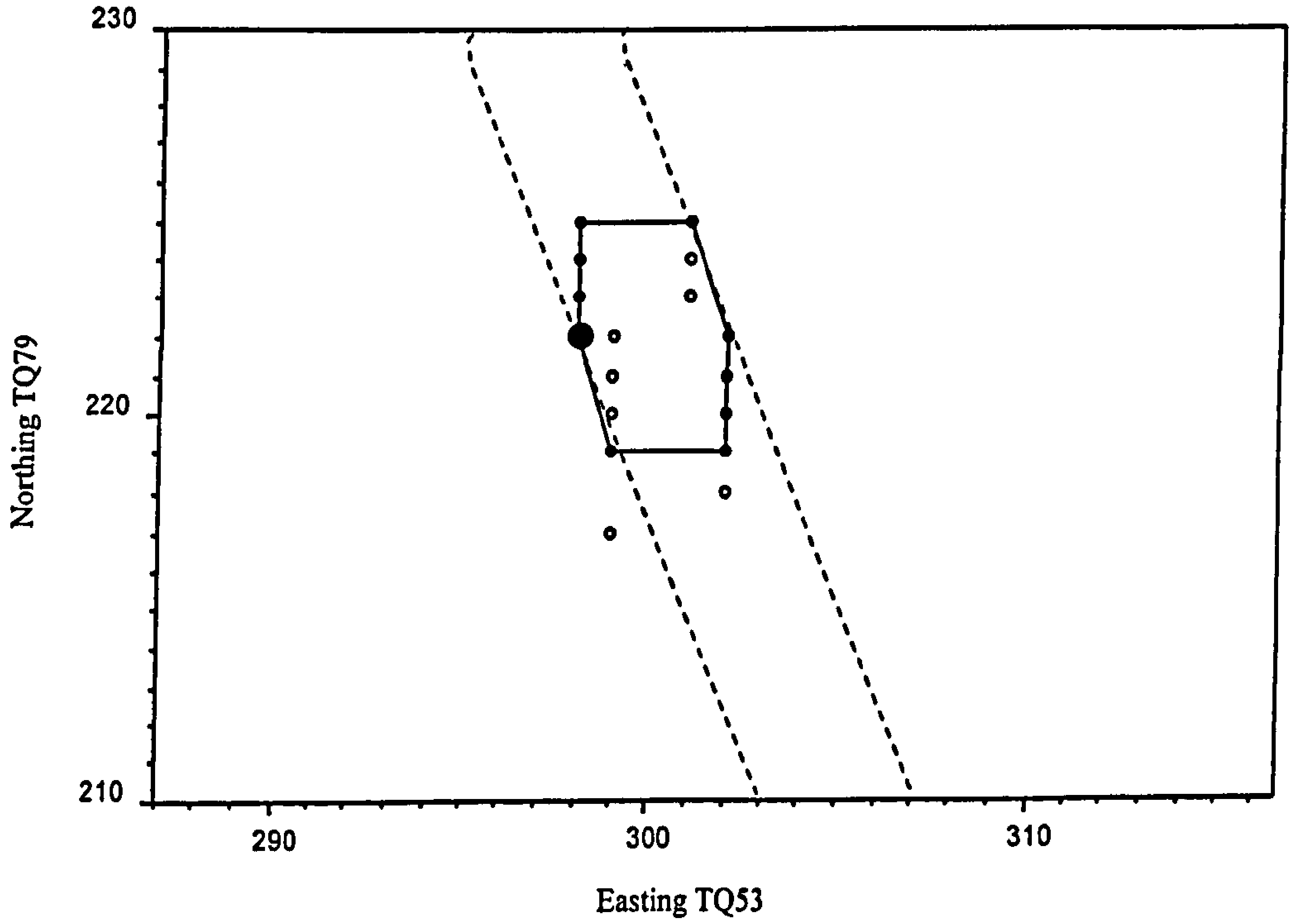


Figure 4.2 95% Minimum Convex Polygon for **Vole A♀ 6 November 1998**
(— MCP, ---- Ditch, ○ Fix, ● Nest site)

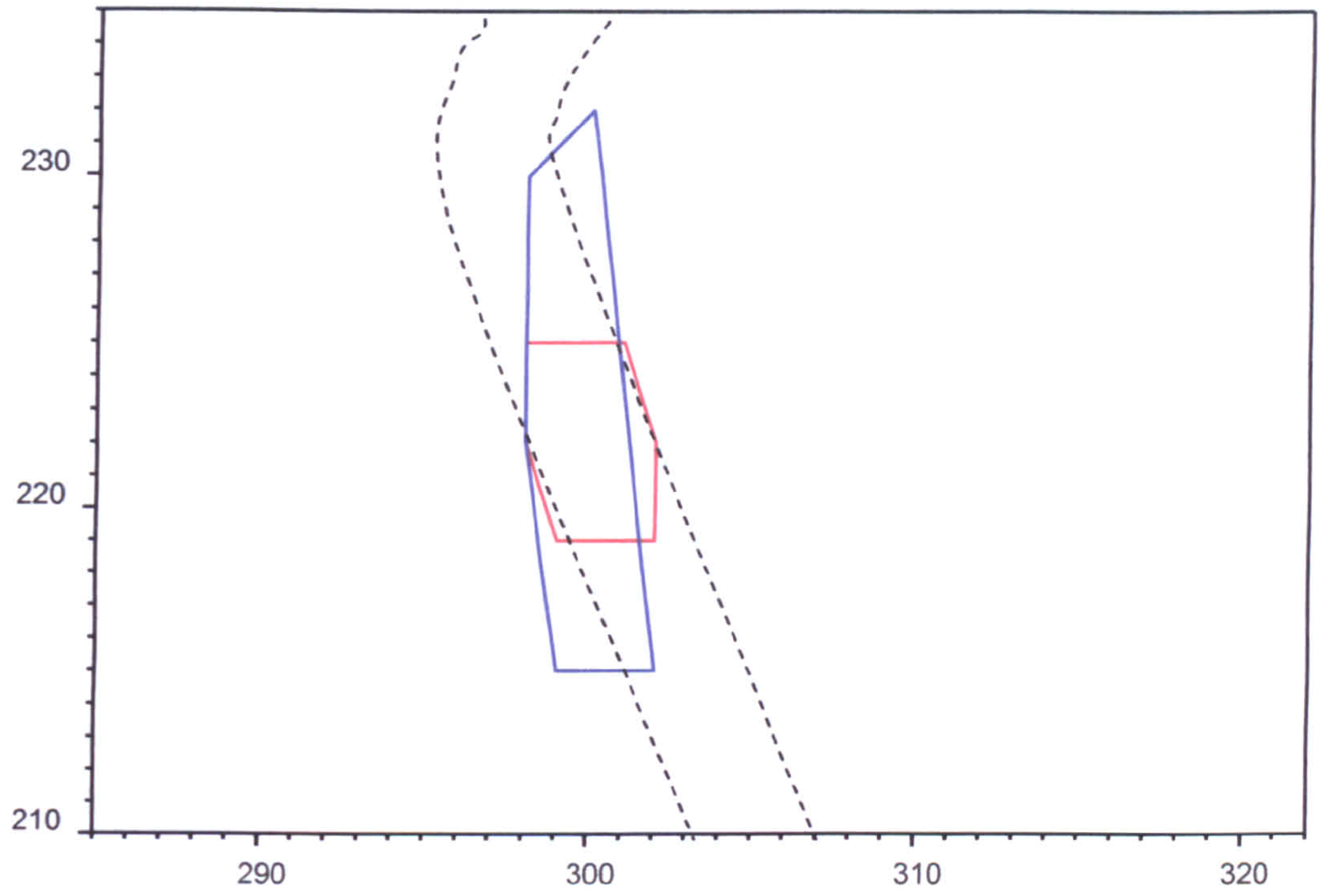


Figure 4.3 95% Minimum Convex Polygons for **Vole A♀**
(— 6 November 1998, — 10 December 1998, ---- Ditch)

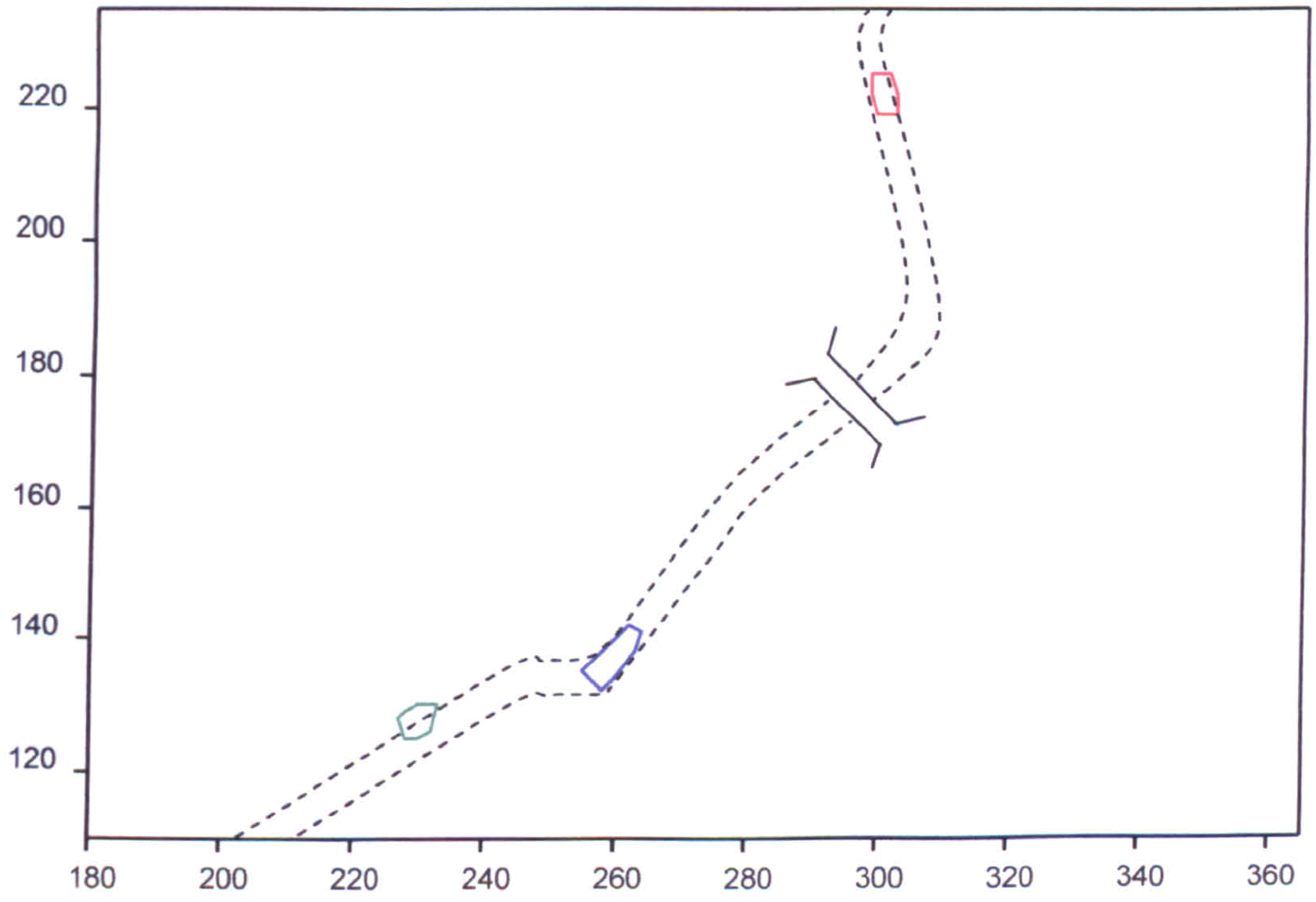


Figure 4.4 95% Minimum Convex Polygons for **Vole A♀, Vole B♀and Vole C♀ 6 November 1998**
(— Vole A♀, — Vole B♀, —Vole C♀, ---- Ditch)

The home range of each water vole in each session was calculated from the MCPs and shown in Table 4.1. In addition, for those water voles radio-tracked on a ditch, the range length was calculated to provide a comparison with published data[1].

Home ranges calculated using 95% MCPs varied considerably in size ranging from 2m^2 (FR♂ 16 November 1999) to 7488m^2 (E♂ 1 March 2000) with a mean of 427m^2 (±168.6; N = 48). The mean home range for males on a ditch was 732m^2 (±437.4, N=18) whilst for those males on a pond the mean home range was 307m^2 (±126.4, N = 11). The mean home range for females on ditch was 100m^2 (±20.2, N = 13) and on a pond 445 (±128.0, N =6). The length of home ranges also varied considerably ranging from 7m (A♀ 6 November 1998) to 230m (E♂ 1 March 2000) with a mean of 60m (±13.5, N = 18) for males and 27 (±4.9; N = 13) for females.

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[1] Fixes from different, but close together, sessions were not grouped to estimate home ranges as examination of the MCPs indicated that home ranges moved between sessions. Such grouping may therefore have resulted in a greater inaccuracy in the estimation.

Table 4.1 Water vole home ranges (as determined by 95% Minimum Convex Polygons) and length of watercourse occupied by the range based on radio-tracking data.

Vole	Date	Number of fixes	Home Range (m^2)	Range length (m)
A♀	6 November 1998	179	21	7
	10 December 1998	331	46	18
B♀	6 November 1998	179	39	11
	10 December 1998	189	153	30
C♀	6 November 1998	178	22	7
E♂	12 January 2000	144	68	19
	15 February 2000	109	109	22
	1 March 2000	111	7488	230
	11 March 2000	144	98	32
	21 March 2000	192	465	65
	15 April 2000	96	95	39
F♂	12 January 2000	48	85	44
	18 January 2000	98	107	31
G♀	16 February 2000	96	79	28
	1 March 2000	96	79	25
	11 March 2000	95	66	30
	21 March 2000	190	221	60
	15 April 2000	95	257	63
H♂	16 February 2000	95	136	58
	1 March 2000	111	37	19
	11 March 2000	96	145	45
	21 March 2000	192	3409	170
	15 April 2000	96	136	115
D♂	16 November 1999	96	65	-
	23 November 1999	157	66	-
	30 November 1999	96	71	-
EM♀	16 November 1999	91	150	-
	23 November 1999	161	214	-
	30 November 1999	96	383	-
	14 December 1999	48	794	-
J♂	16 February 2000	20		-
	22 February 2000	112	499	-
K♂	16 February 2000	20		-
	22 February 2000	112	1338	-
	6 March 2000	144	530	-
L♂	22 February 2000	111	216	45
	6 March 2000	88	315	32
FR♂	16 November 1999	96	2	-
	22 November 1999	161	4	-
HE♀	16 November 1999	96	250	-
	22 November 1999	161	879	-
I♂	14 December 1999	48	7	-
MO♂	16 February 2000	112	128	-
	6 March 2000	144	668	-
N♂	20 August 2000	96	60	20
	2 September 2000	96	181	67
	9 September 2000	96	26	22
O♀	20 August 2000	96	126	26
	2 September 2000	96	90	34
Q♀	9 September 2000	96	101	15

A Mann Whitney U test was used to compare the medians of home ranges areas of males and females and of water voles in ditches and ponds. There was no significant difference in the medians of the home range areas of males (N = 11) and females (N = 9) (U = 273.50, NS) or water voles on ditches (N = 12) and ponds (N = 8) (U = 210.50, NS).

A Mann Whitney U test was also used to compare home range lengths of males (N = 5, Median = 41.5, IQ = 43.5) and females (N = 7, Median = 26, IQ = 19) tracked on ditches. A significant difference in home range length between males and females was found (U = 59.00, $P<0.05$).

Overwinter (December to February) mean home range areas and lengths were calculated for male and female water voles on ditches. The mean overwinter male home range area on a ditch was 120m^2 (±21.3; N = 6) and the mean female area 92m^2 (±31.6; N = 3). The mean range length for males was 37m (±6.2; N = 6) and for females 25m (± 3.7). Due to an insufficient number of data points the mean overwinter home range area for water voles on a pond was not calculated, however, male overwinter home ranges varied from 7m^2 to 1338m^2 (refer to Table 4.1). A single female was tracked for one session during the winter (EM♀ 14 December 1999), her home range area at this time was 794m^2 (refer to Table 4.1).

Long distance movements to new home ranges during radio-tracking sessions contribute to the overall home range size calculated. These fixes could have been excluded from the home range calculation, however in all cases the individuals regularly moved between the two areas during the session in which the first movement was recorded and could therefore reflect their true, albeit temporary, home range.

An interpretation of the MCP plots presented in Appendix 2 is provided below.

The home range of A♀ expanded between November 1998 and December 1998. The nest site remained in the same location for both sessions. The home range of B♀ was also larger in December 1998. Again the nest site remained in the same location. Range length also increased in December 1998 for A♀ and B♀. C♀ was tracked in November 1998 and then subsequently found dead in December 1998. The corpse of

C♀ was located over 500m from the November location in an underground chamber approximately 3m from a ditch. There was no overlap between the home ranges of A♀, B♀ and C♀ in either November or December 1998.

E♂ had a similar home range size and length in January and February 2000. In March 2000, the apparent home range increased dramatically as the animal relocated to occupy a new home range downstream. By 11 March 2000, E♂ had relocated again to a different ditch where it remained until the 21 March 2000 session. The home range size and length increased temporarily on 22 March 2000 before contracting again in April 2000. The home range size and length of F♂ did not differ considerably between to two sessions in January. The nest site remained in the same location, at the southern end of the home range. In February 2000 the transmitter from F♂ was found in a fox scat. G♀ remained in the same location throughout the study. Home range size remained constant throughout 16 February 2000, 1 March 2000 and 11 March 2000. This then increased in both the 21 March 2000 and 15 April 2000 sessions. H♂ also remained in a similar location throughout 16 February 2000, 1 March 2000 and 11 March 2000 retaining the same nest sites. By the 11 March 2000 session, H♂ had established a new nest site to the south of the first and was using both. By 21 March 2000 the vole had extended its home range much further to the south. By 15 April 2000, H♂ still had an extended home range but retaining the second nest site. The home ranges of G♀ and H♂ overlapped in the 16 February 2000 session. By 1 March 2000 the home ranges were not overlapping but adjacent and in all subsequent sessions home ranges overlapped. H♂'s home range was consistently larger that that G♀.

D♂ retained the same nest site throughout the study and had a similar home range size through all three sessions in November 1999. The transmitter on D♂ subsequently failed and although observed the animal was not possible to recapture. EM♀ retained the same nest site throughout the three November 1999 sessions. Home range increased during 30 November 1999 to encompass approximately half of the area of the pond (pond 2) and by 14 December 1999 a new nest site was used. The home range of J♂ was not calculated for 16 February 2000, however in the 22 February 2000 session its home range encompassed almost half of the pond (Pond 2). The home range of K♂ included almost the entire pond (Pond 2) in both 22 February 2000 and 6 March 2000. K♂ and J♂ had overlapping ranges, however, J♂'s nest site was outside of K♂'s home range. D♂ and EM♀ had overlapping home ranges during the 16, 22 and 30 November 1999 sessions. EM♀ had a consistently larger home range than D♂.

L♂ moved home range at the end of the 6 March 2000 session to a new site approximately 150m away. Whilst not intensively tracked in this new home range *adhoc* fixes suggest that L♂ remained in this new home range for at least several weeks subsequently.

FR♂ retained the same nest site during 9 and 22 November 1999 sessions and the home range size was similar. Most of the fixes were located underground on the bank. HE♀ retained that same nest site during 9 and 22 November 1999, with an increase in home range size during 22 November 1999. All of the fixes for I♂ were located on the bank, underground. This transmitter failed after the first radio-tracking session. During the 16 February 2000 session MO♂ had two nest sites. In the 6 March 2000 session MO♂ had moved to a new nest site (an aboveground resting place within emergent vegetation) in the centre of the pond (Pond 1), the home range size also increase with the animal now utilising and area radiating out from the nest at the centre.

During the 2 September 2000 session N♂'s home range increased from the previous session, extending further south. By the 9 September session N♂'s home range had contracted having shifted to the south of the original location. O♀ occupied two nest sites in the 19 August 2000 session and only one in 2 September 2000. The 2 September 2000 nest site was located aboveground in emergent vegetation within the ditch. Q♀ occupied a single nest site on the bank of the ditch in the 9 September 2000 session. The transmitter for Q♀ was subsequently found several hundred metres away from the ditch. No corpse was recovered. The home ranged of N♂ and O♀ overlapped during the 20 August and 2 September 2000 sessions.

Home range area versus cumulative fixes

As home range estimation can be influenced by the number of fixes taken, the percentage of the final home range (MCP) determined at each fix was plotted for each radio-tracking session. Figure 4.5 shows a typical plot. The majority of plots showed the characteristic plateau of home range size as the number of fixes increases, indicating that sufficient fixes were collected. However, in a small number of cases (EM♀ 14

December 1999; F♂ 18 January 2000; H♂ 16 February 2000; J♂ 22 February 2000; N♂ 20 August 2000; N♂ 2 September 2000) this plateau was not reached, suggesting that the number of fixes may be inadequate to estimate home range size.

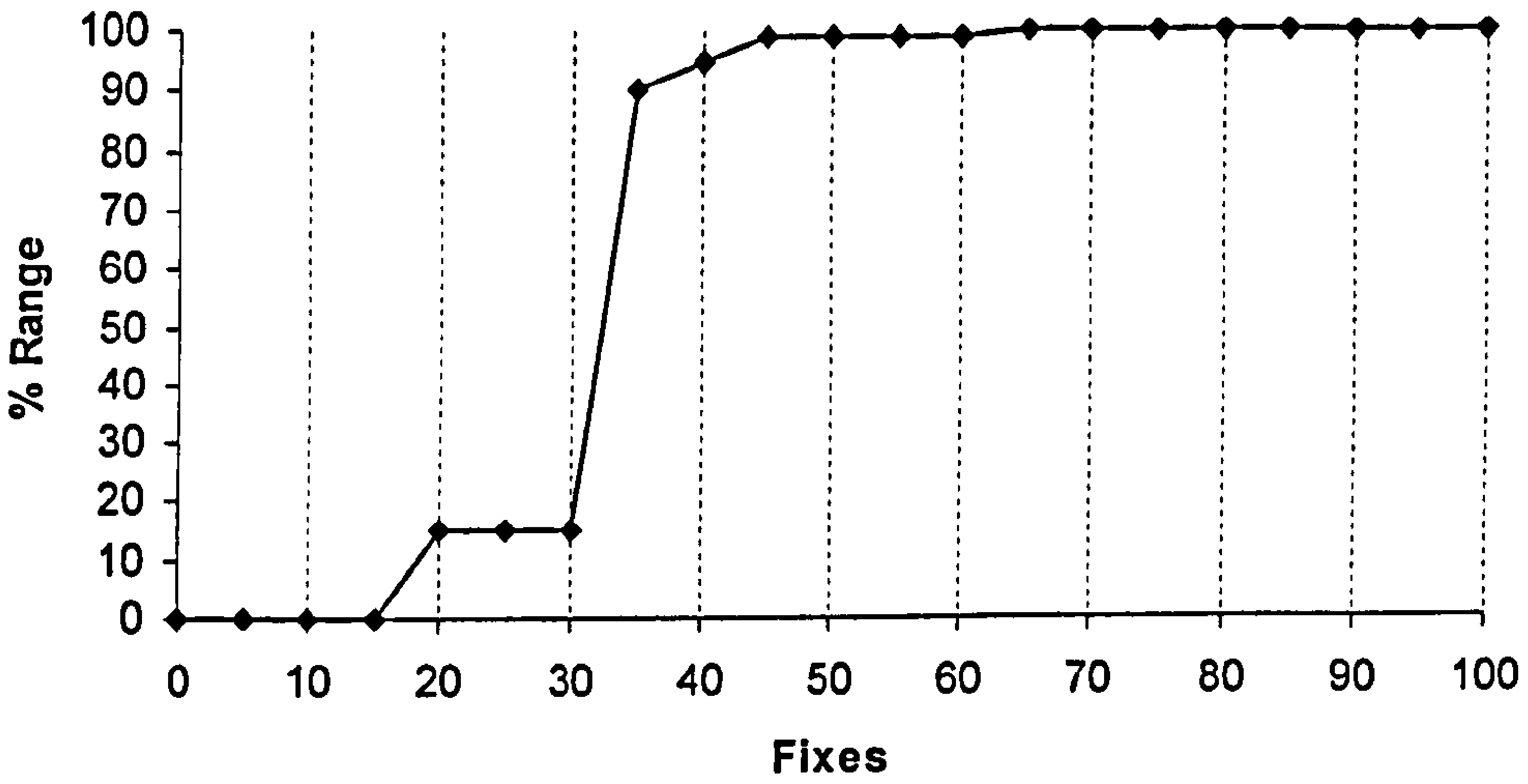

Figure 4.5 – Percentage of Minimum Convex Polygon (MCP) size against cumulative fixes for D♂ 23 November 1999.

4.3.2 Grid cells

Grid cell plots were created using Wildtrak for all water voles for each radio-tracking session. All plots are provided in Appendix 3. Figure 4.6 presents an example of a grid cell plot.

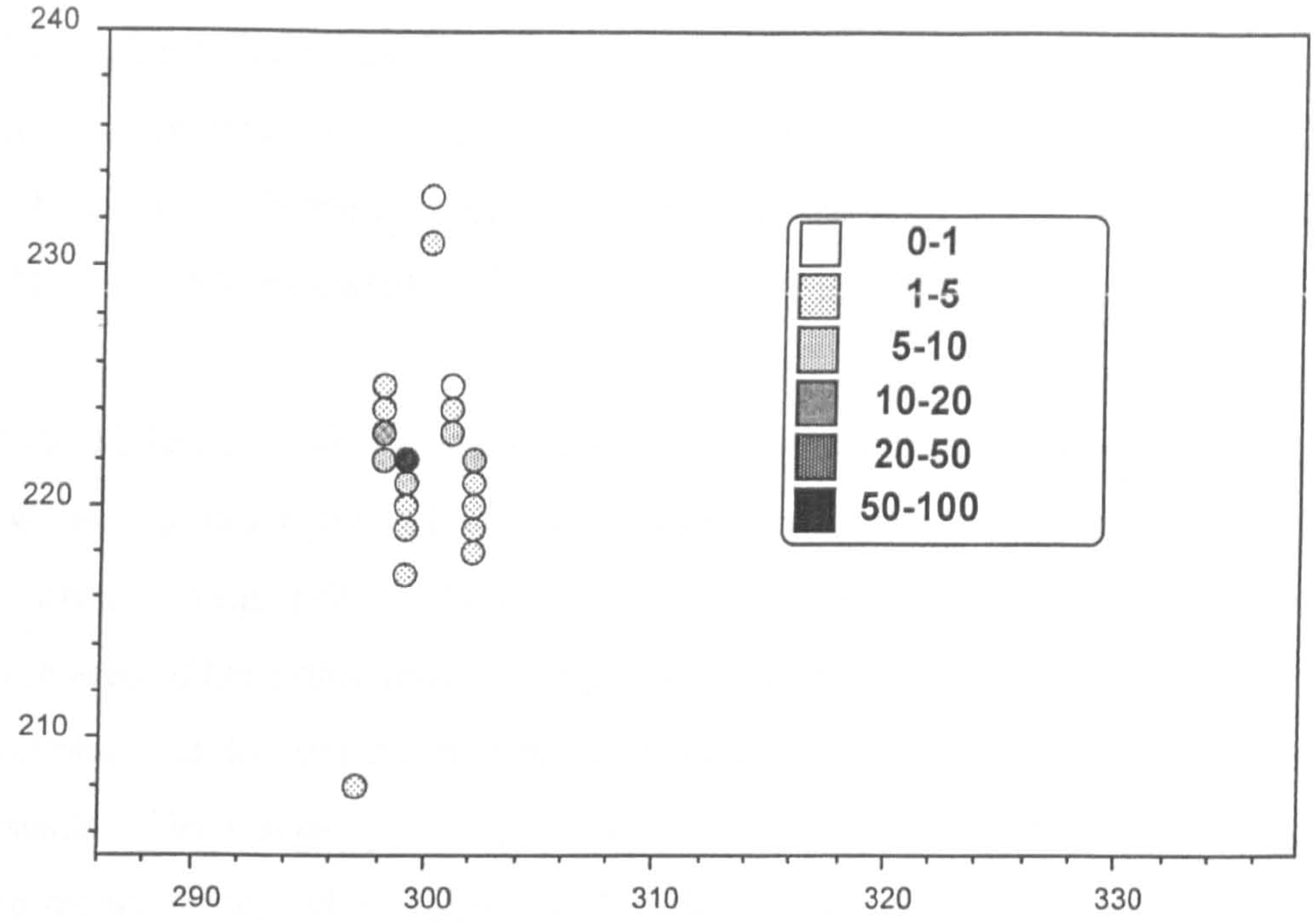

Figure 4.6 Grid Cell Plot (1m cells) for **Vole A♀ 6 November 1998** (N=179 fixes)

The majority of grid cell plots show the highest density of fixes at a single location, usually the nest site. It was noted that water voles would often move location underground, within a burrow system. Several nest chambers were identified within close proximity to each other, although as locations were only identified to 1m accuracy this observation is not seen on the grid cell plots.

A♀ (6 November 1998 and 10 December 1998) visited most locations within its home range on more than one occasion, however the majority of activity was centred on the nest site. B♀'s (6 November 1998 and 10 December 1998) activity was also centred around its nest site although in general the grid cell plot indicates that the majority of the home range was regularly used. The grid cell plot for C♀ also indicates that most activity was centre on the nest site. However, a moderate density of fixes is also shown on the opposite bank.

For E♂ 12 January 2000, activity was centred on the nest site with the remainder of the home range being little used. In the 15 February 2000 session, the majority of fixes were located in the nest site, however other areas of the home range were regularly visited. Plots for 1 March 2000 show a distribution of fixes throughout the apparent home range, with no nest site identified. In the 21 March 2000 session, E♂ ranged widely over his home range with a nest site in the centre. Fixes for E♂ in the 15 April 2000 session were distributed relatively evenly across the home range.

In the 12 January 2000 session, fixes for F♂ were centred on the nest site with only a few visits to other parts of the home range. By 18 January 2000, F♂ ranged more widely and frequently over the home range. Whilst retaining a nest site, G♀ used a large area of her home range throughout all radio-tracking sessions although short excursions up to 40m downstream were seen in the 21 March 2000 and 15 April 2000 sessions. H♂'s activity generally concentrated around a nest site, however, more than one fix was recorded at majority of locations within the large home range.

In the 16 and 23 November 1999 sessions, the plots indicate that D♂ had several areas within the home range where activity was concentrated, with few excursions. D♂'s activity was centred on the nest site with only brief excursions beyond this area. EM♀ activity was generally centred on the nest site, although she also spent time some distance from the nest site, ranging widely around the periphery of her home range. In the 16 February session, the plots indicate that fixes for J♂ were concentrated in a small area. In fact in this session J♂ did not move above ground. In the 22 February 2000 session, J♂ ranged widely although a large number of fixes were recorded at the nest site. K♂ also ranged widely using with several areas of high activity. In the 6 March 2000 session, K♂ had two nest sites at either end of his home range.

Fixes for L♂ were distributed across his home range, with a nest site identified in the 22 February 2000 session. A single fix was obtained at the end of the 6 March session some 500m from the original home range. L♂ subsequently remained in this location and was occasionally observed here for a further three weeks after the transmitter had ceased to function.

The plots show fixes for FR♂ centre around a nest site. In fact, this animal did not leave his burrow system during either the 16 or 22 November 1999 sessions. HE♀'s activity was centred on a nest site in both the 16 November 1999 and 22 November

1999 sessions, although a number of single fixes were obtained at distant points within the home range. All of the fixes for I♂ were located within his burrow system. The plots for MO♂ show fixes concentrated at a few scattered points within the home range.

Whilst no specific nest site was identified for N♂ during the 20 August 2000 or 9 September sessions, activity was concentrated in one area with occasional single fixes further a field. In the 2 September 2000 session a nest site was identified and fixes were concentrated within the vicinity. Nest sites were identified for O♀, however, fixes were distributed relatively evenly throughout the home range in both the 20 August 2000 and 9 September sessions. Fixes for Q♀ were concentrated around a nest site with occasional forays up to 20m away.

4.3.3 Movement

Wildtrak was used to calculate movement parameters for each water vole during each session. Parameters calculated comprised the minimum distance moved and the mean speed using all fixes and using moving fixes only. The results are presented as tables in Appendix 4. An example of one of these tables is provided as Table 4.2.

Table 4.2 Distance and speed parameters for **Vole A♀** based on fixes out of the nest site

Date	Minimum distance moved (m)	Mean speed (all fixes; m/min)	Mean speed (moving fixes; m/min)	Fixes (all)	Fixes (moving)	Percentage moving fixes
06/11/98	89	0.155	0.311	38	19	50
07/11/98	98	0.081	0.176	82	38	46
08/11/98	38	0.048	0.106	42	17	40
Mean (±SD)	75	0.087 (±0.068)	0.187 (±0.099)	162	74	46
10/12/98	172	0.122	0.28	78	27	35
11/12/98	178	0.126	0.269	82	32	39
12/12/98	82	0.062	0.289	90	20	22
13/12/98	33	0.105	0.367	22	7	32
Mean (±SD)	116	0.104 (±0.101)	0.282 (±0.166)	272	86	32

The smallest minimum distance moved was for I♂ on 14 December 1999 (17m), however this calculation only used 11 fixes. The mean minimum distances moved were therefore examined. The smallest mean minimum distance moved was for H♂ during the 1 March 2000 session (58m). The largest mean minimum distance moved was for L♂ (762m) during the 6 March 2000 session.

A Spearman Rank correlation was used to examine the relationship between the mean distances moved and home range area and length. A positive correlation of 0.617 (d.f.=49, $P \leq 0.01$) was found between mean distance moved and home range area. A positive correlation of 0.446 (d.f.=49, $P \leq 0.05$) was found between mean distance moved and home range length.

In all cases the mean speed of movement, based on all fixes, was below 0.6m/min. The mean speed of movement based on moving fixes ranged from 0.106m/min (A♀ 8 November 1998) to 2.715m/min (MO♂ 7 March 2000).

For those water voles tracked in November and December (1998 or 1999; A♀, B♀, D♂, EM♀, FR♂, I♂ and HE♀) the percentage of moving fixes generally decreased over time. For all other voles the percentage of moving fixes remained relatively constant (*e.g.* N♂ and O♀) or increased slightly (*e.g.* HE♀). The highest percentage of moving fixes was recorded for N♂ (20 August 2000; 69) and B♀ (6 November 1998; 69). The lowest percentage of moving fixes was recorded for E♂ (12 March 2000; 15).

4.3.4 Activity patterns

Activity codes were plotted against time to examine the data for trends in activity. These graphs are not presented in this thesis due to their large number and size, however Figure 4.7 presents an example of the graphs used to examine the data. No trends in the time of activity (activity code 1 or 2) or inactivity (activity code 0) were observed either within the data for each water vole or between water voles. The graphs suggested that activity generally occurred in discrete periods followed by a period of rest. These active periods were usually between 1.5hrs and 4hrs with maximum of 7.75hs (L♂ 6 March 2003). Rest periods between the active periods varied from 0.5hrs to 4.5hrs.

To examine the data for differences in activity between day and night, the percentages of daytime and nighttime fixes with each activity code were calculated for each water vole and each radio-tracking session. Table 4.3 presents the results of this analysis.

No trends were observed in the data and the percentages of fixes appear to be relatively between different voles and over time.

To examine the data for differences in the percentages of fixes for each activity between day and night, the data were converted to proportions and a Mann Whitney U test used.

For activity code 0 there is a significant difference in the proportion of fixes between day (Median = 51.95, IQ = 15.43) and night (Median = 45.91, IQ = 15.37) (U = 838.00, N = 50, P<0.01). For activity code 1 there is no significant difference in the proportions between day and night (U = 983.50, N = 50, NS). For activity code 2 there was no significant difference between day.

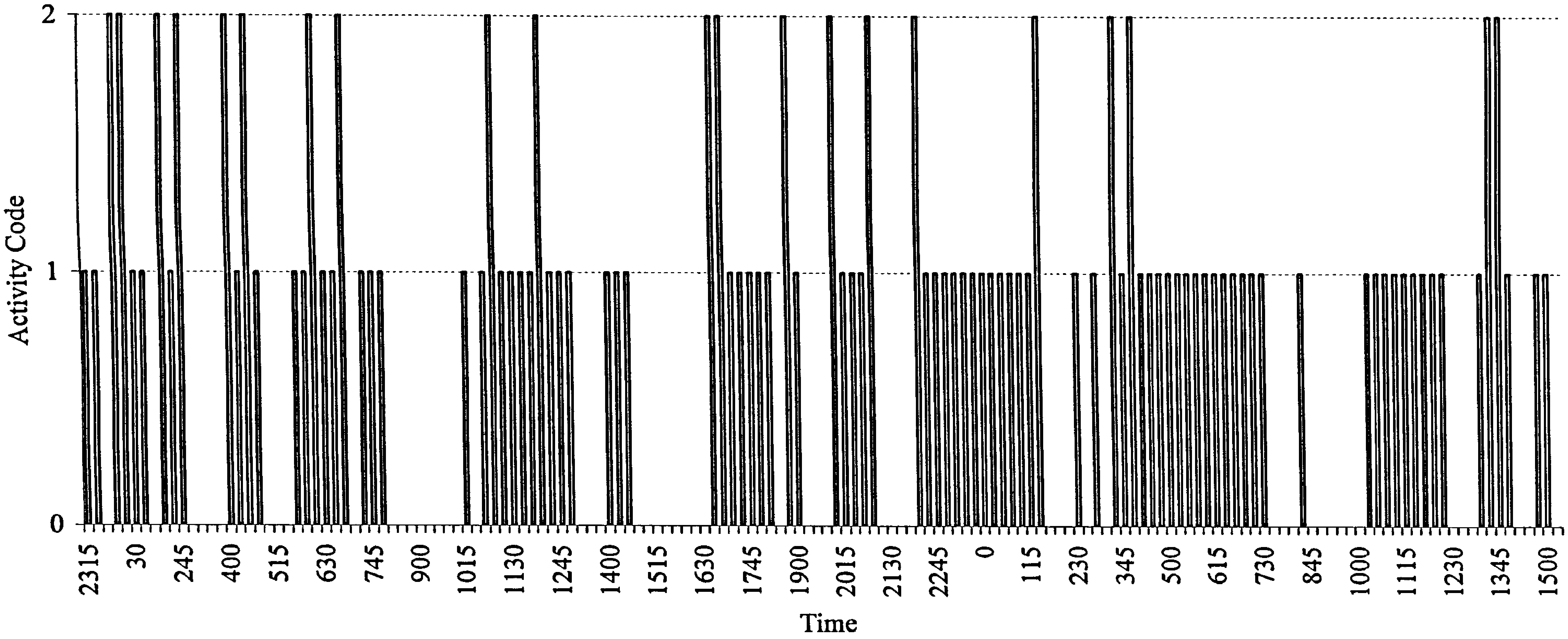

Figure 4.7 Activity codes plotted against time for water vole D♂ during 23 November 1999 radio-tracking session (Activity code 0 = inactive, activity code 1 = active but remaining in same location, activity code 2 = active moving)

Table 4.3 Percentage of fixes for each activity code grouped by night and day as determined by sunset and sunrise times (Activity code 0 = inactive, activity code 1 = active but remaining in same location, activity code 2 = active moving)

Vole	Session	Day			Night		
		0	1	2	0	1	2
A♀	06 November 1999	59.70	29.85	10.45	45.54	44.64	9.82
	10 December 1999	50.00	45.56	4.44	57.68	36.10	6.22
B♀	06 November 1999	65.52	24.14	10.34	46.28	40.50	13.22
	10 December 1999	47.37	47.37	5.26	50.00	42.35	7.65
C♀	01 November 1999	100.00	0.00	0.00	48.65	37.84	13.51
D♂	16 November 1999	60.53	31.58	7.89	34.48	41.38	24.14
	23 November 1999	50.70	43.97	5.63	25.58	54.65	19.77
	30 November 1999	66.67	30.30	3.03	39.68	53.97	6.35
E♂	12 January 2000	51.06	44.68	4.76	46.39	41.24	12.37
	15 February 2000	56.25	43.75	0.00	42.86	53.25	3.90
	01 March 2000	57.14	33.93	8.93	47.27	43.64	9.09
	11 March 2000	70.45	29.55	0.00	67.31	30.77	1.92
	21 March 2000	43.18	51.14	5.68	40.38	53.85	5.77
	15 April 2000	46.15	51.92	1.92	27.27	63.64	9.09
EM♀	16 November 1999	48.48	27.27	18.18	43.10	34.48	22.41
	22 November 1999	57.53	27.40	15.07	37.50	45.45	17.05
	30 November 1999	58.97	23.08	17.95	40.35	38.60	21.05
F♂	12 January 2000	20.00	80.00	0.00	45.45	45.45	9.09
	18 January 2000	40.63	46.88	12.50	40.63	50.00	9.38
FR♂	16 November 1999	61.22	22.45	16.33	76.60	21.28	2.13
	22 November 1999	46.48	43.66	9.86	67.78	24.44	7.78
G♀	16 February 2000	44.74	44.74	10.53	72.41	17.24	10.34
	01 March 2000	45.45	52.27	2.27	48.08	48.08	3.85
	11 March 2000	65.91	50.00	6.82	64.71	35.29	0.00
	15 April 2000	50.00	50.00	0.00	32.56	65.12	2.33
H♂	16 February 2000	54.29	45.71	0.00	54.90	27.45	17.65
	01 March 2000	43.62	51.60	4.79	45.02	52.13	2.84
	11 March 2000	50.26	49.74	0.00	40.38	53.85	0.00
	21 March 2000	40.00	55.00	5.00	52.36	45.25	2.39
	15 April 2000	34.62	57.69	7.69	38.64	56.82	4.55
HE♀	16 November 1999	57.89	42.11	0.00	51.72	29.31	18.97
	22 November 1999	77.46	15.49	7.04	60.67	28.09	11.24
I♂	14 December 1999	42.11	57.89	0.00	55.17	34.48	10.34
	16 November 1999	57.89	26.32	15.79	74.14	20.69	5.17
	22 November 1999	46.48	43.66	9.86	67.78	24.44	7.78
J♂	16 February 2000	65.00	15.00	20.00			
	22 February 2000	56.86	35.29	7.84	42.62	44.26	13.11
K♂	16 February 2000	70.00	30.00	0.00			
	22 February 2000	50.00	34.62	15.38	20.00	66.67	13.33
	06 March 2000	46.67	28.33	8.33	38.10	44.05	17.86
L♂m	22 February 2000	52.83	39.62	7.55	50.00	32.76	17.24
	06 March 2000	29.55	61.36	9.09	34.09	47.73	11.36
MO♂	22 February 2000	84.62	15.38	0.00	48.33	45.00	6.67
	06 March 2000	71.19	28.81	0.00	48.24	43.53	8.24

Vole	**Session**	**Day**			**Night**		
		0	**1**	**2**	**0**	**1**	**2**
N♂	02 September 2000	57.41	33.33	9.26	59.52	35.71	4.76
	09 September 2000	33.33	55.56	11.11	21.43	73.81	4.76
	20 August 2000	59.68	38.71	1.61	35.29	58.82	5.88
O♀	19 August 2000	61.29	32.26	6.45	44.12	50.00	5.88
	02 September 2000	42.59	46.30	11.11	50.00	42.86	7.14
Q♀	09 September 2000	35.19	57.41	7.41	16.67	78.57	4.76

4.3.5 Static interactions

Wildtrak was used to examine the data for static interactions between water voles with adjacent home ranges. Analysis was undertaken on the data for EM♀ and D♂ for 16, 23 and 30 November 1999; G♀ and H♂ 16 February 2000, 1, 11 and 21 March 2000 and 15 April 2000; N♂ and O♀ 19/20 August 2000 and 2 September 2000; N♂ and Q♀ 9 September 2000; and K♂ and J♂ 22 February 2000. The results are presented in Appendix 5, with a summary provided as Table 4.4.

Table 4.4 Static interaction analysis for all simultaneously radio-tracked pairs of water voles with adjacent home ranges

Vole	Fixes used	Fixes total	Range cells	Overlap cells	% range shared
Vole EM♀ 16 Nov 99	91	91	10	3	30
Vole D♂ 16 Nov 99	96	96	10	3	30
Both			17	3	17.6
Vole D♂ 23 Nov 99	157	157	24	9	37.5
Vole EM♀ 23 Nov 99	161	161	26	9	34.6
Both			41	9	22
Vole D♂ 30 Nov 99	96	96	16	8	50
Vole EM♀ 30 Nov 99	96	96	23	8	34.8
Both			31	8	25.8
Vole G♀ 16 Feb 00	96	96	15	1	6.7
Vole H♂ 16 Feb 00	86	86	11	1	9.1
Both			25	1	4
Vole G♀ 1 Mar 00	96	96	10	0	0
Vole H♂ 1 Mar 00	111	111	12	0	0
Both			22	0	0
Vole G♀ 11 Mar 00	95	95	14	2	14.3
Vole H♂ 11 Mar 00	96	96	18	2	11.1
Both			30	2	6.7
Vole G♀ 21 Mar 00	190	190	17	7	41.2
Vole H♂ 21 Mar 00	192	192	55	7	12.7
Both			65	7	10.8
Vole G♀ 15 Apr 00	95	95	20	6	30
Vole H♂ 15 Apr 00	96	96	26	6	23.1
Both			40	6	15
Vole N♂ 20 Aug 00	96	96	32	8	25
Vole O♀ 19 Aug 00	96	96	38	8	21.1
Both			62	8	12.9
Vole N♂ 2 Sep 00	96	96	20	9	45
Vole O♀ 2 Sep 00	96	96	23	9	39.1
Both			34	9	26.5
Vole N♀ 9 Sep 00	63	96	10	0	0
Vole Q♀ 9 Sep 00	96	96	22	0	0
Both			32	0	0
Vole K♂ 22 Feb 00	112	112	22	8	36.4
Vole J♂ 22 Feb 00	112	112	21	8	38.1
Both			35	8	25.8

With the exception of G♀ and H♂ 1 March 2000 and N♂ and Q♀ 9 September 2000, all pairs analysed shared grid cells. It is noticeable that all pairs, with the exception of J♂ and K♂, are male and female not single sex.

4.3.6 Dynamic interactions

The data were examined for dynamic interactions between water voles. The analysis used the pairs of animals with overlapping home ranges as identified in the static interaction analysis (Section 4.3.4). The results are presented in Appendix 6 with an example provided as Table 4.5.

Table 4.5 Dynamic interaction analysis between **Vole D♂ and Vole EM♀ 16 November 1999.** The proportion of paired (observed) fixes plus unpaired (expected) fixes at given separation increments. Probabilities that the excess or deficit of pair fixes may result from random variation are obtained from the 2-tailed binomial distribution.

Pair: Vole D♂ 16 Nov 99 Vole EM♀16 Nov 99				
Separation(m)	**Observed**	**Expected**	**Difference**	**P**
19-20	0	0.0024	-0.0024	1
18-19	0	0.0097	-0.0097	1
17-18	0	0.0091	-0.0091	1
16-17	0.033	0.0161	0.0169	0.1805
15-16	0.033	0.0116	0.0214	0.0896
14-15	0	0.0002	-0.0002	1
13-14	0.0659	0.1508	-0.0849	0.019
12-13	0.022	0.085	-0.063	0.0235
11-12	0	0.0338	-0.0338	1
10-11	0.0879	0.0372	0.0507	0.0202
9-10	0	0.0077	-0.0077	1
8-9	0	0.0059	-0.0059	1
7-8	0	0.0117	-0.0117	1
6-7	0.022	0.0086	0.0134	0.1838
5-6	0	0.0023	-0.0023	1
4-5	0.011	0.01	0.001	0.6002
3-4	0	0.0035	-0.0035	1
2-3	0	0.0016	-0.0016	1
1-2	0	0.0174	-0.0174	1
0-1	0.0989	0.2314	-0.1325	0.0017
0	0.5604	0.2773	0.2832	0
	<= 1 m.	> 1 m.	Totals	
Paired	60	31	91	
Unpaired	4152	4038	8190	
Totals	4212	4069	8281	

The results can be interpreted in terms of mutual attraction or repulsion. From the example in Table 4.4, D♂ and EM♀ showed an attraction to each other at 0m (P=0) and 10-11m ($P<0.05$). At 0-1m ($P<0.01$), 12-13m ($P<0.05$) and 13-14m ($P<0.05$) the animals were repelled. Given the relatively small home range sizes of water voles only the interactions at 0 and 0-1m are considered to be valid in relation to water vole behaviour. It is likely that the other significant interactions are due to the small sample size (Todd, 1993). In the 23 November 1999 session, D♂ and EM♀ showed an attraction at 0m (P=0) and 6-7m ($P<0.05$) and repulsion at 14-15m ($P<0.001$). In the 30 November 1999 session these two individuals showed an attraction at 0m ($P<0.05$).

In the 16 February 2000 session, G♀ and H♂ showed an attraction at 5-6m ($P<0.01$). No significant interactions were observed in the 1 or 21 March 2000 sessions. In the 11 March 2000 session these two individuals showed repulsion at 0m ($P<0.05$) and an attraction at 13-14m ($P<0.001$) and 16-17m ($P<0.001$). H♂ and G♀ showed an attraction at 8-9m ($P<0.01$) and 10-11m ($P<0.05$) in the 15 April 2000 sessions.

During the 20 August 2000 session, N♂ and O♀ showed an attraction at 13-14m ($P<0.01$). An attraction was also shown in the 2 September session at 0-1m (P=0) and 18-19m ($P<0.05$). No significant interactions were observed in the September session.

4.3.6 Autocorrelation

Autocorrelation analysis was undertaken using Wildtrak. The analysis used a minimum separation interval of 15 minutes (the time between each fix) and a maximum of 600 minutes. Wildtrack calculates the Schoener index. Figures 4.8 and 4.9 illustrate examples of plots of the Schoener Index against time (inter-fix interval) for two different water voles during two different radio-tracking sessions. The minimum time interval where fixes may be considered to be independent is the smallest interval with a Schoener's Index not significantly less than 2 and followed by at least two intervals also not significantly less than 2. In the example shown in Figure 4.8, the minimum time interval where fixes are considered independent is 100 minutes, however, in the example shown in Figure 4.9 the time interval is 435 minutes.

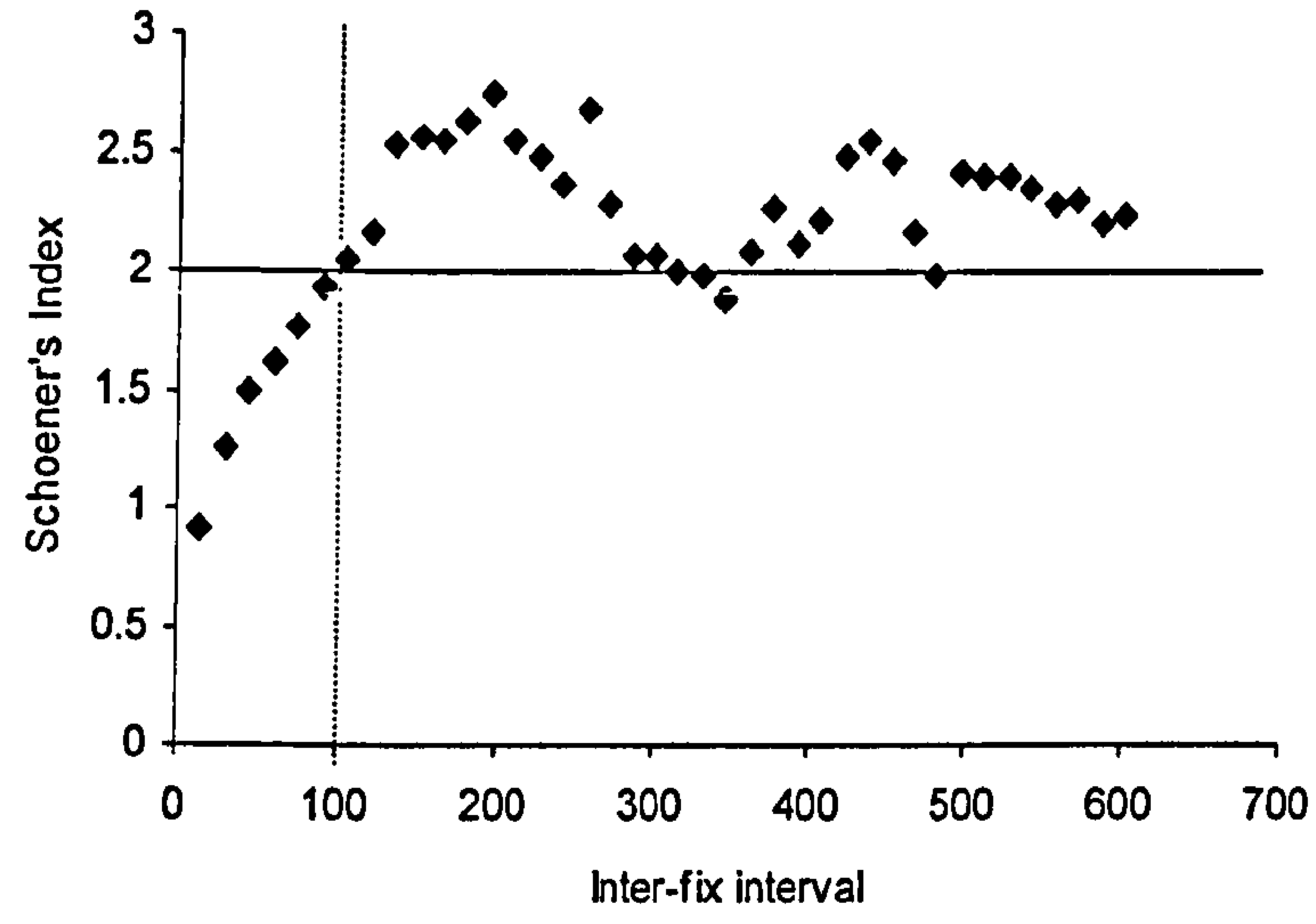

Figure 4.8 Plot of Schoener's index against inter-fix interval for vole Q♀ 9 September 2000. Vertical broken line indicates the minimum time interval where fixes may be considered independent.

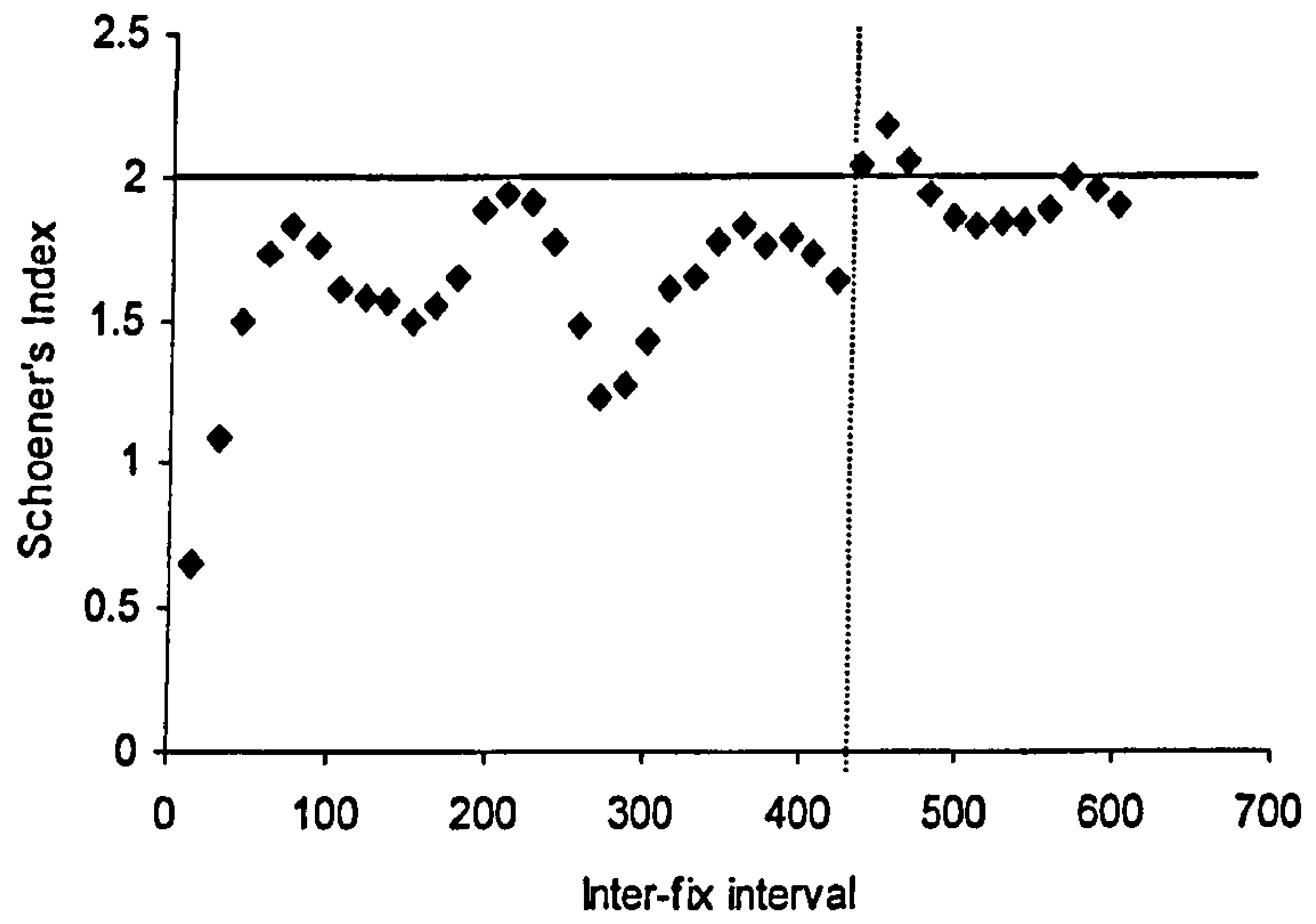

Figure 4.9 Plot of Schoener's index against inter-fix interval for vole A♀ 6 November 1998. Vertical broken line indicates the minimum time interval where fixes may be considered independent.

4.3.7 Summary

MCPs were plotted for each vole in each radio-tracking session. MCPs were used to calculate home range size (m^2) and range length (m). Home range size varied from between $2m^2$ and $427m^2$ whilst range length varied from 7m to 230m.

Two water voles, both male, changed their home range location in March 2000, with one male relocating on two occasions within this period. The majority of vole undertook extensions and contractions in home range during the course of the study.

One transmitter was found in a fox scat suggesting predation, whilst another was found some 300m from its origin with no corpse present. A third transmitter was found attached to the decomposing corpse of a water vole in a burrow approximately 500m from its previously known home range.

Grid cell plots were created for all water voles in all sessions. In the majority of cases activity was centred on a nest site. The remainder of the home ranges were used to a greater or lesser extent.

The minimum distance moved by each water vole during each 24hr period was calculated. The smallest distance moved was 17m and the largest was 762m. The speed of movement, using all fixes, was below 0.6m/min in all cases. The speed of movement calculated on moving fixes ranged from 0.106m/min to 2.715m/min. For voles tracked in November and December the percentage of moving fixes generally decreased over time.

The data were examined for activity patterns. The results suggest that activity generally occurred in discrete periods of 1.5 to 4hrs followed by a period of inactivity (0.5 to 4.5hrs). A significant difference between the percentage of inactive fixes during the day and night was identified.

Static interaction analysis was performed on all water voles that were tracked simultaneously with adjacent home ranges. All pairs of individuals with overlapping home ranges comprised a male and a female. Overlap varied from 6.7% of the individuals' home range to 50%.

Pairs of voles were examined for evidence of dynamic interactions. Two pairs showed an attraction to each other at a separation distance of 0m. One pair showed an attraction at 0-1m and another pair showed repulsion at 0-1m.

Autocorrelation analysis revealed that there a range of minimum time intervals where fixes may be considered to be independent for different water voles during different radio-tracking sessions.

4.4 DISCUSSION

A total of 19 water voles were radio-tracked as part of the current study the majority of which were adult males (12). The aim of the study was to examine overwinter behaviour. Due to time constraints and the difficulty of intensive radio-tracking during cold conditions some session were undertaken in August and September and some also continued into March and April.

4.4.1 Home range

Based on Minimum Convex Polygons (MCP) the home ranges in the current study varied from $2m^2$ to $7488m^2$. Home range length of those animals tracked on ditches varied from 7m to 230m. The highest estimates of home range were obtained when water voles undertook movements possibly to look for new home ranges, potentially confounding the estimates of home range size. Fixes obtained during these movements were not excluded from the calculations of home range as in all cases the animals returned to their original location during the session, making determination of the actual home range boundary impossible, however the use of 95% MCPs will have limited this to cases where individuals made prolonged excursions from their home range. Movements are discussed in detail in Section 4.4.2.

Overall there was no significant difference in the size of male and female home range areas. This is contradictory to some studies, based on range length, which have reported males to have larger home ranges than females (*e.g.* Leuze, 1976) however it is supported by Barreto and Macdonald (2000) who found males and females to have similar home ranges and Woodall (1977) who found that males and females have similar ranges during September to May. However, all of the studies mentioned above used range home length as opposed to area. Analysis of home range lengths for water voles tracked on ditches in the current study revealed a significant difference between males and females with mean range lengths of 60m and 27m respectively. This indicated that males have longer home range than females as supported by a number of other studies (*e.g.* Leuze, 1976; Woodroffe 1988). Efford (1985) reported males as having home ranges 2.5 times larger than females during the breeding season. A similar relationship for males and females is suggested in the current study, albeit during winter.

On Pond 2 vole EM♀'s home range size increased from 16 November 1999 to 14 December 1999. A similar increase was also seen for HE♀ on Pond 1 between 16 and 22 November 1999, although this appears to be driven by occasional excursions. This is in contrast to the decrease seen for water voles on ditches and reported in the literature. The increase in home range size for EM♀ was associated with a change in home range. The large increase in home range size may therefore have been due to exploratory behaviour, with the home range size subsequently decreasing and stabilising if EM♀ had continued to be radio tracked. The shift in home range may have been due to competitive exclusion by another water vole, disturbance associated with observers or an attempt to locate further food sources.

There was no significant difference in home range sizes of water voles on ponds and ditches. However, a great deal of variation was seen between individuals. It is likely that home range size is dependent on a number of factors including the density of water voles and the abundance of food. Additionally, the method of home range size estimation has limitations which can account for variability. This is discussed in further detail later in this Chapter.

One of the disadvantages of MCPs as a method of estimating home ranges is that the home range estimate increases as the number of fixes increases until a certain point at which there should be no or minimal increase (refer to Section 4.2.3.1). A small sample size may therefore result in a biased home range estimate. However, in the current study there was no correlation between the number of fixes and the home range estimate ($r = 0.06$, NS). This was also found to be the case in a radio-tracking study of the giant kangaroo rat (*Dipodomys ingens*) in the USA (Braun, 1985). Another disadvantage of using MCPs is that polygon may include areas that are not within the animal's home range (refer to Section 4.2.3.1). In the current study, in some instances it is likely that this occurs and produces an overestimate of home range size.

In fossorial water voles overwintering in rough grassland, Jeppsson (1987) recorded home ranges of 15 to 53m^2 during September to April. In the current study the majority of home ranges were greater than 53m^2. It is perhaps not appropriate to compare home ranges of vole on a watercourse to fossorial voles, however, those water voles tracked on the ponds may provide a more suitable comparison. In the current study, mean home ranges of water voles from the ponds were 307m^2 for males and 445m^2 for females. The difference between the home ranges on the two studies may be due to the habits of fossorial water voles, which overwinter spending most of the time feeding on roots and rhizomes underground (Jeppsson, 1987). A population of water voles living in grass tussocks on a marsh were also studied by Jeppsson (1987) although not during the winter. Average males home ranges between May and August ranged from 1154m^2 to 1795m^2 and female home ranges 1644m^2 to 4104m^2. These home ranges are considerably larger than in the current study, possibly as the marshland voles were studied during the breeding season when home ranges are known to increase in size (Leuze, 1976).

Studies of home ranges of water voles living along watercourses tend to consider home range length as opposed to area. On a river in the UK, Barreto and Macdonald (2000) reported average male home range lengths of 64.5m to 550m and average female lengths of 62m to 163.3m during the summer, based on radio-tracking data. Radio-tracking of water voles on the River Itchen in the UK, revealed average range lengths of 22.26m for males and 30.23m for females during November to January (Jordan and Netherton, 1999). They also reported ranges to increase in late February or March at the onset of the breeding season, with average lengths during the period of February to April of 131.28m for males and 47.13m for females. The range lengths in the current study are smaller than those summer range lengths reported by Barreto and Macdonald (2000) and the spring home ranges reported by Jordan and Netherton (1999). The mean range lengths between November and January were 15m (N=5) for females and 31m (N=3) for males. This compares favourably with those ranges recorded by on the River Itchen although the in the current study males had longer home ranges than females. Differences between the two studies may be caused by different estimation techniques (the current study estimate range length based on MCP analysis and Jordan and Netherton (1999) used actual distances observed) and the low sample size in the current study. February to April mean range lengths were 47m (N=5) for females and 73m (N=12) for males. The mean female range length is very similar to that recorded on the River Itchen, however whist greater then the females the male home range length much smaller than recorded by Jordan and Netherton (1999). As previously discussed, differences in the two studies may result from different estimation techniques. In addition the study by Jordan and Netherton (1999) was undertaken on a river as opposed to a ditch and unlike the current study they did not report an instances of water voles utilising both banks. Therefore the actual area of bank used by water voles in the current study was consistently greater than on the River Itchen.

In the current study, mean range lengths showed an increase between January or February and April as seen by Jordan and Netherton (1999). These overall increases are primarily contributed by voles E♂, G♀ and H♂. Leuze (1976) and Efford (1985) also reported an increase in range size in during this period. It appears likely that the increase in home range length coincides with the beginning of the breeding season. In general home range length determined from live trapping studies tend to be larger than those from radio-tracking data. Pelikan and Holisova (1969) reported trapping based winter water vole observed range lengths of 500m for males and 80m for females on a narrow brook in the Czech Republic, well in excess of those recorded in here. In the current study, the Observed Range Length (ORL) was calculated from live-trapping data (Section 2.3.8; Chapter 2). For Aveley, the maximum mean ORL for females was 87.50m in May 2000 and 70m for males in July 2000 . During, the winter period, only the mean ORL of males could be calculated due to limited captures. This varied from 3m to 28m which, surprisingly, is broadly comparably with those obtained from radio-tracking data, adding weight to the accuracy of the estimates obtained using MCPs. In addition, plots of cumulative fixes against percentage home range (MCP) for each vole during each radio-tracking session, in general, indicated that sufficient fixes were taken to reliably estimate home range size. In a small number of samples, insufficient fixes may have been collected, however, in the absence of any other data, the MCPs produced at least provide an approximation of home range size for these samples.

When the data were examined for autocorrelation (Section 4.3.6), it was clear the data are strongly autocorrelated. Many statistical analyses require independence of fixes and therefore autocorrelated fixes are eliminated (Harris *et al*, 1990). However, in the current study this would result in a loss of a substantial proportion of the data, reducing the accuracy of the home range estimation. De Solla *et al* (1999) recommend that the number of observations be maximised for home range estimation even at the expense of autocorrelation. For the purpose of home range estimation in the current study, autocorrelated data were retained.

4.4.2 Utilisation of home range

Grid cell analysis was used to examine the utilisation of home ranges. In many cases the majority of activity was centred on one or two points, identified as nest sites. Jordan and Netherton (1999) and Ashby *et al* (1969) also report that winter activity tends to centre around one burrow system. In the current study, many fixes were located underground within 1m of the nest sites, indicating that the animals were moving within underground burrow systems. Strachan and Jefferies (1993) report a complex burrow system with several entrances and multiple nest chambers supporting the findings of the current study. They also describe water voles as spending the majority of time during January and February below ground feeding on stored food and rhizomes. Holisova (1970) found that roots and rhizomes occurred in the diet throughout the year but significantly increased in September. Muskrats are also known to increase their intake of rhizomes during autumn and winter (Campbell and MacArthur, 1998). The nest site or other centre of activity was often located within the middle of the home range. However, in some cases it is noticeable that the nest site was located on the extreme edge of the home range (*e.g* F♂ 12 and 18 January 2000; G♀ 11 March 2000). It is possible that, whilst not measured, in these cases the locations of water vole nest sites were limited by the suitability of the banks. It was noted that in some areas localised poaching of the banks by cattle had made them shallow and compacted, and therefore potentially unsuitable for a nest site.

The majority of the grid cell plots show the pattern described above, with the home range size being increased by relatively few fixes further away from the nest site. The fixes may relate to daily home range patrols, as described by Woodroffe (1988) or to forays during which the animal is investigating areas outside of its home range looking for food, a mate or a new home range. In some cases, most notable for E♂, G♀ and H♂, the estimated home range was influenced by these forays and subsequent movements of the home range. When an animal made such a home range move during a radio tracking session, it was not considered appropriate to estimate the size of the two home ranges separately. The reason for this being that during such a move, the individual would travel between the two home ranges using nest sites at both, thereby rendering it impossible to determine the boundaries of either home range. Home range moves and other movements are discussed further in Section 4.4.3.

The distribution of fixes for water voles within the ponds focussed primarily around the perimeters where vegetation was present. A notable exception was MO♂ during the 6 March 2000 session, when he established a nest site in the centre of the pond. This nest site was located in a small stand of sea club-rush. On further examination, no nesting material or burrow was present suggesting that this was a temporary nest site, possibly to facilitate foraging or because his previous nest site had been disturbed.

4.4.3 Movements and dispersal

A number of male water voles in the current study undertook movements to new home ranges (E♂, MO♂, L♂ and N♂). Female home ranges increased in size but, with the exception of EM♀, no movements to new home ranges were seen. E♂ initially extend his home range downstream (1 March 2000) whilst still using his previous nest site and then subsequently established a new home range on an adjacent ditch (11 March 2000) before moving upstream to a third home range. MO♂ moved from a home range along the margins of Pond 1 into the centre. At the end of the study L♂ moved across an area of tussocky grassland to a new ditch. Whilst not recorded, *adhoc* fixes suggested that L♂ remained in this location for several weeks. N♂ initially extended his home range before settling in a new home range downstream. Approximately 30% of fossorial water voles have been reported to leave their burrows at least once to settle in new location not more than 100m from their original site (Saucy, 1987). Efford (1985) found long distance dispersal movements to be more common in males and he also recorded a preference for downstream movements as seen in the current study. Barreto and Macdonald (2000) suggest that water voles tend to use a small sector of a larger home range for several days before switching to a new burrow. This may explain the movements of N♂ but not so for E♂ or L♂ who moved to completely new ditches.

Stoddart (1970a) describes long and short distance movements of water voles. He reported the long distance movement, away from the geographical confines of the population, of an adult female. It seems likely that the movements seen by E♂ and L♂ were similar in nature to this long distance movement. The long distance movements of E♂ and L♂ both occurred in the spring (March 2000) at the start of the breeding season. This suggests that these movements may have been an attempt to locate potential mates and establish breeding territories. Stoddart (1970a) also recorded short distance permanent or semi-permanent range shift movements of two male water voles. He described these as movements of home range within the geographical confines of the group due to sites becoming vacant by the death or emigration of the occupant. Whilst there is no evidence to support the death or emigration of previous occupants, it seems likely that the movement seen by MO♂ and N♂ were of a similar nature. Interestingly the home range shift by N♂ occurred at the end of the breeding season and therefore was unlikely to be associated with breeding behaviour, but perhaps provides further evidence that the move was due to the disappearance of a previous occupant.

The percentage of moving fixes was calculated for each water vole (Section 4.3.3). In this analysis the definition of a moving fix was a fix outside of the nest site where the location of the animal was different at successive time intervals. The percentage of moving fixes therefore relates to movements as opposed to being a measure of activity. For those voles radio-tracked in November and December the percentage of moving fixes decreased with time, suggesting that the water voles spent a greater amount of time in individual locations and undertook less short or long distance movements approaching winter. For water voles radio-tracked at other times of the year little or no change was seen in the percentage of moving fixes. However, both short and long distance movements during the spring have already been discussed. This suggests that, for water voles, the percentage of moving fixes does not provide a useful measure of actual movements.

The distances moved by individual water voles during each session were calculated. The mean daily minimum distance travelled within a session for males ranged from 16.10m to 761.69m. The lower distance was recorded for I♂ who remained within his burrow system for the duration of the session. The upper distance was recorded for E♂ during one of his long distance movements. The mean daily minimum distance travelled for females ranged from 74.91m to 279.48m. The lowest of these distances was recorded for A♀ during the 6 November 1998 session, whilst the highest was for G♀ during the 2 March 2000 session. A positive correlation was found between the mean distance travelled and home range area and length indicating that the distance travelled increases as the home range size increases. The only comparable published study, on a ditch in Russia, reported males as covering 100m to 1400m and females 20m to 300m during their active period (Rogov *et al*, 1992). These results are not dissimilar to the current study however they do not provide enough detail to enable discussion of the relevance of this.

4.4.4 Activity patterns

Analysis of activity codes failed to reveal any relationship between water vole activity and time of day. In contrast, observations of the activity of water voles in an outdoor enclosure in Sweden suggested that the majority of activity occurs during the day from November to May, with an increase in activity correlated with sunrise and a decrease with sunset (Lund, 1970). Gaisler and Zejda (1973) also report activity to be higher during the day and in the evening, based on live trapping data. Also using live trapping data, Stoddart (1969) reported a preference for diurnal activity. Knight (1975) used bait stations to record activity of water voles during the summer and found activity to be distributed throughout the day with peaks at dawn and dusk, and least activity at night. Observations by Ashby *et al* (1969) suggested the existence of a rhythm of activity throughout the day and night, with each period of activity consisting of up to four visits above ground and being followed by a an absence of an above ground siting for two or three hours. It is important to note that the published accounts of water vole activity have only considered above ground activity, whilst the current study did not discriminate between above and below ground activity. Jordan and Netherton (1999) report water voles spending an average of 71.5% of their time below ground in January and 40.5% in April. This supports anecdotal observations from the current study and would undoubtedly account for variation between the activity patterns in the published accounts and the current study. It is also important to recognise that different environmental factors may be influencing water voles at different sites, such as vegetation type and density, presence of predators or other disturbances including observer disturbance.

The data in the current study suggest that activity occurred within discrete blocks between 1.5hrs to 4hrs with rest periods between 0.5hrs and 4.5hrs. This may be similar to the rhythm observed by Ashby *et al* (1969). As water voles are herbivores, specialised in food with a high cellulose content, their activity may relate to their metabolism. Unfortunately, in the current study, it was not possible to record the behaviour that a water vole was performing at each of the fixes.
Although not measured in the current study, weather conditions appeared to have no effect on water vole activity. Gaisler and Zejda (1973) determined that above ground activity continued at temperatures around 0°C, during rain and wind of medium velocity. A study in Russia, reported higher water vole activity levels on warm cloudy nights than on dry clear nights (Nikolaev and Chertova, 1962) as seen in other small mammals (Gurnell and Flowerdew, 1995). They also found captures of water voles increased in wet periods and activity was seen to increase in windy conditions. It should be noted that the aforementioned study examined the behaviour of water voles in a ploughed field, which are likely to be adapted to living in more open conditions than then water voles in the current study.

4.4.5 Interactions

In the current study a number of static interactions were found between males and females, where individuals' home ranges overlapped. The analysis used grid cells as the basis for the overlap as opposed to MCPs, therefore the overlap more correctly refers to shared 1m grid cells rather that home range. With the exception of two male voles on Pond 2 (K♂ and J♂ 22 February 2000), no overlap was found between same sex individuals. It is possible that same sex non-radio-tracked individuals may have been present. Additionally, the small number of radio-tracked individuals limited the number of possible pairings of voles. However, the results suggest that individuals excluded same sex individuals from their home range. This is supported by the findings Jeppsson (1987) who found in marsh living water voles, male home ranges overlapped with females and that males always excluded other males from their home ranges, except when the number of females was very low. This has also been reported in fossorial water voles, where male home ranges overlapped the whole home ranges or one or more females, and that adult males and females defend their territory against same sex adults (Saucy, 1987). In addition, Leuze (1976) reported adult females to maintain exclusive home ranges throughout the year, however she also found that males ranges overlapped each other. Ashby *et al* (1969) also reported considerable overlap in male home ranges. It is worth noting that the studies discussed above all consider home range overlap during the breeding season. In the current study, the majority of radio-tracking took place outside of the breeding season. Jeppsson (1987) noted that few individuals overlapped outside of the breeding season, with most animals living a solitary existence

Saucy (1987) suggests that monogamy is the rule for fossorial water voles but that males are occasionally polygamous, whilst Jeppsson (1987) suggests that marsh living male and female water voles may both exhibit polygamy or monogamy. It may be that the mating system of water voles is more complex as seen in other rodents, for example, Townsend's voles (*Microtus townsendii*) exhibit territoriality and monogamy in the spring and subsequently have overlapping ranges and are polygamous in the summer (Lambin and Krebs, 1991). Marinelli and Messier (1993) found both male and female muskrats to be territorial with males overlapping one or more female home ranges, like water voles, with monogamy as the basic mating system although polygamy was common.

The social system of water voles is thought to be maintained by males' latrines. Leuze (1976) demonstrated that males established latrines at the ends of females' territories. By removing the latrines, females extended their territories and entered into aggressive interactions with their neighbours. In the current study, dynamic interactions between individuals were examined. Due to their small size, interactions between the movements of water voles at greater than 5m are not considered to be significant. It is likely that the interactions seen at distances of greater than 5m were due to the small sample size. Two pairs of water voles, showed an attraction for each other at 0m (D♂ and EM♀ 23 and 30 November 1999, N♂ and O♀ 2 September 2000). It is of note that these interactions occurred towards the end of the breeding season. One male and female showed a repulsion at 0m at the beginning of the breeding season (G♀ and H♂ 11 March 2000). No other significant interactions were observed or recorded. Leuze (1976) describes overt and ritual antagonism over home ranges between adult females in early spring, whilst Efford (1985) reports that females rarely behaved aggressively. Ashby *et al* (1969) did not observe any aggressive encounters between individuals and Jeppsson (1987) found that an individuals' movement was not affected by the movement of other individuals. No same sex interactions were observed in the current study. This may be in part due to the low number animals radio-tracked, particularly females, and also the study being outside of the breeding season. Efford (1985) reported that males and females did not share refuges either within or outside of the breeding season. In contrast the majority of the findings of this study and others, the MCPs show the home ranges for EM♀, during the two sessions in which she interacted with D♂, are larger and completely encompass the home ranges of D♂. Whilst no nest sites were recorded for D♂ or EM♀ during these two sessions, the grid cell analysis shows that they both frequently used one location. It cannot be determined whether this was a nest or feeding site or whether both animals were there at the same time, however the attraction seen at 0m suggests that they were together. Given the location of this point, on the edge of Pond 2, it seems likely that this was a nest site, a finding in contrast to Efford's study.

4.4.6 Mortality

Three of the tracked voles died during the study, two assumed to be through predation, probably by foxes, and one through an unknown cause. Fossorial water voles in Switzerland have been shown to be a major prey item for foxes (Weber and Aubry, 1993) and it is possible that water voles in the UK may be of local importance to some foxes. Foxes were observed hunting along the edges of watercourses in the current study and were observed to dig in the area of known water vole nest sites. It is considered unlikely that fitting radio-collars to individuals increased their risk of predation. A study in Finland showed that the mobility of collared voles (*Clethrionomys glareolus, Microtus agrestis* and *M. epiroticus*) was only affected on the first day of fitting and that collars did not increase the risk of predation from avian predators (Korpimäki *et al*, 1996). Leuze (1976 and 1980) studied the amount of aboveground activity of collared water voles before and after the attachment of transmitters. She found that activity was only reduced for 36 hours after attachment. The mortality in the current study, is more likely to be attributable to the overall high winter mortality rates recorded Jordan and Netherton (1999) and Carter and Bright (2003) of 74% and 64% respectively. Both studies found that predation by mustelids was the chief cause of mortality. In the current study, Weasel (*Mustela nivalis*) were observed to predate water voles in the study area, however, this was predominately during the summer months.

CHAPTER 5 GENERAL DISCUSSION

The current study used several different techniques, namely live-trapping, field sign counts and radio-tracking, to examine aspects of the ecology of water voles. Whilst each of these techniques provides important data on water vole ecology, there are many instances in which the results can be brought together to give a more coherent and robust analysis. This section aims to draw connections between the previous three chapters and discuss the significance of the results.

Chapter 2 presents the results of extensive live-trapping programmes undertaken at five sites in the south of England. Two of these sites, Bovington and Whitemead, suffered extinction during the study and therefore the trapping programme was curtailed. However, two of the sites, Aveley and Hilliers, were live-trapped for 24 months. Chapter 3 presents an analysis of latrines and their relationship with water vole numbers, which was undertaken at all five sites throughout the duration of the trapping programme. Chapter 4 presents the results of radio-tracking studies on water voles within the Aveley site and adjacent ponds.

5.1 THE ECOLOGY OF WATER VOLES IN DIFFERENT HABITATS

5.1.1 Populations and social structure

In Chapter 2, peaks and troughs were seen in the number of water voles captured, with a similar pattern seen at each of the sites. These were explained in terms of changes in the population size due to emigration, immigration, deaths and births. Few water voles were captured during the winter period at any site, suggesting a small overwinter populations. However, data from the radio-tracking study may provide further information on the behaviour of water voles, particularly in winter. Water voles were found to spend more time in individual locations approaching winter, thereby reducing the probability their being captured in the live-trapping programme. This may, in part, explain the decrease in numbers captured during the winter months. Additionally, during the radio-tracking study, observations suggest that at least some water voles spent a large proportion of time underground, thereby further reducing the chance of capture. However it is not considered that this would account for the particularly low numbers captured.

Dispersal movements from the individual's original home range were also observed, however, it seem probable that there would be an equal chance of animals moving into the study site as moving out, unless there was a net dispersal of animals from the site due to a deterioration in the quality of habitat. Deterioration in site quality undoubtedly occurred due to the natural loss of vegetation cover during the winter, and the additional pressures of poaching by cattle at Aveley. However, none of the water voles, that were observed dispersing, moved to areas that appeared substantially different in terms of vegetation cover. The fact that winter numbers decreased at all sites, including Hilliers where no alternative sites were nearby, suggests that this is not a likely cause of the decrease in numbers captured over winter.

The small overwinter population of water voles means that there may be a bottleneck effect. This appears to be overcome by the dispersal of adults prior to the breeding season. This was observed at Aveley, where water voles had a wide range of alternative sites (ditches). At Hilliers, the relative isolation of the watercourse may mean that dispersal has less of an effect. Although not studied using radio-tracking techniques, there appeared to be limited opportunities for dispersal of water voles, either to or from the site. At Hilliers, this isolation has been caused by humans through intensive agricultural practices. The long term future of Hilliers may therefore be limited. Such fragmentation of water vole populations has been observed at other sites and has been cited as one of the primary reasons for the national decline of water voles (Strachan and Jefferies, 1993). Stewart *et al* (1999) reported water voles in coastal sites mat be less influenced by gene flow than inland sites, due to greater isolation of the coastal populations.

A decline in numbers was seen at both Aveley and Hilliers over the course of the study. Reasons for this decline have already been discussed, such as the introduction of grazing at Aveley and the cutting of bankside vegetation at Hilliers. Many small mammal populations show dramatic variations in numbers between years, often linked to predator populations (*e.g.* Erlinge, 1974). Weber *et al* (2002) report seven year population cycles of water voles in mountainous habitats in Switzerland, with seven years between peaks in population size. Populations of two predators, long-eared owl (*Asio otus*) and polecat (*Mustela putorius*), were linked to annual changes in water vole numbers. Annual cycles in water vole populations in the UK have not been studied and in the absence of further data it is not possible to determine whether water voles at the sites in the current study are also subject to similar annual cycles. It is worth noting that in the three years following the study water vole populations appear to have declined even further (pers. obs.; Wells, pers. comm). Severe flooding of both sites, during the winter of 2000/1, appeared to have an immediate effect on numbers. At Hilliers, water voles were observed sheltering in areas of higher ground up to 200m from the watercourse, thereby rendering them more susceptible to predation. Continue poaching by cattle at Aveley, combined with the wet conditions, appeared to make the study ditch less suitable for water vole in the years following the study. These factors are highly likely to have influenced the continued decline of animals at both sites. Further study may reveal recovery of the populations or their extinction. In the case of Aveley, water voles were present in the majority of the ditches throughout the site, therefore recovery is likely to be aided by recruitment from other parts of the site. Conversely, the population at Hilliers is relatively isolated and therefore more susceptible to extinction. However, Telfer *et al* (2003) recorded dispersal through unsuitable habitat over several hundred metres, which can be important for the recolonisation of previously occupied sites. It is therefore possible, that were the Hilliers population to go extinct, dispersal from populations in neighbouring catchments may eventually result in the colonisation of the site.

Benge (1999) compared the density of water voles from a number of study sites, based on published data and data from the current study. The comparison revealed that the density of water voles recorded at Hilliers during August 1998 was higher than any other site. This high density may be, in part, due to the isolation of the site. However, all animals captured appeared to be in good condition, suggesting that the habitat (before the vegetation cut) could support this density of water voles. Whilst Hilliers is undoubtedly an important site for water voles, its' isolation from other populations suggest that it may not be viable in the long term. Conversely, Aveley is situated on a grazing marsh with an extensive ditch network and therefore isolation is not considered to be an issue. The densities recorded at Aveley and Rainham were also higher than at most other sites previously recorded. In response to this, the Inner Thames Marshes has been established a National Key Site for water vole, for which the management of the site will be closely monitored (Bright and Carter, 2000).

The live-trapping study showed that water voles were most active between 22:00h and 06:00h, suggesting a preference for night-time activity. Radio-tracking at Aveley revealed no relationship between time of day and activity. However, both the measure of activity and the timescales used in the two studies were markedly different. In addition, the traps may have had an effect on water vole behaviour; with animals possibly favouring investigating traps during the night time. It should be noted that radio-tracking was also only undertaken at one site and local environmental variables may influence activity patterns.

Home range lengths and areas were estimated from the radio-tracking data for Aveley, whilst Observed Range Lengths (ORL) were calculated from the live-trapping data. In both cases a great deal of variation was seen, although no obvious difference between sites was observed. The limitations of ORL based on live-trapping have previously been discussed (Chapter 2), as have those of home range estimation using radio-tracking (Chapter 4). The mean ORLs varied from zero to 87.50m for females, zero to 70m for males and 36.67m for juveniles. Mean home range lengths estimated using radio-tracking were 27.23m for females and 59.72m for males. It is of note that the mean radio-tracking home range lengths fall within the range of mean ORLs. This suggests that home ranges were likely to have been smaller over winter, as seen by previous authors (*e.g.* Leuze, 1976), when the radio-tracking measurements were taken.

Despite apparent differences in the habitats between the study sites, no obvious differences in populations and social structures were observed. However, it is noted that had radio-tracking taken place at sites other than Aveley, some differences may have been observed. Also, had study at Bovington and Whitemead sites not been affected by the extinction of the water vole populations, further comparisons could have been made.

5.2 THE USE OF LATRINES FOR ESTIMATING WATER VOLE NUMBERS

A relationship was observed between the number of latrines and the number of water voles captured. Generally, from the live-trapping and latrine count data, the number of latrines increased and decreased in relation to the number of animals captured. An absence of latrines was then seen during the winter months. The failure to produce latrines during winter has previously been considered to be due to the breakdown of territories (Strachan and Jefferies, 1993). However, in the radio-tracking study, no evidence of a breakdown in territories was seen. Generally, little overlap was observed between radio-tracked animals and whilst two animals shared the same burrow system, there were no other interactions between animals. It is possible that the radio-tracked water voles were simply interacting with other, un-tracked voles, however, the results do indicate that a breakdown of territories does not occur. A switch from aboveground activity to more activity centred on the burrow system and underground is likely to have an effect on the number of latrines observed.

In the current study, latrines were not divided into those that may have served as territory markers and those that may have been a result of consistent use of a feeding platform. Many of the latrines counted were associated with feeding remains suggesting that they may not have been territorial markers. This being the case, even if a breakdown in territories occurred, some latrines would still have remained and been counted over winter. During 1999 at Aveley and Rainham, latrines were observed over the winter period, suggesting that they were not territory markers but simply associated with feeding. It also perhaps more likely, that the absence of or decline in latrines is due to the described shift from aboveground activity to below ground activity.

It is possible that the scent marking on top of latrines, that has previously been recorded, only occurs during the breeding season. Therefore latrines themselves do not act as territorial markers, but rather those latrines that have been scent marked. As part of the current study, samples of secretions were taken from flank glands and analysed using gas chromatography. Unfortunately, no results were obtained due to a fault with the equipment, however, it was established that these secretions comprised relatively stable elements, which would persist over a long period and therefore have some benefit for scent marking.

Despite the confusion regarding the definition and function of water vole latrines, this study has shown a relationship between water vole numbers and latrines. Predictive equations obtained were similar to those previously obtained by Morris *et al* (1998). However, it must be noted that both studies could only look at the number of water voles captured and not the actual number present. Therefore, the equations obtained probably provide a useful guide to the scale of a population but should not be used to obtain a final number. Where it is necessary to obtain an reliable estimate of water vole numbers, such as where animals need to be relocated as part of mitigation works, live-trapping still provides the most accurate estimate.

5.3 OVERWINTERING BEHAVIOUR OF WATER VOLES IN A GRAZING MARSH SYSTEM

Conclusions on the overwintering behaviour of water voles are made difficult by the low number of captures and the small number of animals that is was possible to radio-track, due to a limited amount of equipment and time. A few conclusions can be made in relation to home range size and trappability. The results of this study suggest that home range may decrease into winter for a brief period before movements or extensions of home range occur leading into the breeding season. No appreciable differences in activity levels were observed. The most conclusive point is that overwinter there is a decline in numbers of water voles, however, it is likely that some of the decline seen may be attributed to a reduction in trappability, perhaps due to more time spent underground, as was anecdotally recorded for some animals and previously discussed. Additionally, it is interesting that latrine usage did not cease over the winter period, or if so only for a brief period. This suggests that in the study sites, either water voles maintained territories overwinter or latrines recorded overwinter were not territorial markers but by-products of favoured feeding locations.

Winter appears to be a key factor in the persistence of water vole populations. A high mortality rate results in a relatively small pool of breeding individuals at the start of the breeding season. Dispersal of water voles at this time is therefore essential to maintain the heterozygosity of the population. Fragmentation of populations, resulting in increased isolation, will inhibit dispersal leading to a loss of genetic diversity in these isolated populations. In addition, these populations will be more susceptible to extinction due to predation from American mink (*e.g* Barreto and MacDonald, 2000).

5.4 IMPLICATIONS OF THE STUDY

The current study employed a range of methods to examine aspects of water vole ecology. The study emphasises the qualities and disadvantages of the methods for different purposes. Live-trapping is undoubtedly the best method for studying and monitoring water vole populations. Ear tagging as a method of marking water voles proved to be unreliable and it is therefore recommended that for future studies either fur clipping or PIT (Passive Integrated Transponders) be used, although these also have disadvantages in terms of longevity and cost respectively. Latrines provide a useful guide to population size, however, despite the findings of the current study and the work by Woodroffe *et al* (199ob), the accuracy of the method cannot be confirmed. The relationship between the two is likely to be dependent on site and environmental variables, and on the definition of a latrine. Few latrines were found at Bovington or Whitemead and it is hypothesised that this is either due to the presence of mink or a non-breeding population. Either way, this provides another variable that may render latrine counts ineffective. Radio-tracking was shown to provide the most useful means of studying water vole home ranges, activity and interactions. However, this is time consuming and expensive, and therefore is unlikely to be appropriate for general monitoring of populations.

Management regimes at the study sites vary from cattle and sheep grazing, bankside vegetation cutting and non-intervention. Cattle were seen to influence the population of water voles at Aveley; the introduction of cattle grazing to the site having a deleterious effect on the population. Poaching of the banks and removal of marginal vegetation are considered to have contributed to making the habitat less suitable for water voles. It is not possible to determine whether sheep grazing at Bovington and Whitemead had an impact on the water vole population as it was in the process of extinction by American mink at the start of the study. However, it is possible that a reduction in bankside vegetation by grazing can increase the ability of American mink to predate water voles. Bankside vegetation cutting at Hilliers also appeared to have a deleterious effect on the water vole population, particularly during the first year of the study. However, it is recognised that, in the absence of either grazing or cutting, bank would become dominated by scrub and become sub-optimal for water voles.

5.5 FURTHER WORK

The current study contributes to and furthers the existing knowledge of water vole ecology. Live-trapping studies of water voles are common in the literature although few are as intensive and long-term as the current study. In order to obtain a better understanding of water vole populations, and possibly their cycles as seen in fossorial water voles, further long-term studies are required. Long-term monitoring of populations over several years may help to provide an understanding of the current rapid decline of the species.

Fragmentation of populations appears to occur relatively often in southern England, in many cases due to changes in agricultural practices and development of semi-natural areas. Further studies on dispersal and metapopulations in these areas to determine the effect that this fragmentation has on water vole populations. In the meantime efforts should be made to prevent further fragmentation by appropriate management and protection of watercourses. The reversal of fragmentation by restoring watercourses and the terrestrial links between them could also have great benefits for populations. Methods of accommodating this reversal within the existing landscape will need to be looked at through both agricultural subsidies and the planning process. Further protection of the water vole through the Wildlife and Countryside Act 1981 (as amended), is currently being considered (Mitchell-Jones pers. comm.) and if implemented should help to further raise the profile of water vole requirements.

In the current study, radio-tracking was limited to a few individuals and was predominately undertaken overwinter. Further work to establish the importance of the winter period for water vole populations is required. Many management operations on watercourses occur in autumn or winter, and therefore may have a substantial impact on the proportion of water voles entering the breeding season. In addition, further work to record their behaviour throughout the year, and in particular their dispersal movements may provide valuable information that would aid conservation and mitigation strategies for water voles. The effectiveness of standard mitigation techniques, such as the displacement of water voles through vegetation cutting and translocation , needs to be examined through further scientific study. The use of radio-tracking techniques is essential to understanding the effect of such mitigation measures on individual animals and populations.

It is not considered a priority to re-examine the relationship between latrines and water vole numbers, as this study demonstrated that although it may provide a useful indication it is fraught with problems. Provided that latrines are only used as a means of estimating the scale of a population as opposed to the numbers in a population, it is a useful technique, and one that can be employed in large scale surveys, such as a national or regional survey.

The current study focussed, to an extent, on water voles within a grazing marsh system (*i.e.* Aveley and Rainham). The results of this study differed from previous research, which has tended to concentrate on river and stream systems. The population dynamics and possibly behaviour of grazing marsh water voles, where a network of interconnecting ditches is present, appear likely to be substantially different to those on rivers and streams. Although, it is recognised that similar studies were not conducted at Hilliers, Bovington or Whitemead. Intensive radio-tracking studies of water vole populations on rivers and streams, may provide valuable information on dispersal. With the rapid decline of the species these habitats, which have the potential to support large concentrations of water voles, are likely to become of greater importance to water vole conservation. Further research on the water voles and habitat management of grazing marshes is essential to ensure that these areas remain important water vole sites.

The long-term effectiveness of various management techniques in retaining and enhancing water vole populations should be monitored, specifically through live-trapping and radio-tracking techniques

APPENDICES

APPENDIX 1

Table A1.1 Number of individuals (*N*) in each month used in calculation of mean water vole weights

Month	**Aveley**			**Hilliers**			**Rainham**		
	Males	**Females**	**Juveniles**	**Males**	**Females**	**Juveniles**	**Males**	**Females**	**Juveniles**
Aug-98	8	16	27	10	34	12	1	3	1
Sep-98	11	18	21	6	15	0	0	4	18
Oct-98	3	6	2	6	6	0	2	4	5
Nov-98	0	0	1	0	0	0	0	0	0
Dec-98									
Jan-99									
Feb-99									
Mar-99	4	8	0	6	4		3	5	
Apr-99	4	6	0	5	4	6	3	3	6
May-99	5	8	0	4	7	22	5	1	10
Jun-99	3	4	0	10	12	23	6	3	2
Jul-99	3	1	0	15	15	18			
Aug-99	2	6	6	10	18	3			
Sep-99	4	4	6	6	11	0			
Oct-99	4	2	2	1	2	0			
Nov-99	0	0	0	0	0	0			
Dec-99	1	1	0	0	0	0			

Month	Aveley			Hilliers			Rainham		
	Males	**Females**	**Juveniles**	**Males**	**Females**	**Juveniles**	**Males**	**Females**	**Juveniles**
Jan-00	3	2	0	0	0	0			
Feb-00	3	0	0	0	0	0			
Mar-00	4	1	0	2	0	0			
Apr-00	3	1	0	3	4	0			
May-00	3	2	1	2	4				
Jun-00	1	2	3	1	4	8			
Jul-00	4	4	7	5	7	5			

APPENDIX 2

Minimum Convex Polygons

This appendix presents 95% Minimum Convex Polygons for each water vole during each radio-tracking session. The location of each fix is shown using the last three digits of a five digit Ordnance Survey Grid Reference. All water voles were located within Grid Reference TQ54, 79 (ditch) or TQ54, 80 (Pond 1 and Pond 2).

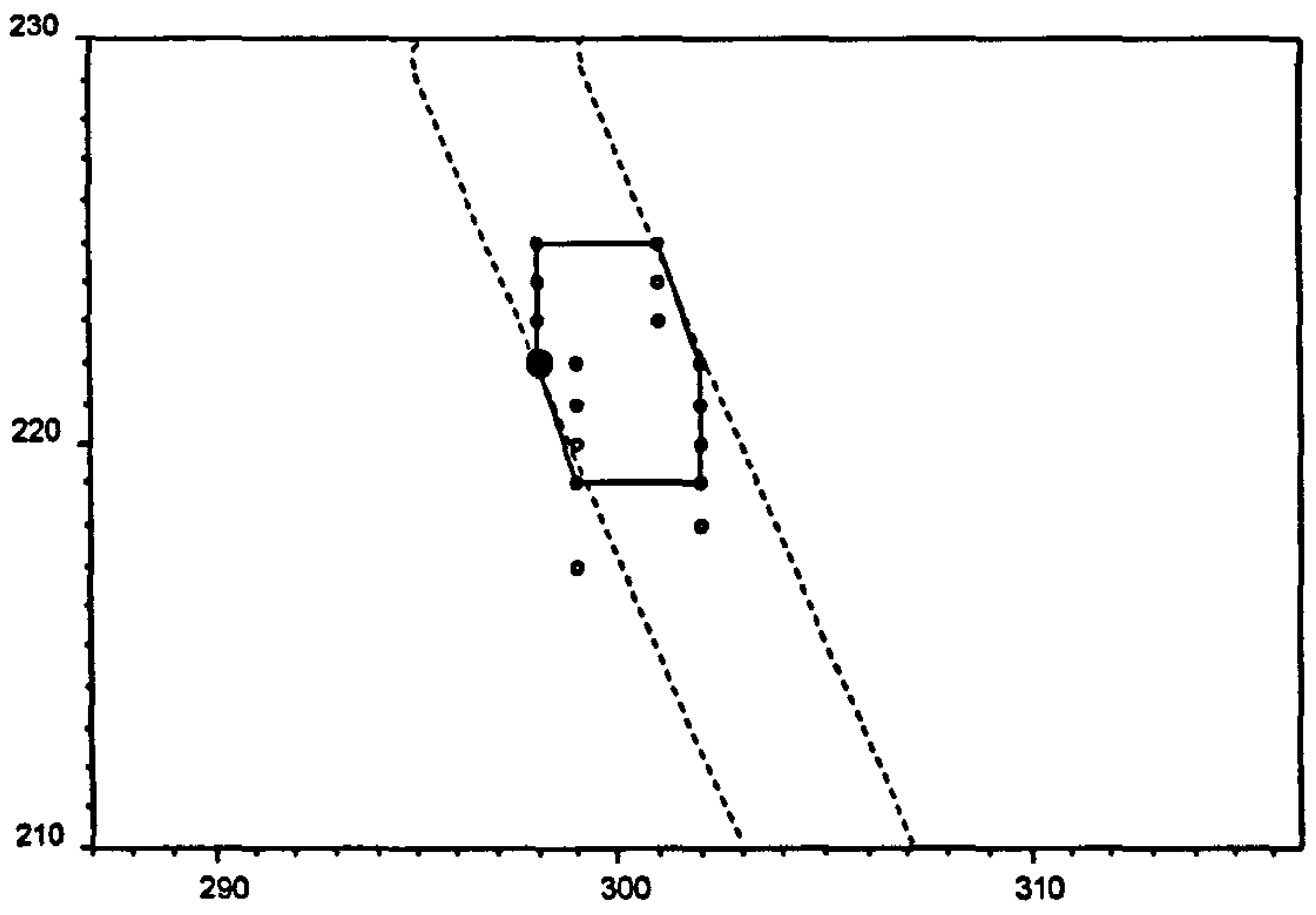

Figure A2.1 95% Minimum Convex Polygon for **Vole A♀ 6 November 1998**
(— MCP, ---- Ditch, • Fix, ● Nest site)

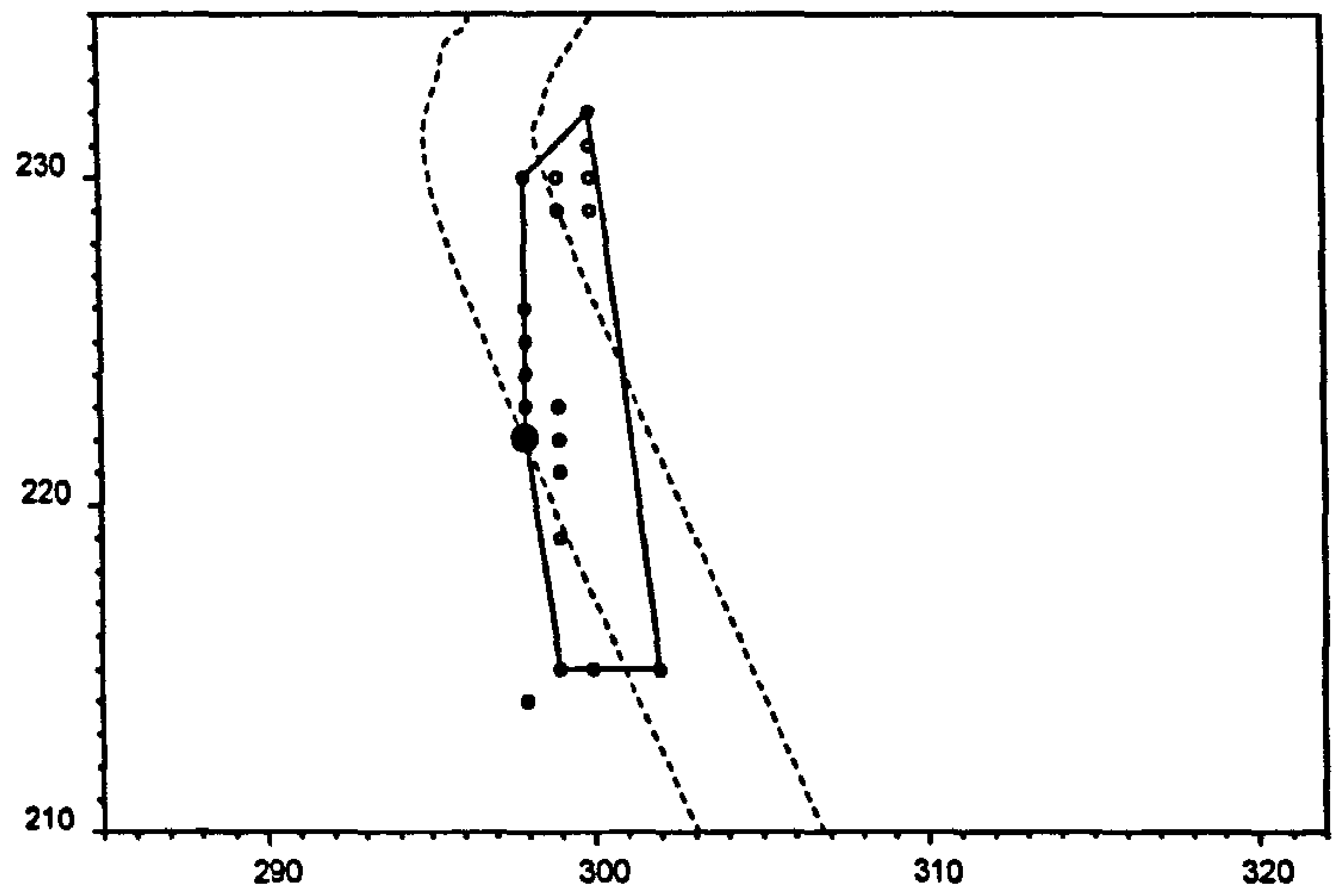

Figure A2.2 95% Minimum Convex Polygon for **Vole A♀ 10 December 1998** (—MCP, ---- Ditch, • Fix, ● Nest site)

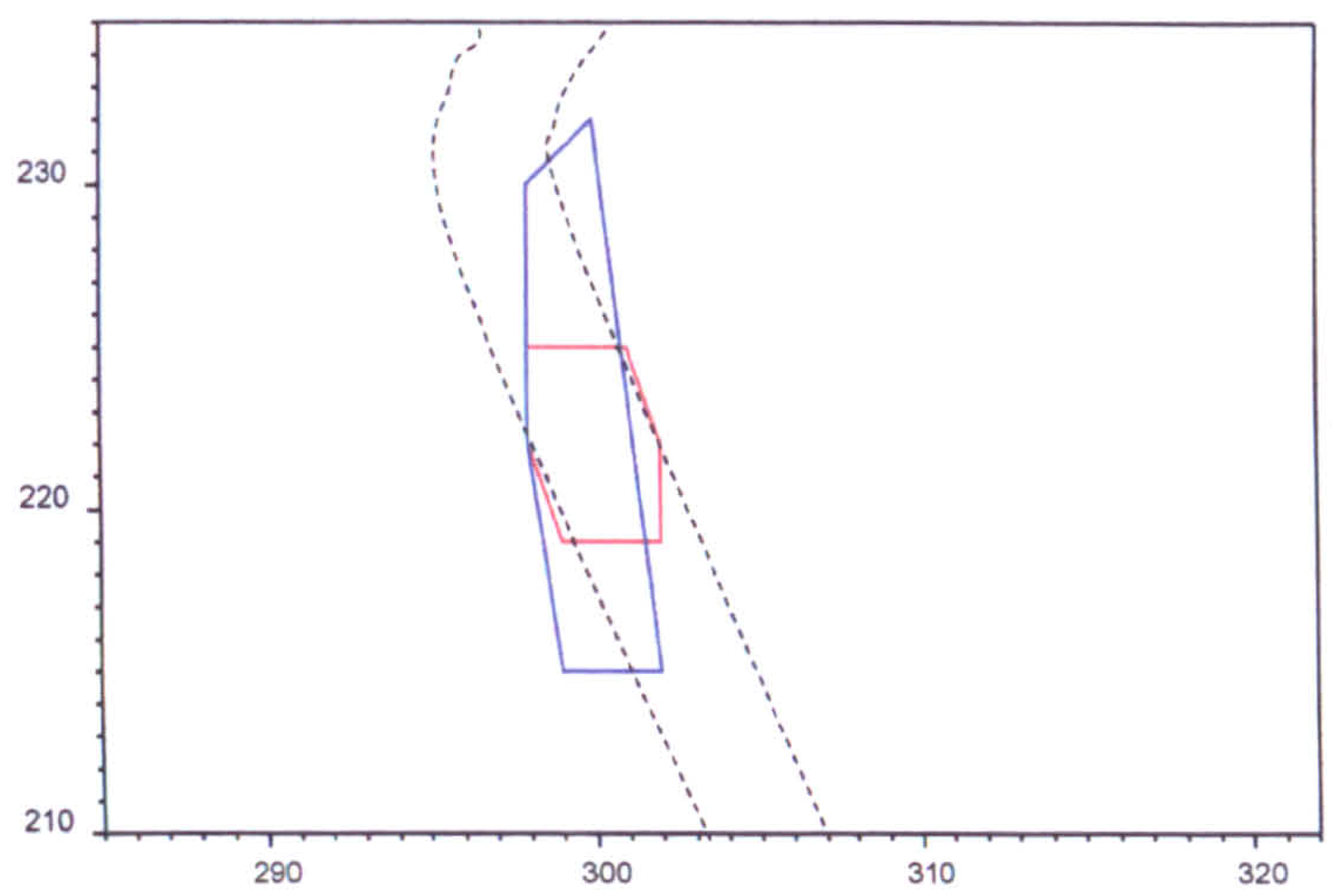

Figure A2.3 95% Minimum Convex Polygons for **Vole A♀**
(— 6 November 1998, — 10 December 1998, ---- Ditch)

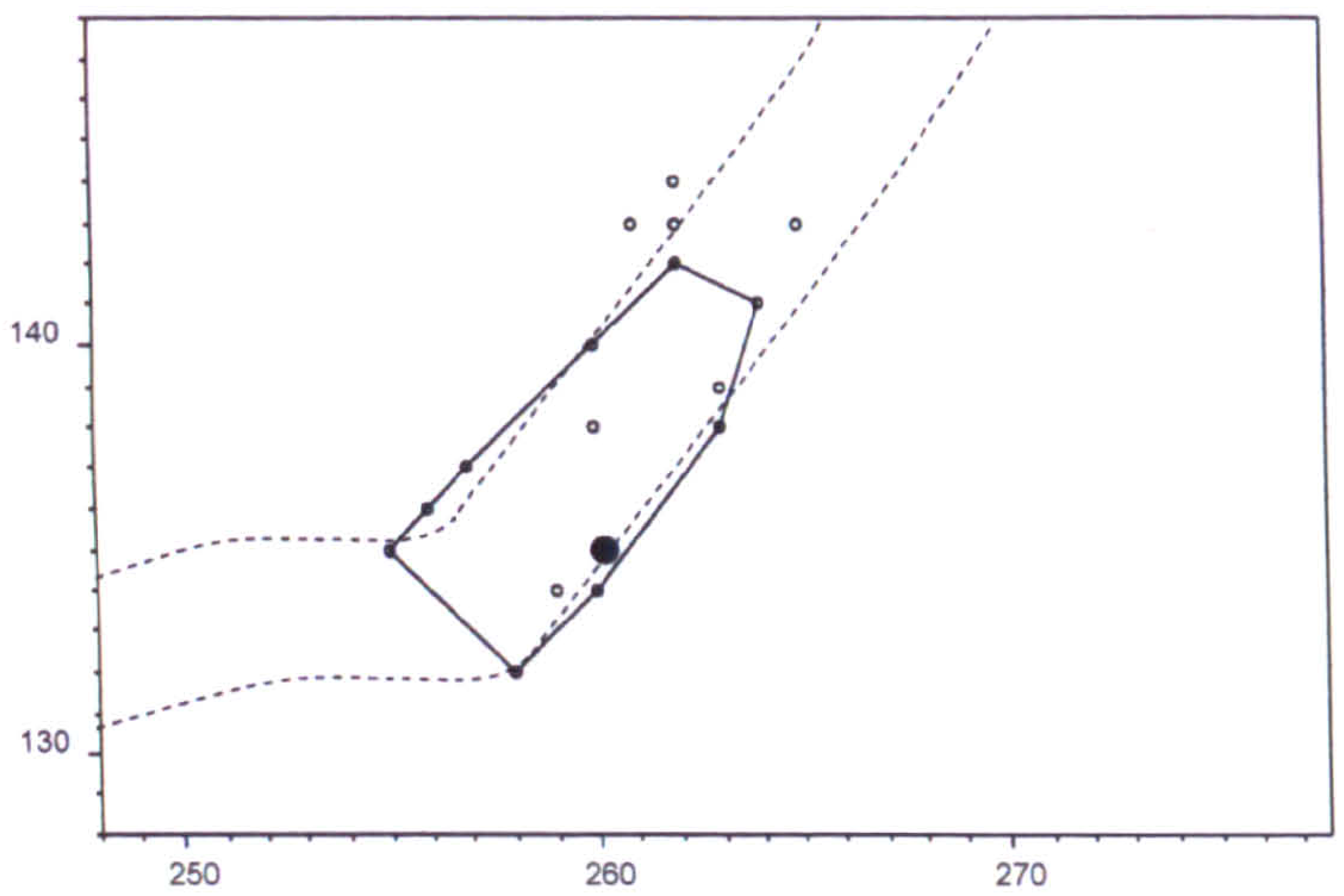

Figure A2.4 95% Minimum Convex Polygon for **Vole B♀ 6 November 1998**
(— MCP, ---- Ditch, ∘ Fix, ● Nest site)

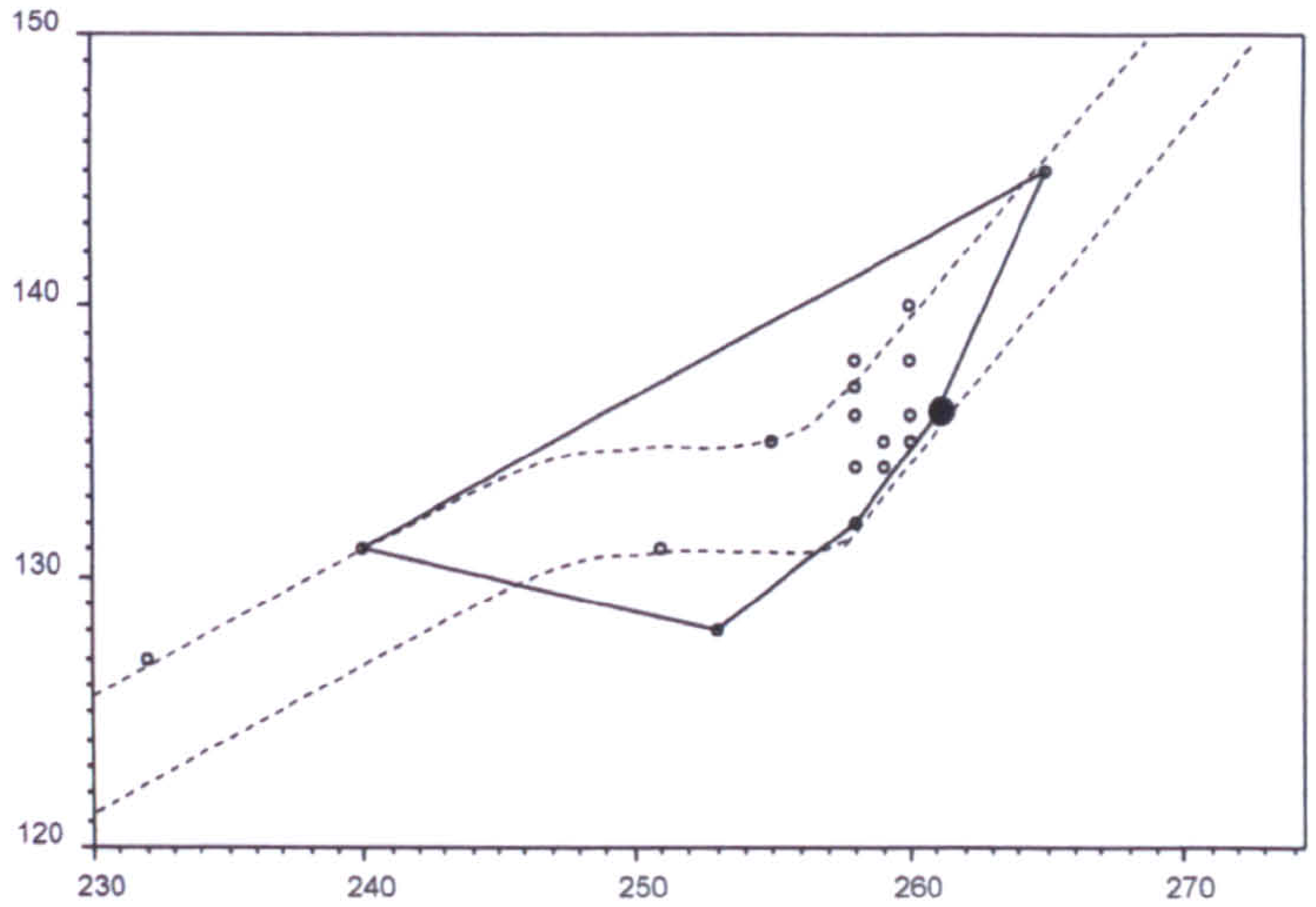

Figure A2.5 95% Minimum Convex Polygon for **Vole B♀ 10 December 1998**
(— MCP, ---- Ditch, ∘ Fix, ● Nest site)

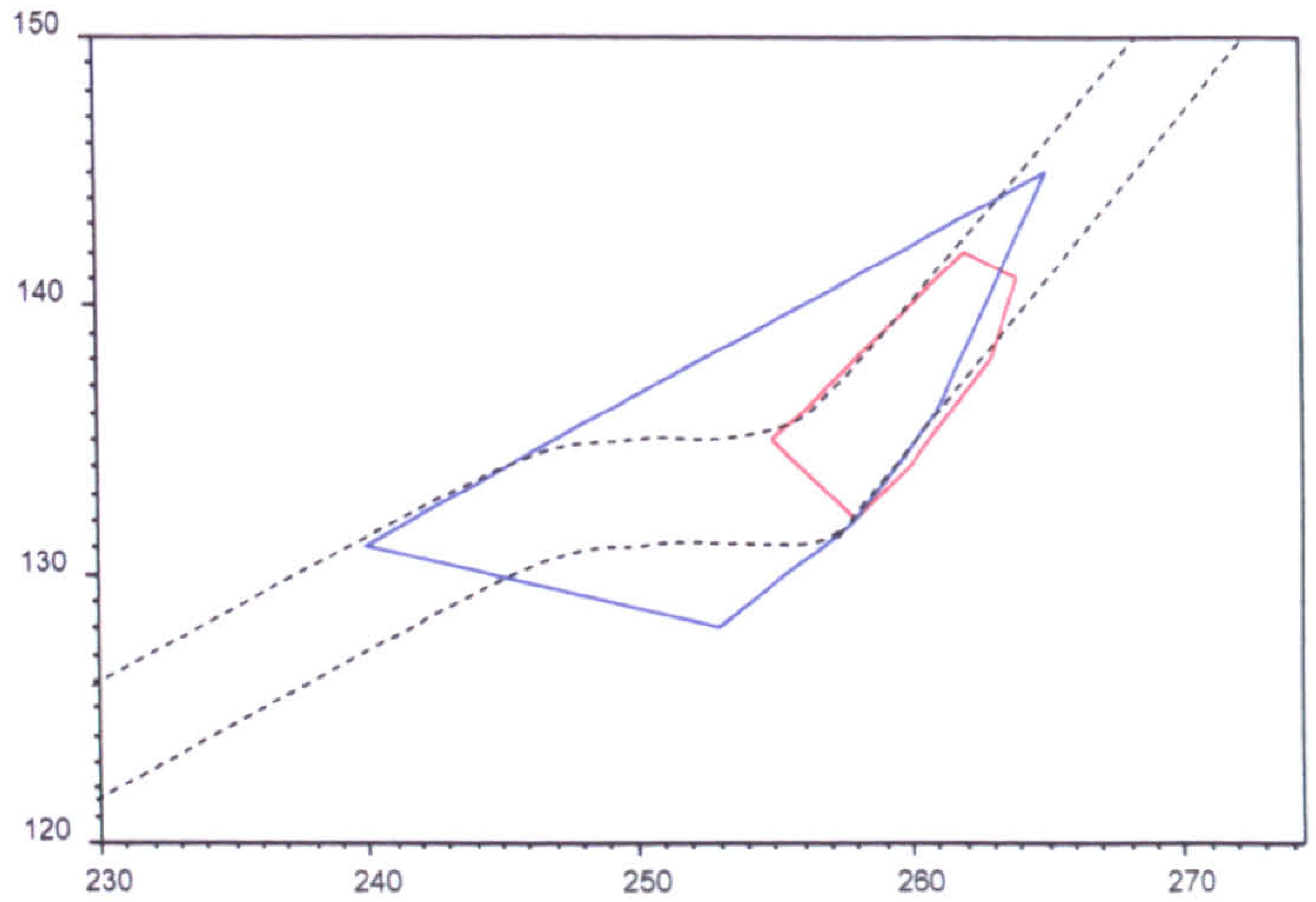

Figure A2.6 95% Minimum Convex Polygons for **Vole B♀**
(— 6 November 1998, — 10 December 1998, ---- Ditch)

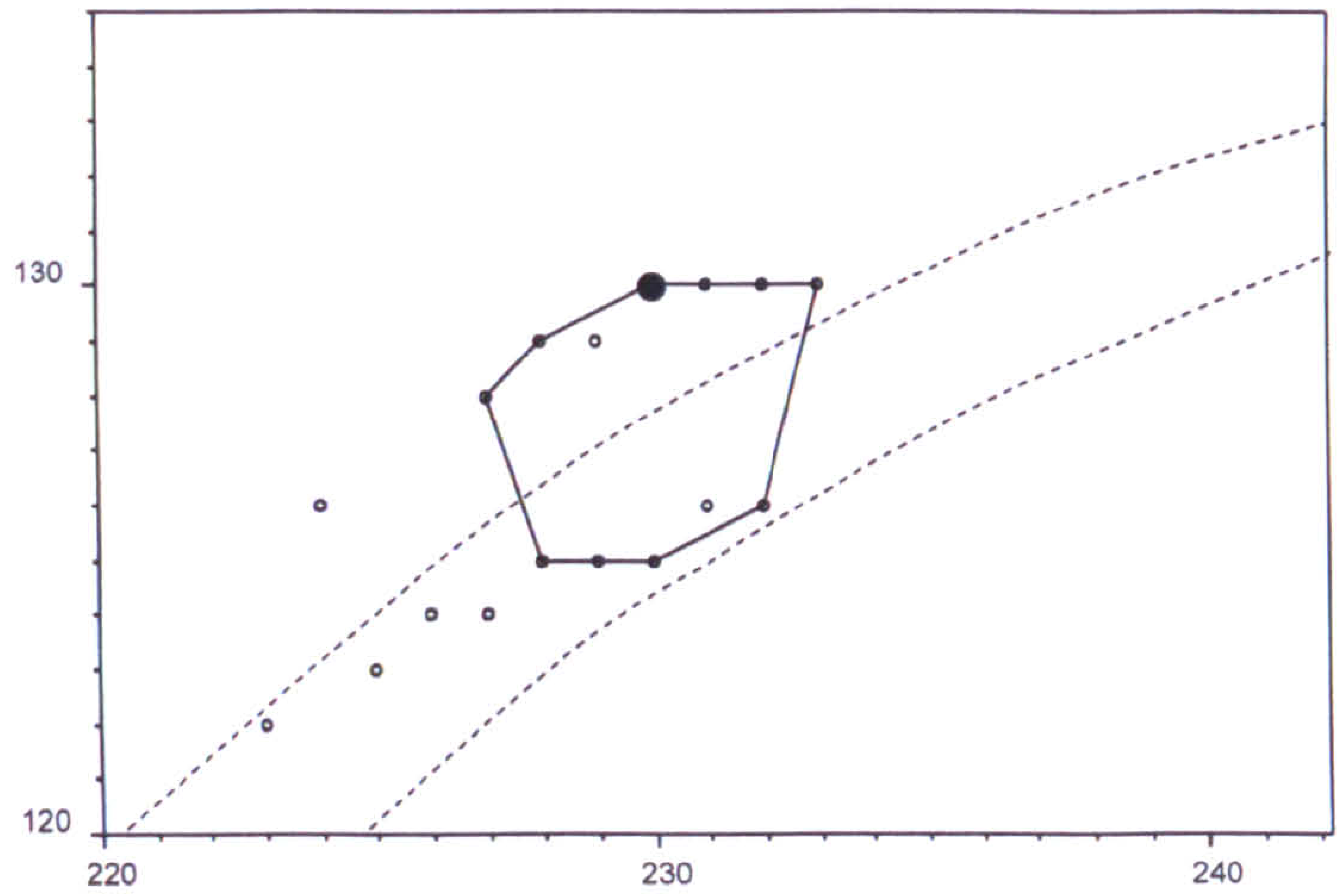

Figure A2.7 95% Minimum Convex Polygon for **Vole C♀ 6 November 1998** (— MCP, ---- Ditch, ∘ Fix, ● Nest site)

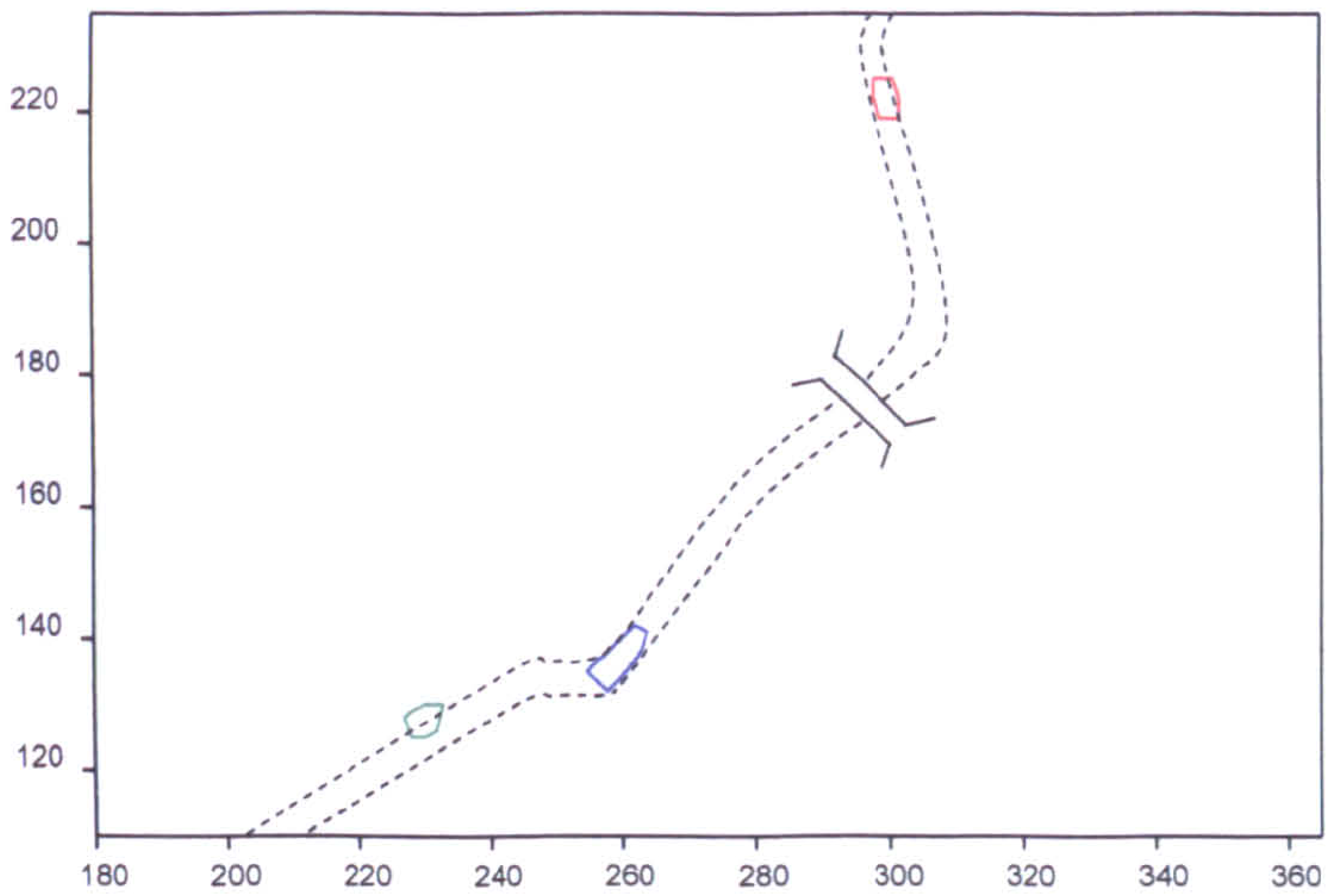

Figure A2.8 95% Minimum Convex Polygons for **Vole A♀, Vole B♀ and Vole C♀ 6 November 1998** (— Vole A♀, — Vole B♀, —Vole C♀, ---- Ditch)

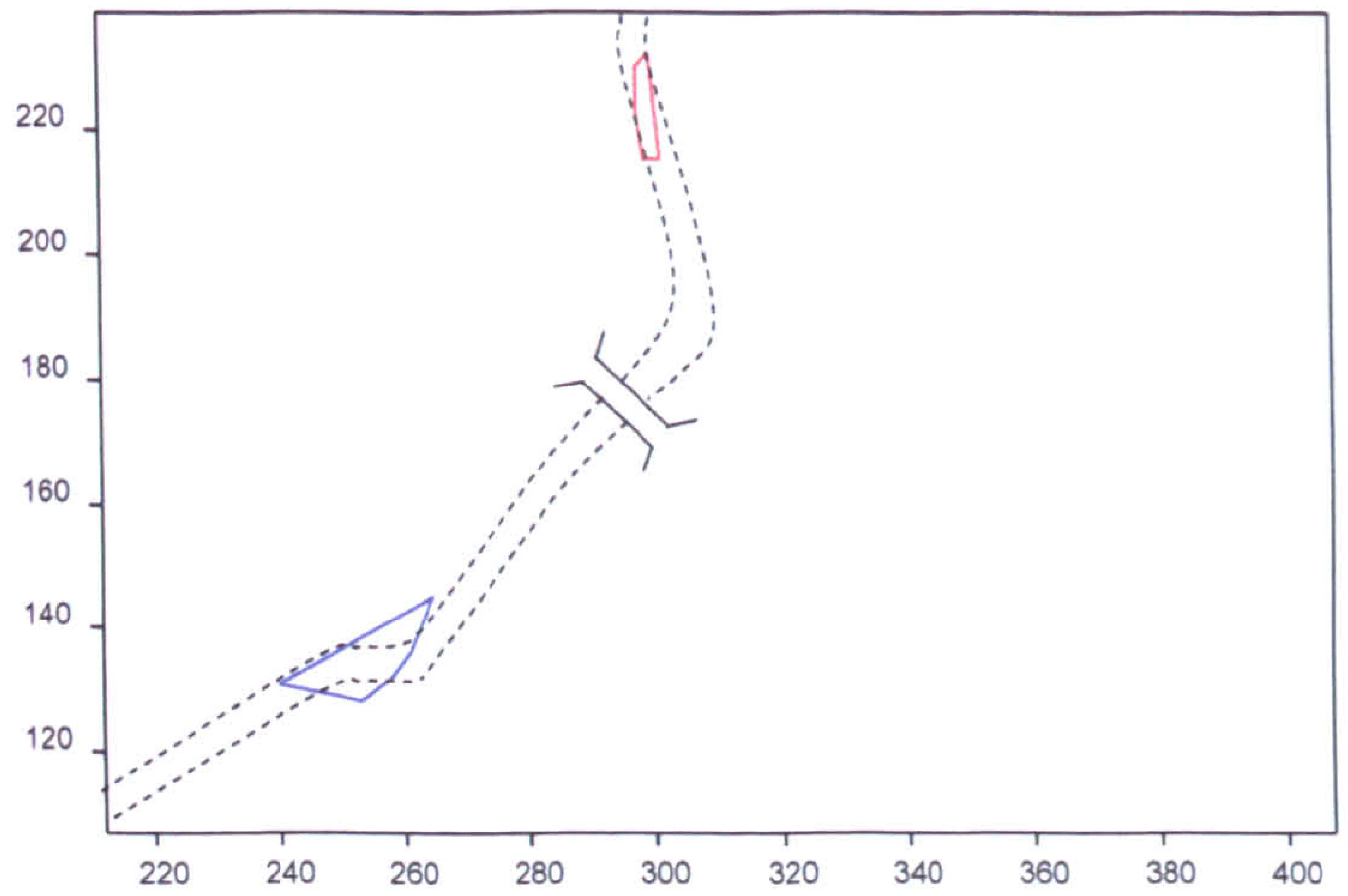

Figure A2.9 95% Minimum Convex Polygons for **Vole A♀ and Vole B♀ 10 December 1998** (— Vole A♀, —Vole B♀, ---- Ditch)

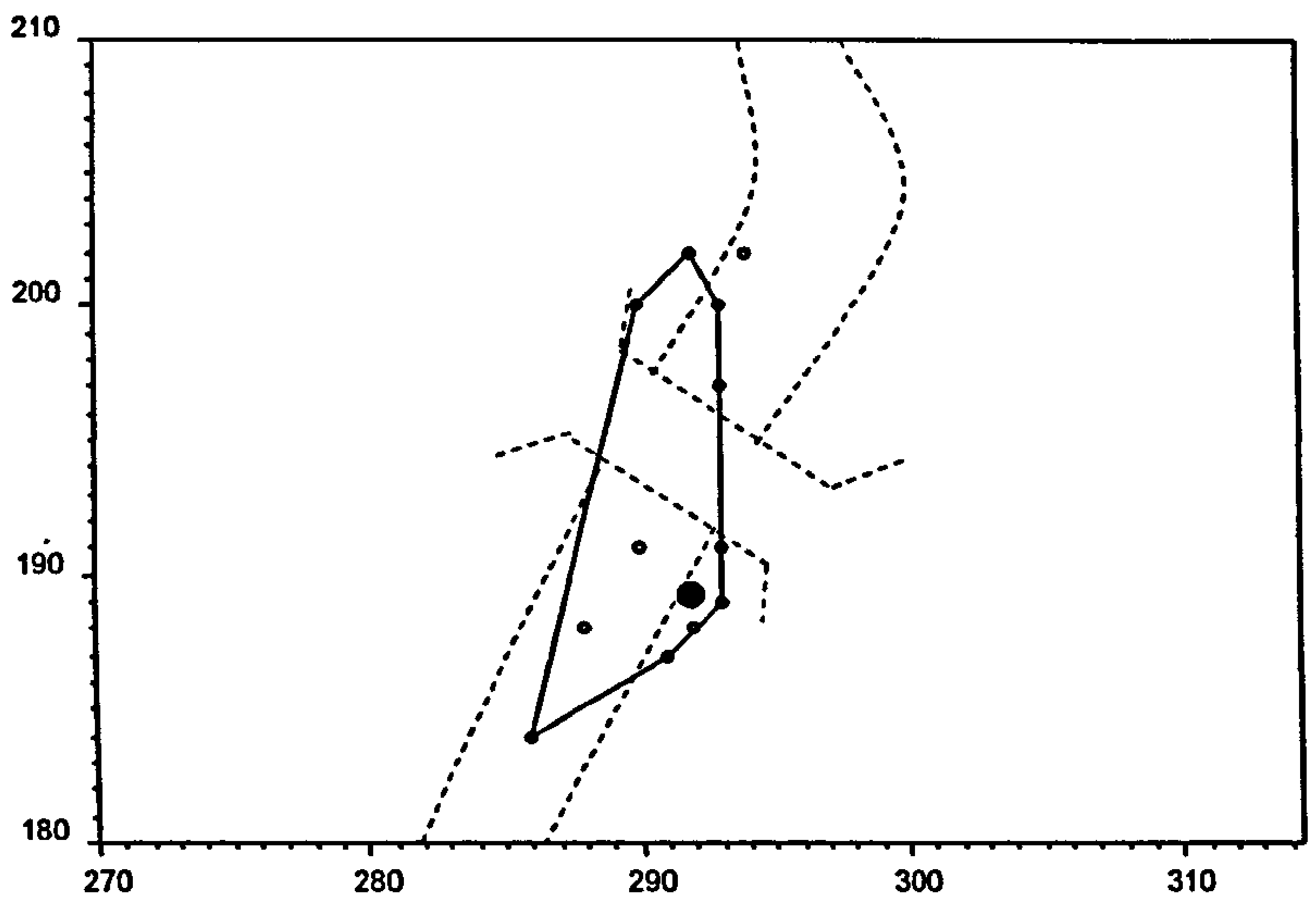

Figure A2.10 95% Minimum Convex Polygon for **Vole E♂ 12 January 2000**
(— MCP, --- Ditch, Fix, Nest site)

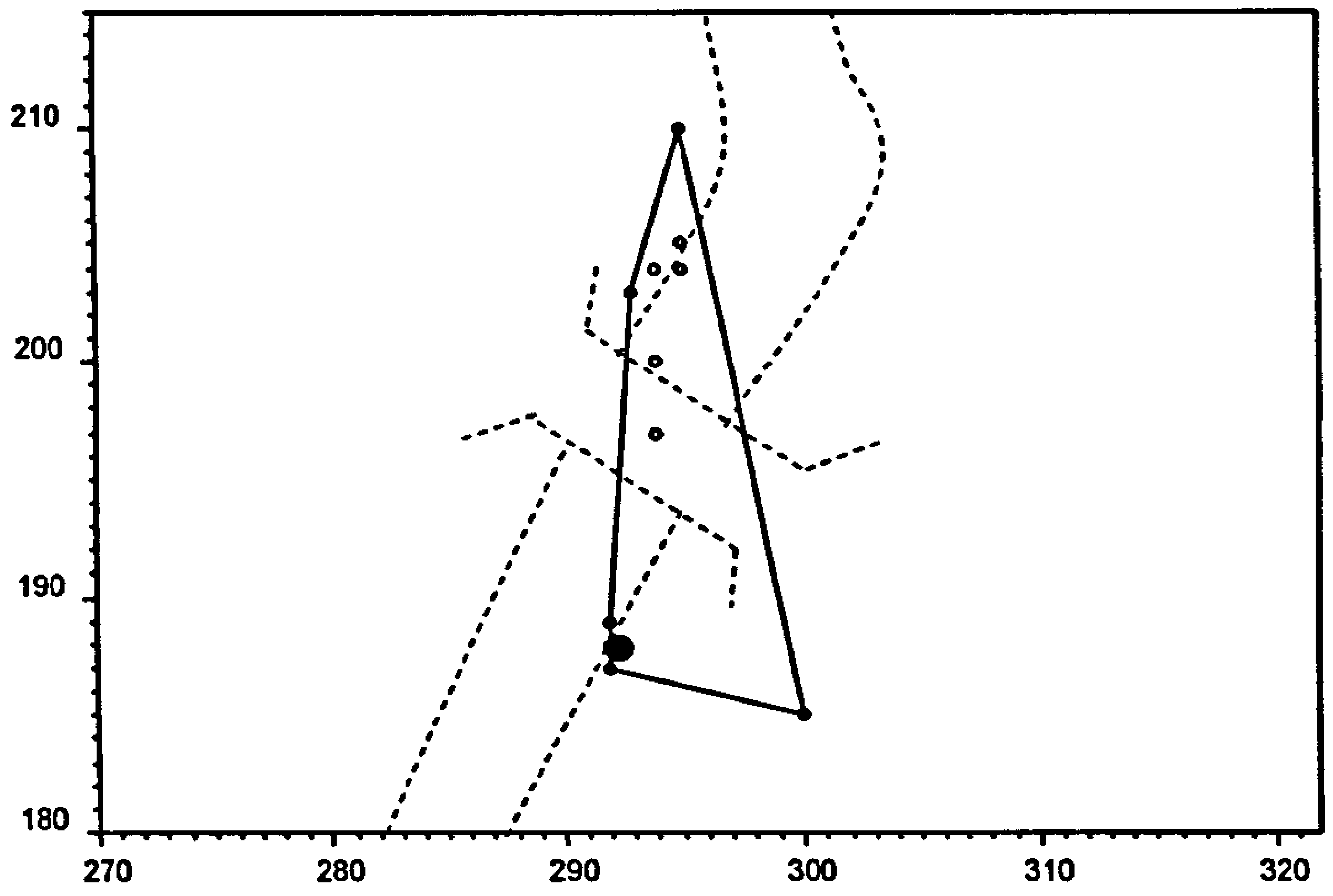

Figure 2.11 95% Minimum Convex Polygon for **Vole E♂ 15 February 2000**
(— MCP, --- Ditch, Fix, Nest site)

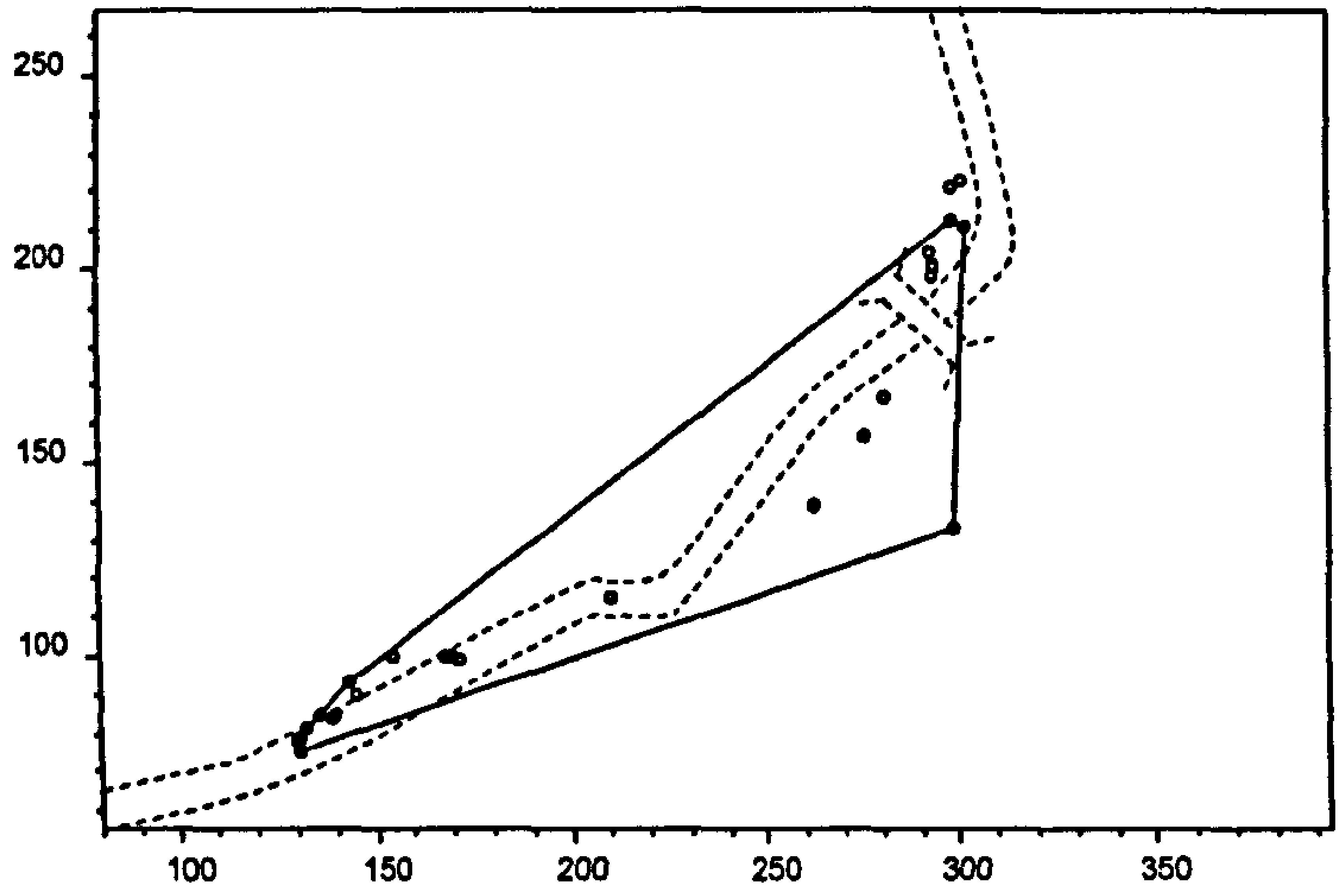

Figure A2.12 95% Minimum Convex Polygon for Vole E♂ **1 March 2000** (— MCP, --- Ditch, ● Fix, no nest site identified)

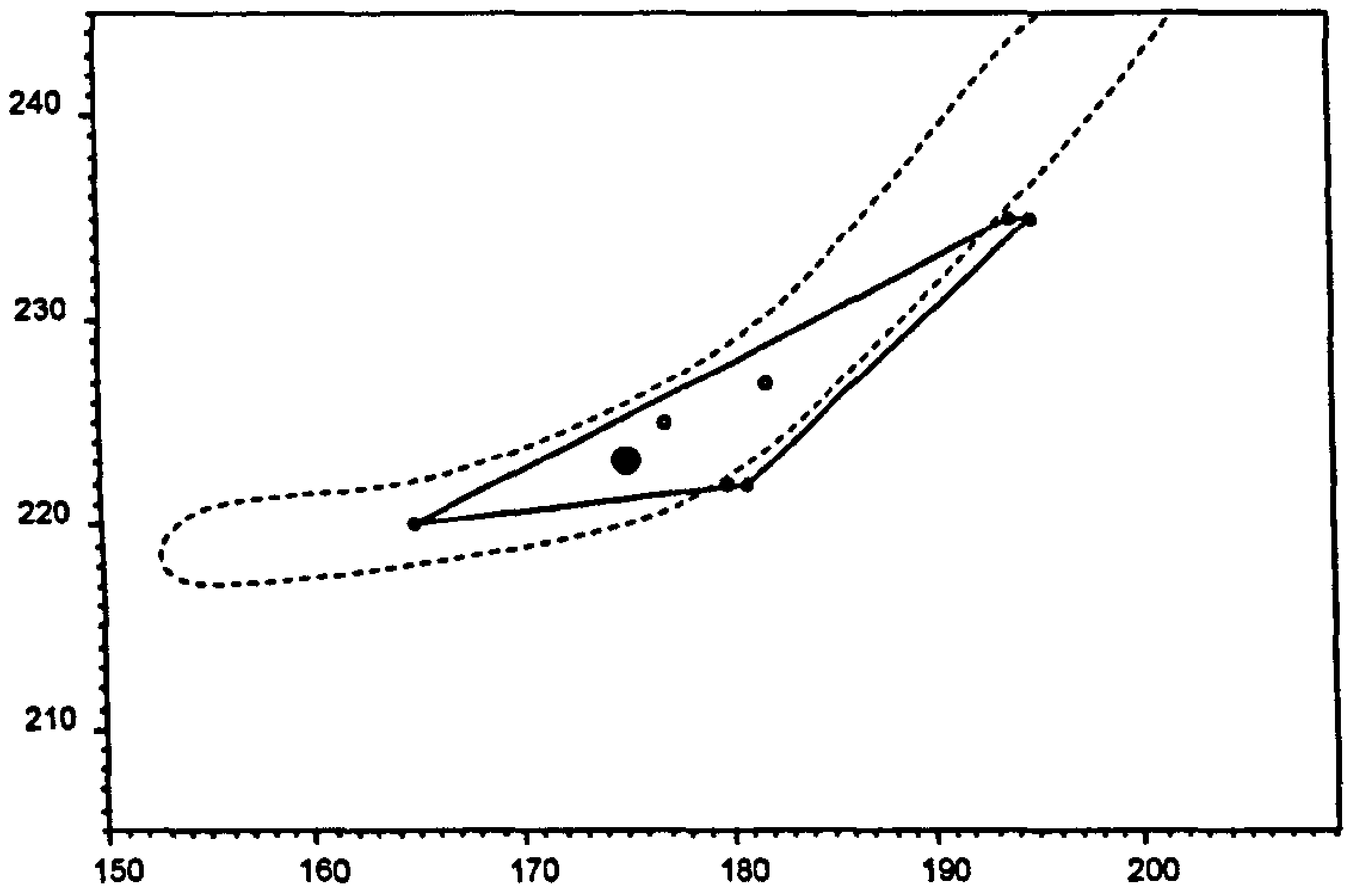

Figure A2.13 95% Minimum Convex Polygon for Vole E♂ **11 March 2000** (— MCP, --- Ditch, ● Fix, ● Nest site)

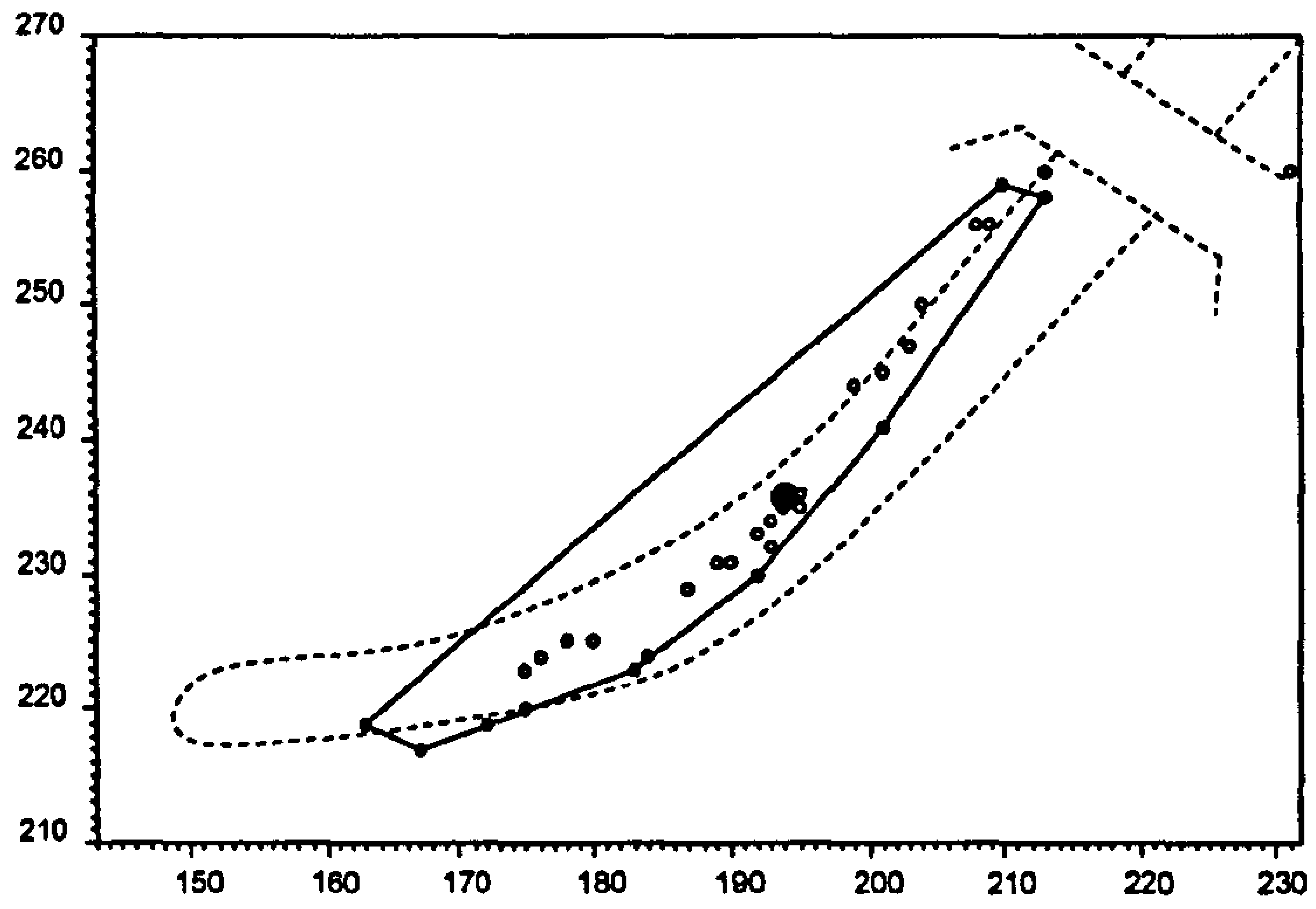

Figure A2.14 95% Minimum Convex Polygon for Vole E♂ **22 March 2000** (— MCP, --- Ditch, ● Fix, ● Nest site)

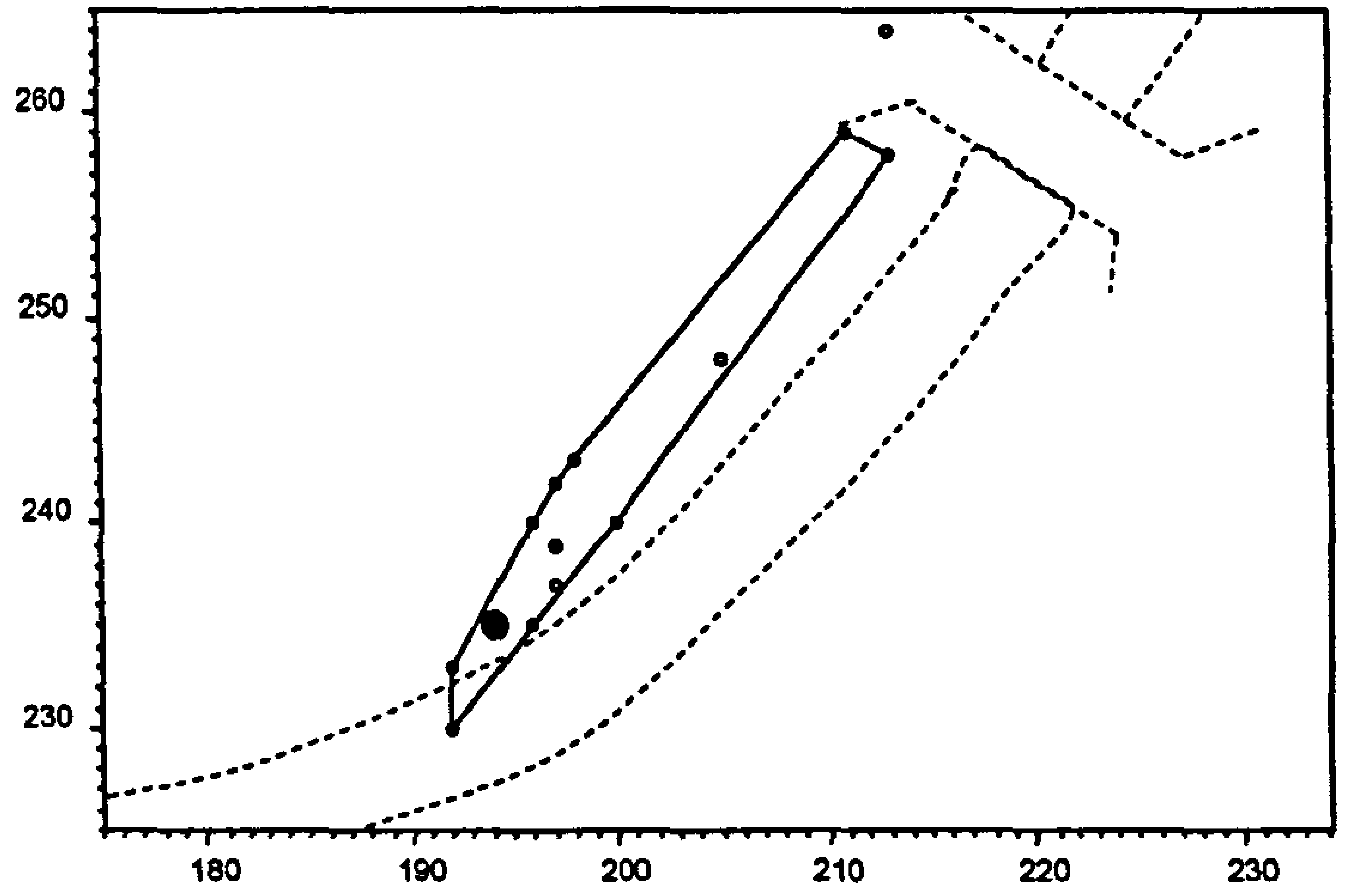

Figure A2.15 95% Minimum Convex Polygon for Vole E♂ **15 April 2000** (— MCP, --- Ditch, ● Fix, ● Nest site)

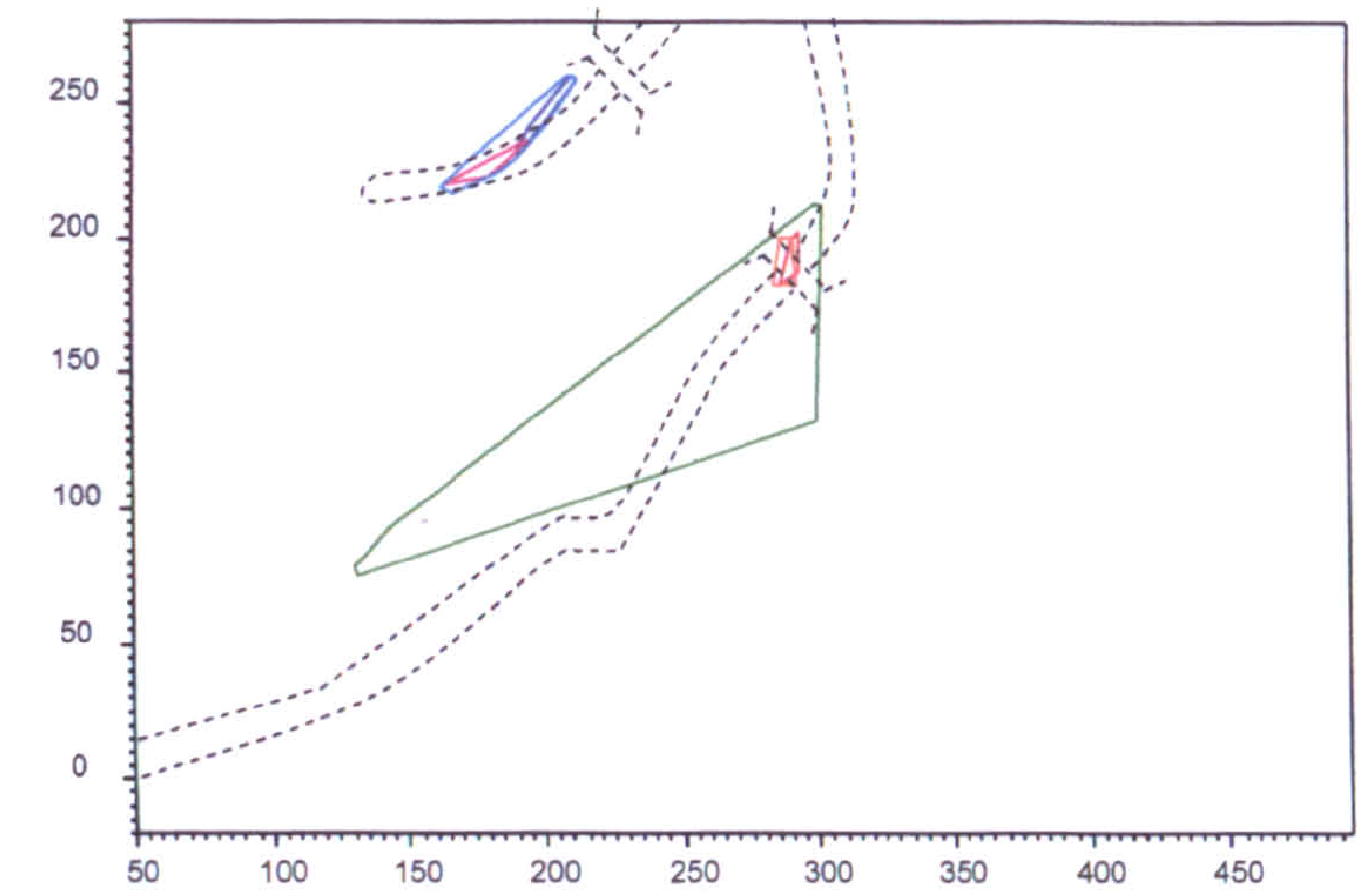

Figure A2.16 95% Minimum Convex Polygons for **Vole E♂**
(— 12 January 2000, — 15 February 2000, — 1 March 2000,
— 11 March 2000, — 22 March 2000, — 15 April 2000,
---- Ditch)

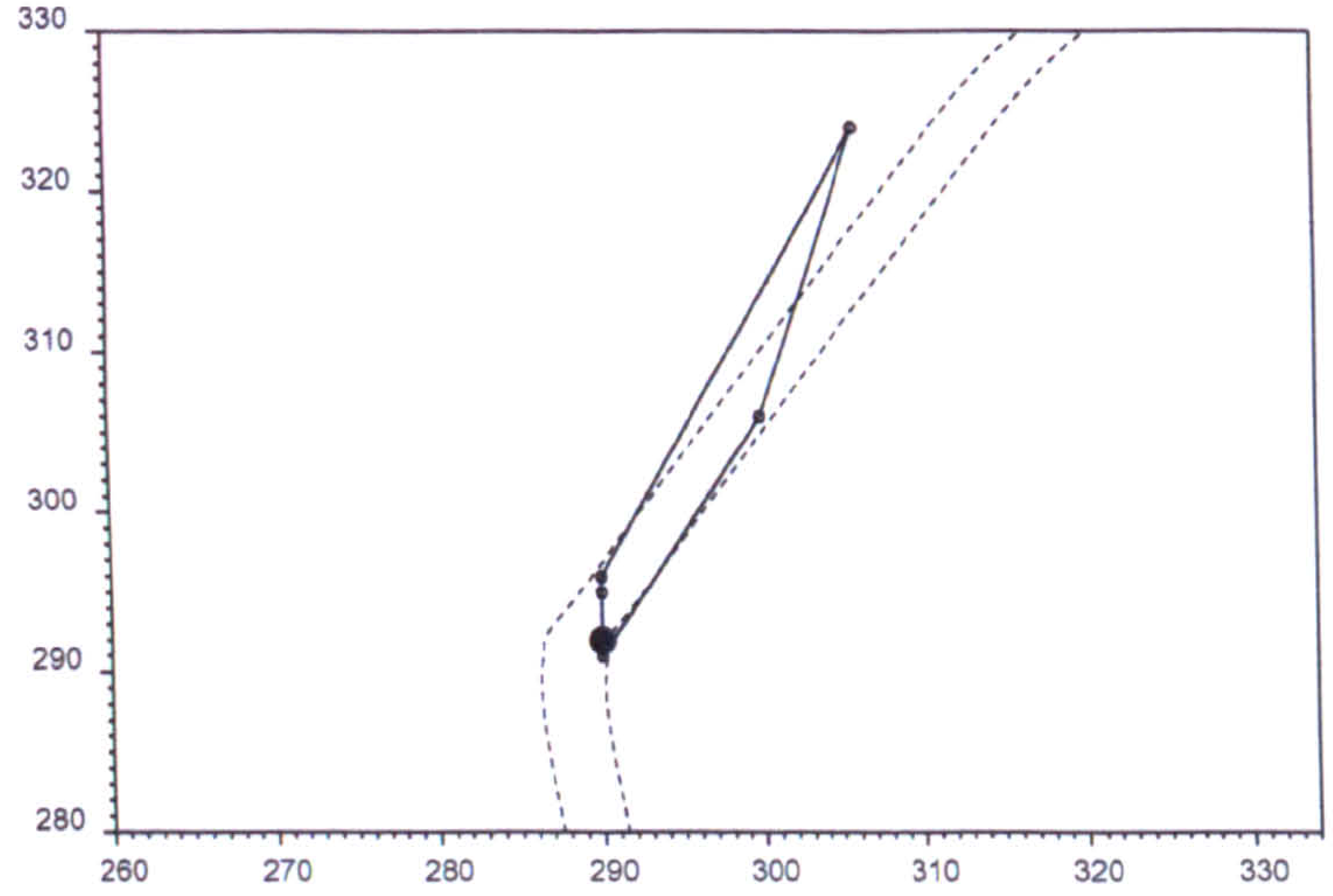

Figure A2.17 95% Minimum Convex Polygon for **Vole F♂ 12 January 2000**
(— MCP, ---- Ditch, ∘ Fix, ● Nest site)

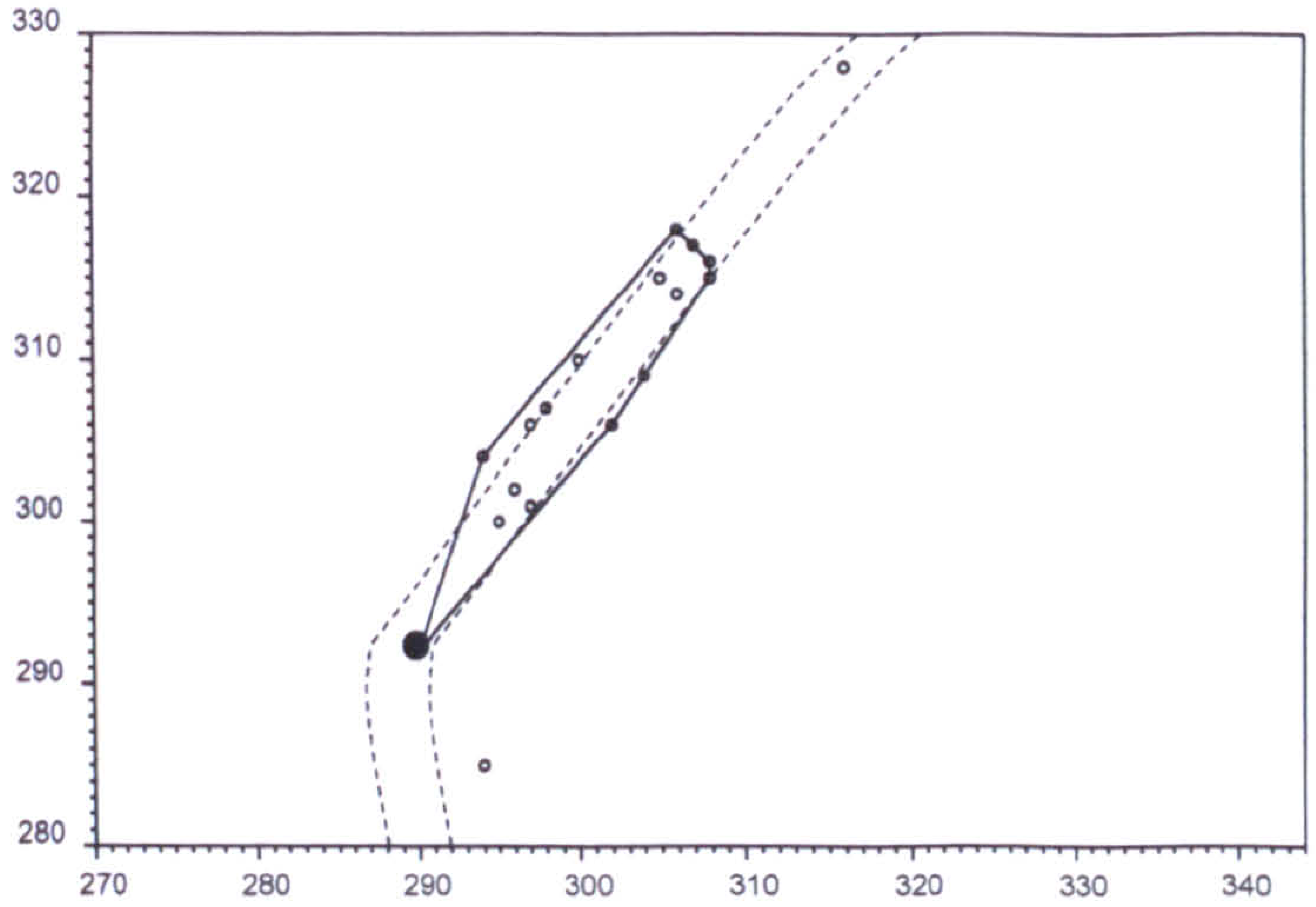

Figure A2.18 95% Minimum Convex Polygon for **Vole F♂ 18 January 2000**
(— MCP, ---- Ditch, ∘ Fix, ● Nest site)

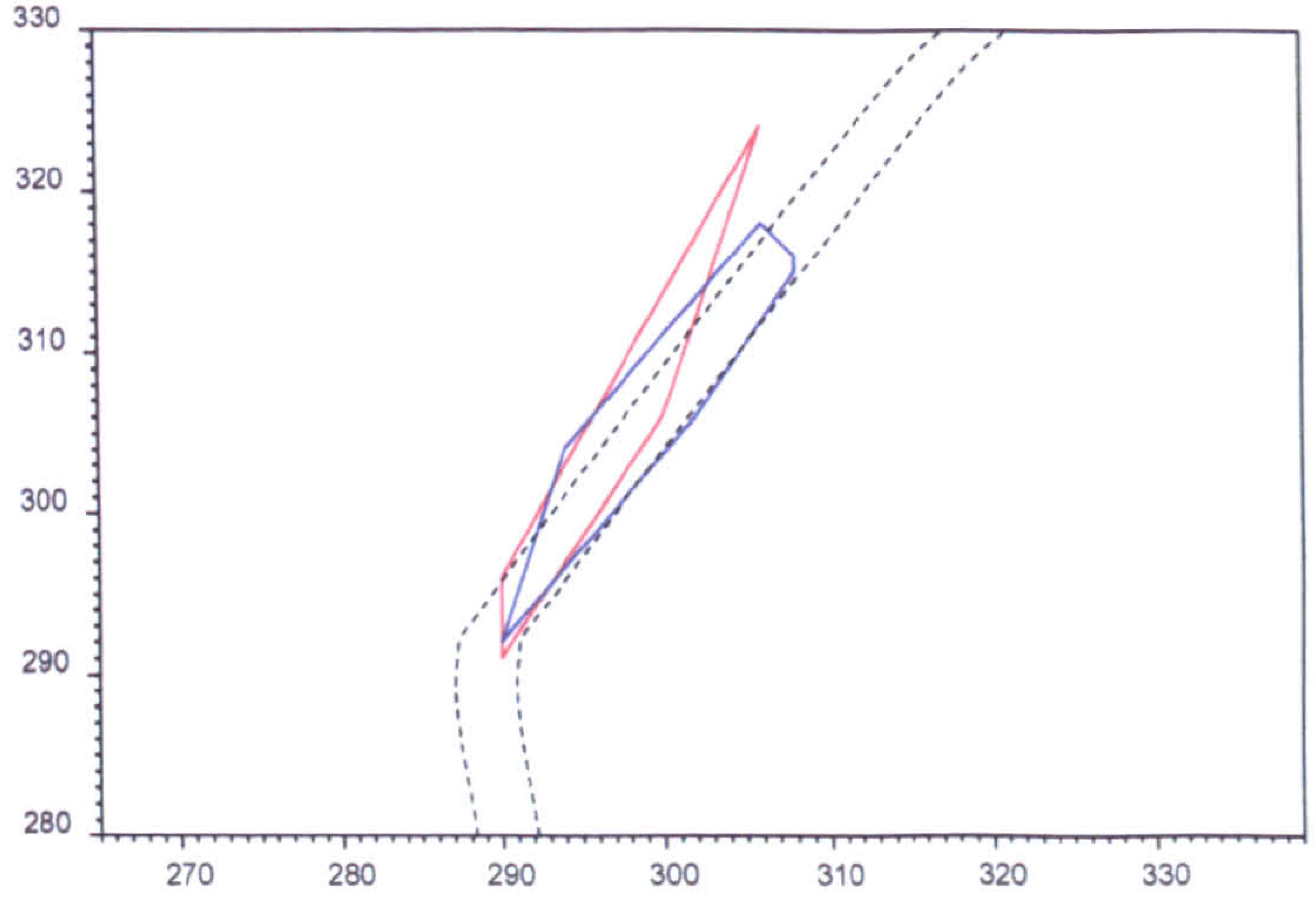

Figure A2.19 95% Minimum Convex Polygons for **Vole F♂**
(— 12 January 2000, — 18 January 2000, ---- Ditch)

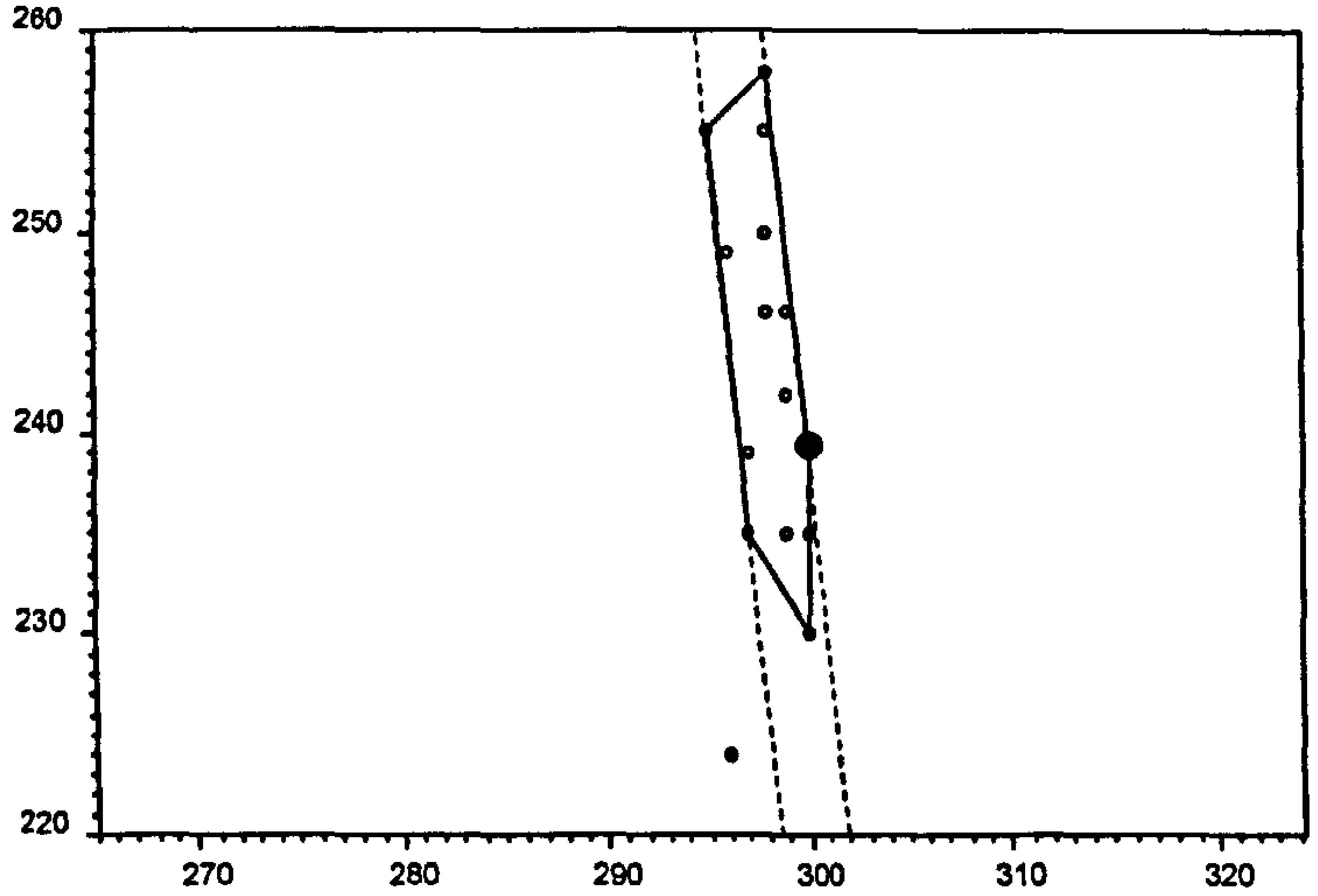

Figure A2.20 95% Minimum Convex Polygon for Vole G♀ 16 February 2000 (— MCP, ---- Ditch, • Fix, ● Nest site)

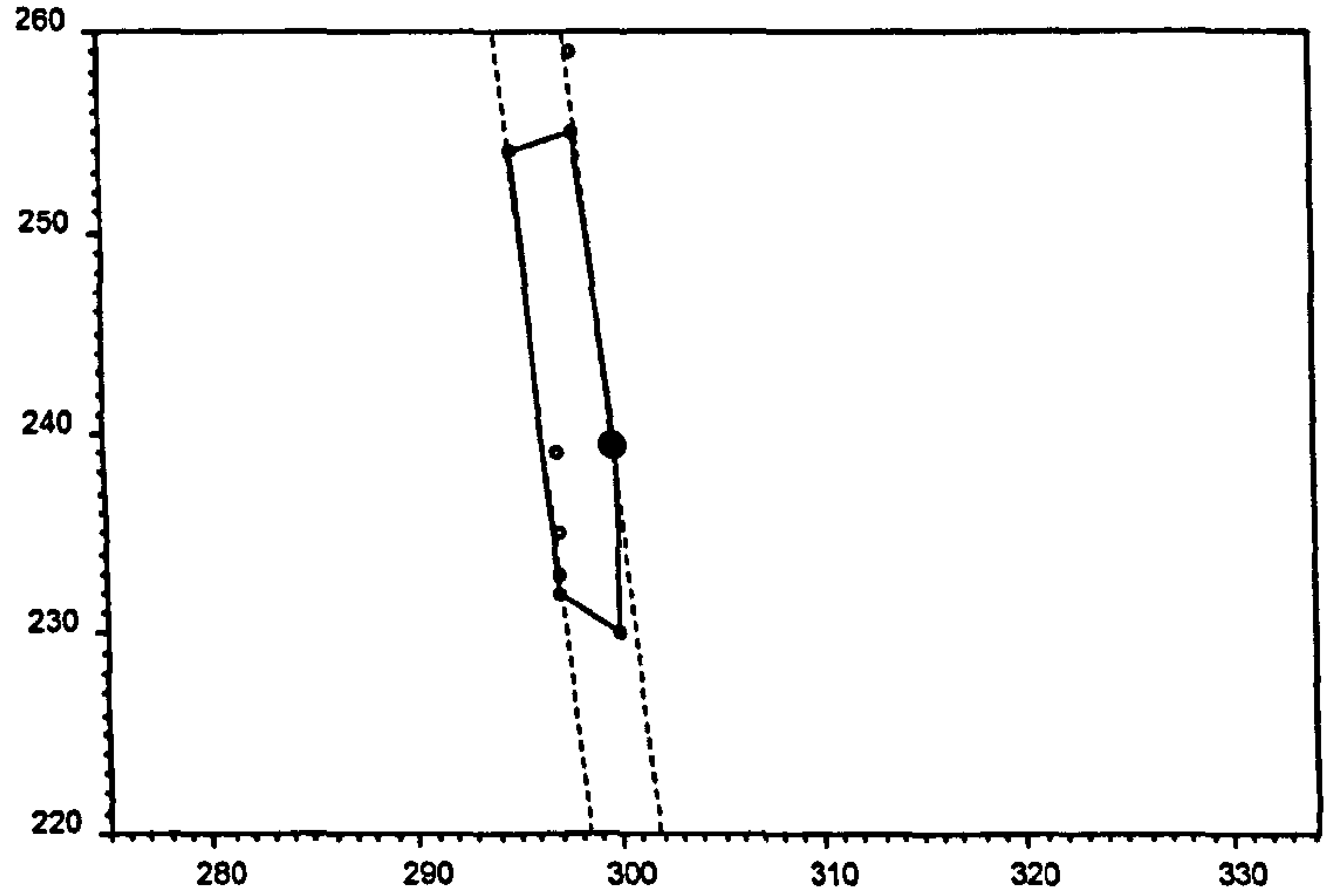

Figure A2.20 95% Minimum Convex Polygon for Vole G♀ 1 March 2000 (— MCP, ---- Ditch, • Fix, ● Nest site)

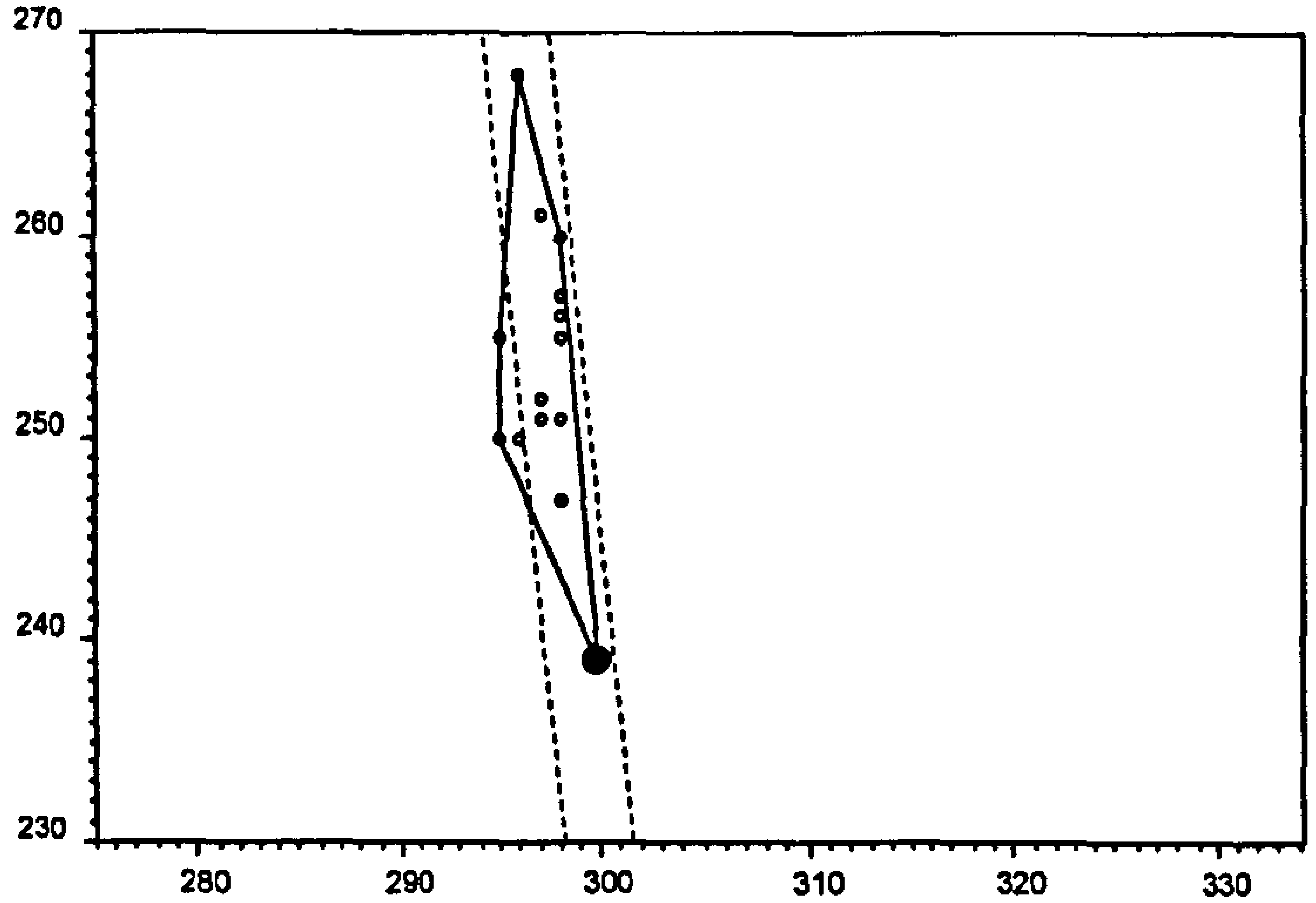

Figure A2.21 95% Minimum Convex Polygon for Vole G♀ 11 March 2000 (— MCP, ---- Ditch, • Fix, ● Nest site)

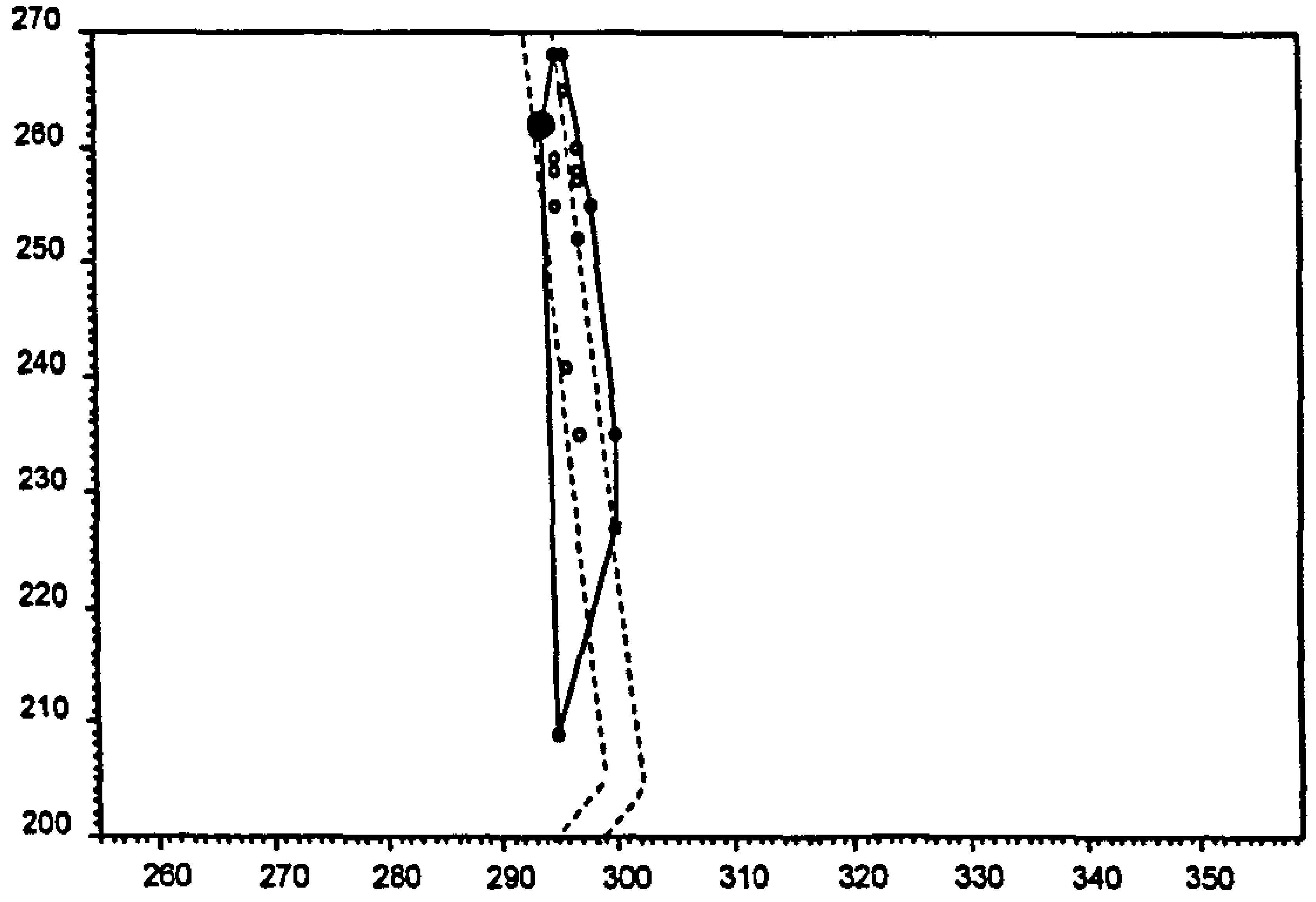

Figure A2.22 95% Minimum Convex Polygon for Vole G♀ 21 March 2000 (— MCP, ---- Ditch, • Fix, ● Nest site)

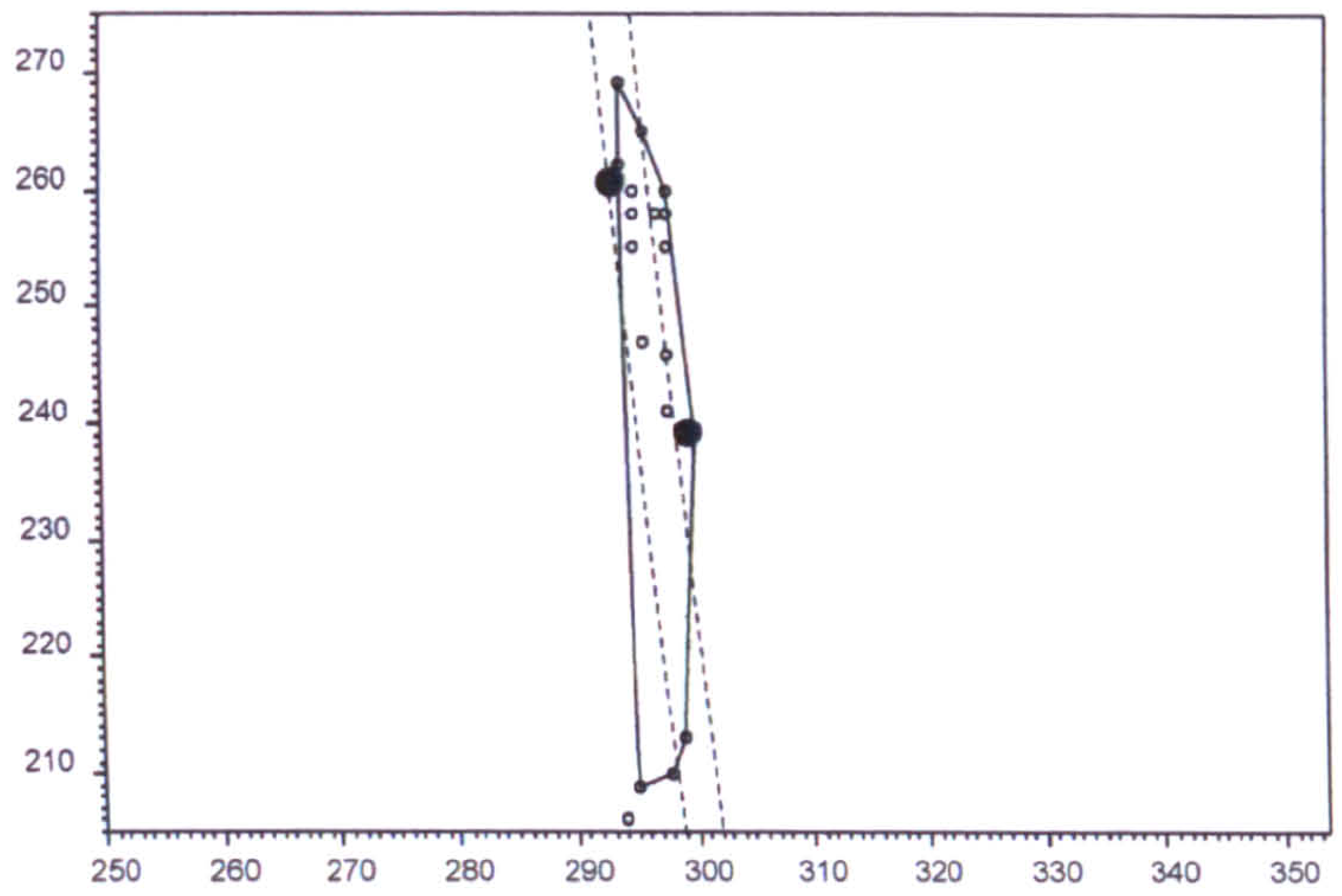

Figure A2.23 95% Minimum Convex Polygon for **Vole G♀ 15 April 2000**
(— MCP, ---- Ditch, ∘ Fix, ● Nest site)

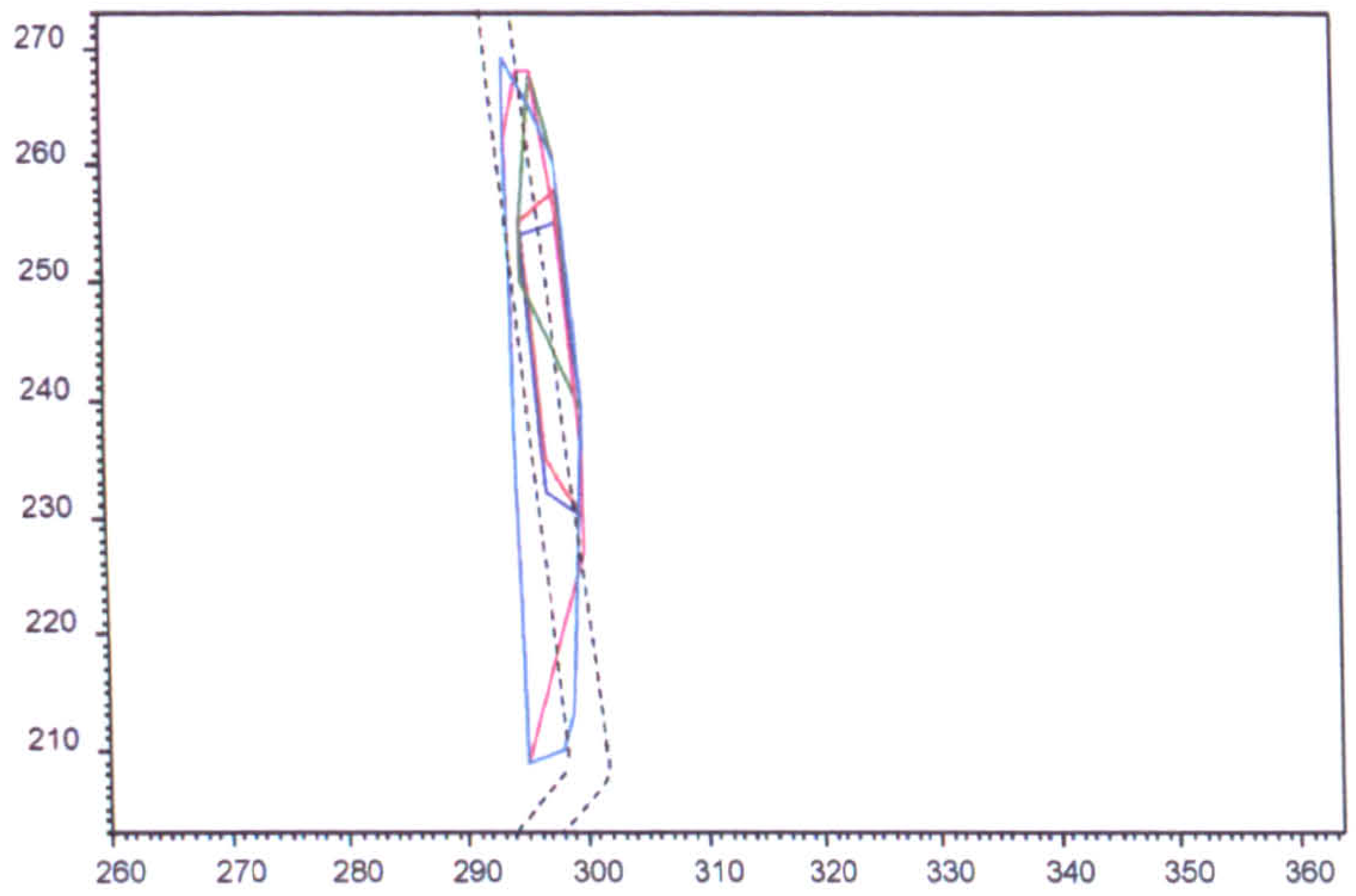

Figure A2.24 95% Minimum Convex Polygons for **Vole G♀**
(— 16 February 2000, — 1 March 2000, — 11 March 2000, —
21 March 2000, —15 April 2000, ---- Ditch)

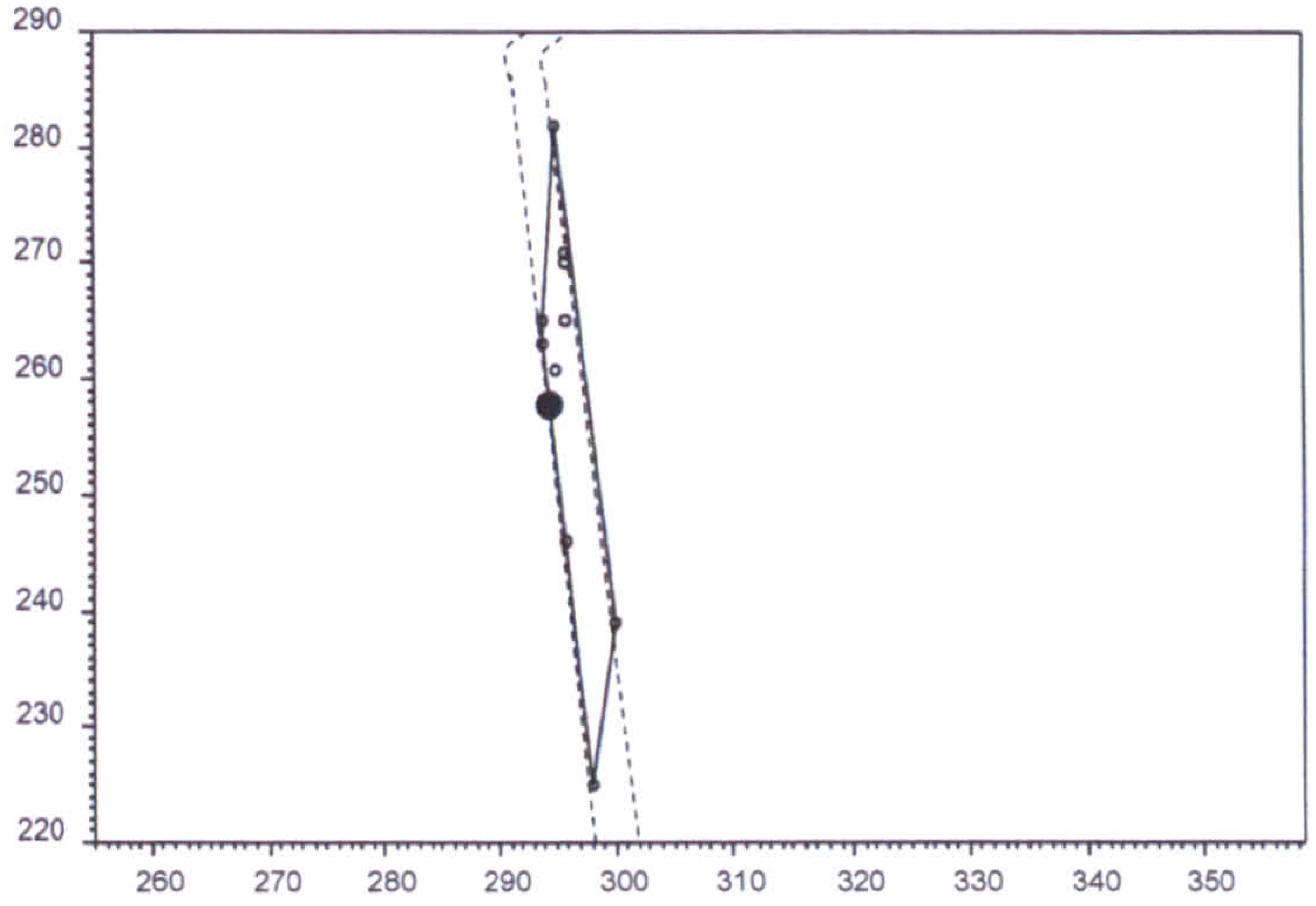

Figure A2.25 95% Minimum Convex Polygon for **Vole H♂ 16 February 2000**
(— MCP, ---- Ditch, ∘ Fix, ● Nest site)

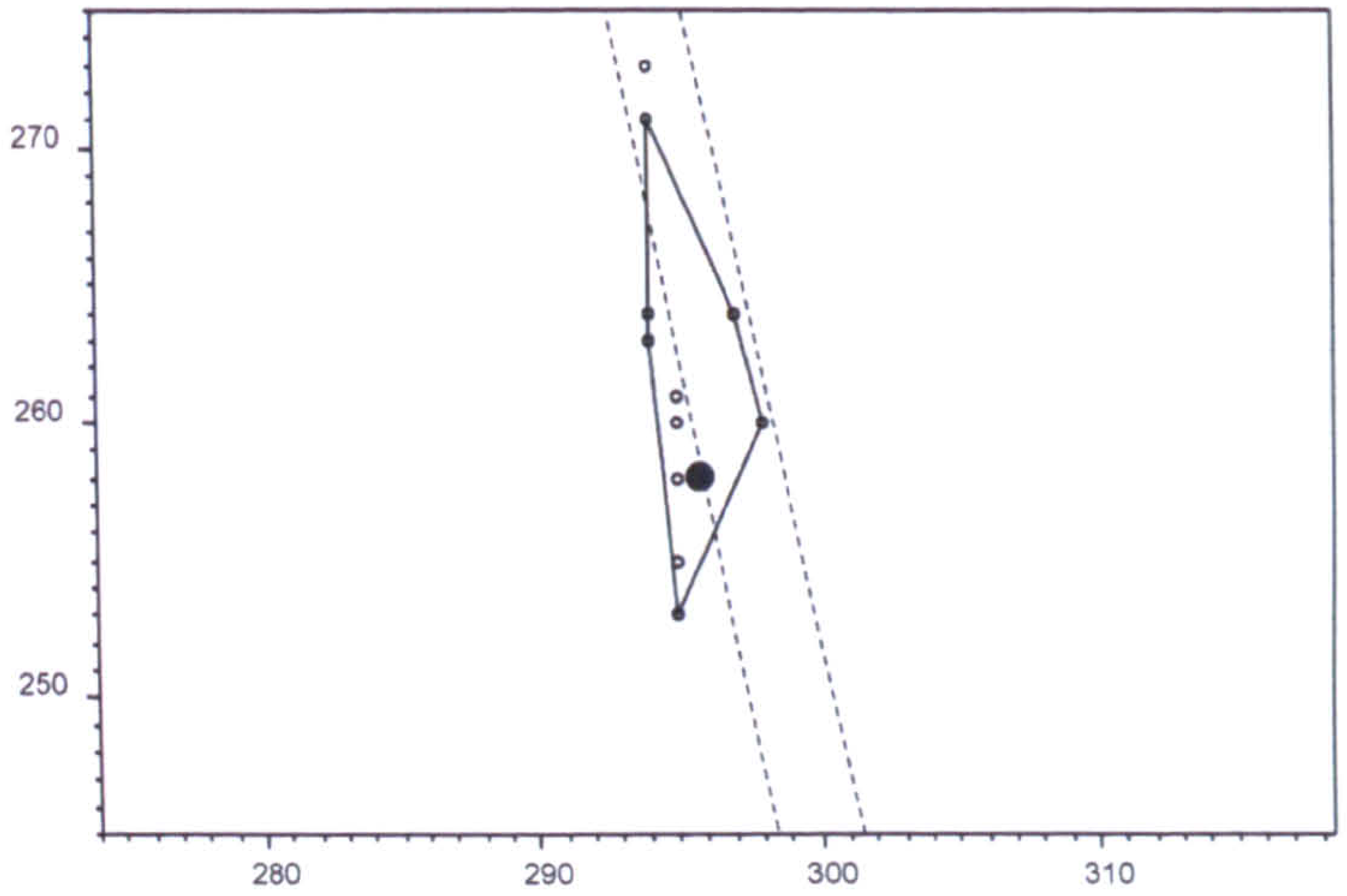

Figure A2.26 95% Minimum Convex Polygon for **Vole H♂ 1 March 2000**
(— MCP, ---- Ditch, ∘ Fix, ● Nest site)

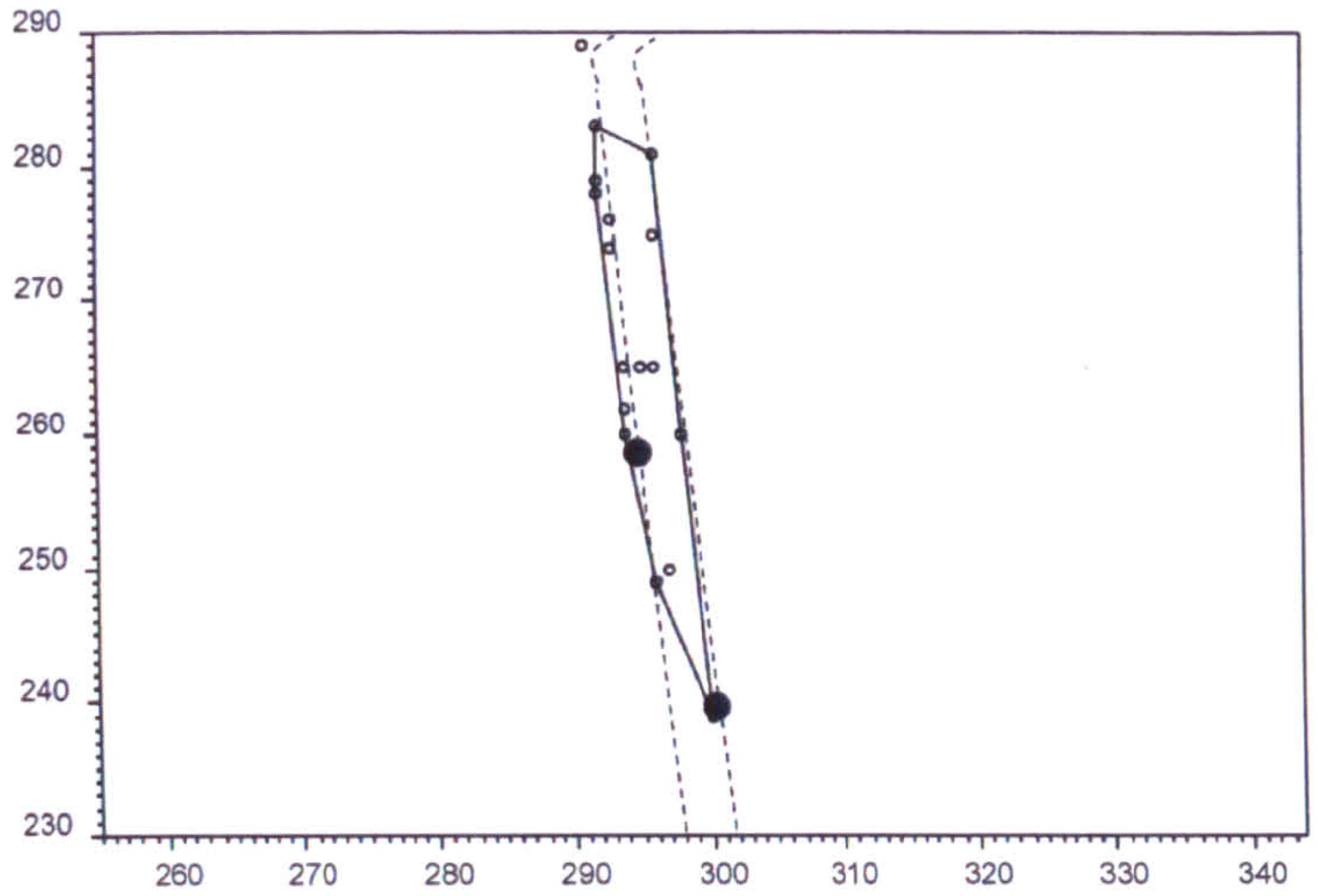

Figure A2.27 95% Minimum Convex Polygon for **Vole H♂ 11 March 2000** (— MCP, ---- Ditch, ∘ Fix, ● Nest site)

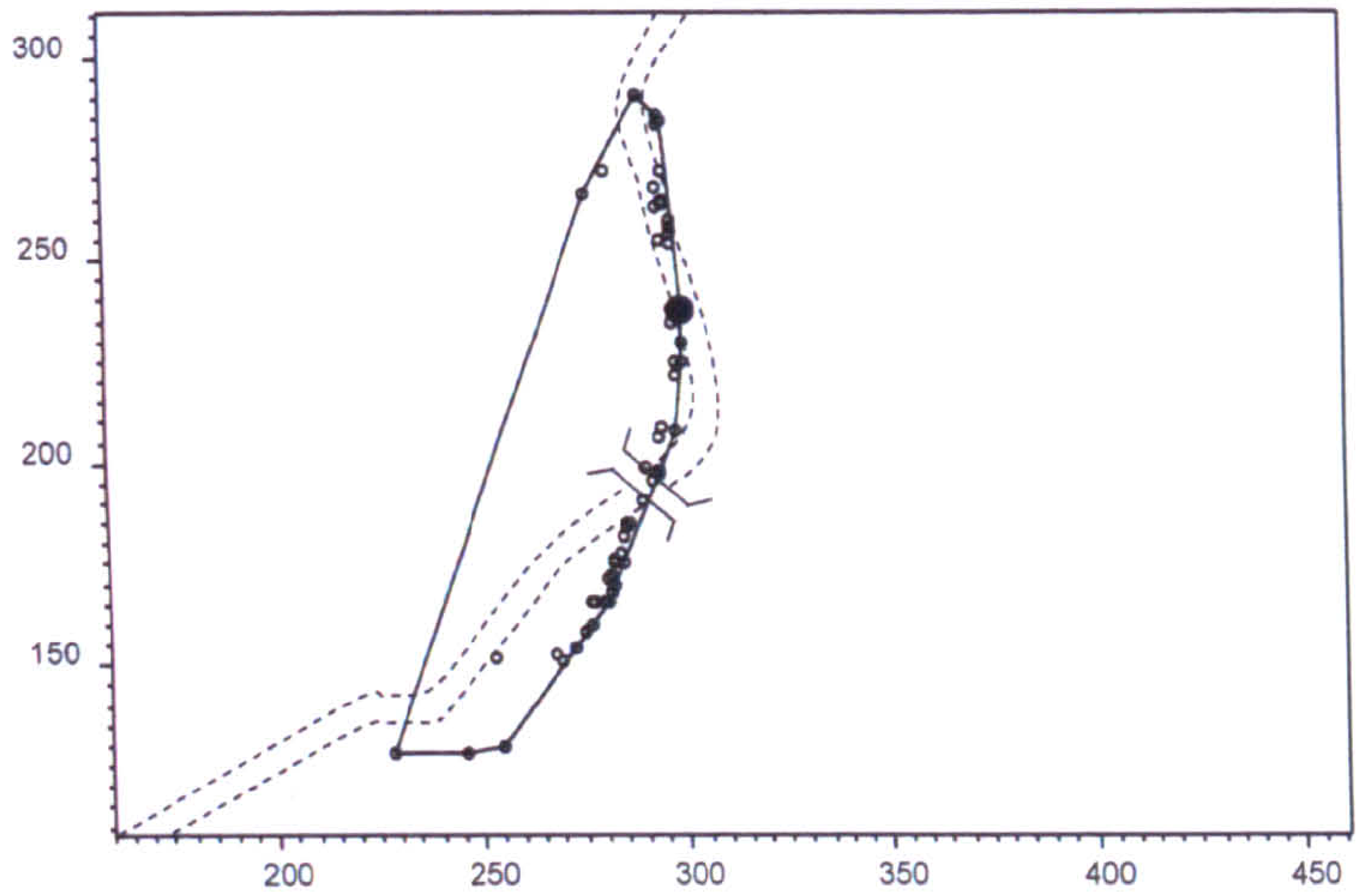

Figure A2.28 95% Minimum Convex Polygon for **Vole H♂ 21 March 2000** (— MCP, ---- Ditch, ∘ Fix, ● Nest site)

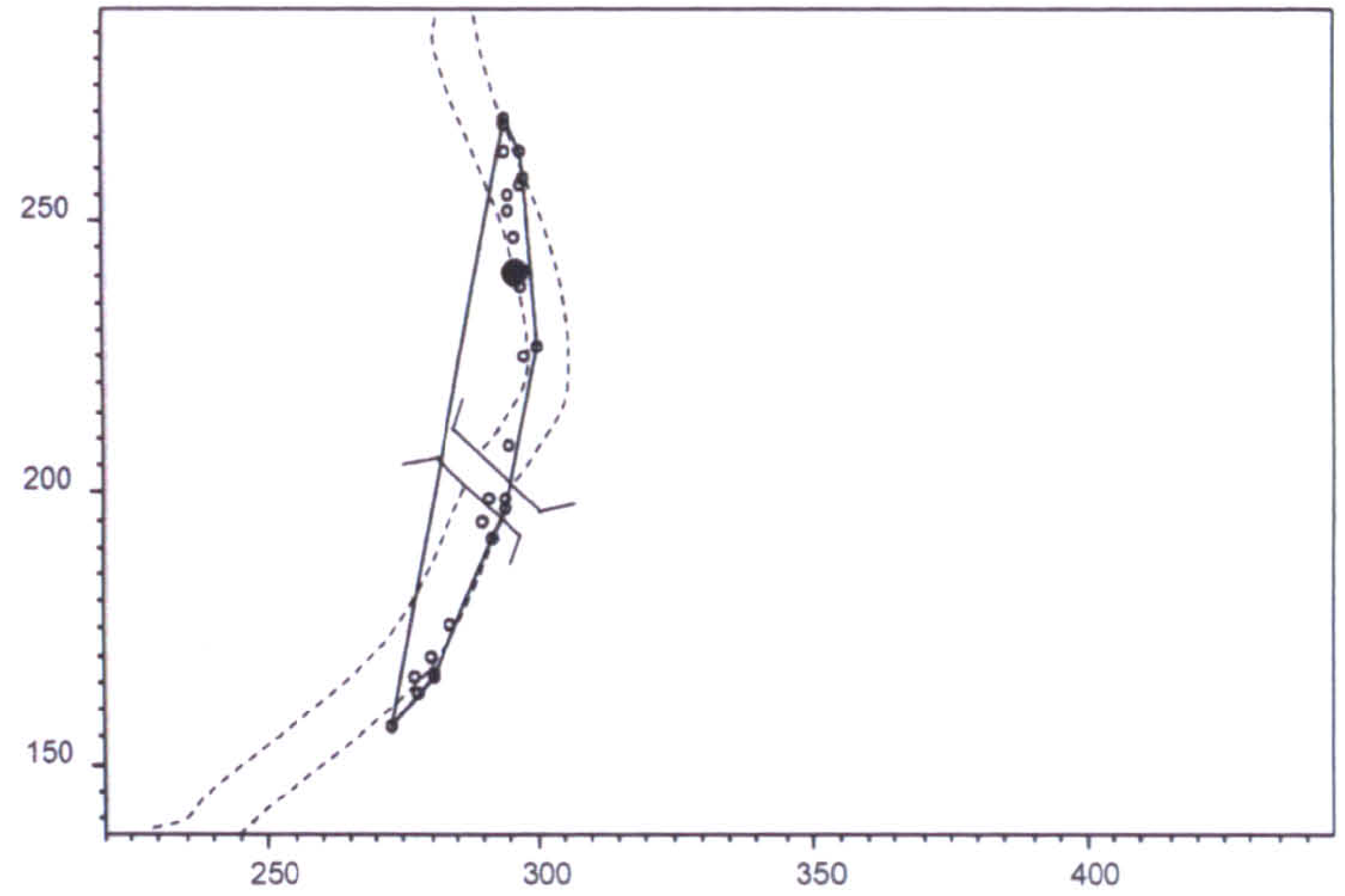

Figure A2.29 95% Minimum Convex Polygon for **Vole H♂ 15 April 2000** (— MCP, ---- Ditch, ∘ Fix, ● Nest site)

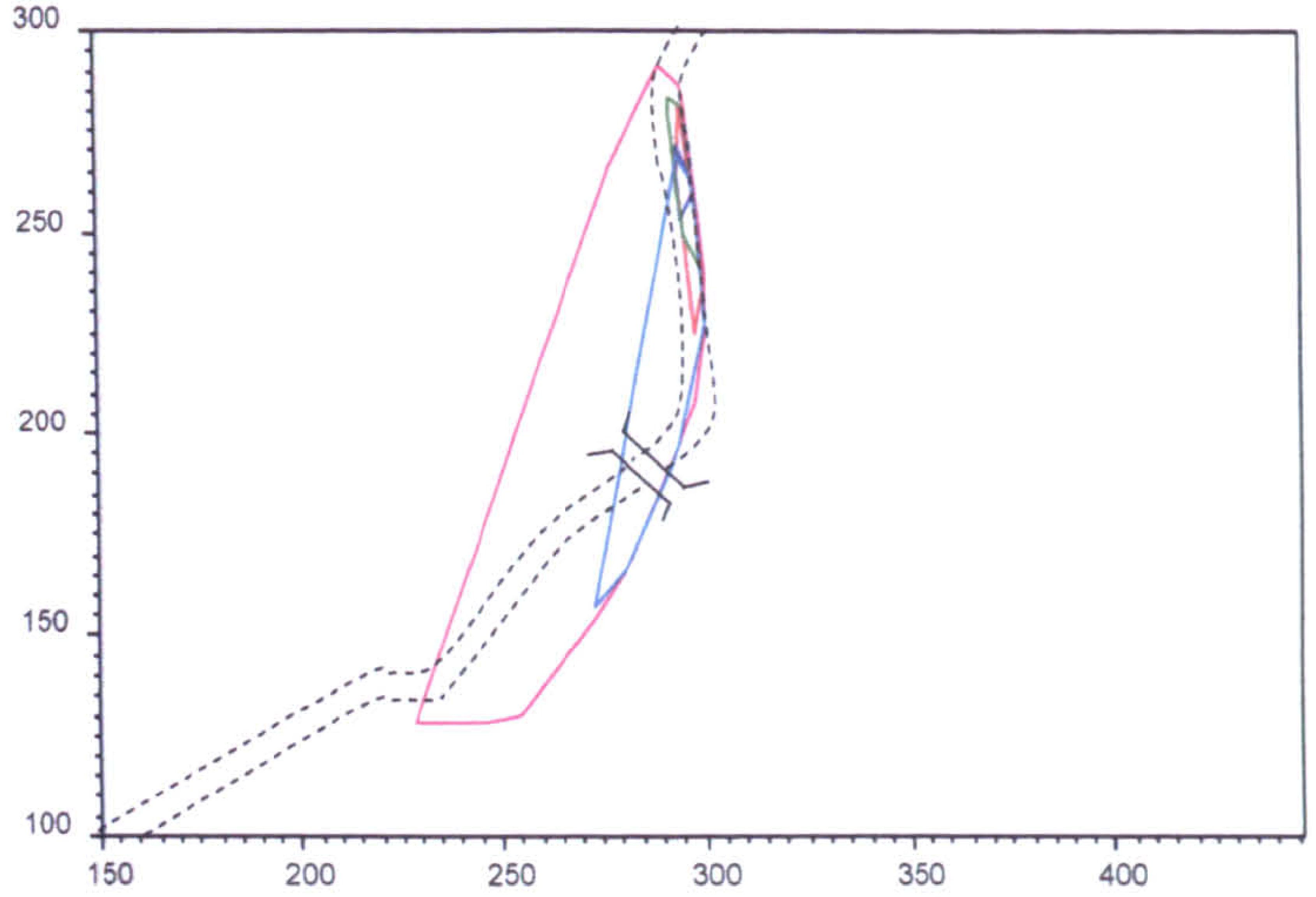

Figure A2.30 95% Minimum Convex Polygons for **Vole H♂** (— 16 February 2000, — 1 March 2000, — 11 March 2000, — 21 March 2000, — 15 April 2000, ---- Ditch)

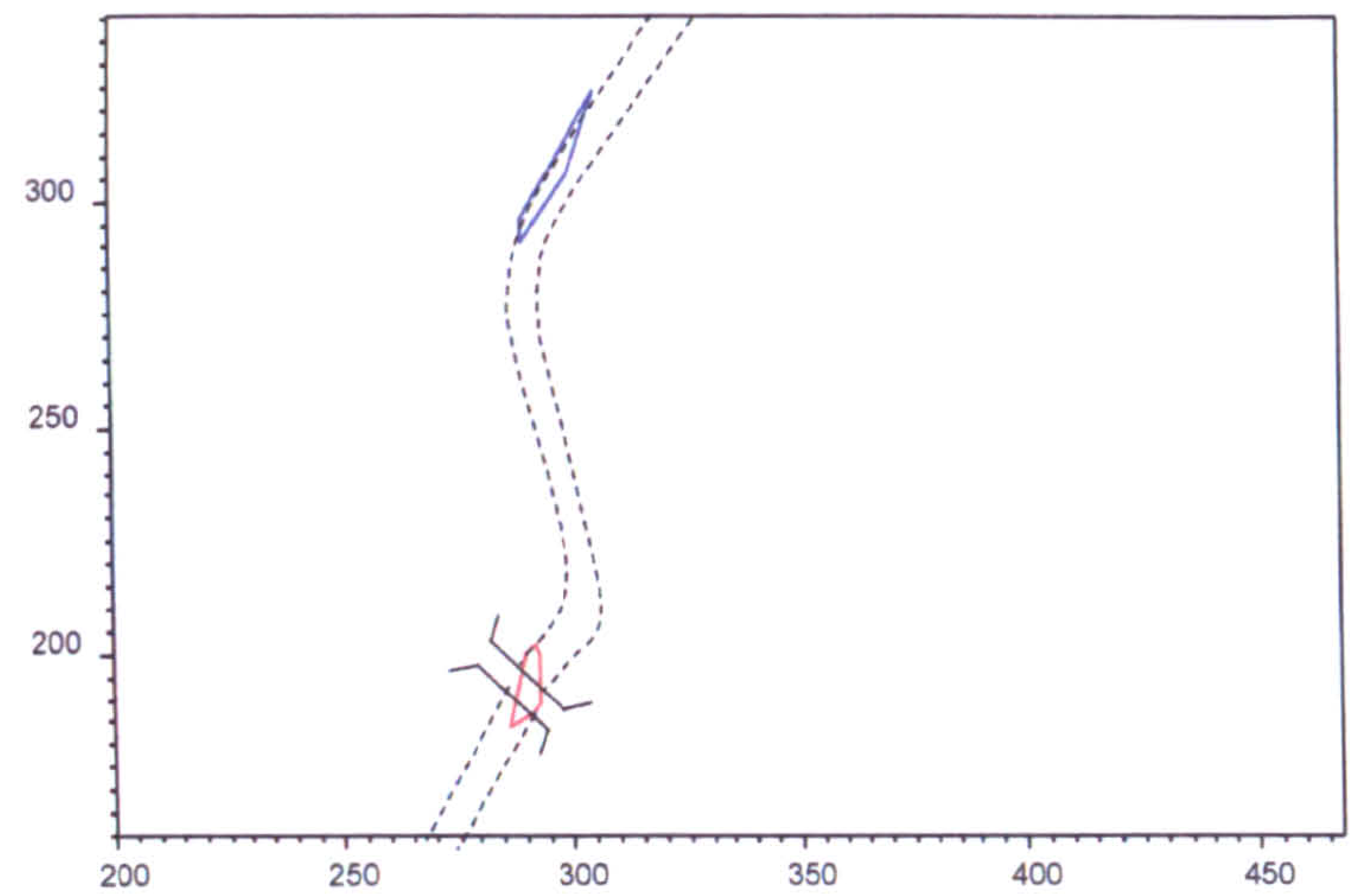

Figure A2.31 95% Minimum Convex Polygons for **Vole E♂ and Vole F♂ 12 January 2000** (— Vole E♂, — Vole F♂, ---- Ditch)

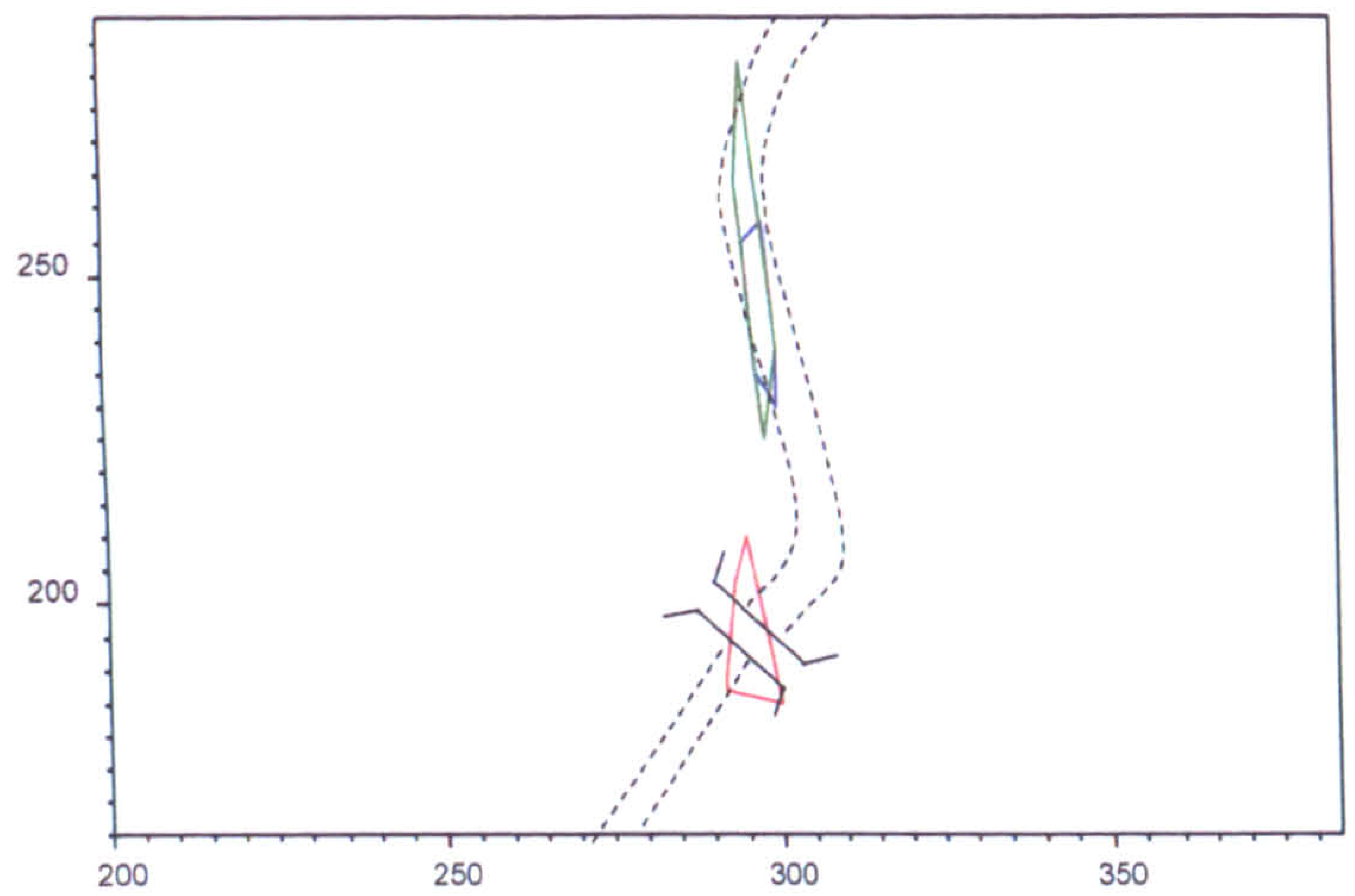

Figure A2.32 95% Minimum Convex Polygons for **Vole E♂, Vole G♀ and Vole H♂ 15/16 February 2000** (— Vole E♂, —Vole G♀, —Vole H♂, ---- Ditch)

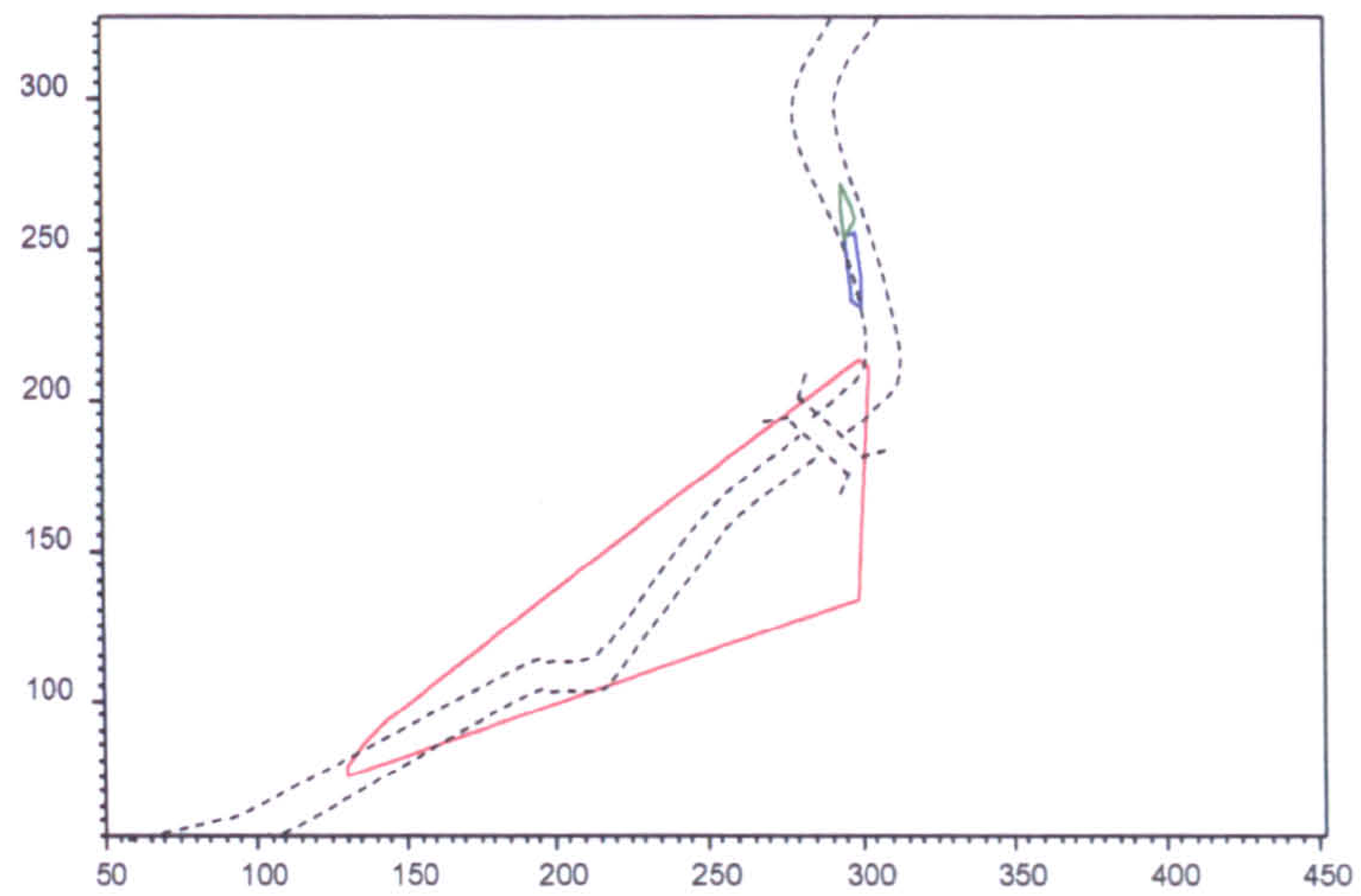

Figure A2.33 95% Minimum Convex Polygons for **Vole E♂, Vole G♀ and Vole H♂ 1 March 2000** (— Vole E♂, — Vole G♀, —Vole H♂, ---- Ditch)

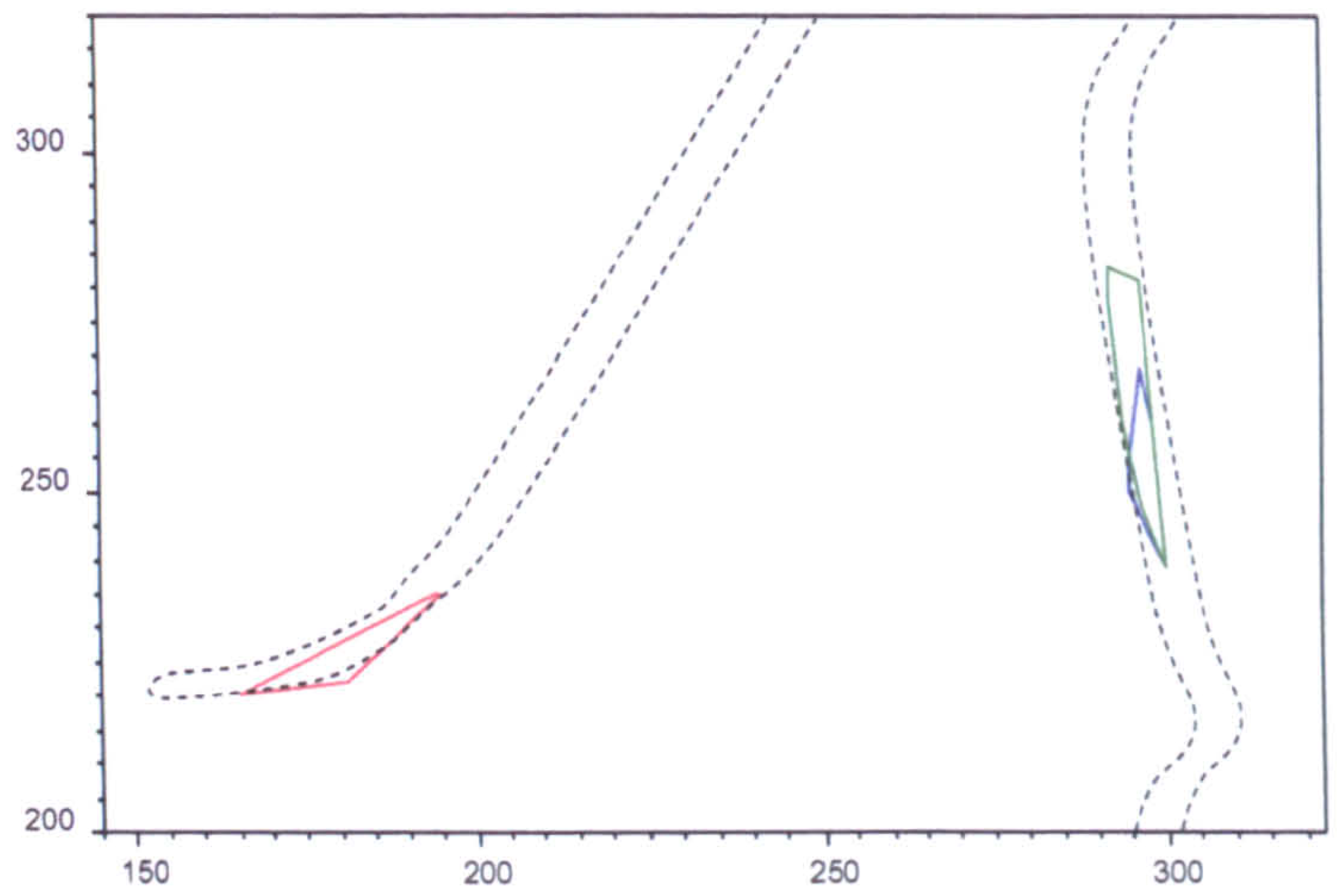

Figure A2.34 95% Minimum Convex Polygons for **Vole E♂, Vole G♀ and Vole H♂ 11 March 2000** (— Vole E♂, — Vole G♀, — Vole H♂, ---- Ditch)

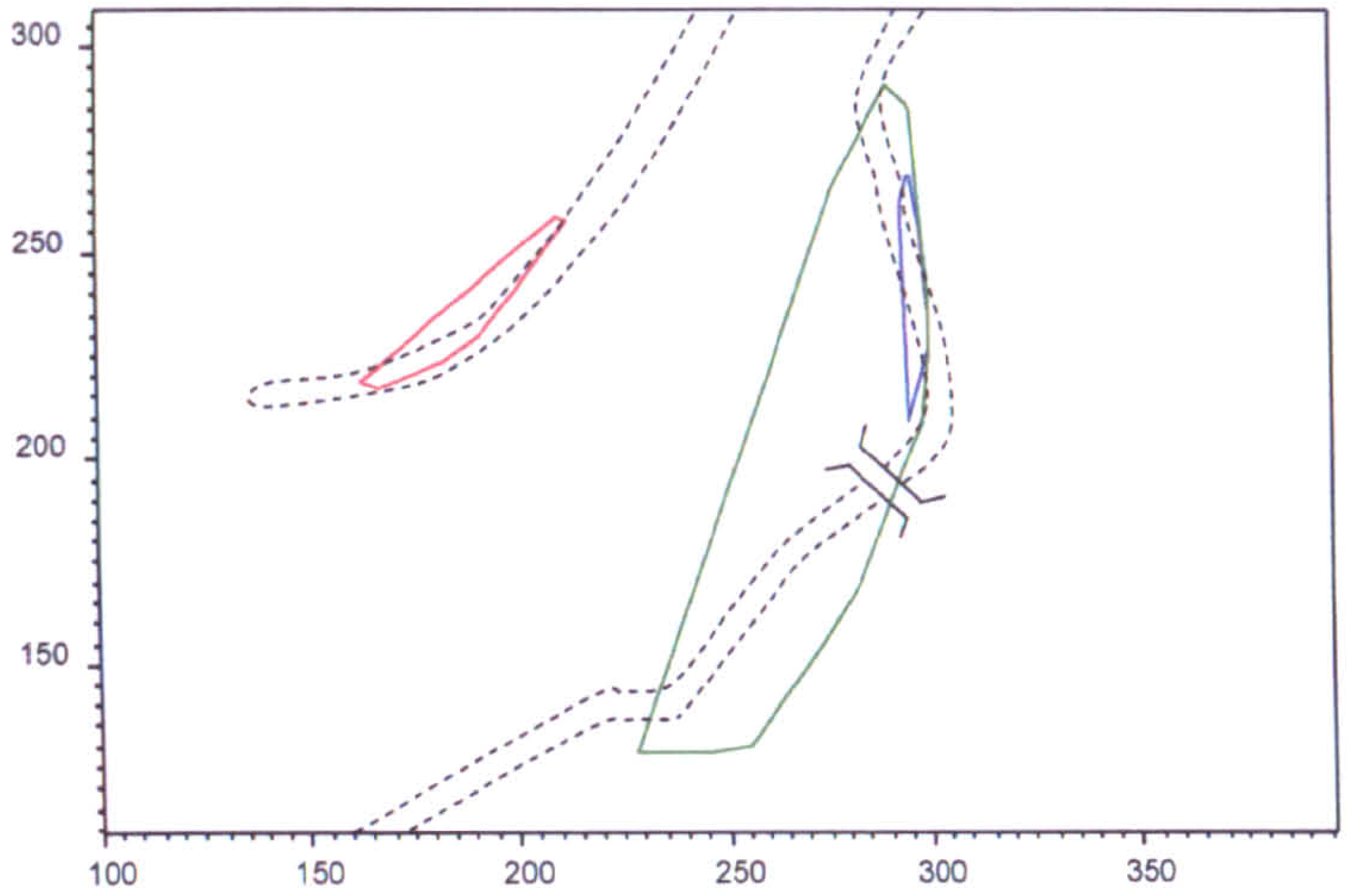

Figure A2.35 95% Minimum Convex Polygons for **Vole E♂ , Vole G♀ and Vole H♂ 22 March 2000** (— Vole E♂, — Vole G♀, — Vole H♂, ---- Ditch)

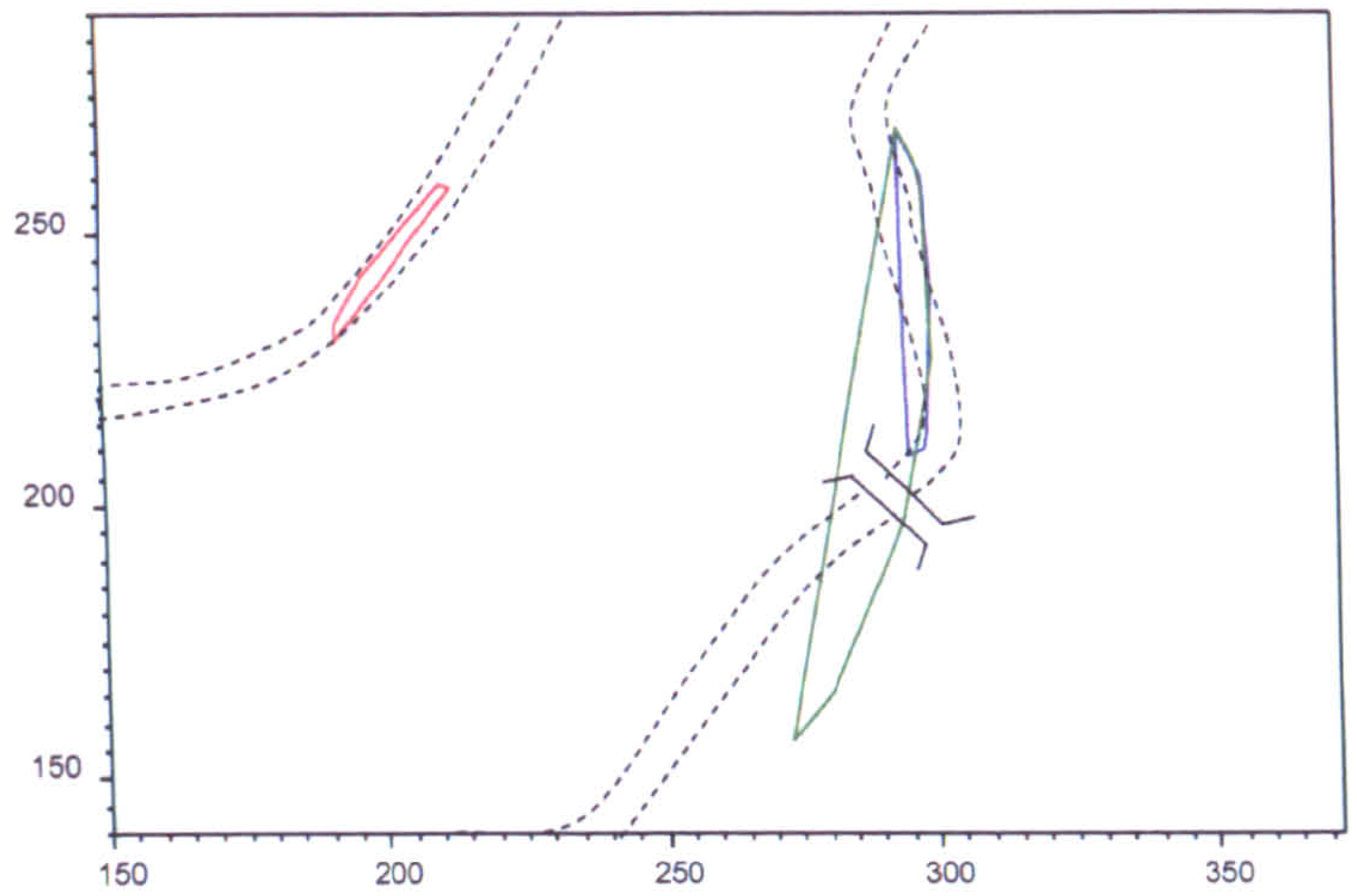

Figure A2.36 95% Minimum Convex Polygons for **Vole E♂ , Vole G♀ and Vole H♂ 15 April 2000** (— Vole E♂, — Vole G♀, — Vole H♂, ---- Ditch)

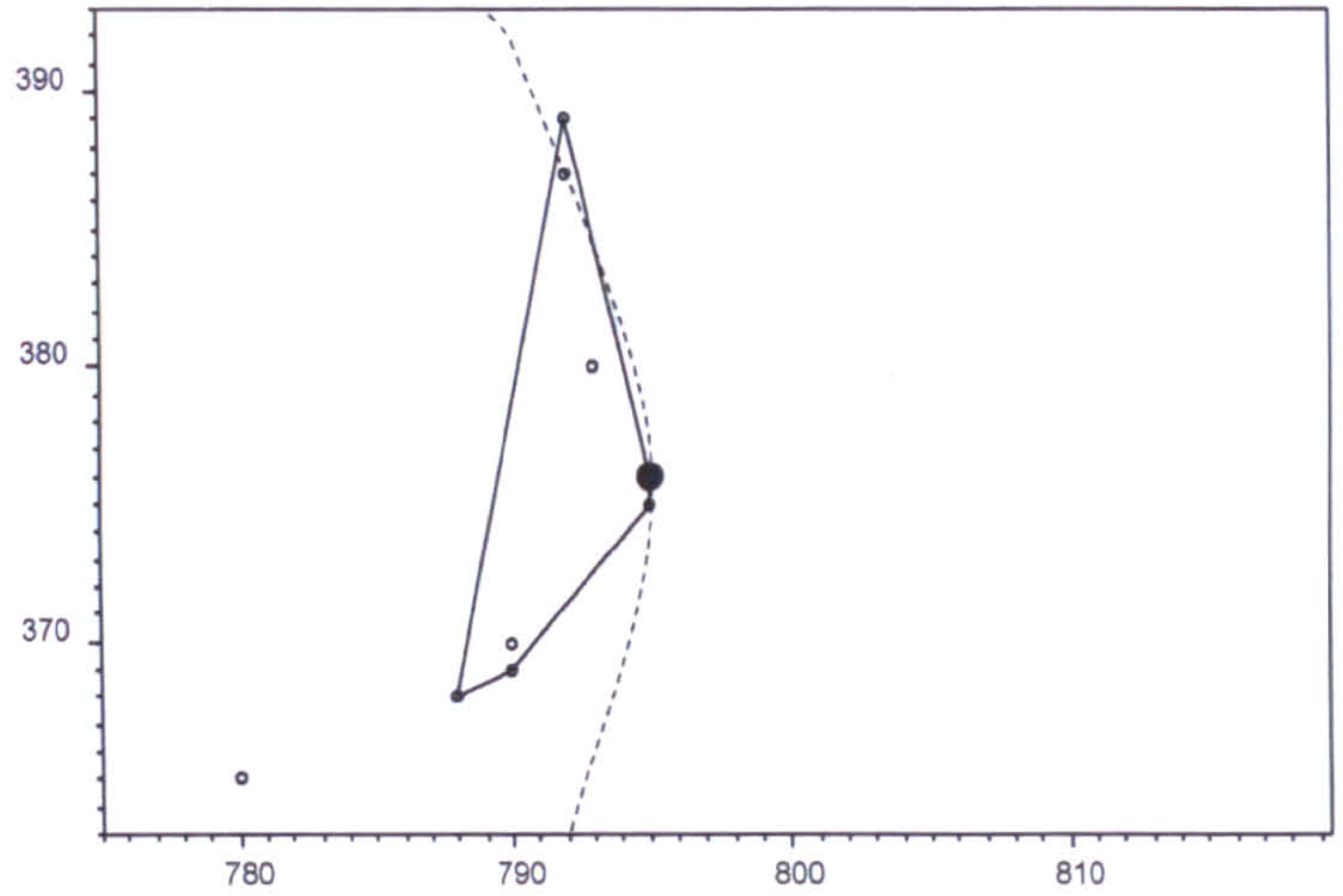

Figure A2.37 95% Minimum Convex Polygon for **Vole D♂ 16 November 1999** (— MCP, ---- Pond, ∘ Fix, ● Nest site)

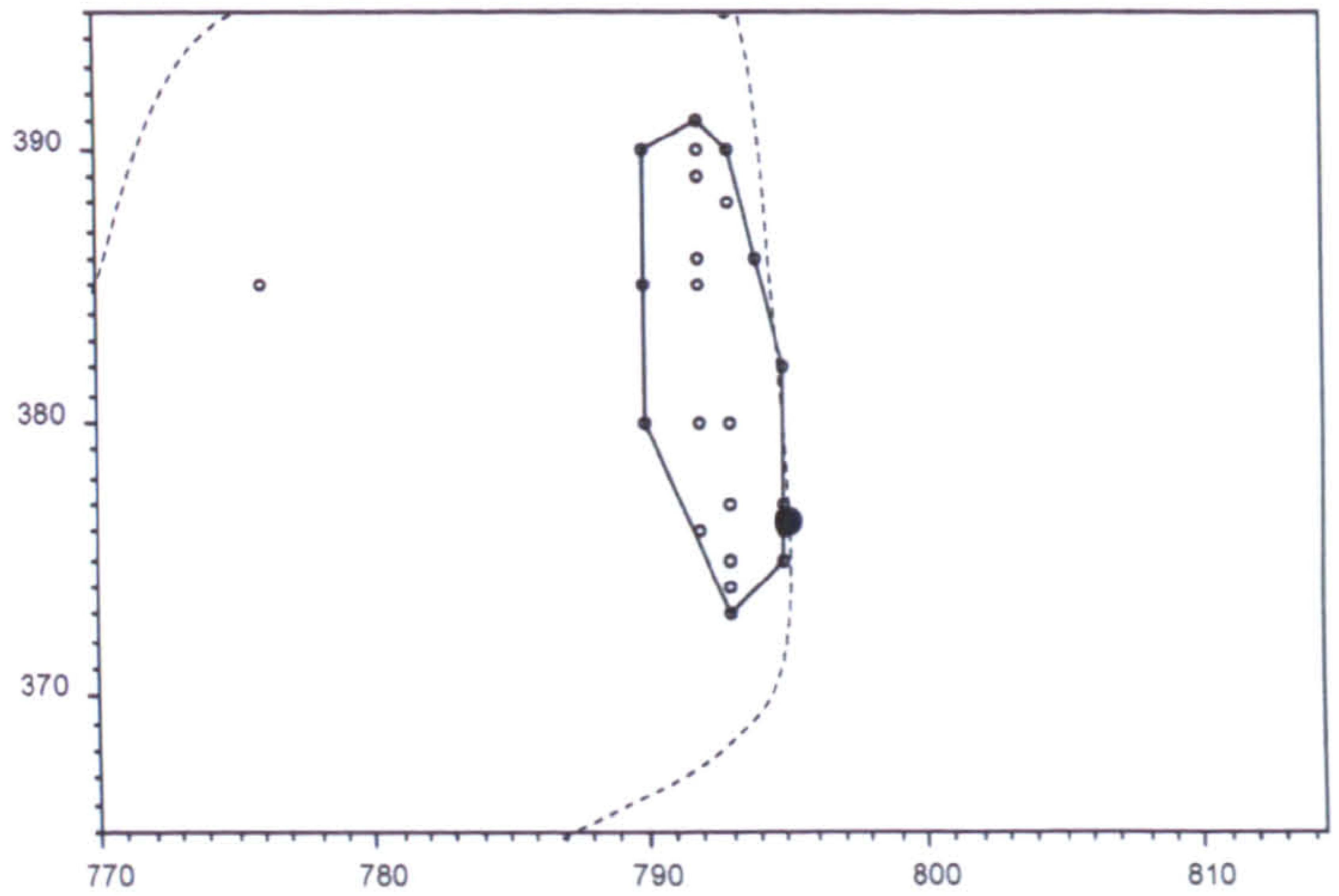

Figure A2.38 95% Minimum Convex Polygon for **Vole D♂ 23 November 1999** (— MCP, ---- Pond, ∘ Fix, ● Nest site)

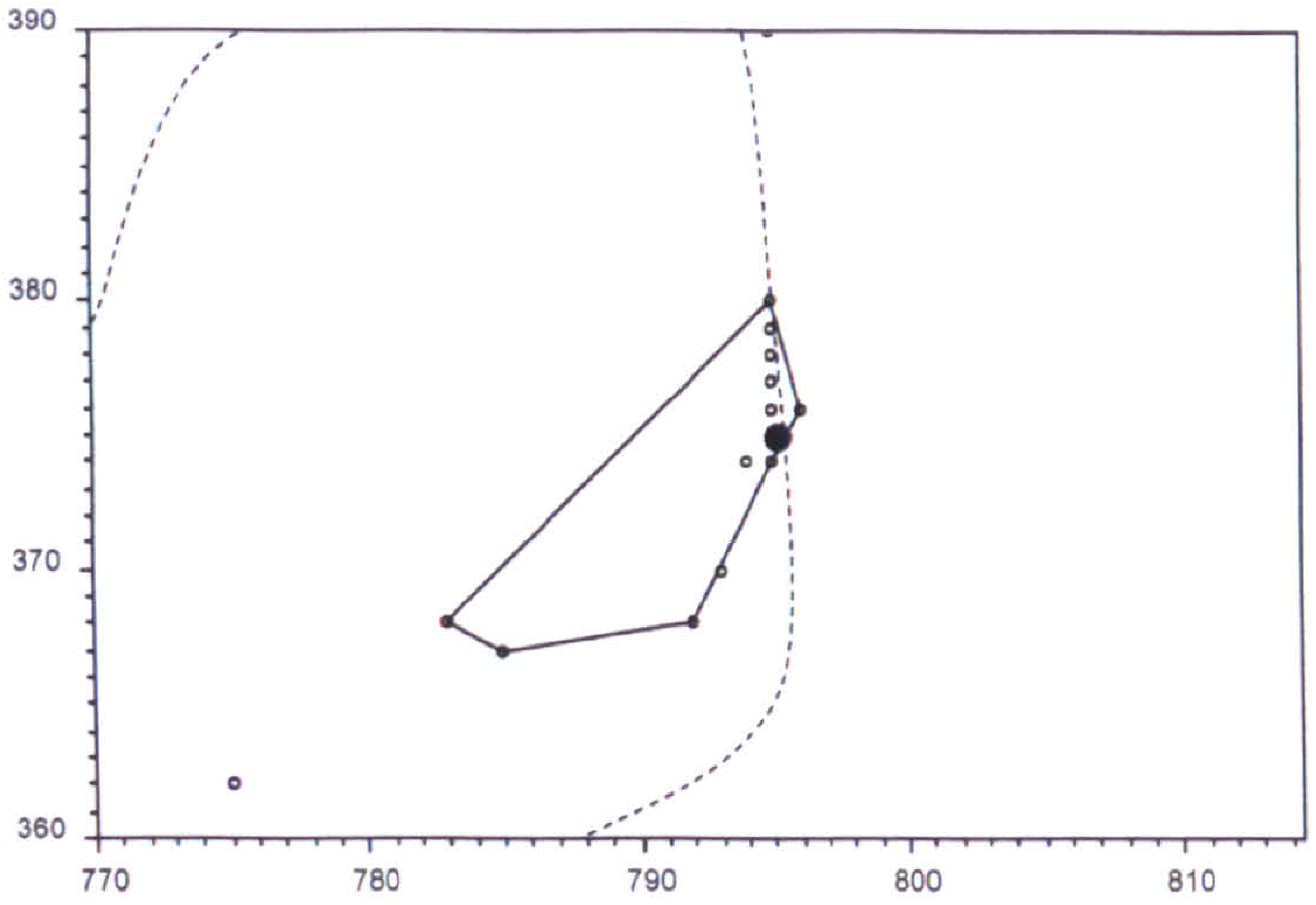

Figure A2.39 95% Minimum Convex Polygon for **Vole D♂ 30 November 1999** (—MCP, ---- Pond, ∘ Fix, ● Nest site)

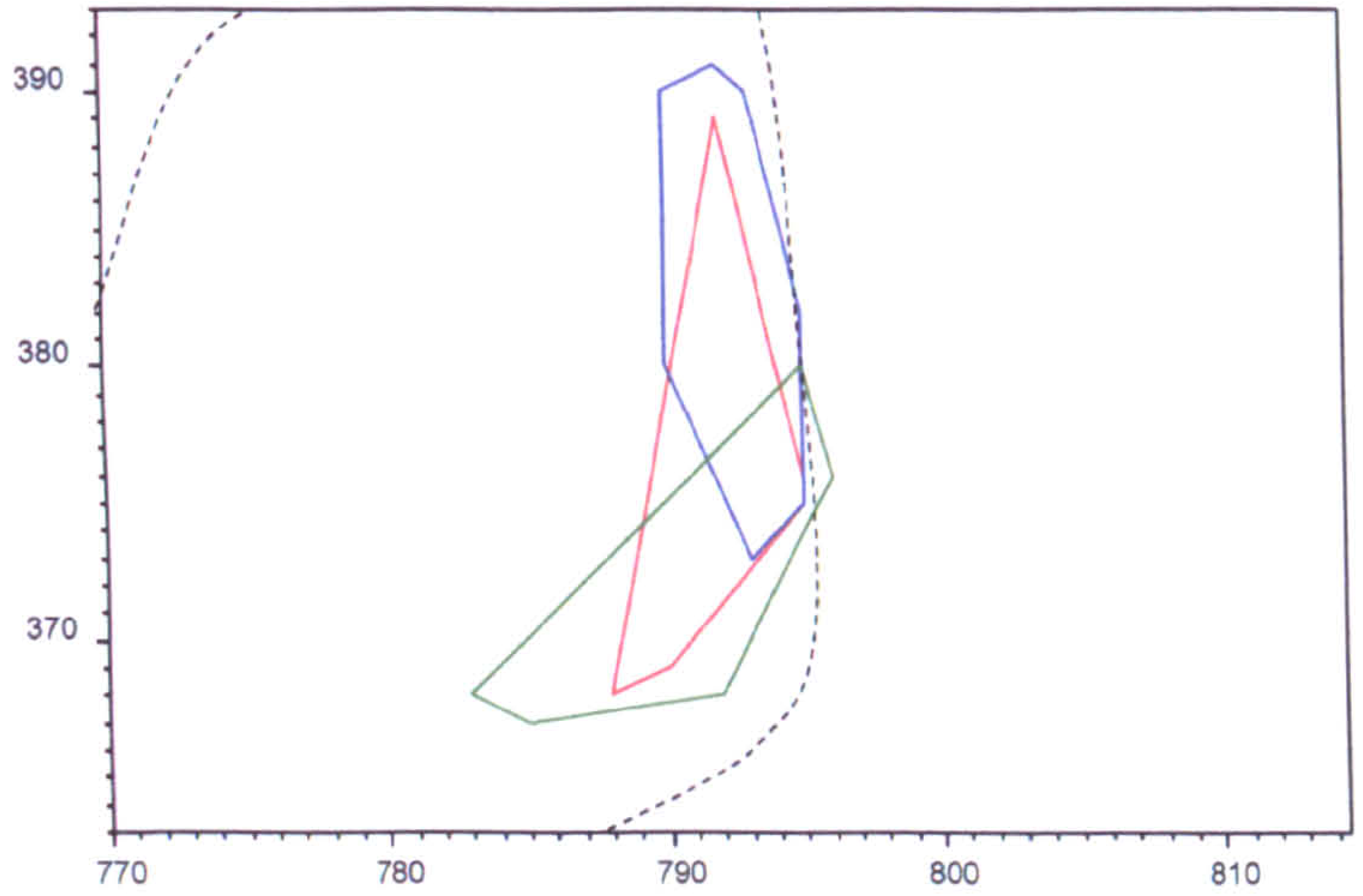

Figure A2.40 95% Minimum Convex Polygons for **Vole D♂**
(— 16 November 1999, — 23 November 1999,
— 30 November 1999, ---- Pond)

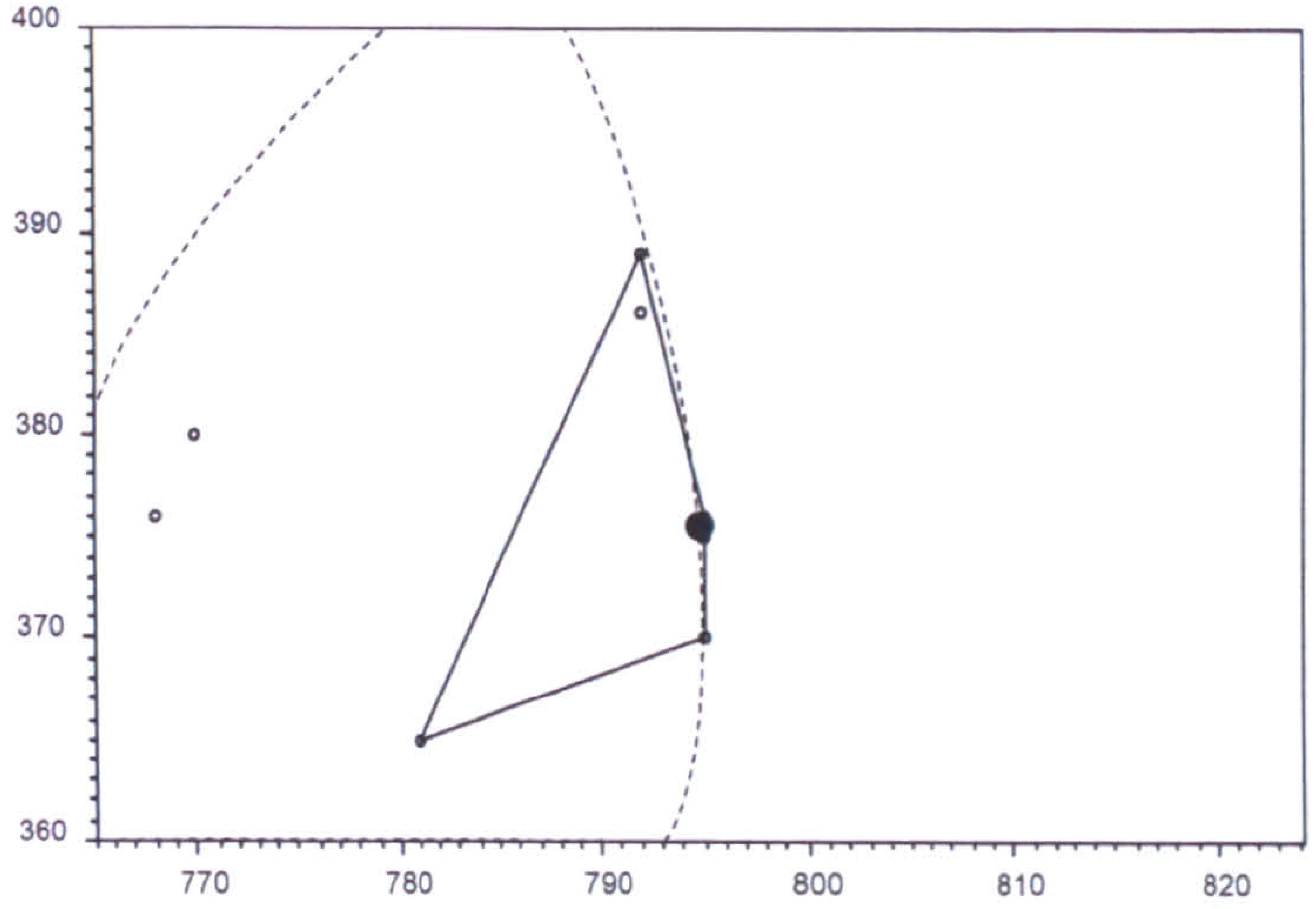

Figure A2.41 95% Minimum Convex Polygon for **Vole EM♀ 16 November 1999** (— MCP, ---- Pond, ∘ Fix, ● Nest site)

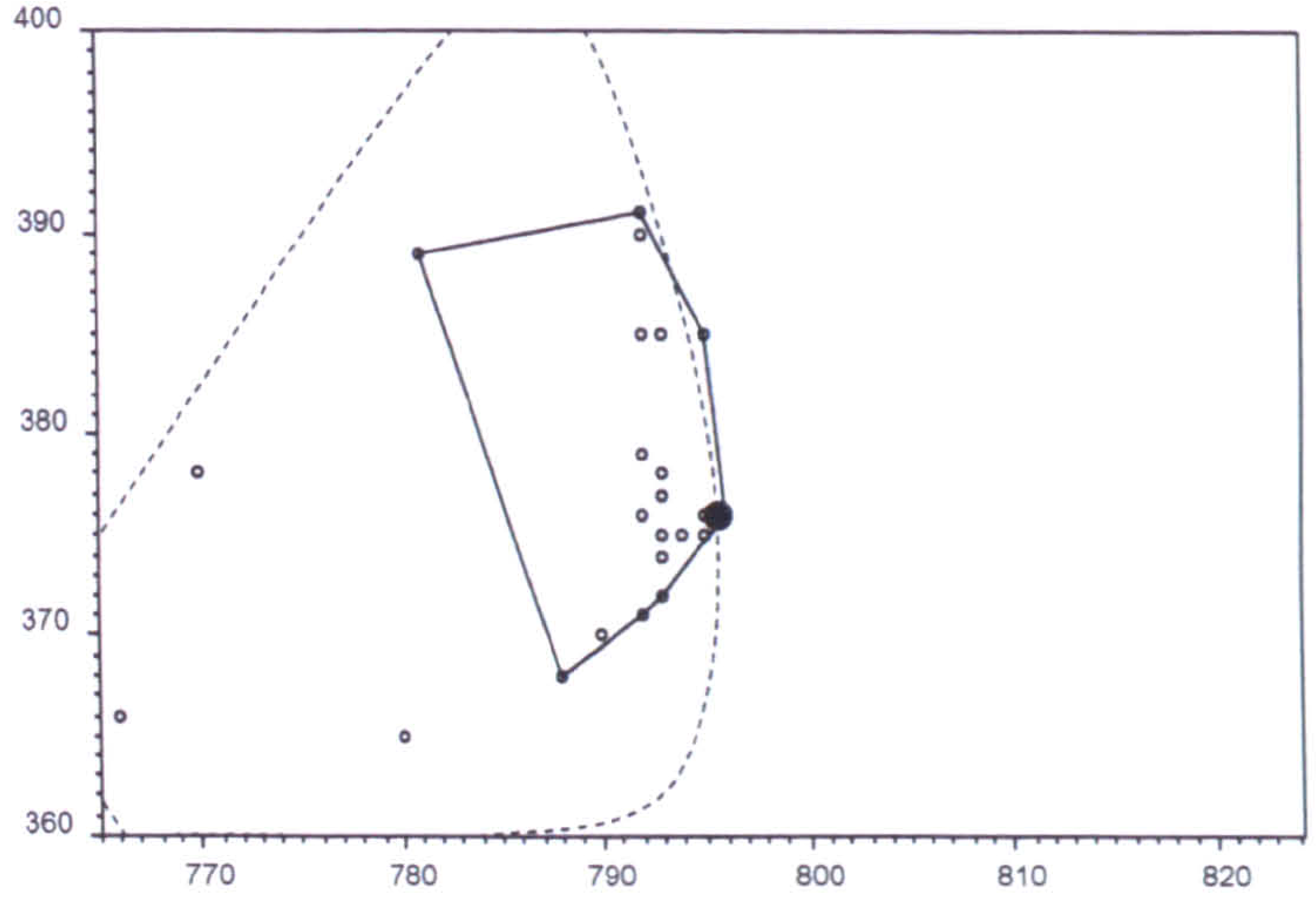

Figure 2.42 95% Minimum Convex Polygon for **Vole EM♀ 22 November 1999** (— MCP, ---- Pond, ∘ Fix, ● Nest site)

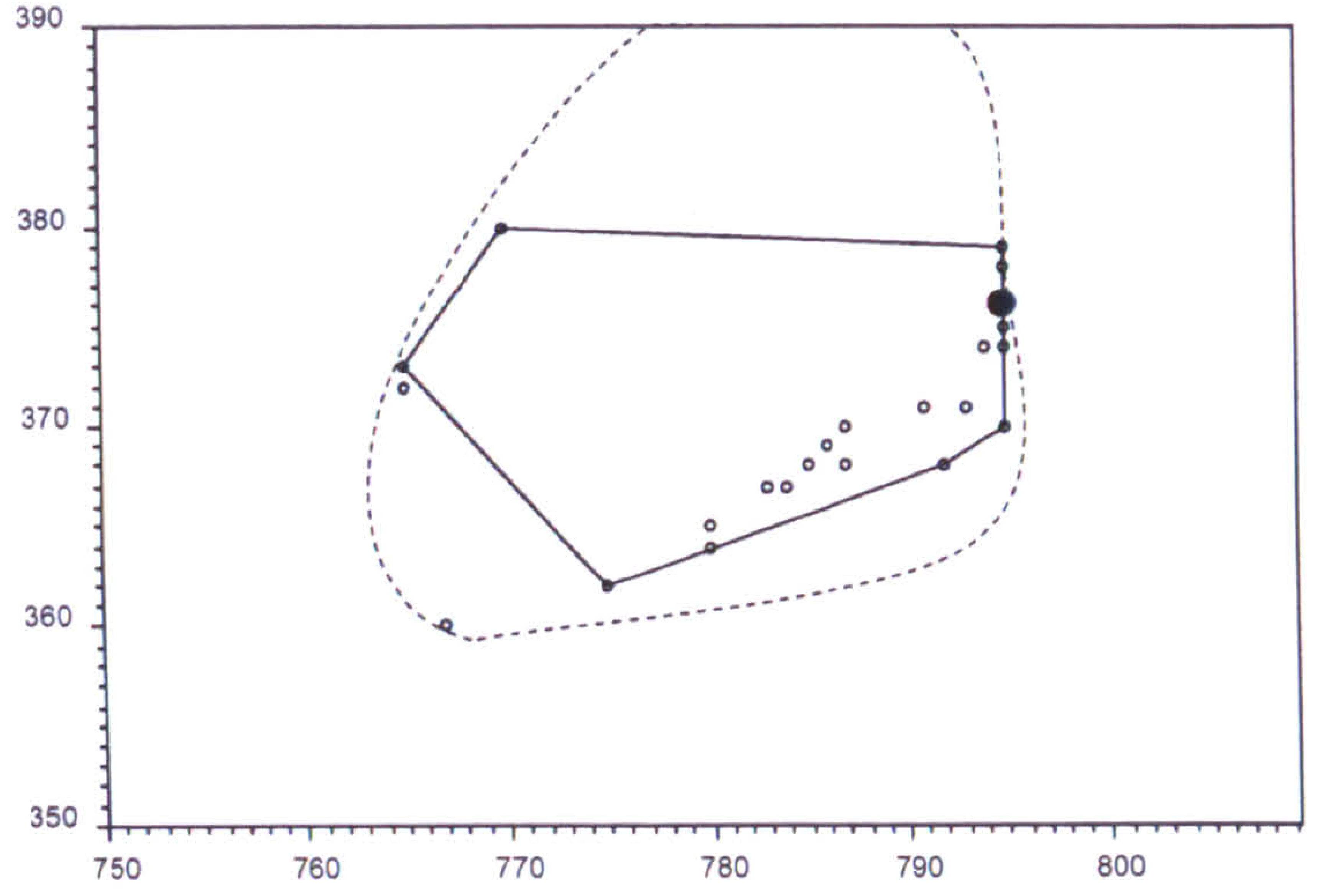

Figure A2.43 95% Minimum Convex Polygon for **Vole EM♀ 30 November 1999** (— MCP, ---- Pond, ∘ Fix, ● Nest site)

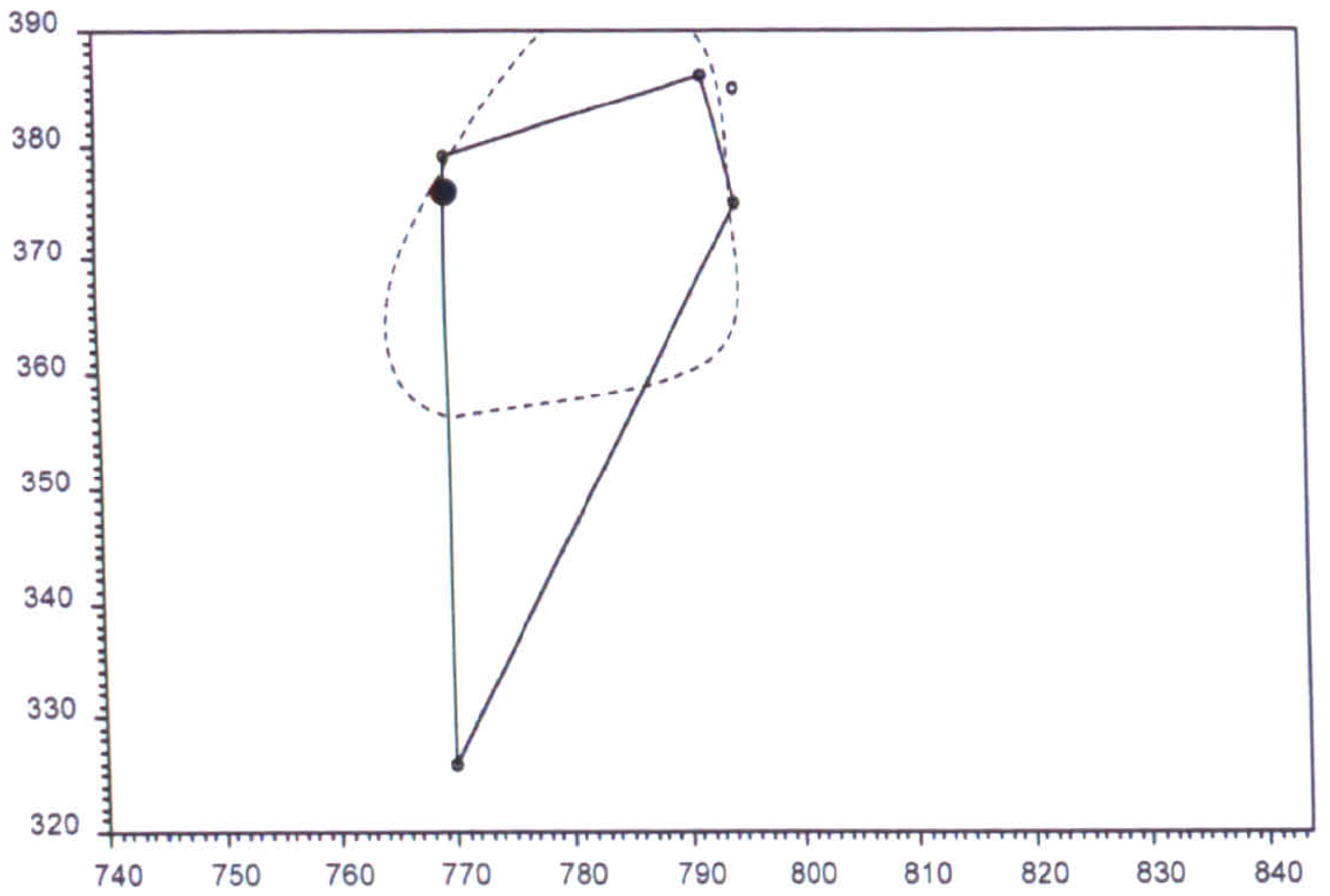

Figure A2.44 95% Minimum Convex Polygon for **Vole EM♀ 14 December 1999** (— MCP, ---- Pond, ∘ Fix, ● Nest site)

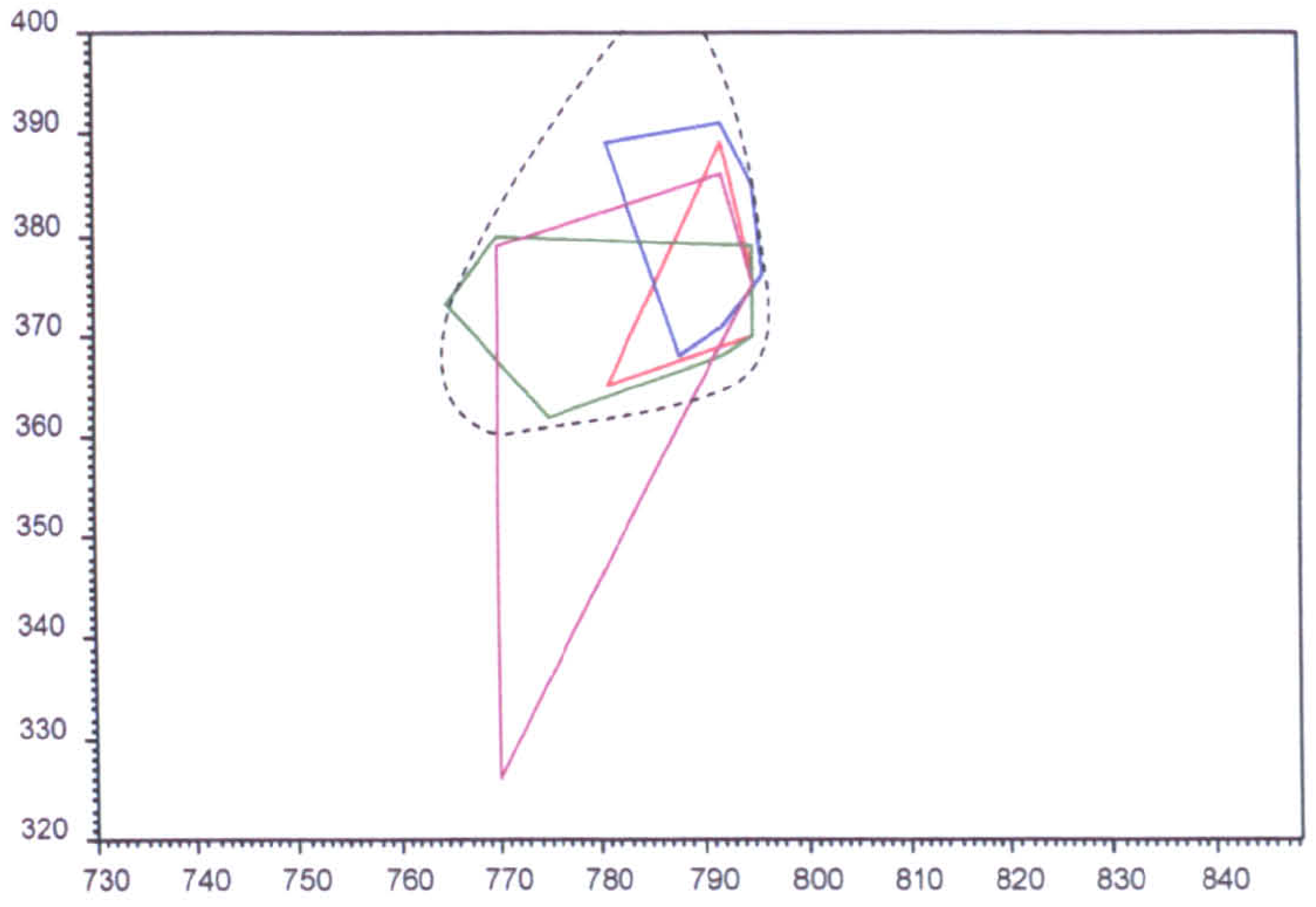

Figure A2.45 95% Minimum Convex Polygons for **Vole EM♀** (— 16 November 1999, — 23 November 1999, — 30 November 1999, — 14 December 1999, ---- Pond)

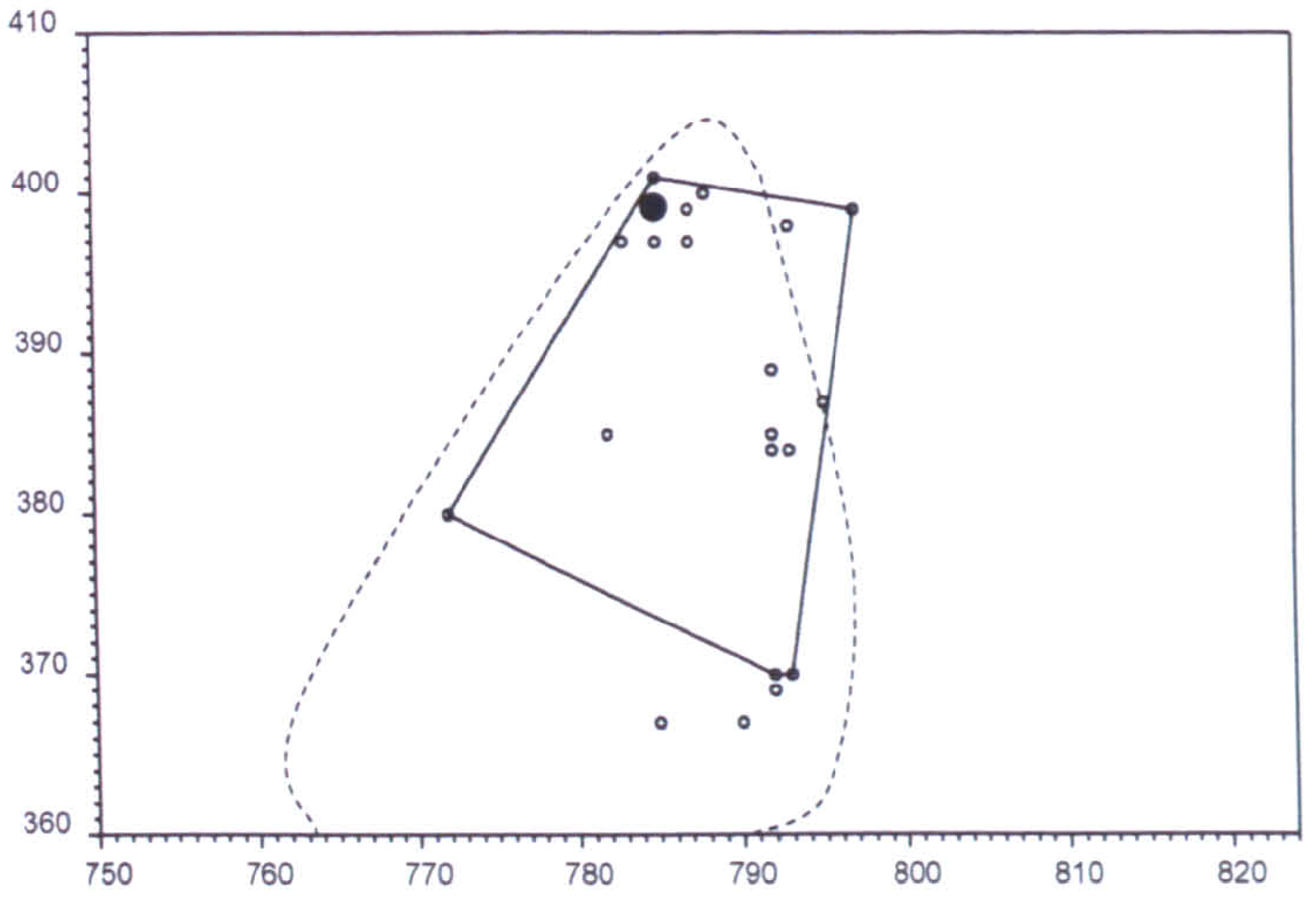

Figure A2.46 95% Minimum Convex Polygon for **Vole J♂ 22 February 2000** (__ MCP, ---- Pond, ∘ Fix, ● Nest site)

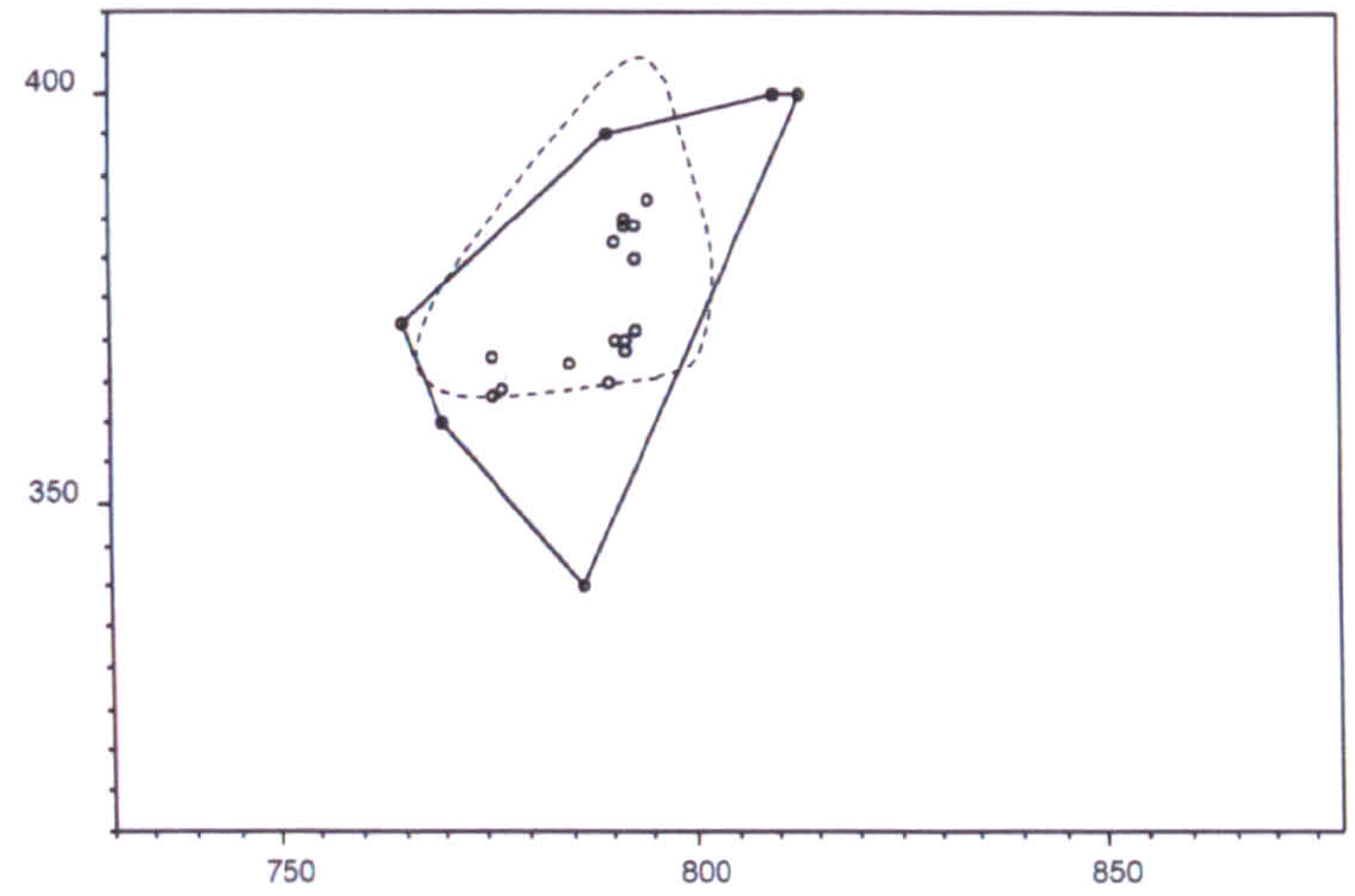

Figure A2.47 95% Minimum Convex Polygon for **Vole K♂ 22 February 2000** (—MCP, ---- Pond, ∘ Fix, ● Nest site)

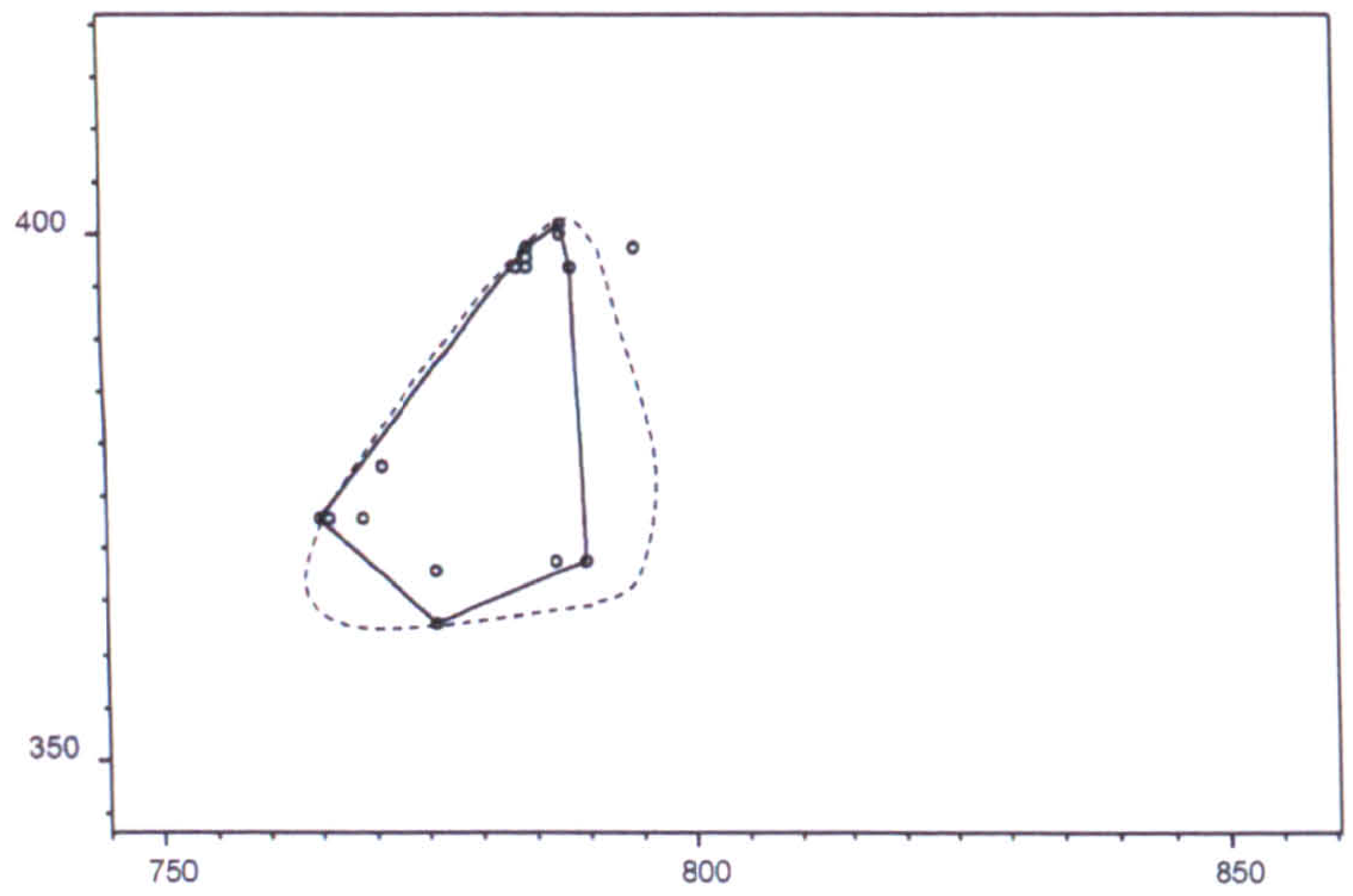

Figure A2.48 95% Minimum Convex Polygon for **Vole K♂ 6 March 2000** (— MCP, ---- Pond, ∘ Fix, ● Nest site)

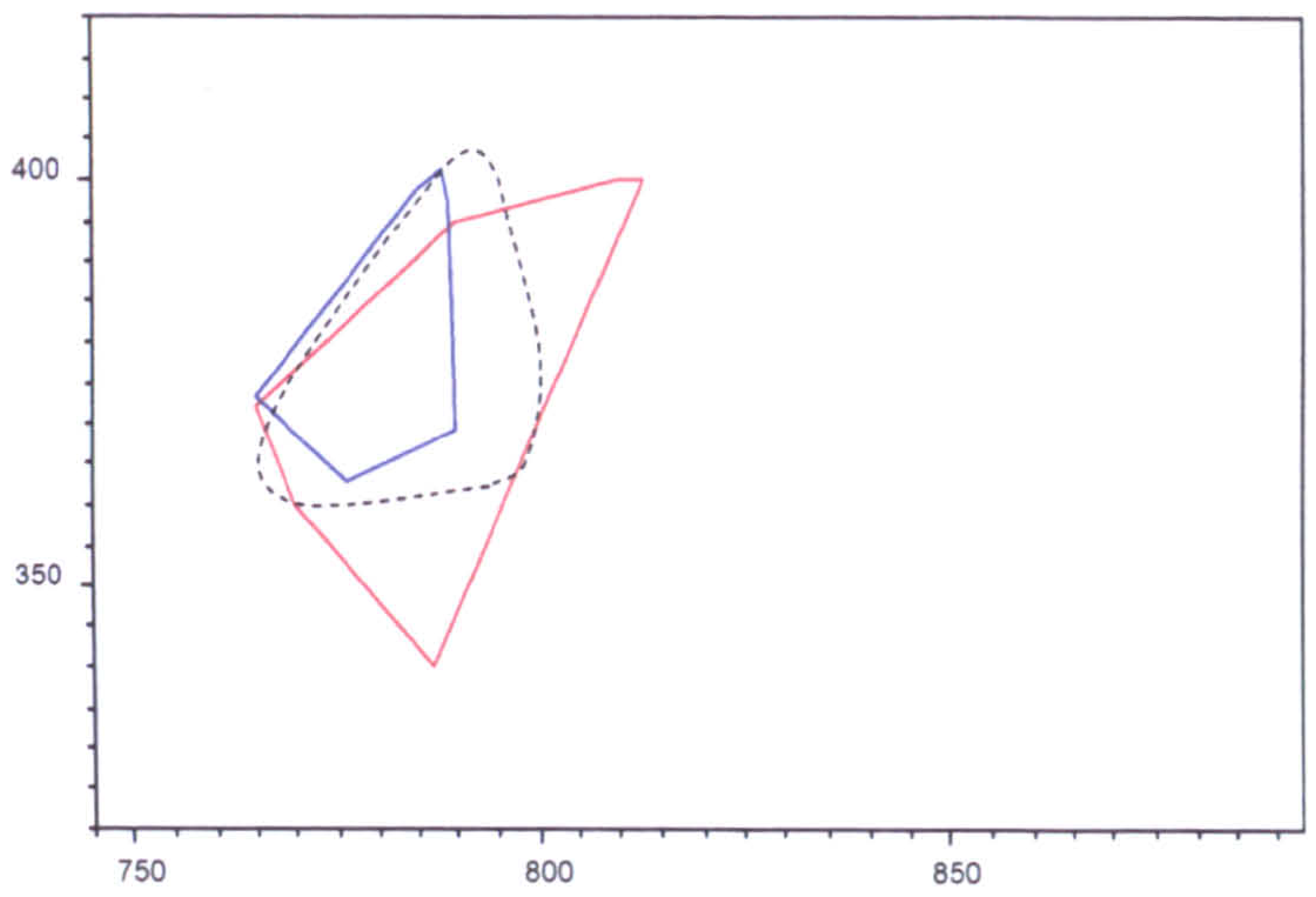

Figure A2.49 95% Minimum Convex Polygons for **Vole K♂** (— 22 February 2000, — 6 March 2000, ---- Pond)

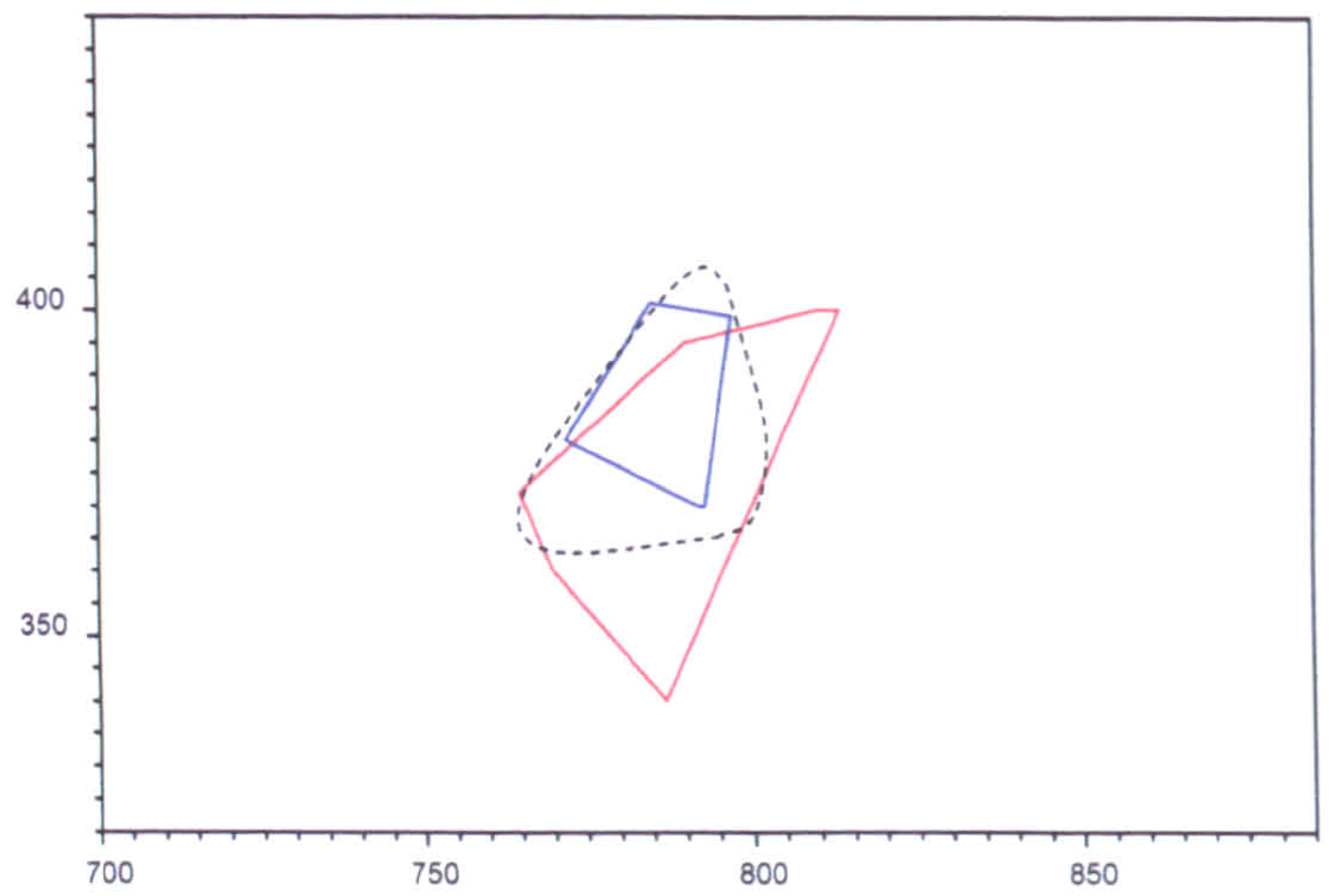

Figure A2.50 95% Minimum Convex Polygons for **Vole K♂ and Vole J♂ 22 February 2000** (— Vole K♂, —Vole J♂, ---- Ditch)

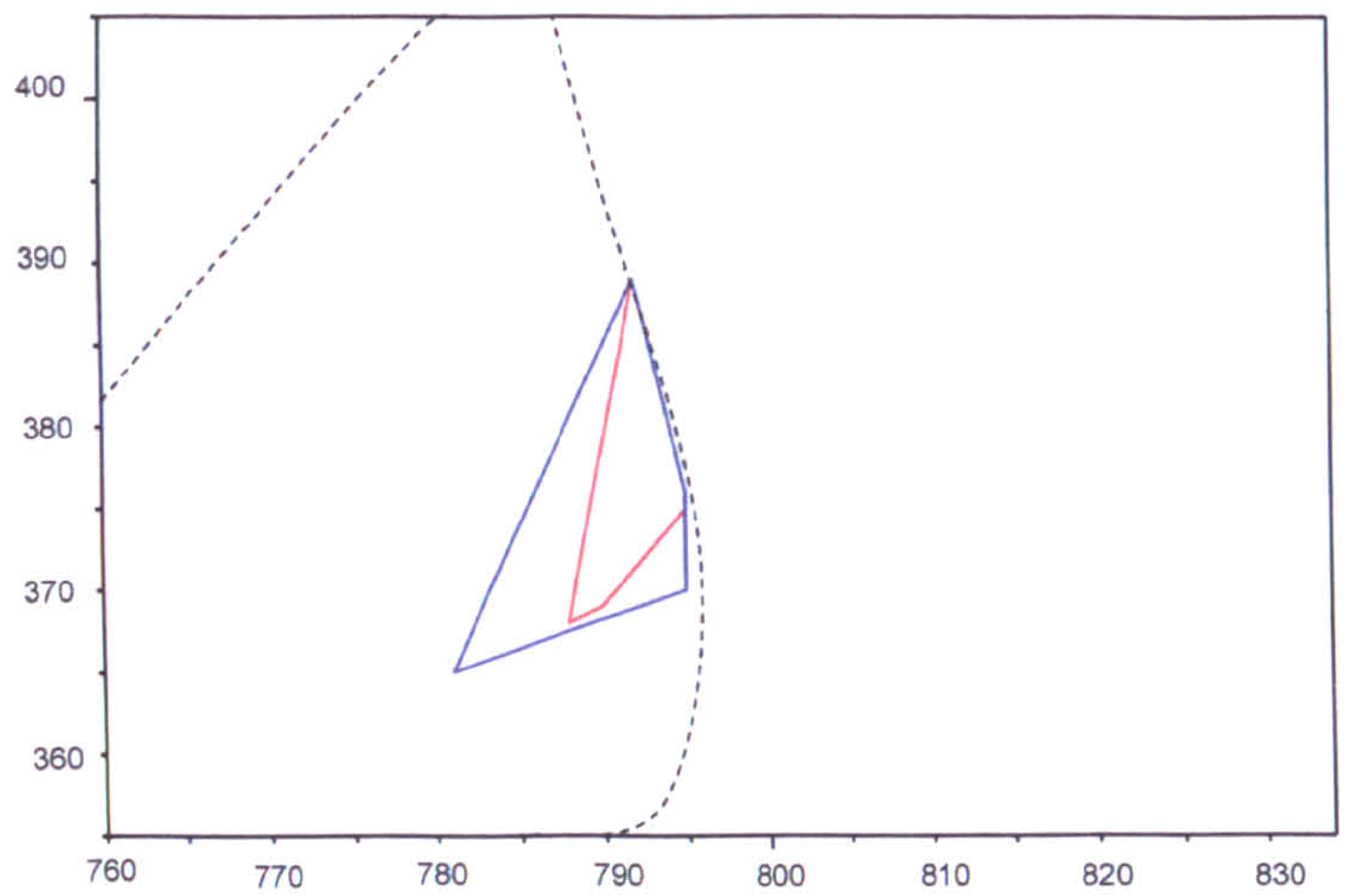

Figure A2.51 95% Minimum Convex Polygons for **Vole D♂ and Vole EM♀ 16 November 1999** (— Vole D♂, — Vole EM♀, ---- Ditch)

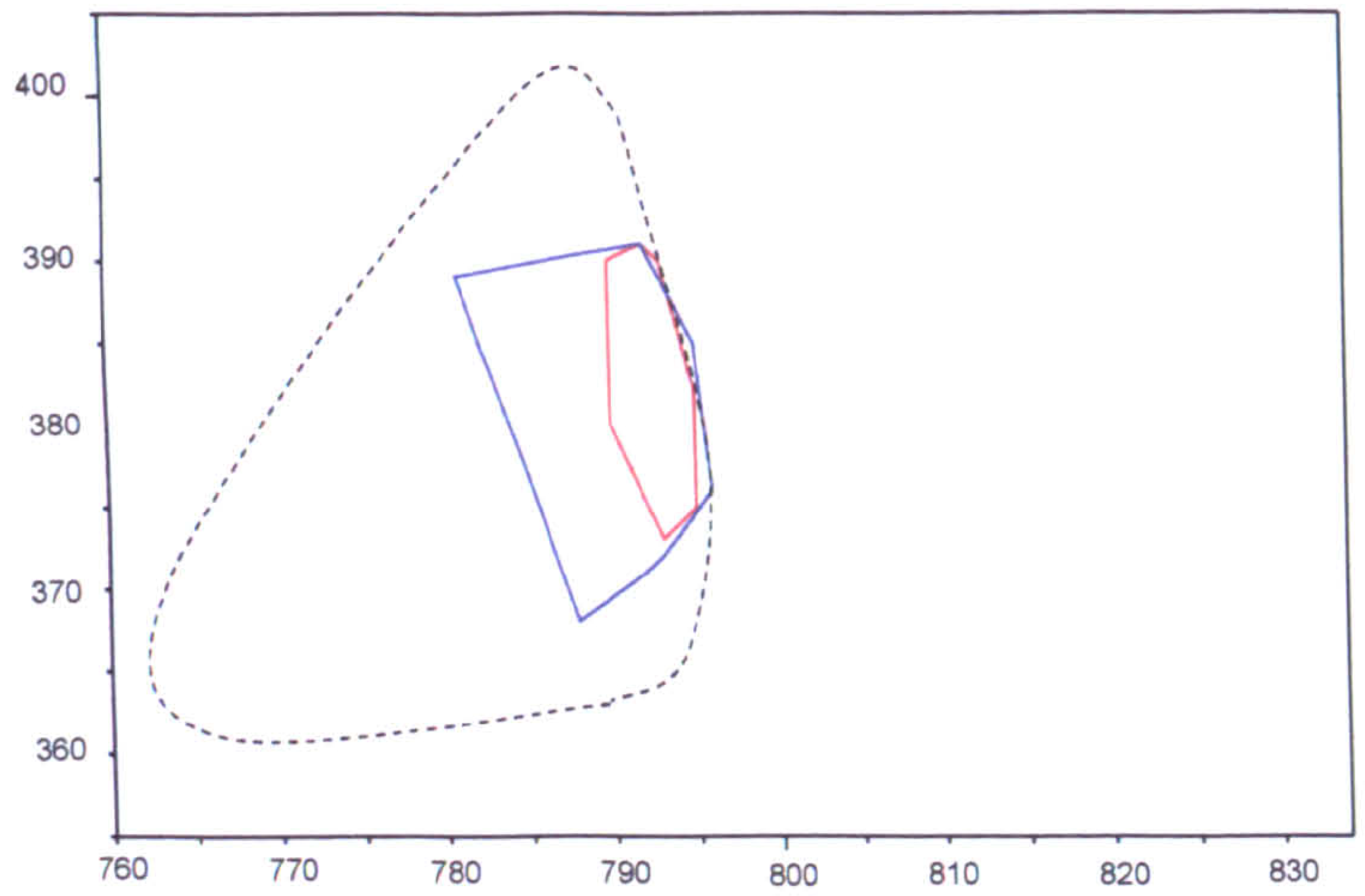

Figure A2.52 95% Minimum Convex Polygons for **Vole D♂ and Vole EM♀ 22 November 1999** (— Vole D♂, — Vole EM♀, ---- Ditch)

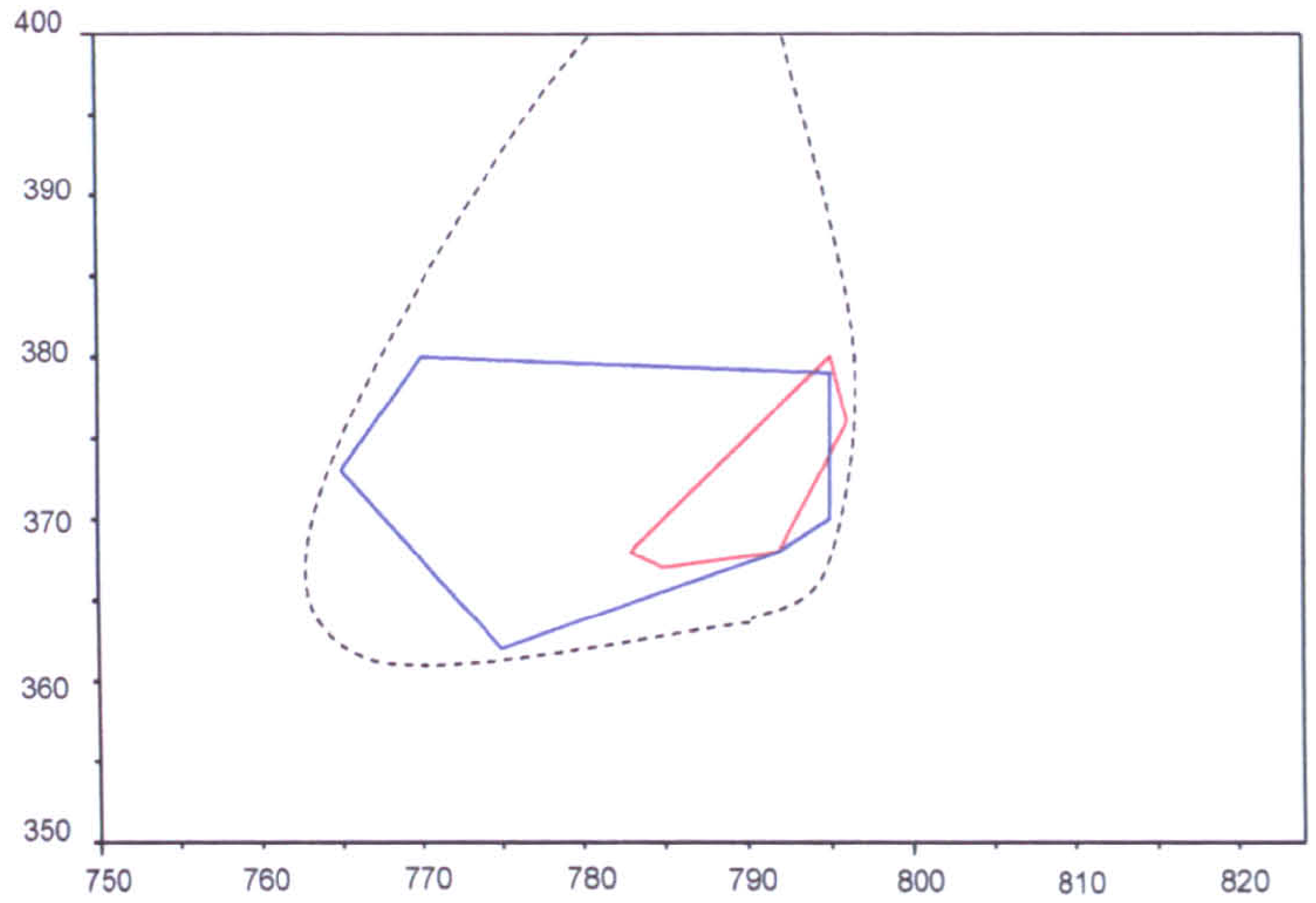

Figure A2.53 95% Minimum Convex Polygons for **Vole D♂ and Vole EM♀ 30 November 1999** (— Vole D♂, — Vole EM♀, ---- Ditch)

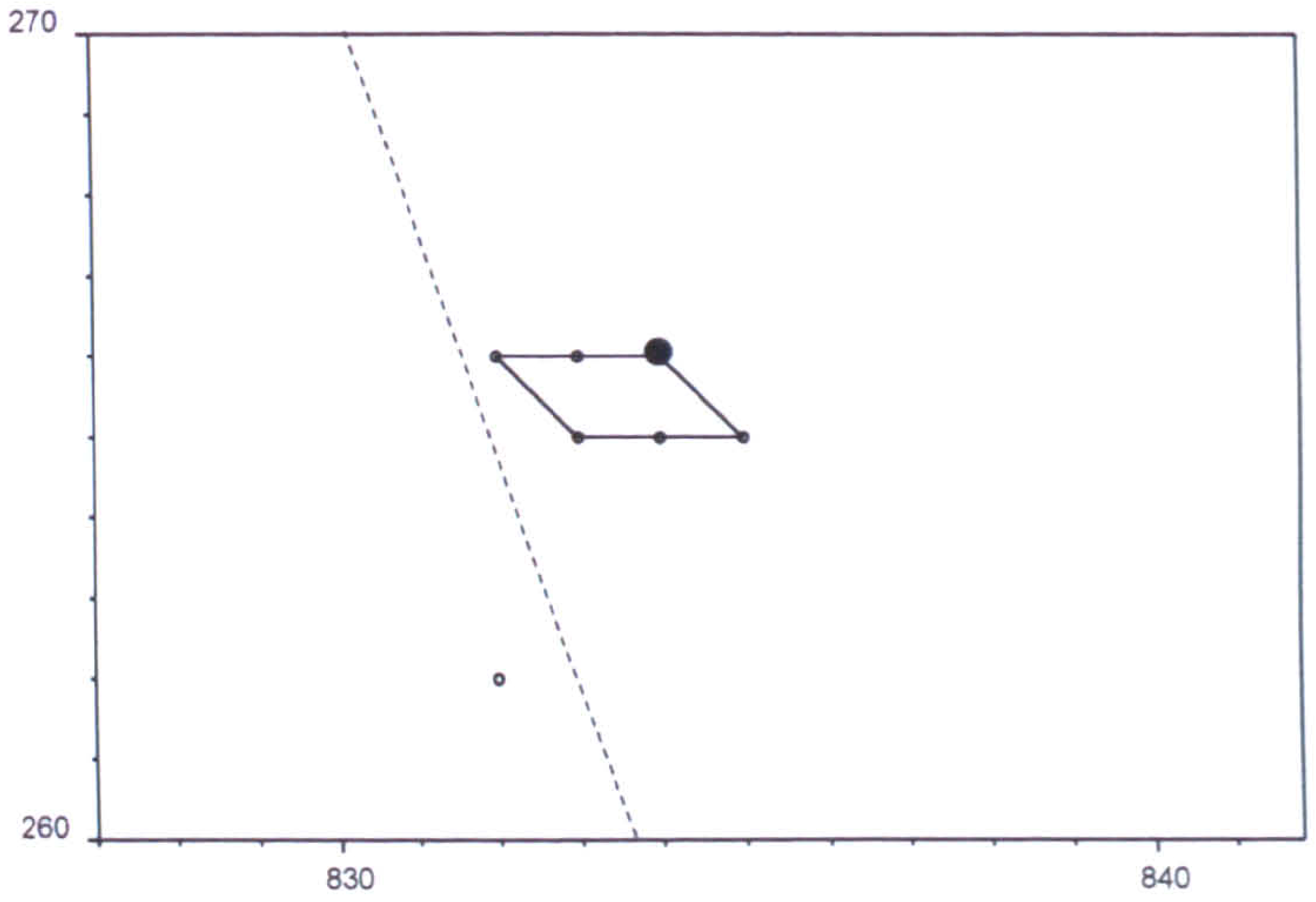

Figure A2.54 95% Minimum Convex Polygon for **Vole FR♂ 9 November 1999**
(— MCP, ---- Pond, ∘ Fix, ● Nest site)

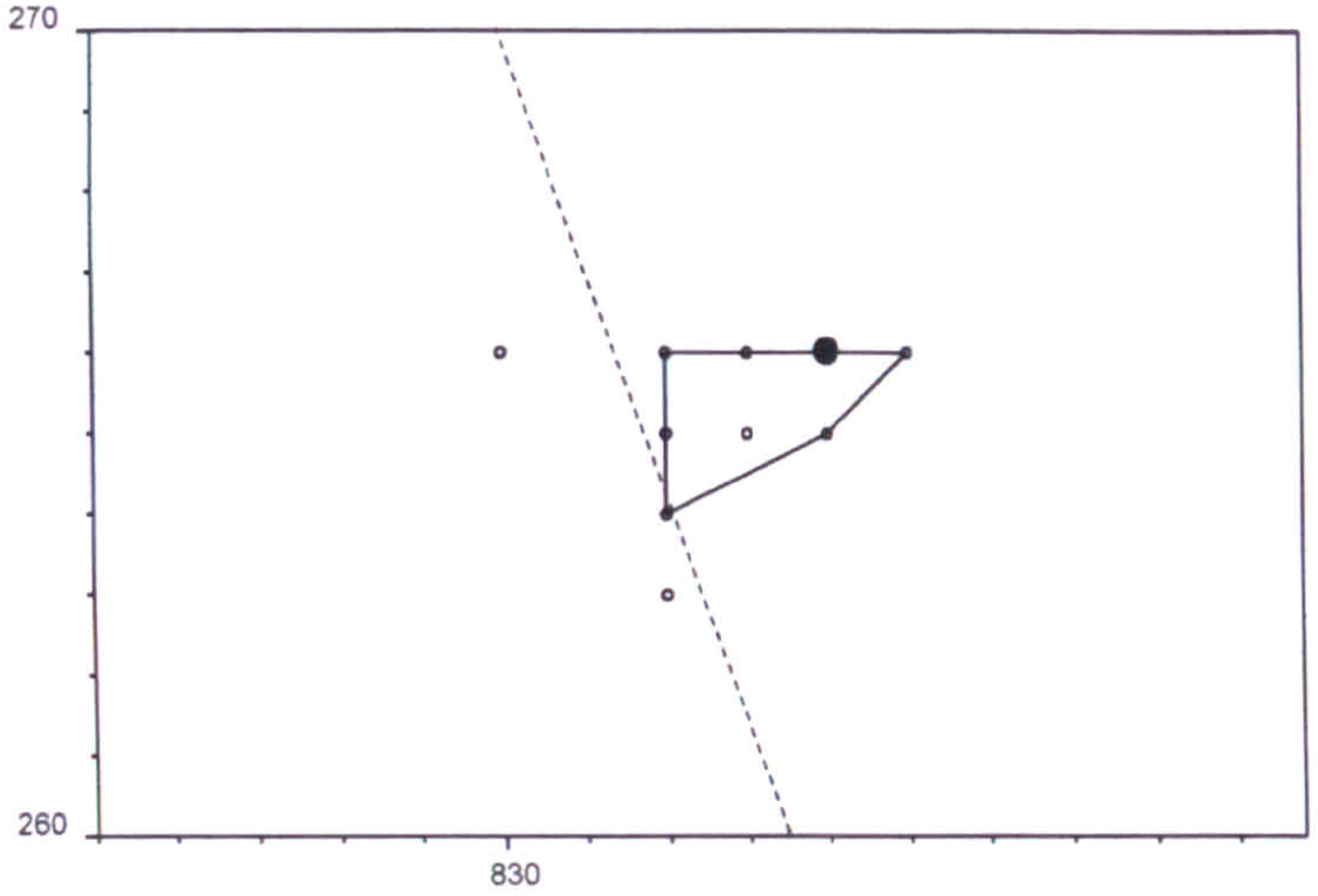

Figure A2.55 95% Minimum Convex Polygon for **Vole FR♂ 22 November 1999**
(— MCP, ---- Pond, ∘ Fix, ● Nest site)

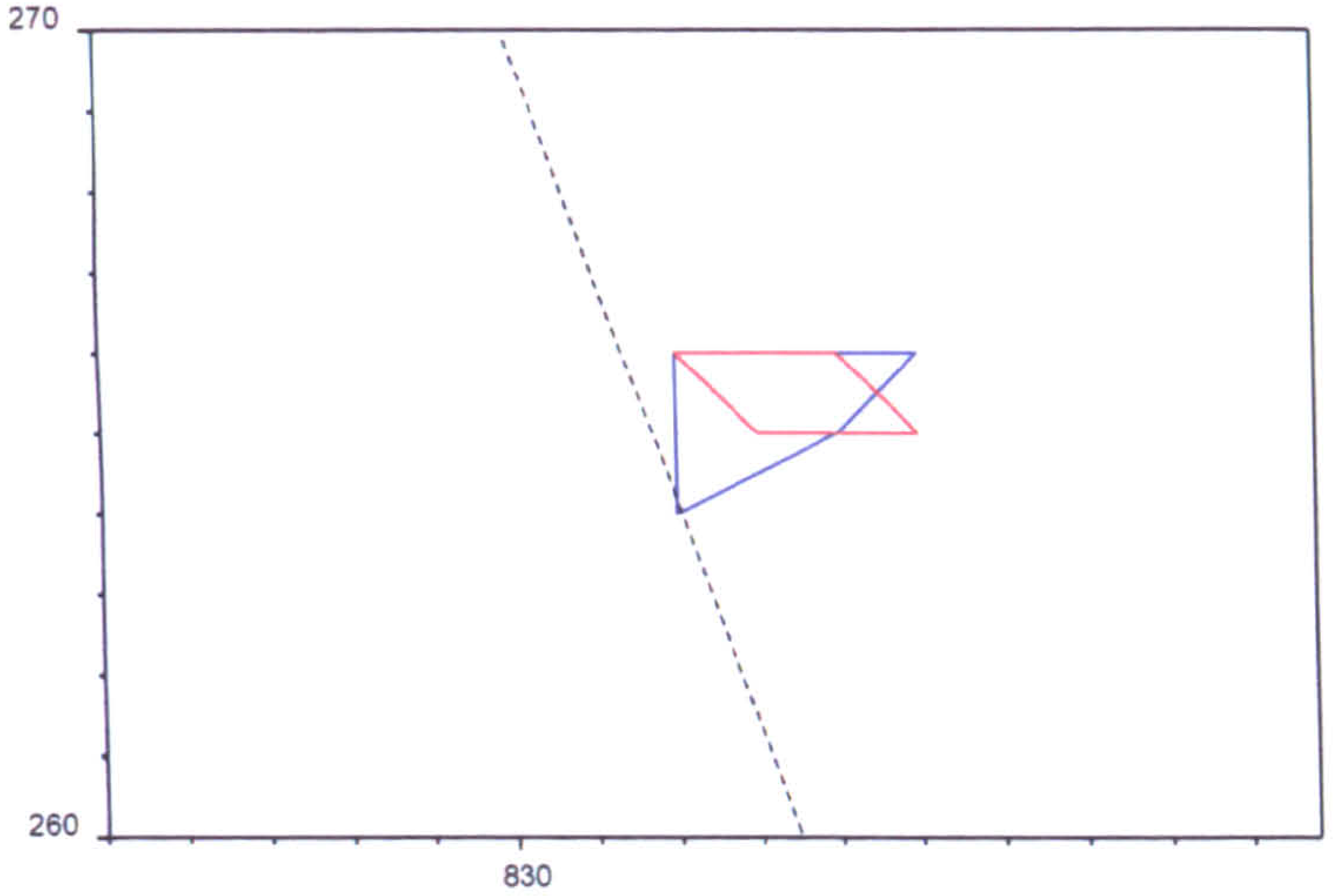

Figure A2.56 95% Minimum Convex Polygons for **Vole FR♂**
(— 16 November 1999, — 22 November 1999, ---- Pond)

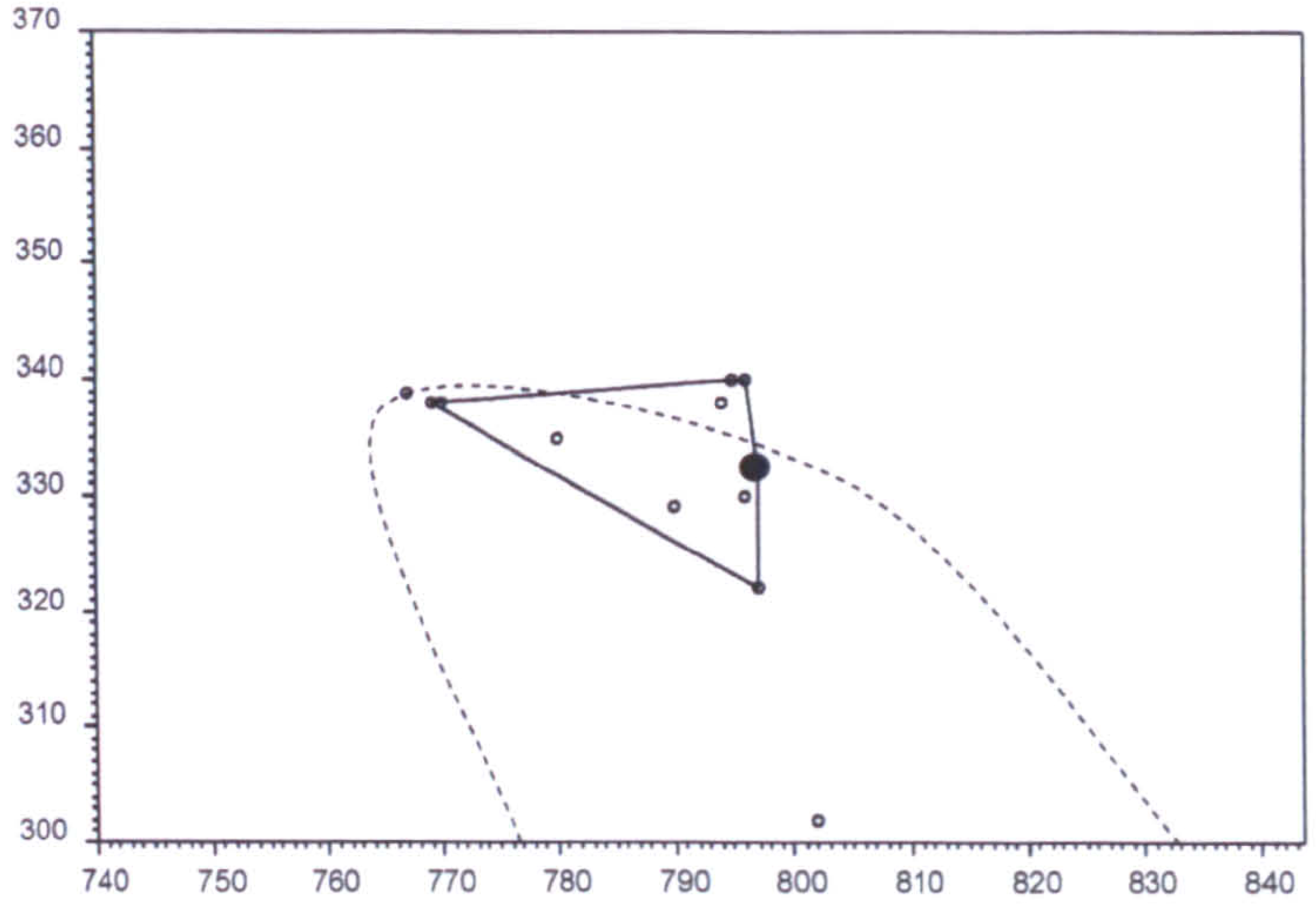

Figure A2.57 95% Minimum Convex Polygon for **Vole HE♀ 16 November 1999**
(— MCP, ---- Pond, ∘ Fix, ● Nest site)

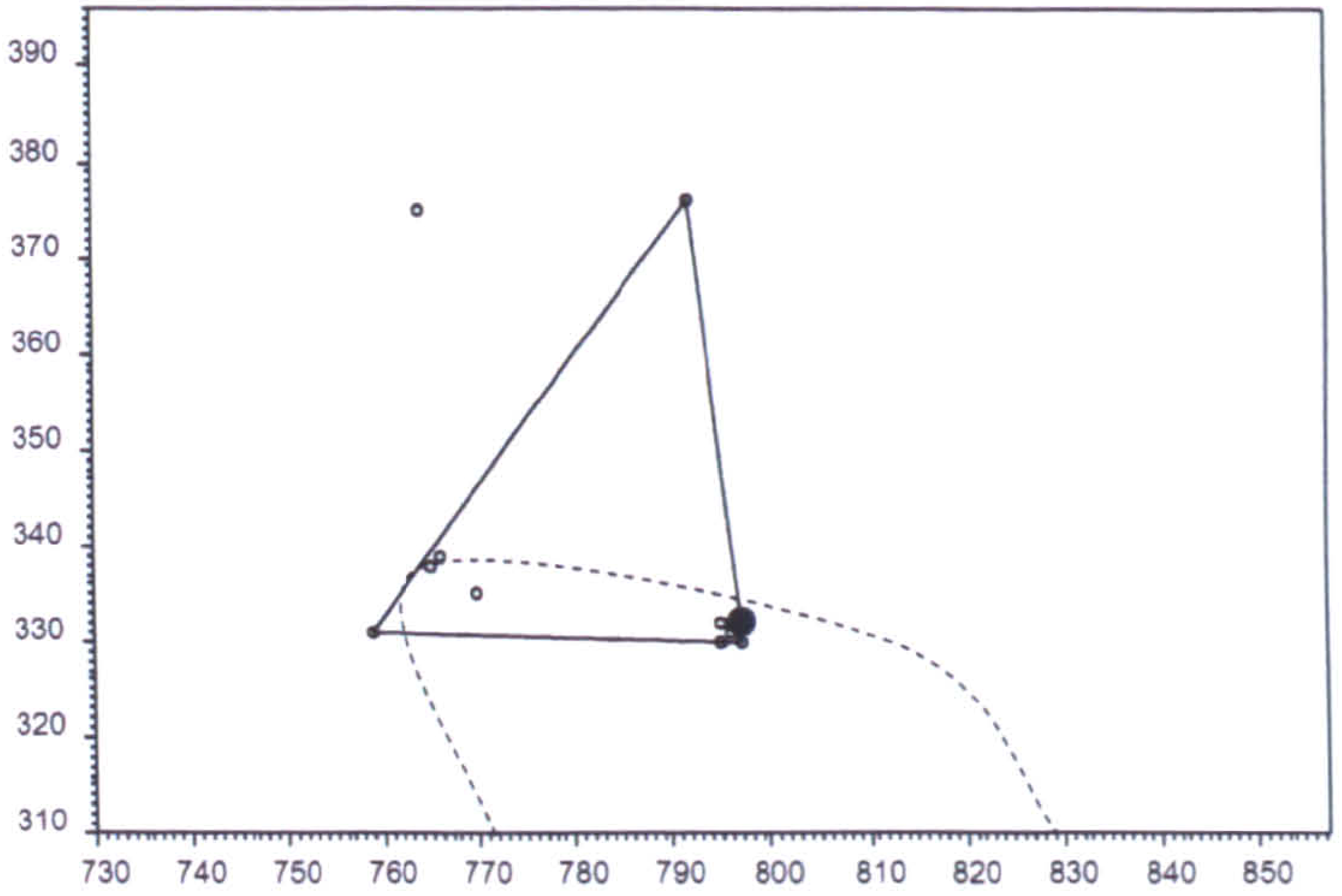

Figure A2.58 95% Minimum Convex Polygon for **Vole HE♀ 22 November 1999** (— MCP, ---- Pond, ∘ Fix, ● Nest site)

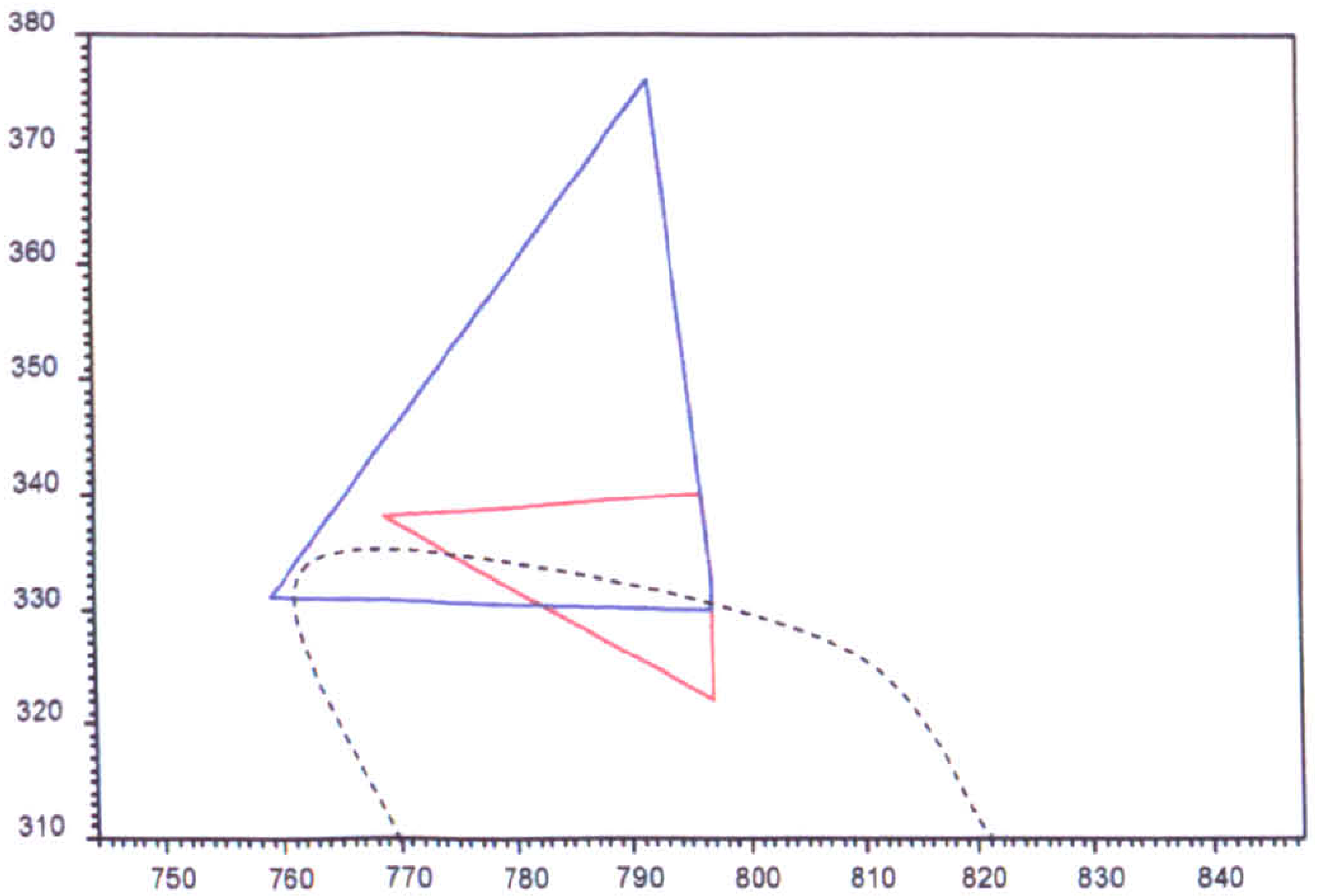

Figure A2.59 95% Minimum Convex Polygons for **Vole HE♀** (— 16 November 1999, — 22 November 1999, ---- Pond)

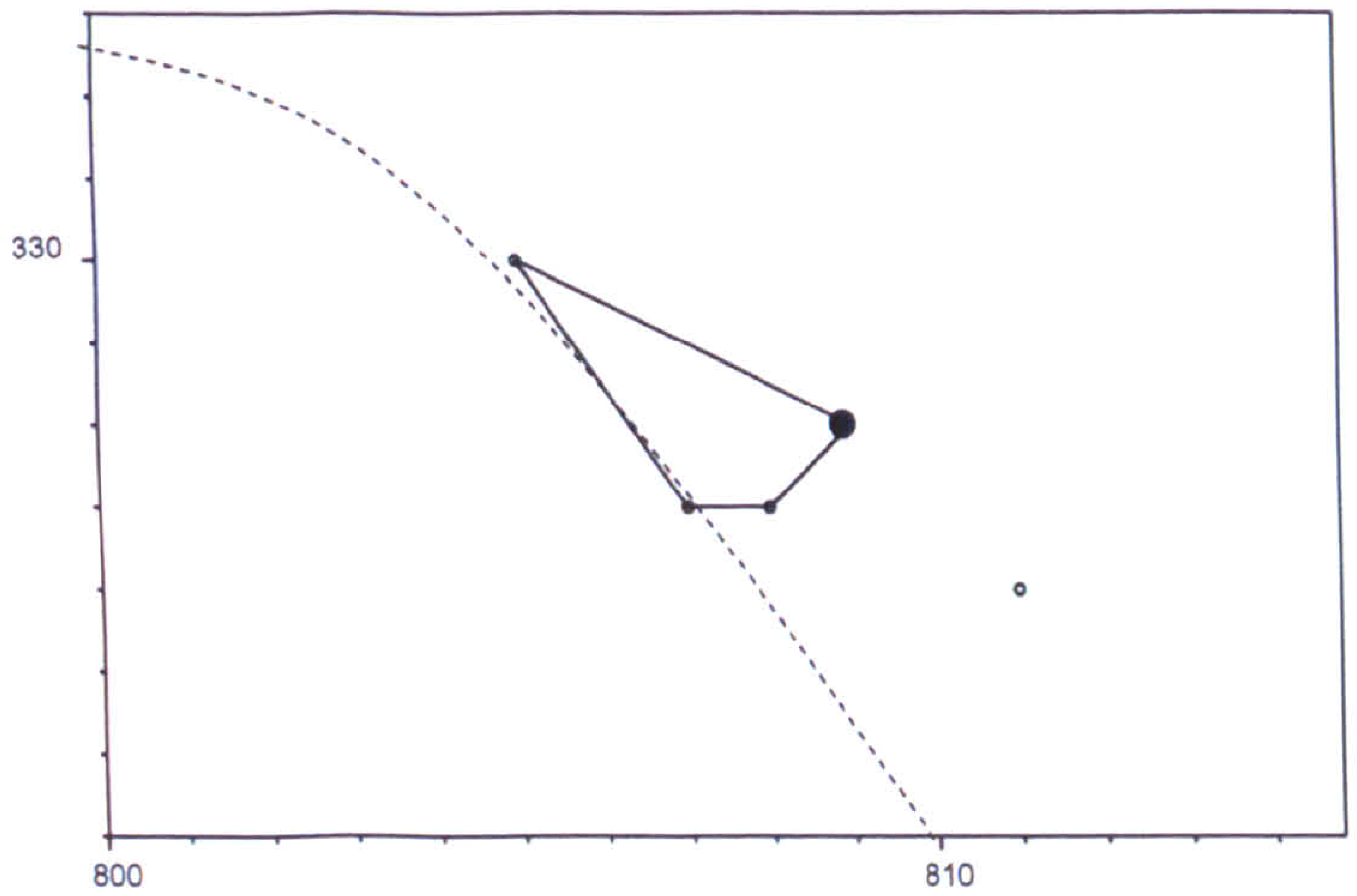

Figure A2.60 95% Minimum Convex Polygon for **Vole I♂ 14 December 1999** (— MCP, ---- Pond, ∘ Fix, ● Nest site)

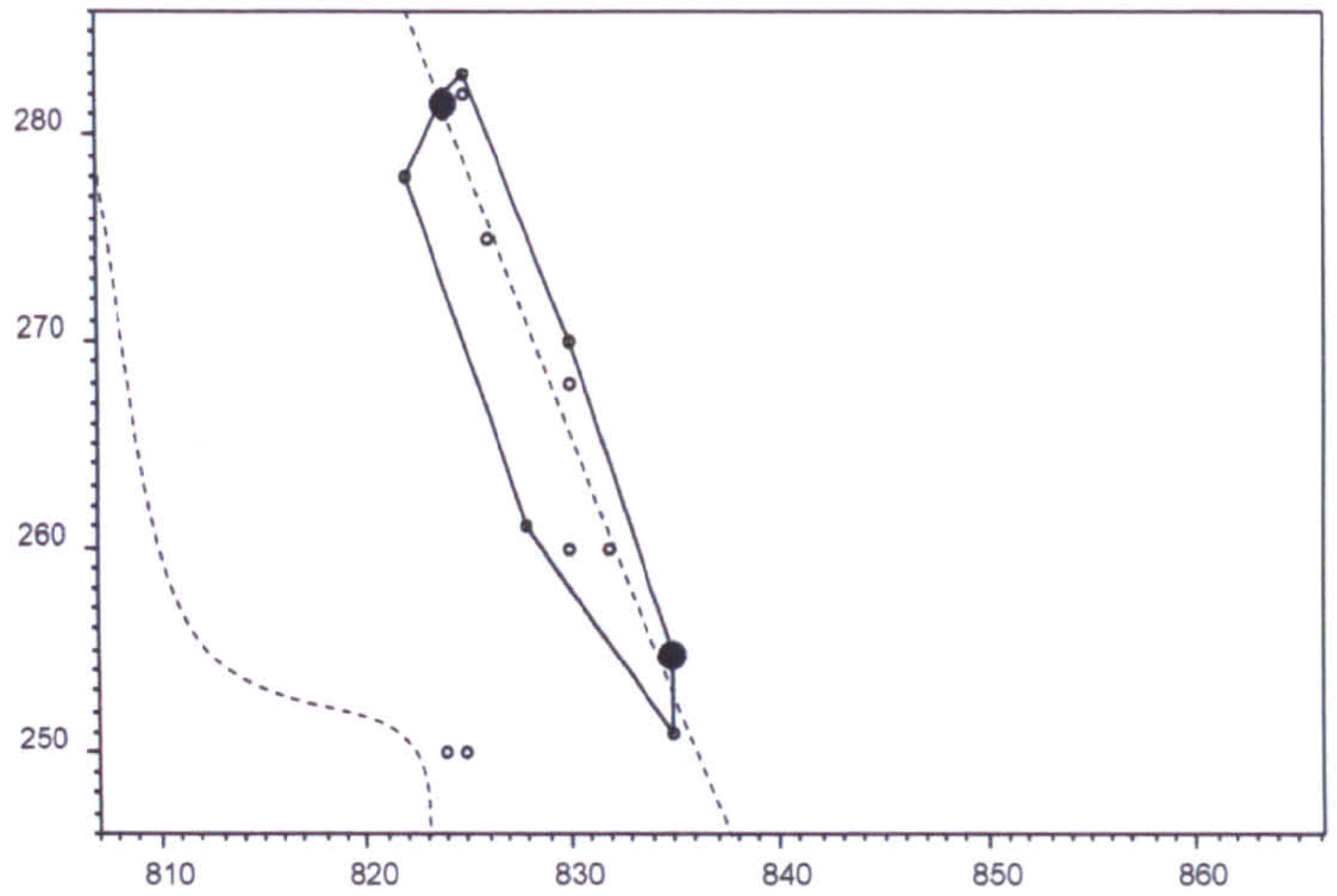

Figure A2.60 95% Minimum Convex Polygon for **Vole MO♂ 22 February 2000** (— MCP, ---- Pond, ∘ Fix, ● Nest site)

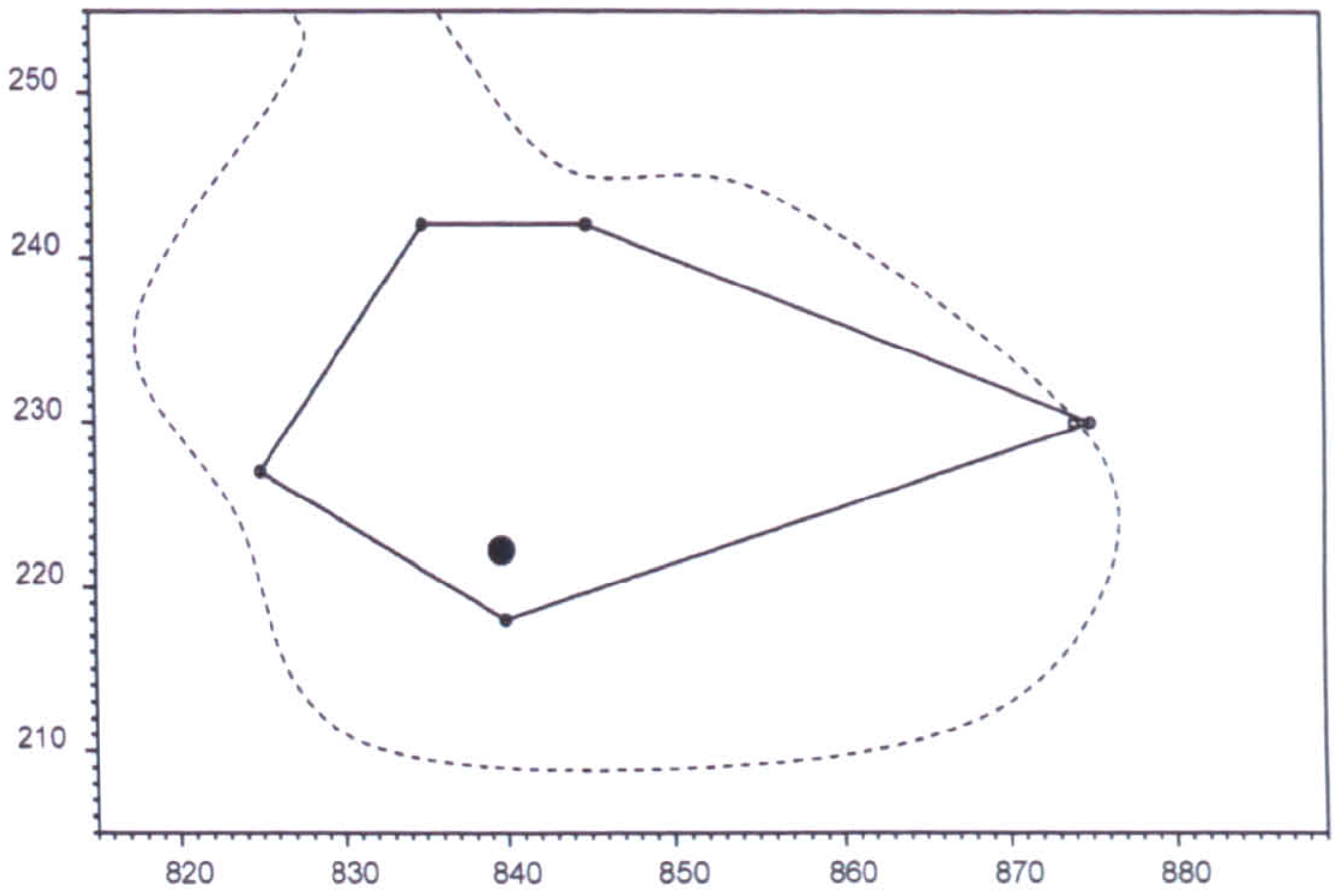

Figure A2.61 95% Minimum Convex Polygon for **Vole MO♂ 6 March 2000** (— MCP, ---- Pond, ∘ Fix, ● Nest site)

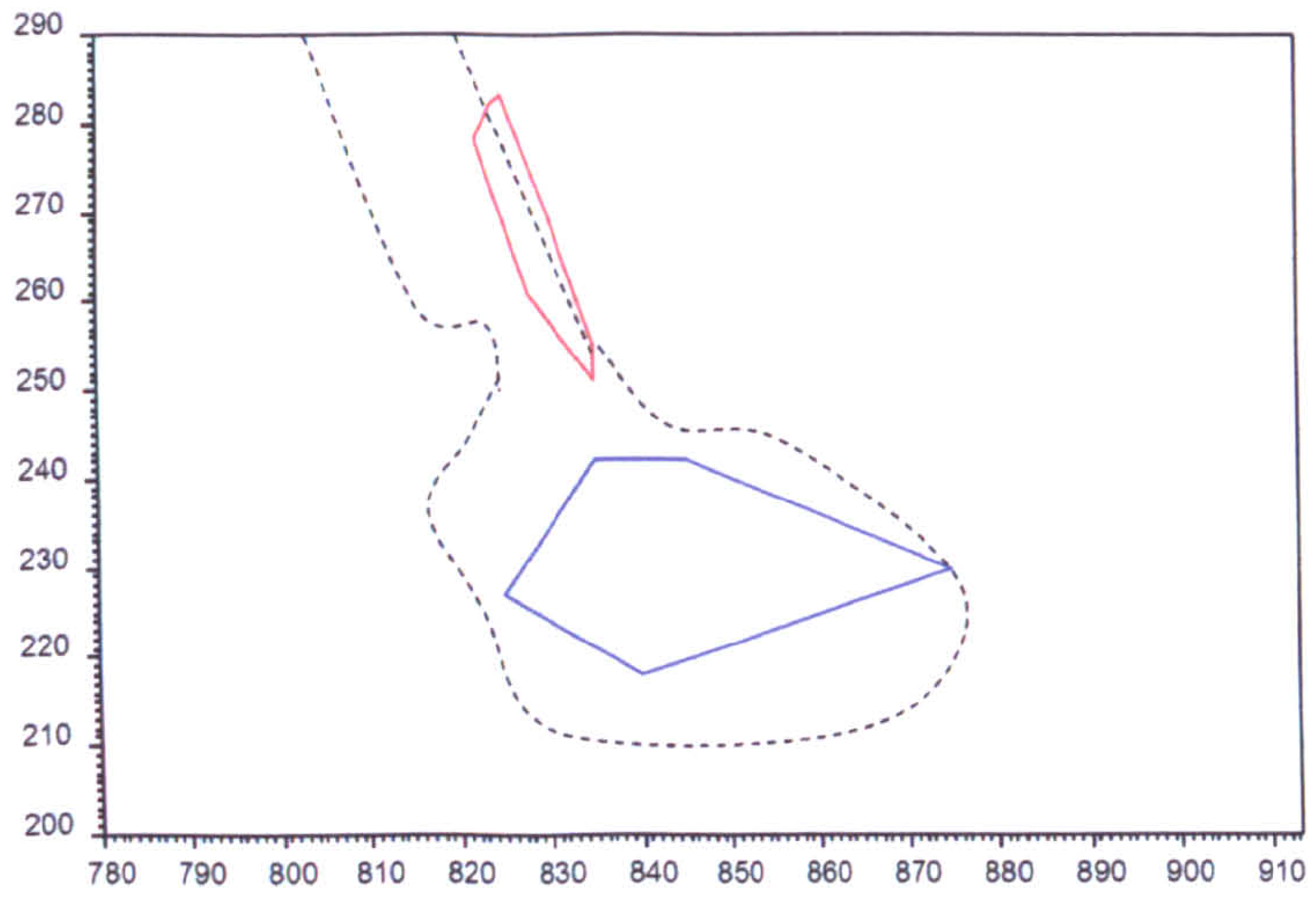

Figure A2.62 95% Minimum Convex Polygons for **Vole MO♂**
(— 22 February 2000, — 6 March 2000, ---- Pond)

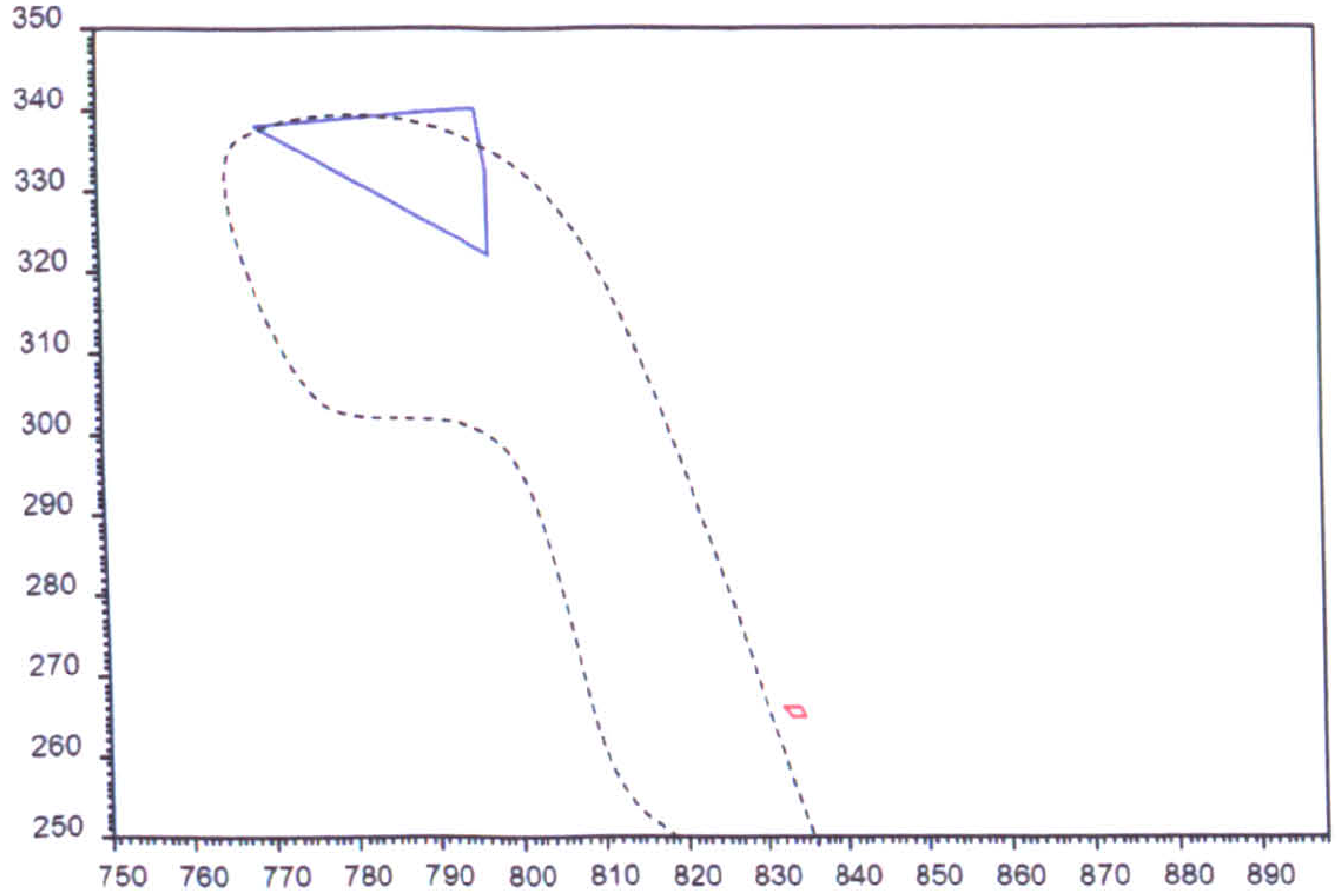

Figure A2.63 95% Minimum Convex Polygons for **Vole FR♂ and Vole HE♀**
16 November 1999 (— Vole FR♂, — Vole HE♀, ---- Pond)

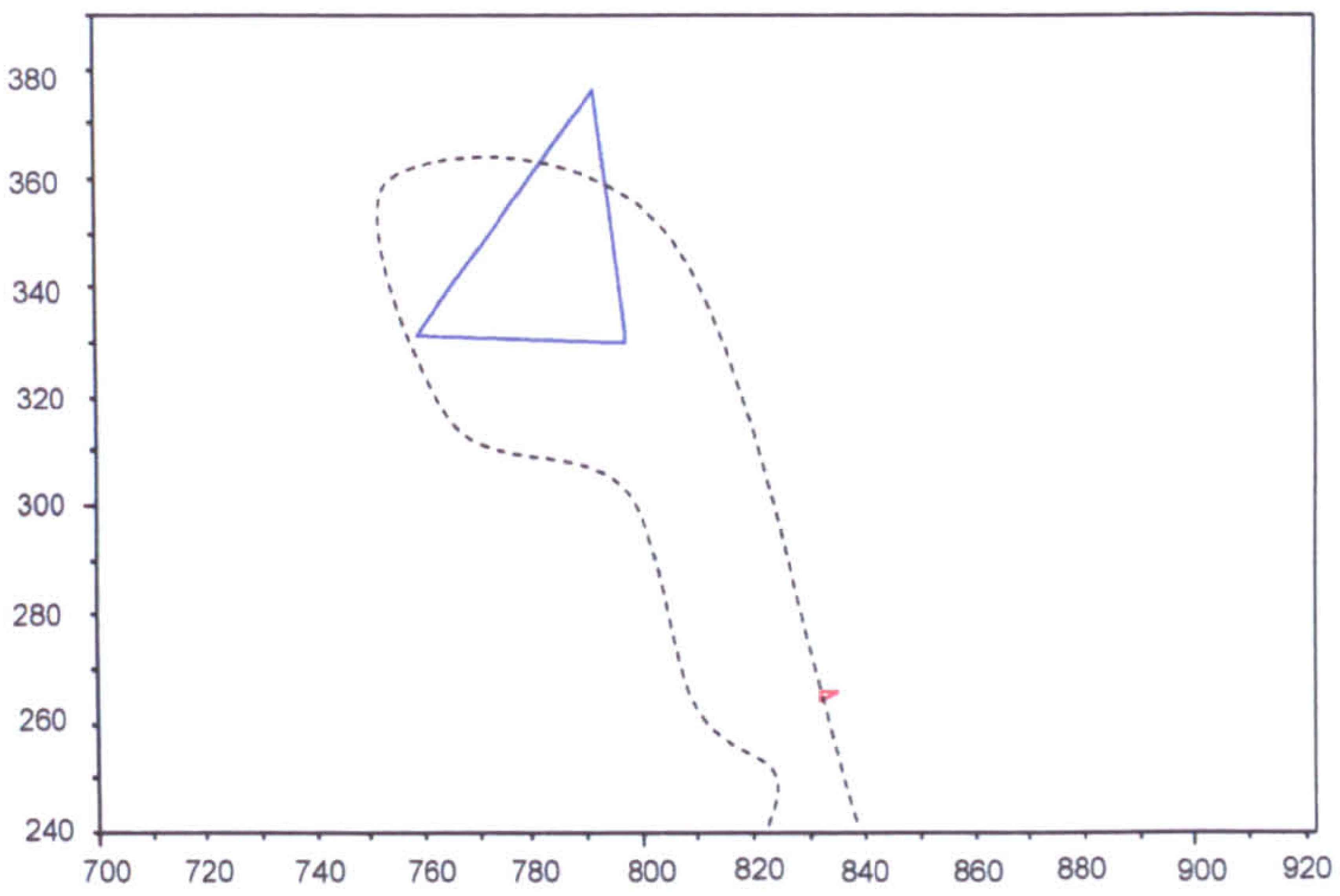

Figure A2.64 95% Minimum Convex Polygons for **Vole FR♂ and Vole HE♀**
22 November 1999 (— Vole FR♂, — Vole HE♀, ---- Pond)

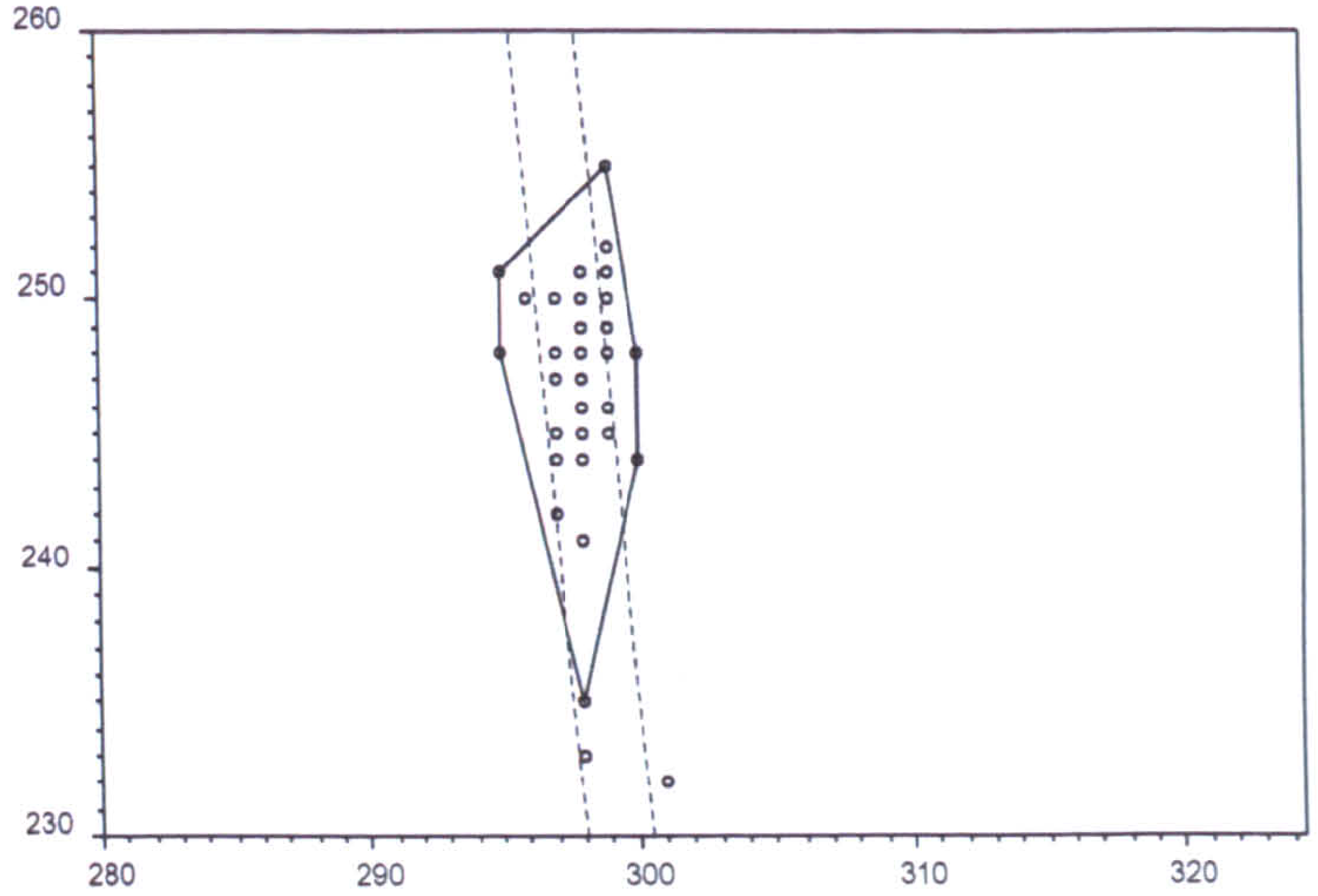

Figure A2.65 95% Minimum Convex Polygon for **Vole N♂ 20August 2000**
(— MCP, ---- Ditch, ∘ Fix, No obvious nest site)

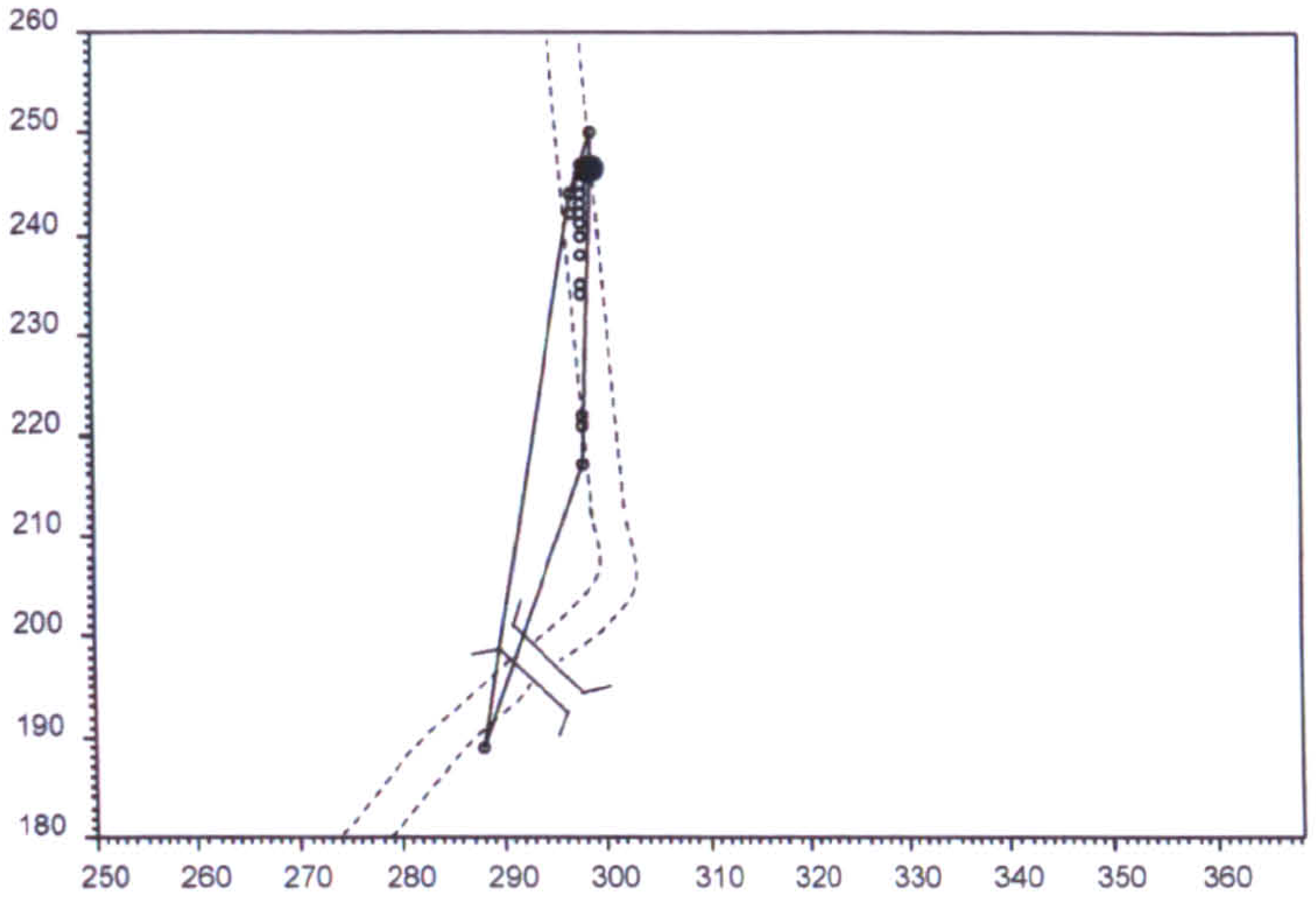

Figure A2.66 95% Minimum Convex Polygon for **Vole N♂ 2 September 2000**
(— MCP, ---- Ditch, ∘ Fix, ● Nest site)

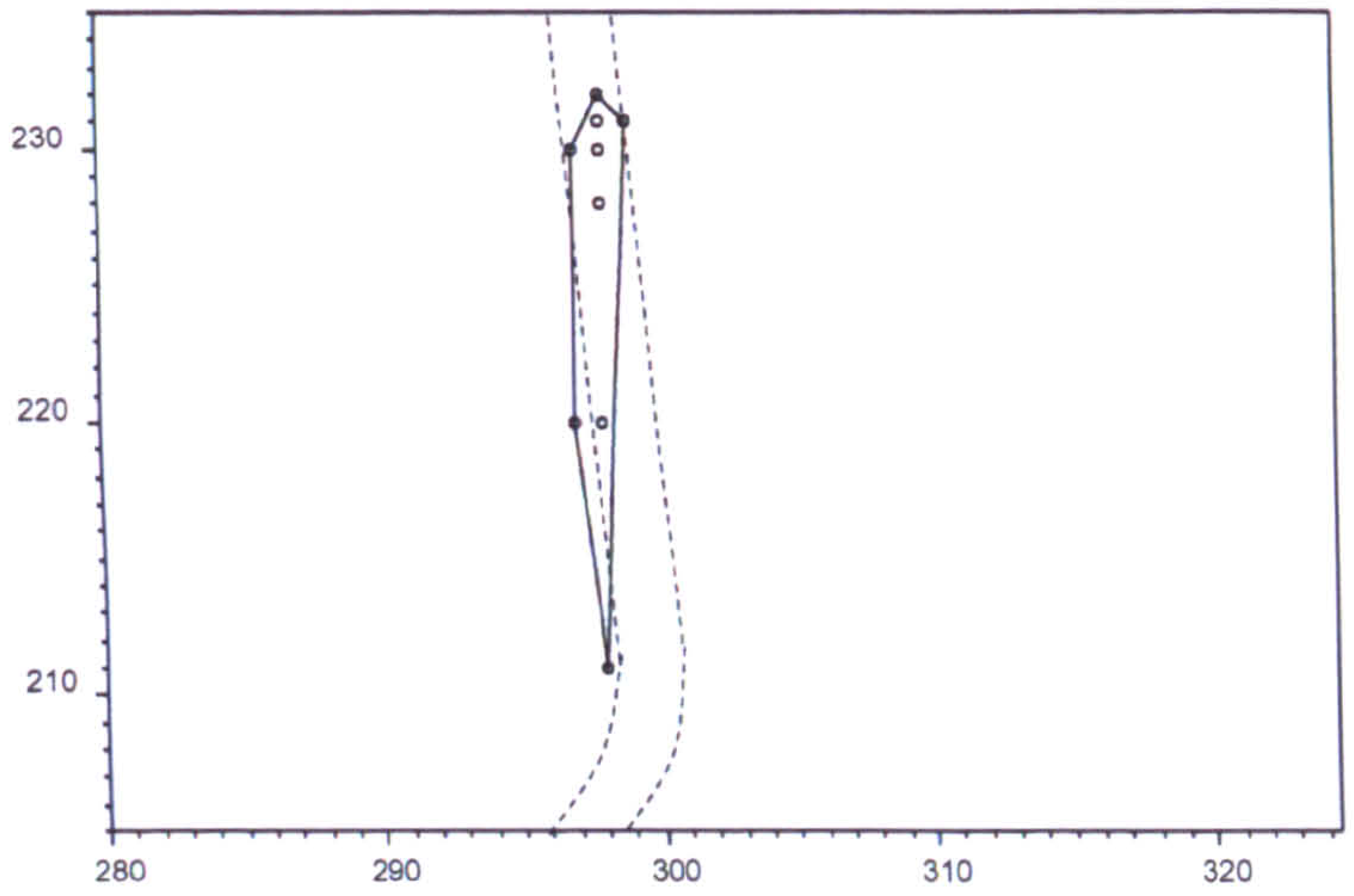

Figure A2.67 95% Minimum Convex Polygon for **Vole N♂ 9 September 2000**
(— MCP, ---- Ditch, ∘ Fix, No obvious nest site)

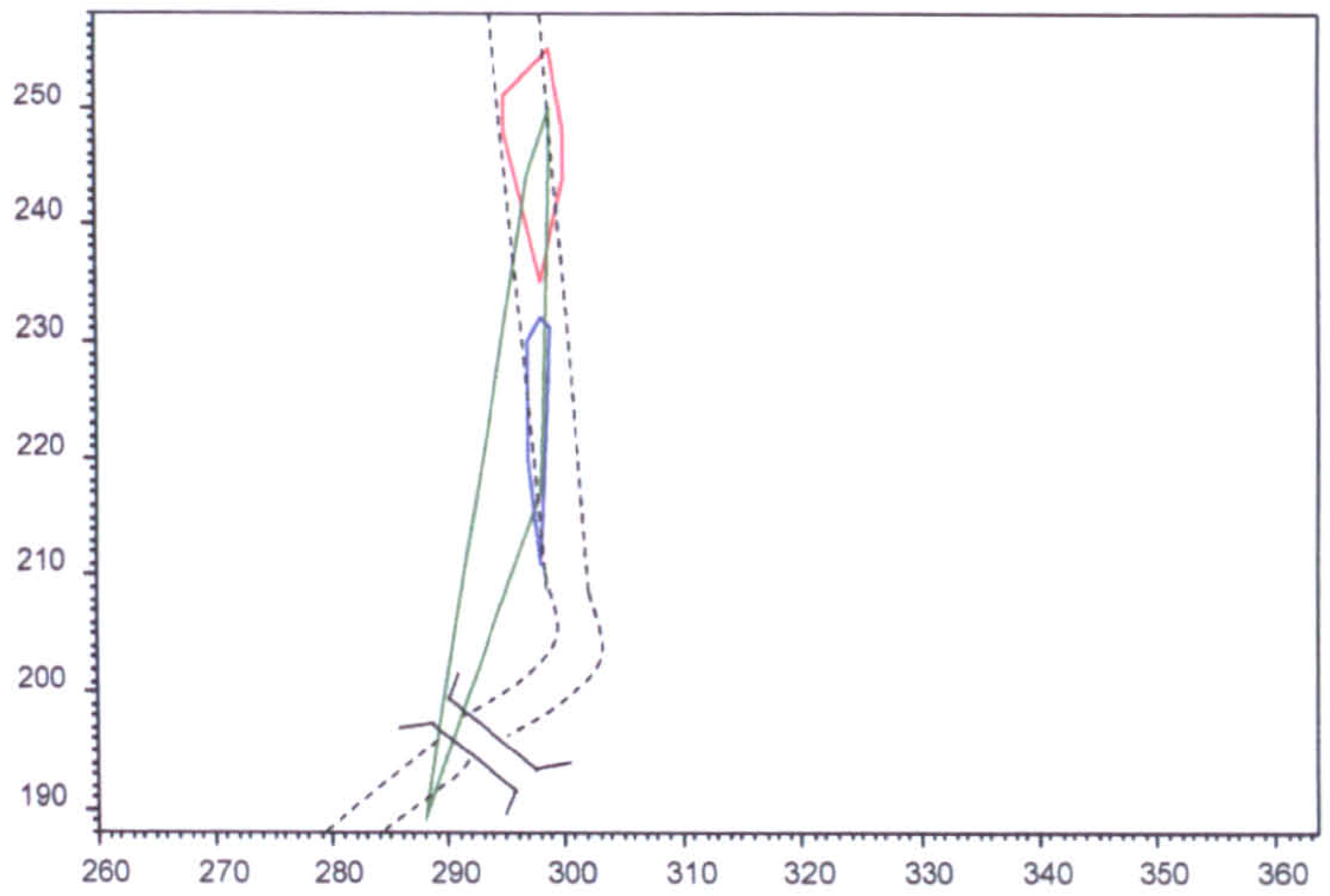

Figure A2.68 95% Minimum Convex Polygons for **Vole N♂**
(— 20 August 2000, — 2 September 2000, — 9 September 2000, ---- Ditch)

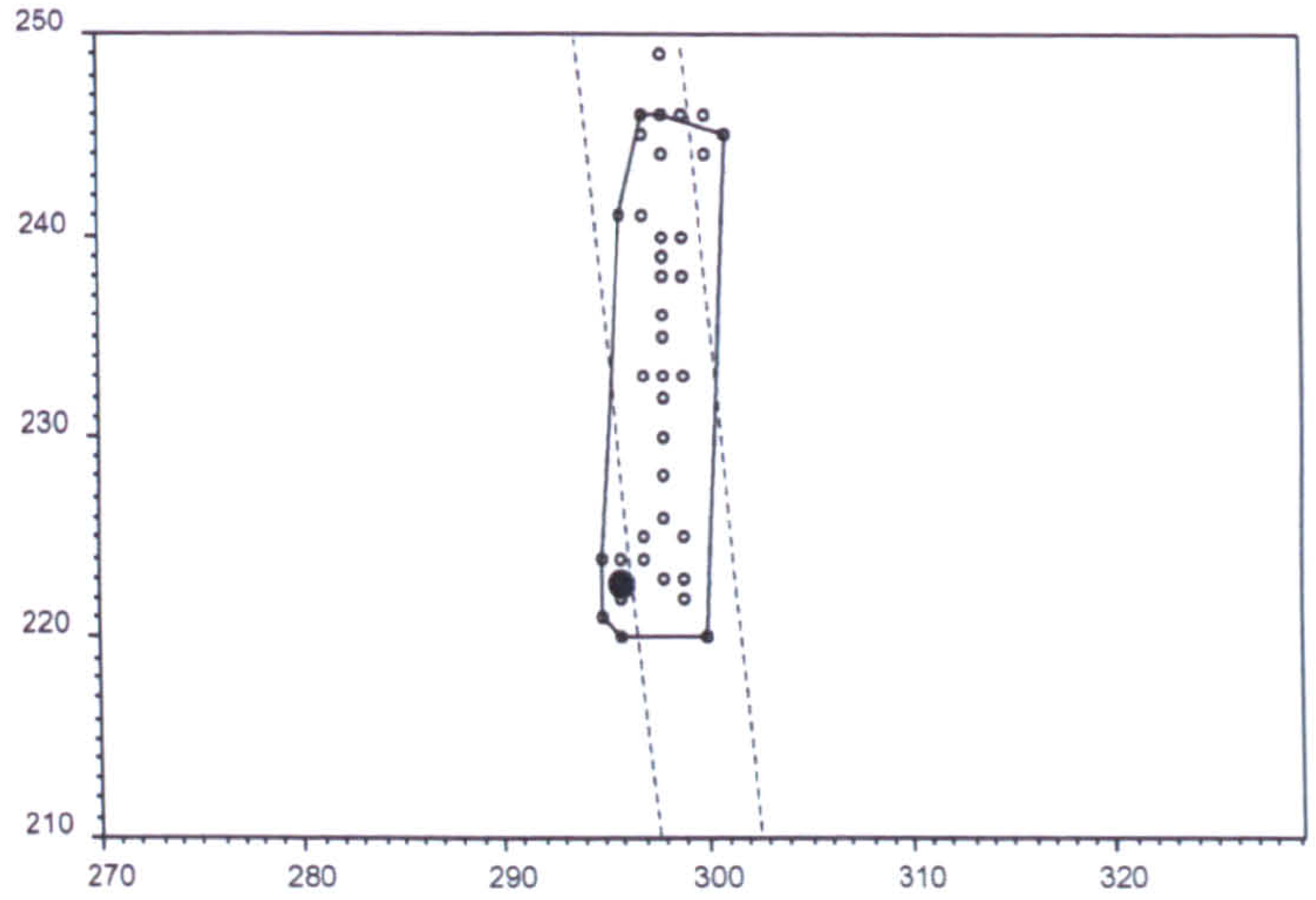

Figure A2.69 95% Minimum Convex Polygon for **Vole O♀ 19 August 2000**
(— MCP, ---- Ditch, ∘ Fix, ● Nest site)

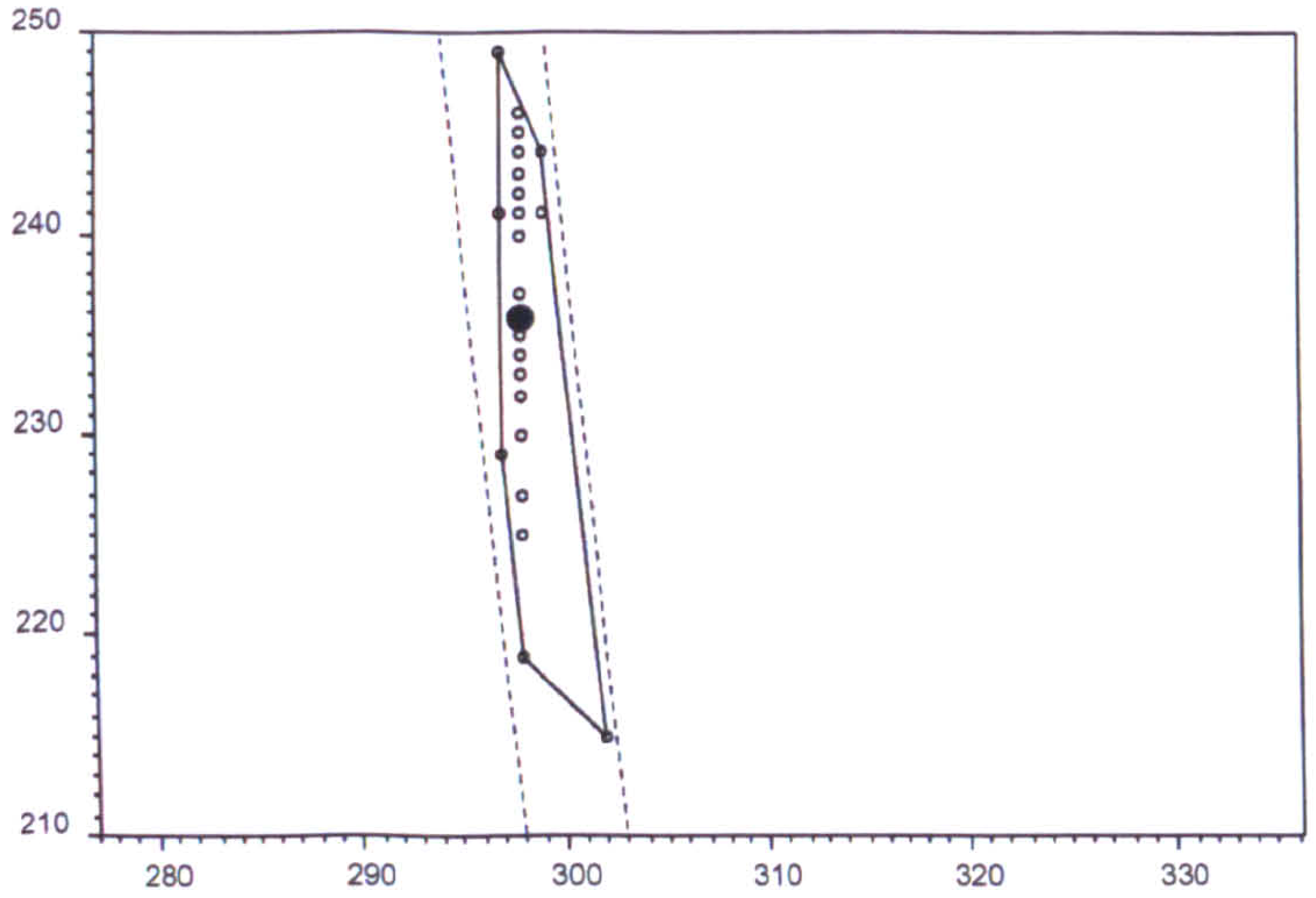

Figure A2.70 95% Minimum Convex Polygon for **Vole O♀ 2 September 2000** (— MCP, ---- Ditch, ∘ Fix, ● Nest site)

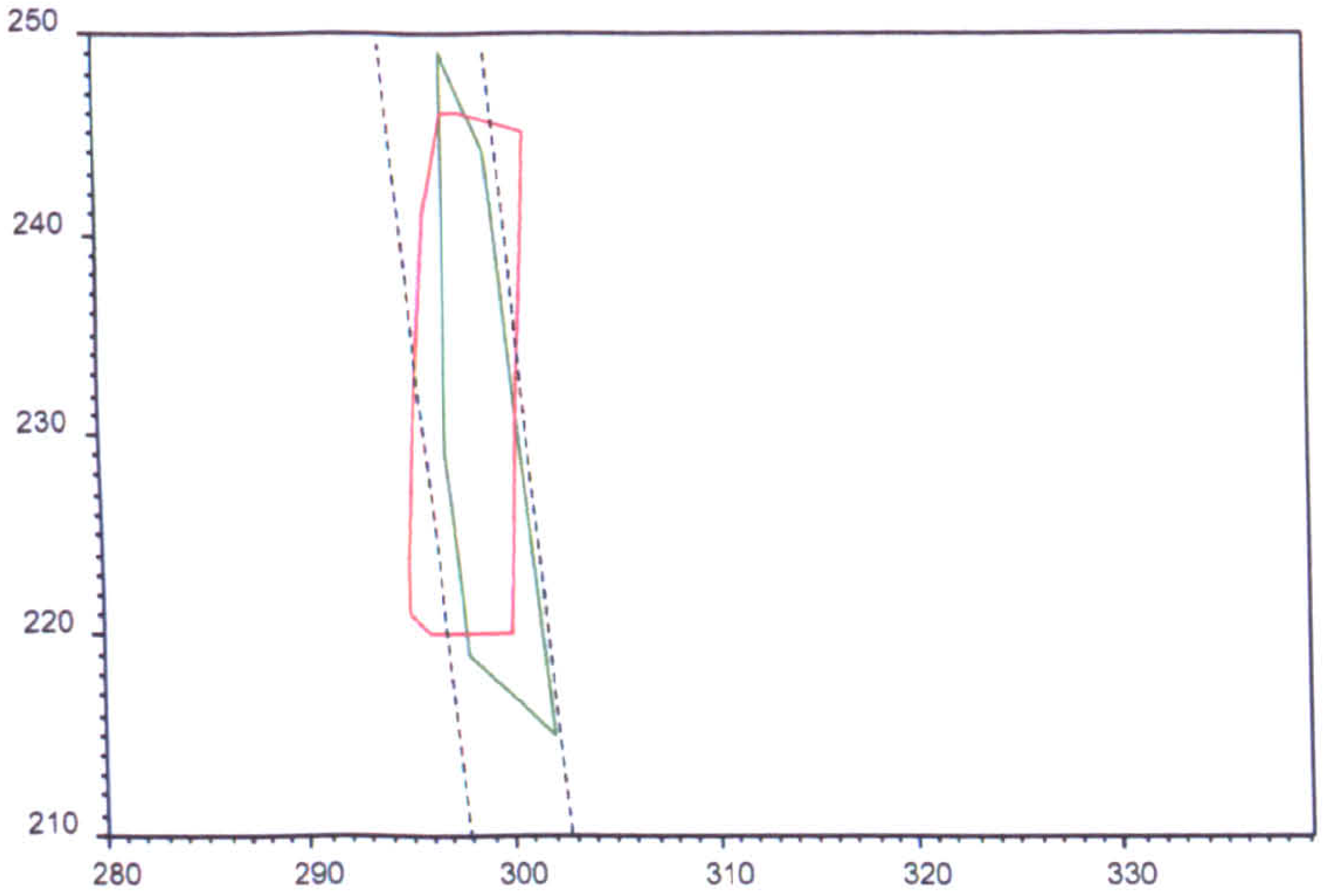

Figure A2.71 95% Minimum Convex Polygons for **Vole O♀** (— 19 August 2000, — 2 September 2000, ---- Ditch)

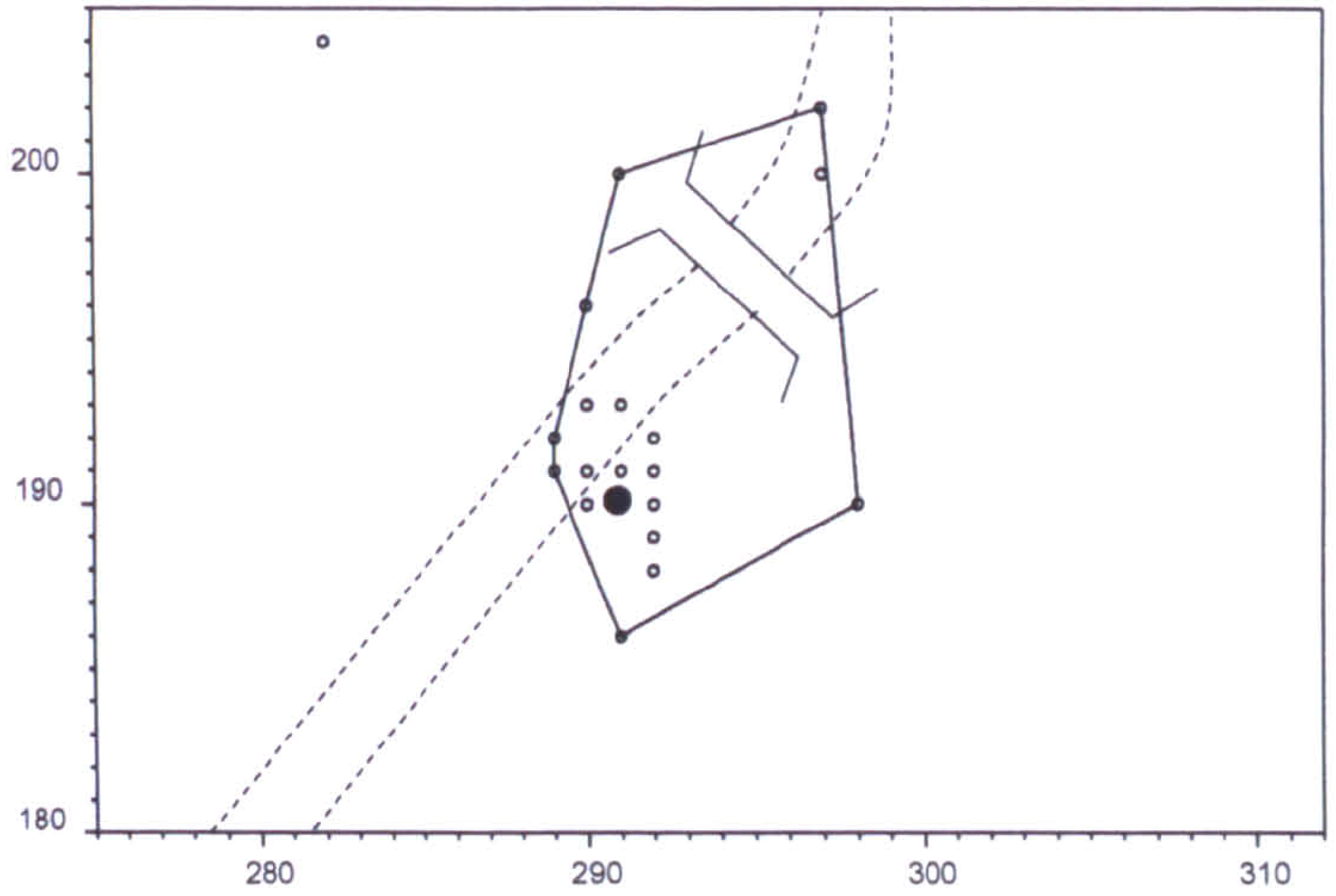

Figure A2.72 95% Minimum Convex Polygon for **Vole Q♂ 9 September 2000** (— MCP, ---- Ditch, ∘ Fix, ● Nest site)

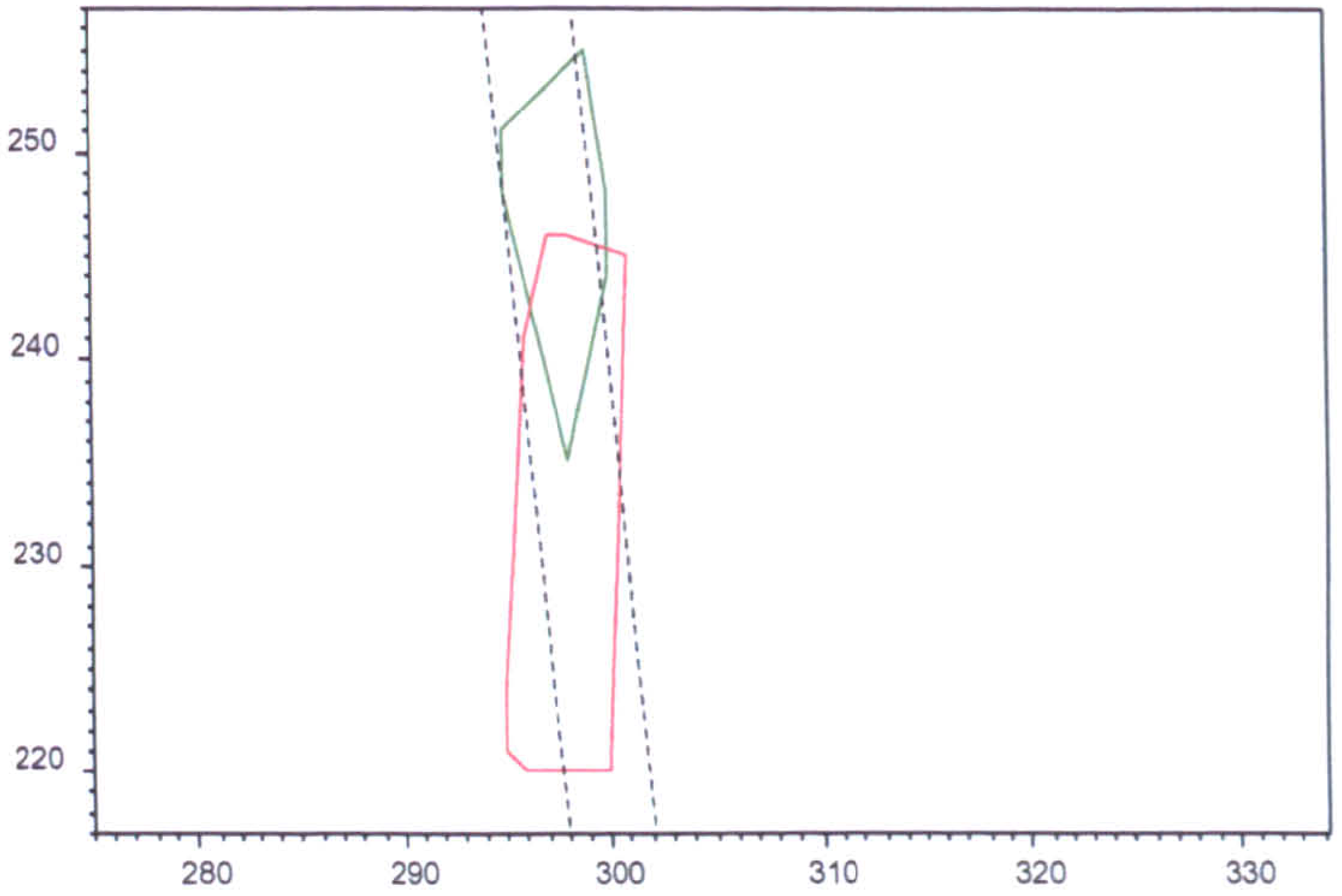

Figure A2.73 95% Minimum Convex Polygons for **Vole N♂ and Vole O♀ 20 August 2000**(— Vole N ♂, — Vole O ♀ , ---- Ditch)

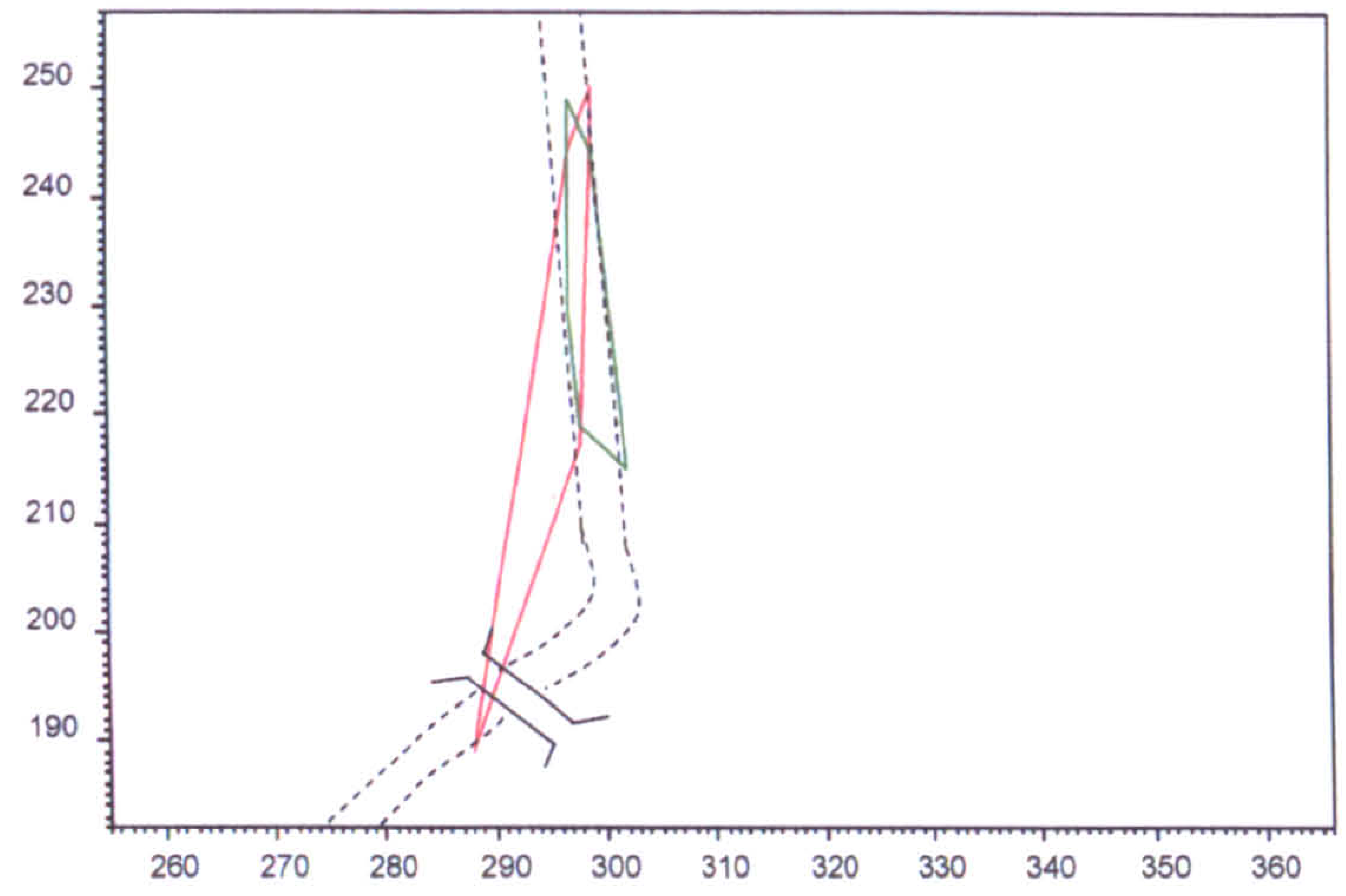

Figure A2.74 95% Minimum Convex Polygons for **Vole N♂ and Vole O♀**
2 September 2000 (— Vole N♂, —Vole O♀, ---- Ditch)

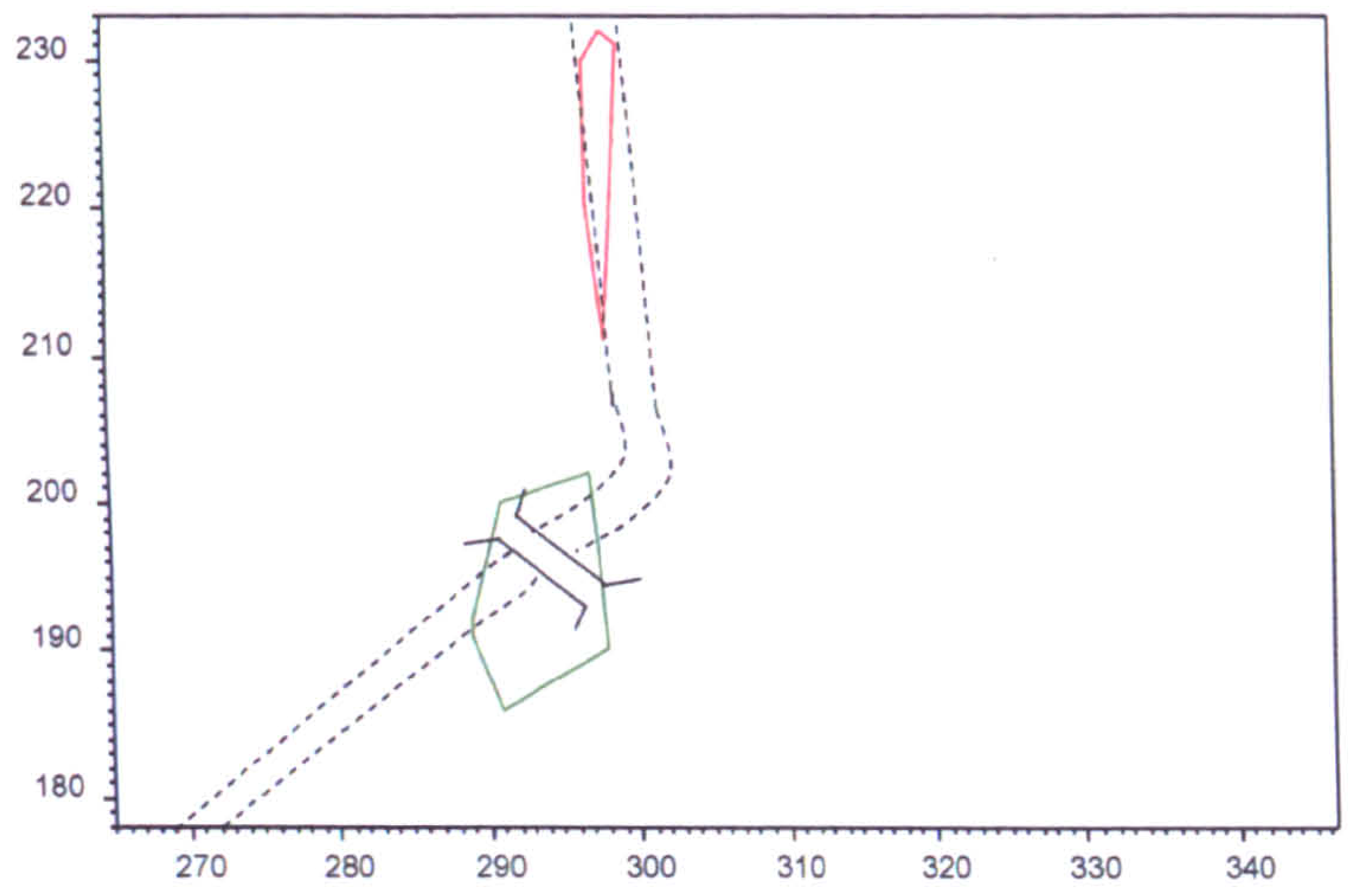

Figure A2.75 95% Minimum Convex Polygons for **Vole N♂ and Vole Q♀**
9 September 2000 (— Vole N♂, —Vole Q♀, ---- Ditch)

APPENDIX 3

Grid Cells

This appendix presents Grid Cell plots for each water vole during each radio-tracking session. The location of each fix is shown using the last three digits of a five digit Ordnance Survey Grid Reference. All water voles were located within Grid Reference TQ54, 79 (ditch) or TQ54, 80 (Pond 1 and Pond 2).

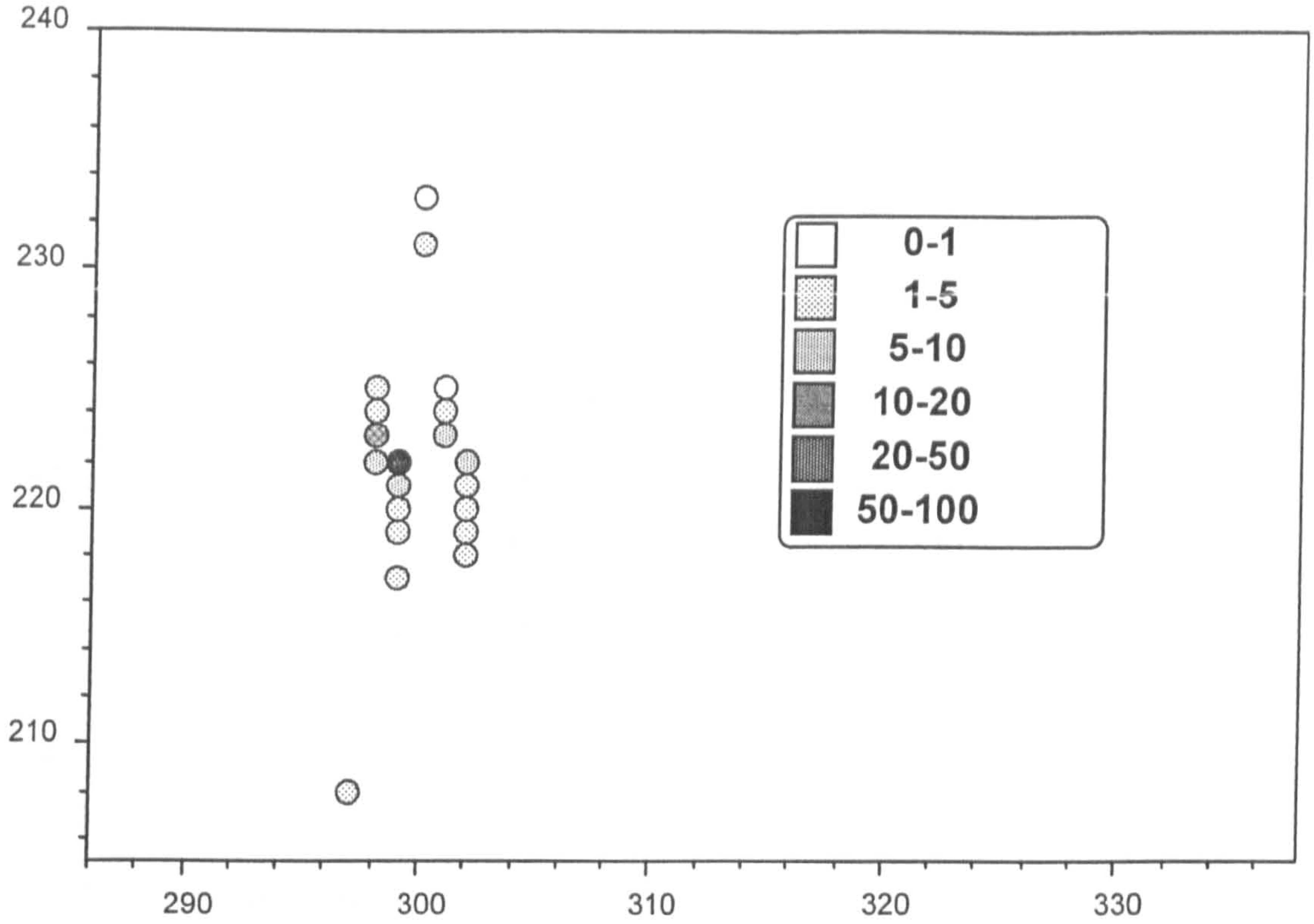

Figure A3.1 Grid Cell Plot (1m cells) for **Vole A♀ 6 November 1998** (N=179 fixes)

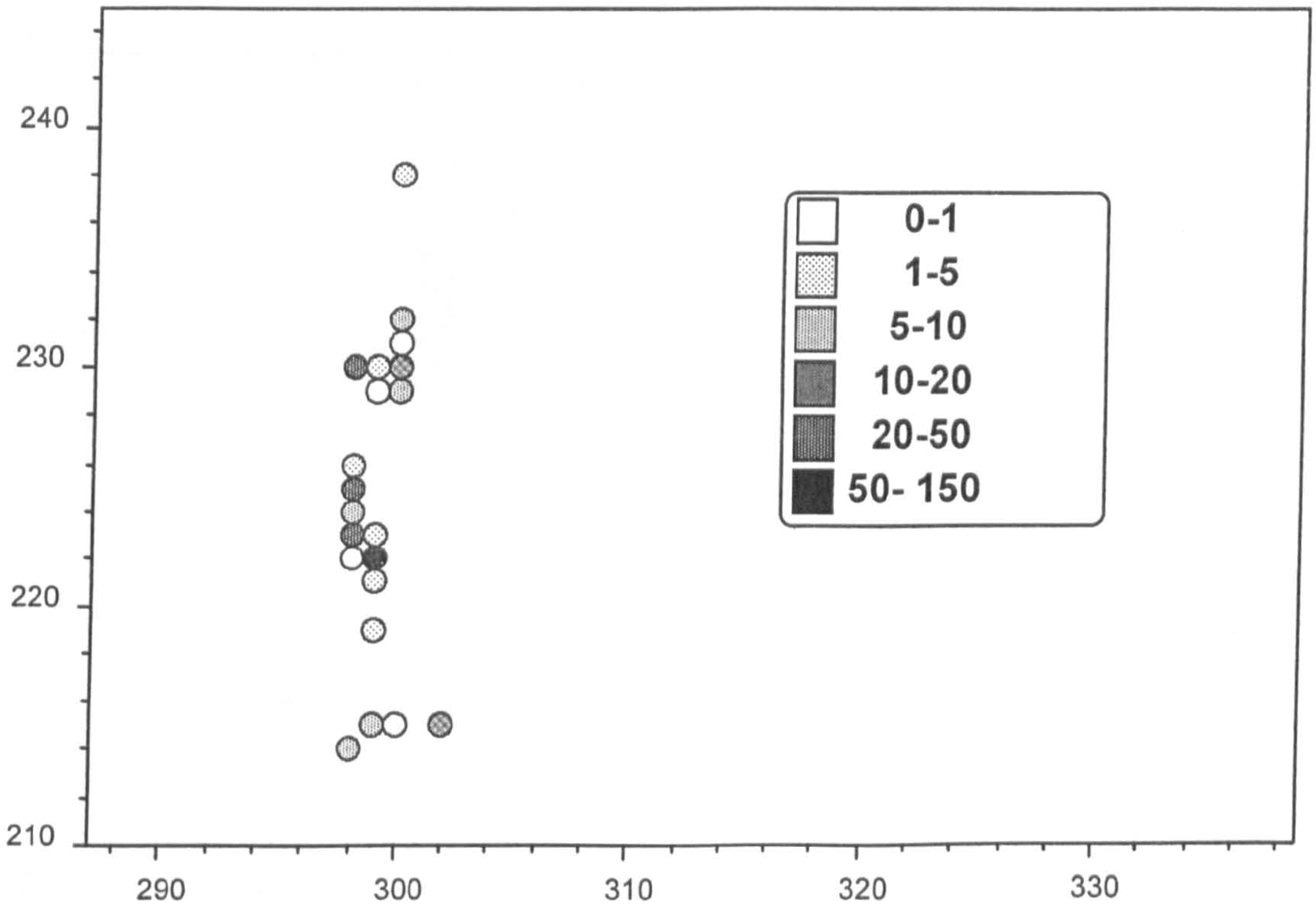

Figure A3.2 Grid Cell Plot (1m cells) for **Vole A♀ 10 December 1998** (N=331 fixes)

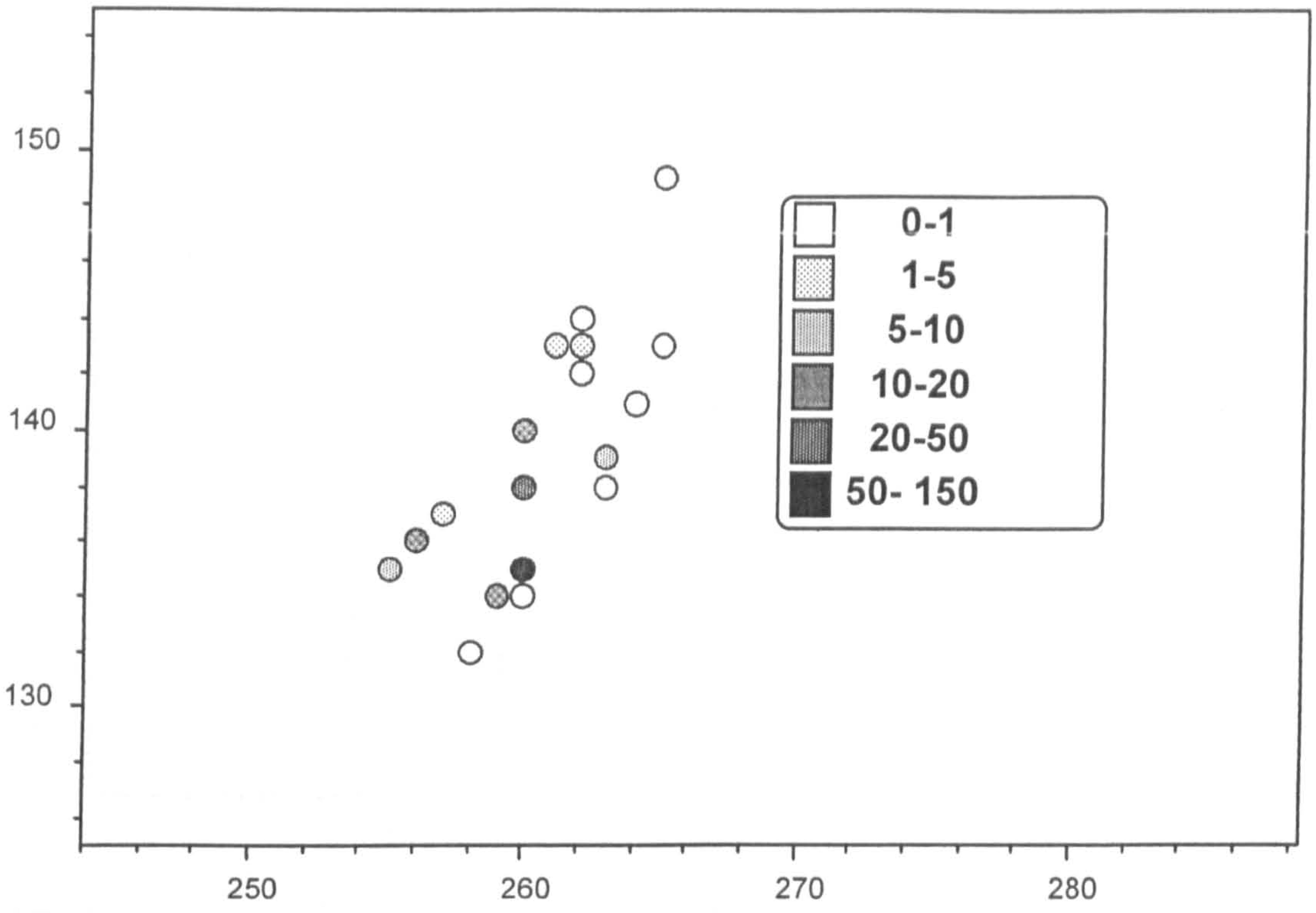

Figure A3.3 Grid Cell Plot (1m cells) for **Vole B♀ 6 November 1998** (N=179 fixes)

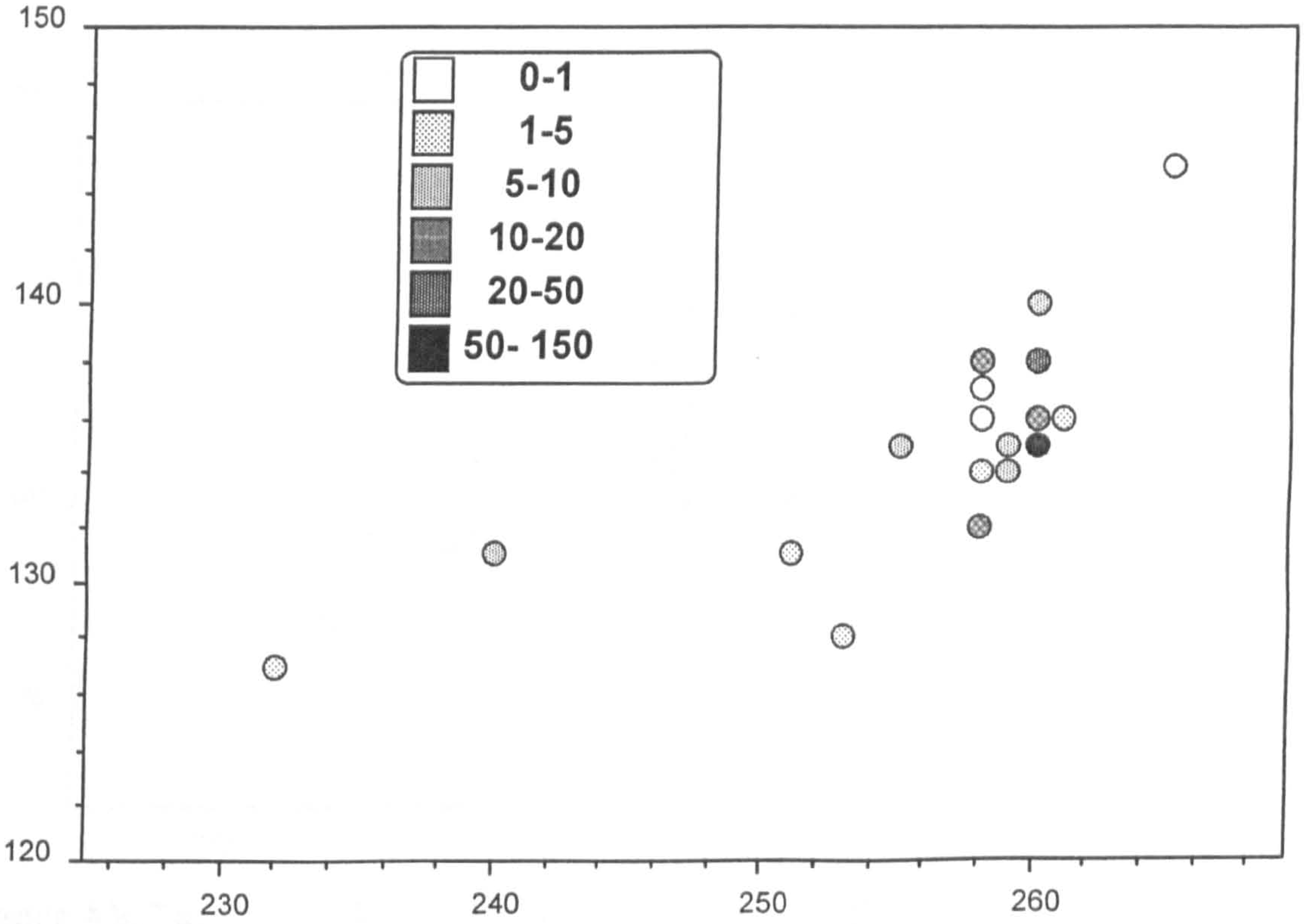

Figure A3.4 Grid Cell Plot (1m cells) for **Vole B♀ 10 December 1998** (N=179 fixes)

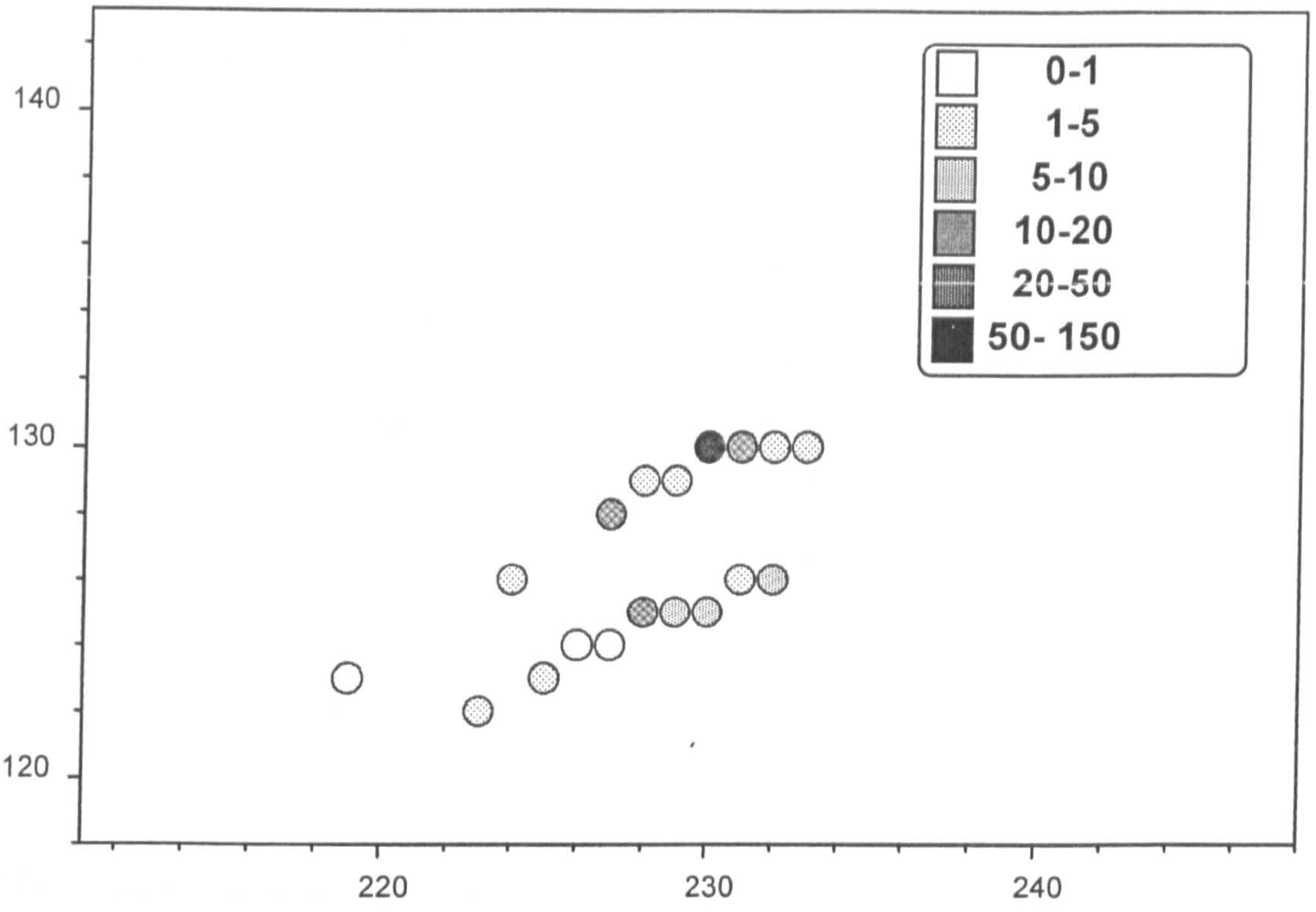

Figure A3.5 Grid Cell Plot (1m cells) for **Vole C♀ November 1998** (N=178 fixes).
Note that on 10 December 1998 Vole C♀ was recorded dead at grid reference 205,906.

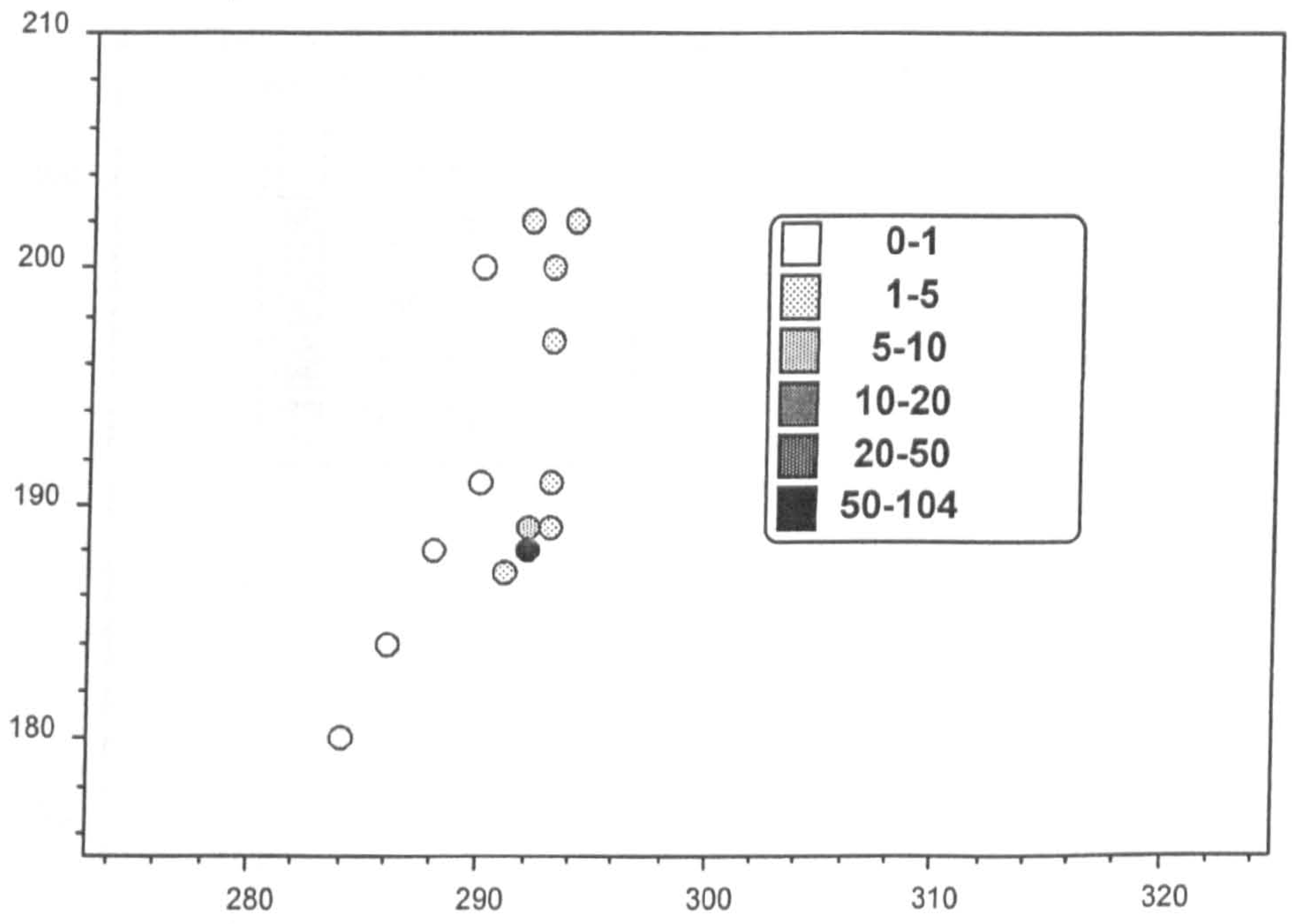

Figure AX.7 a) Grid Cell Plot (1m cells) for **Vole E ♂ 12 January 2000** (N=144 fixes)

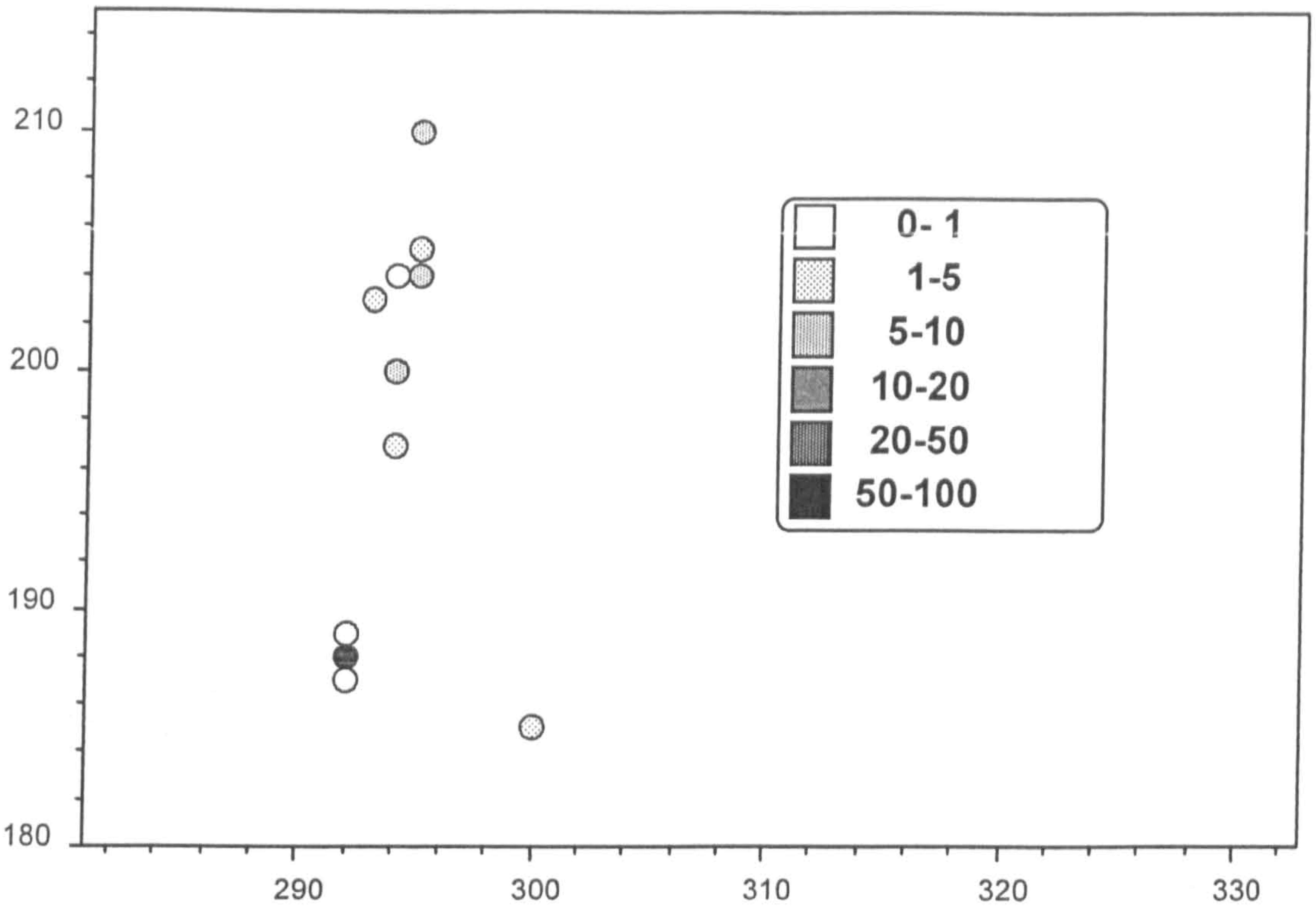

Figure A3.6 Grid Cell Plot (1m cells) for **Vole E♂ 15 February 2000** (N=109 fixes)

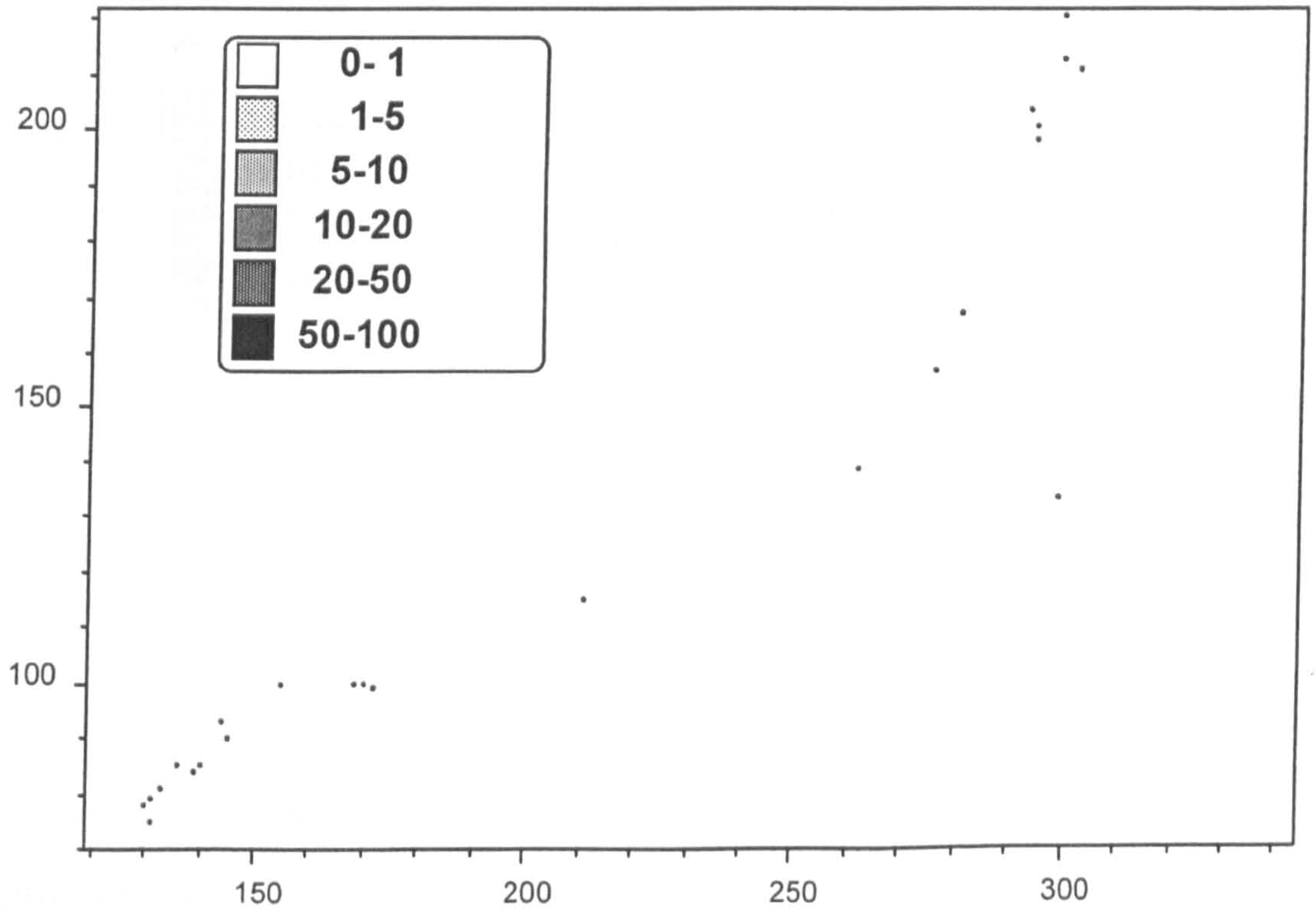

Figure A3.7 Grid Cell Plot (1m cells) for **Vole E♂ 1 March 2000** (N=111 fixes). Refer to Figures A3.7i, ii and iii.

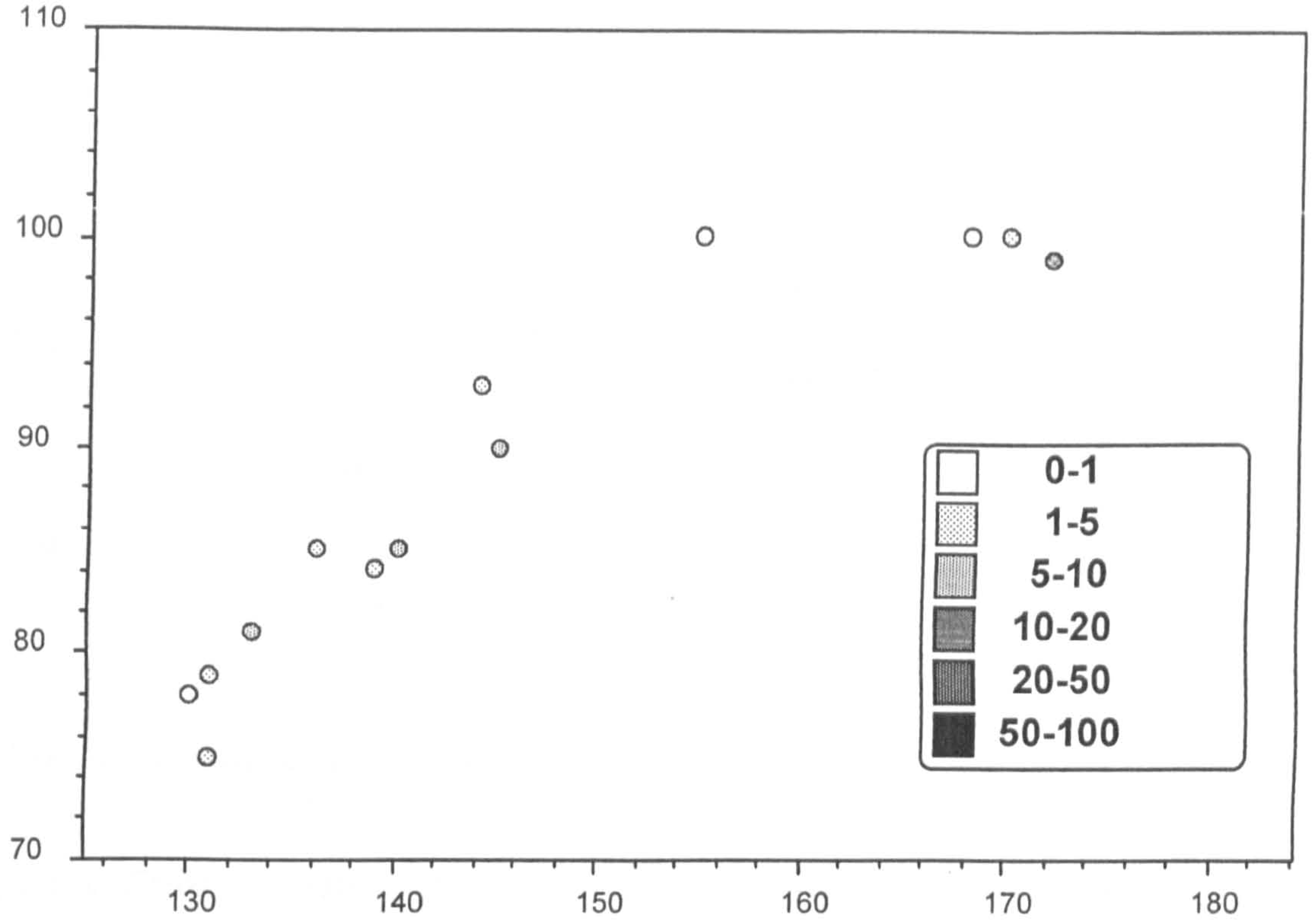

Figure A3.7(i) Grid Cell Plot (1m cells) for **Vole E♂ 1 March 2000**

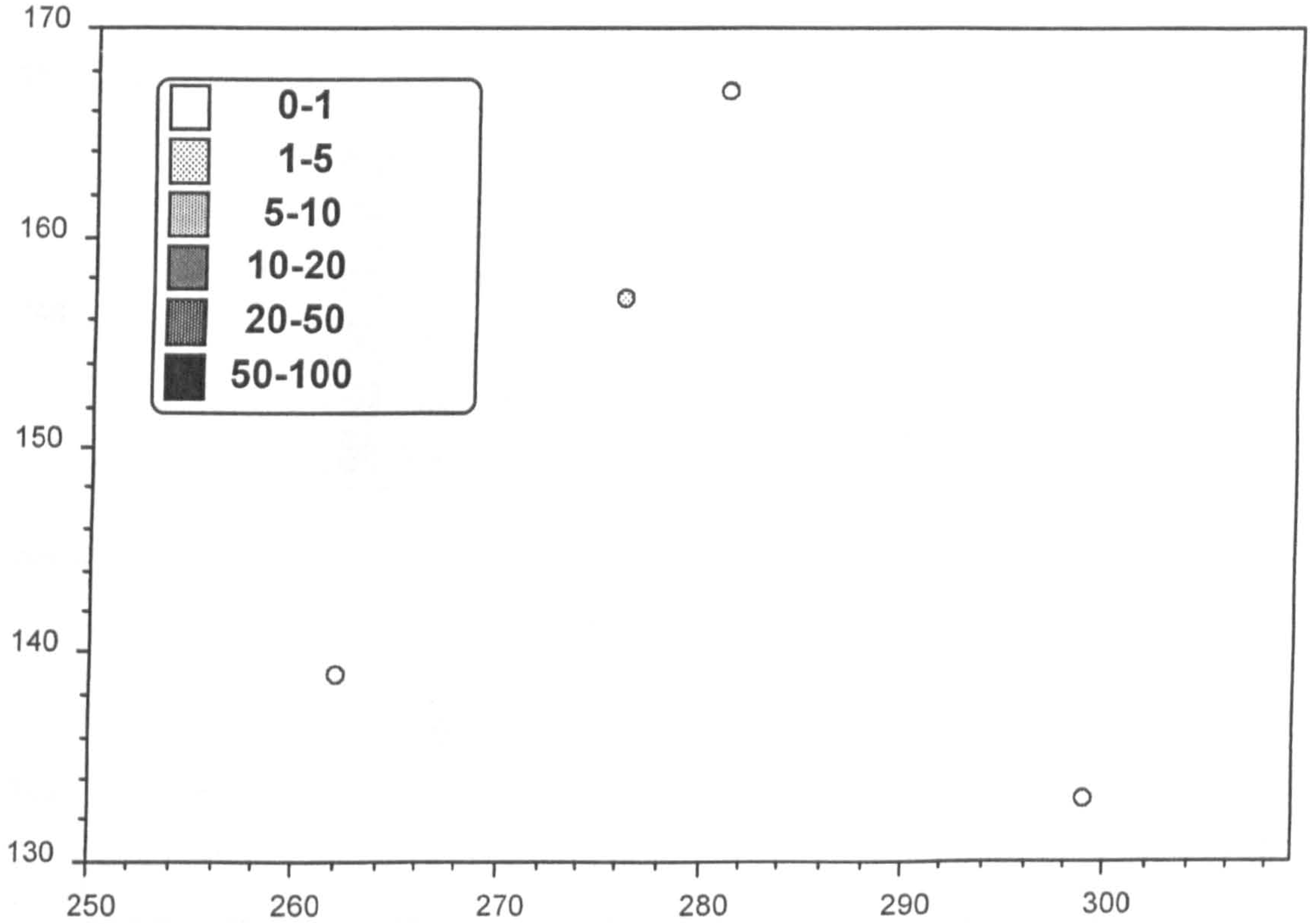

Figure A3.7(ii) Grid Cell Plot (1m cells) for **Vole E♂ 1 March 2000**

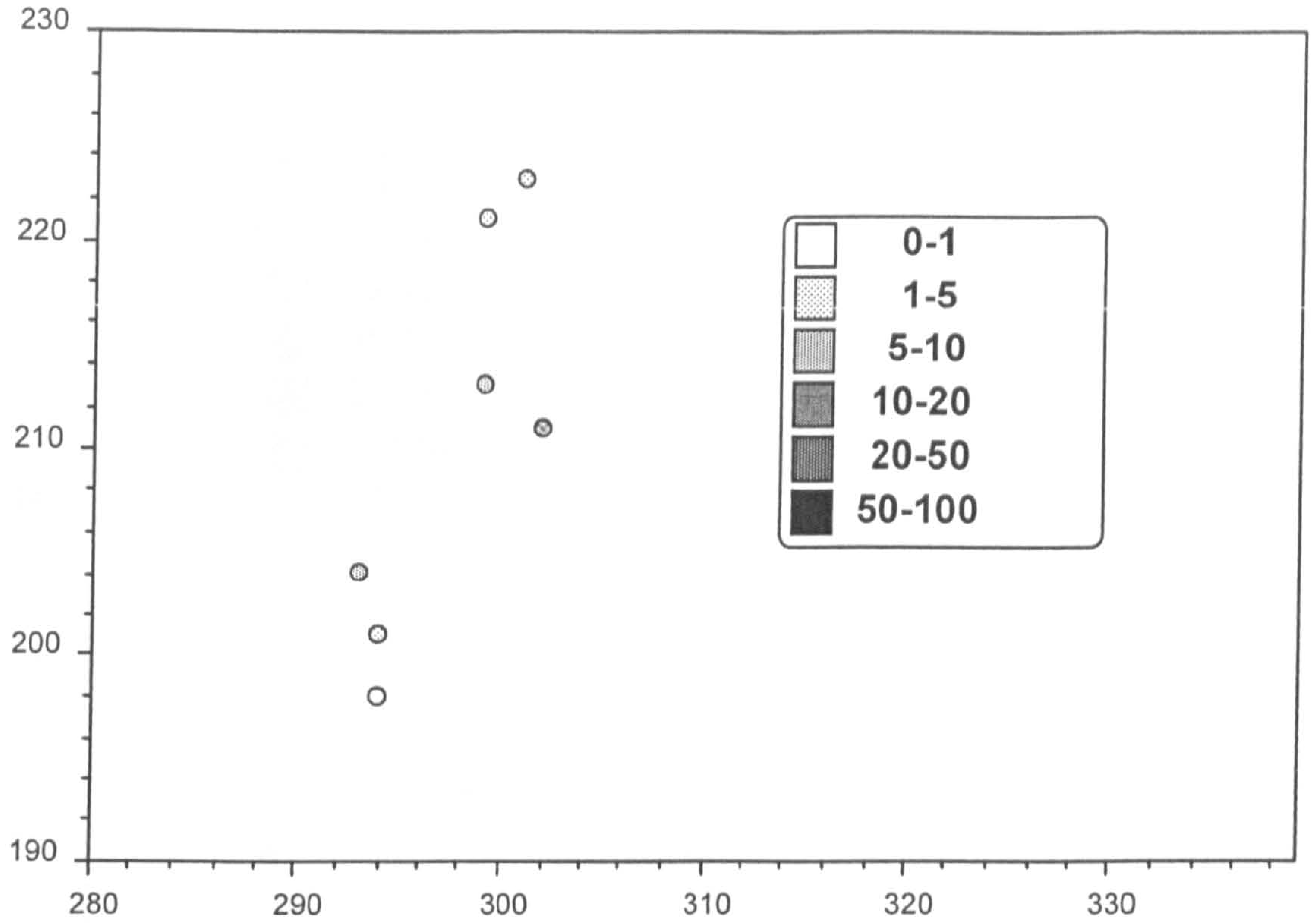

Figure A3.7(iii) Grid Cell Plot (1m cells) for **Vole E♂ 1 March 2000**

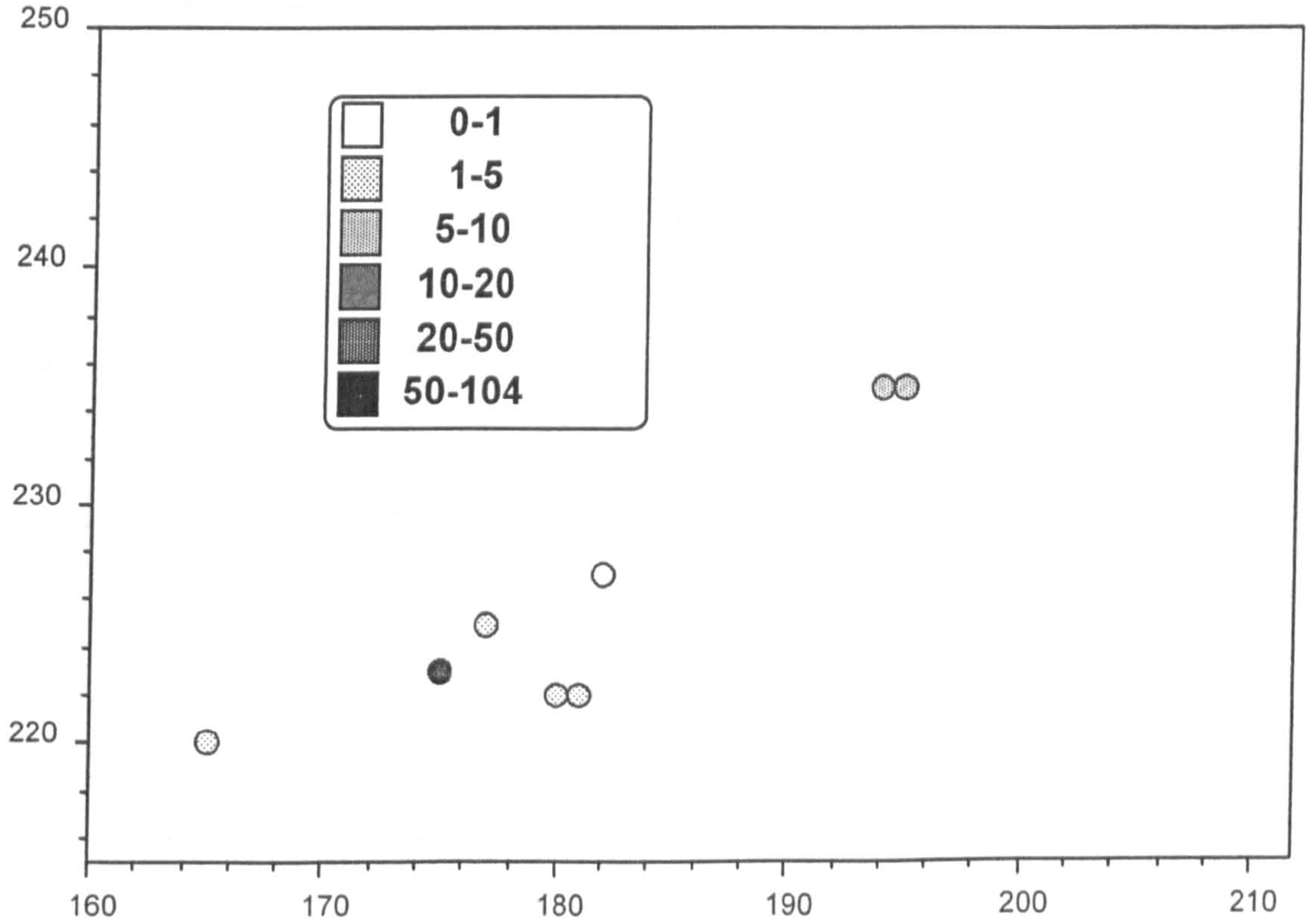

Figure A3.8 Grid Cell Plot (1m cells) for **Vole E♂ 11 March 2000** (N=96 fixes)

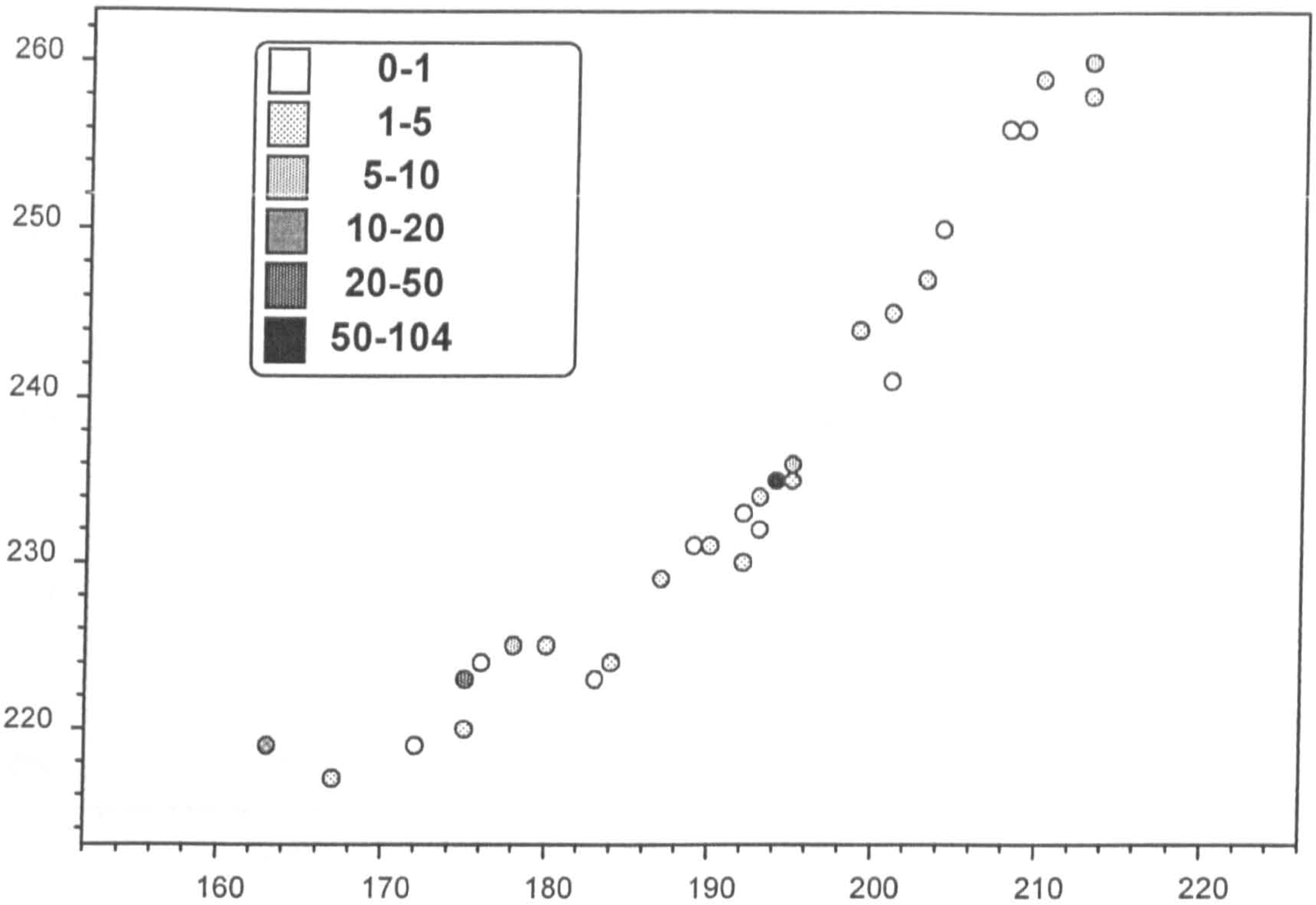

Figure A3.9 Grid Cell Plot (1m cells) for **Vole E♂ 21 March 2000** (N=192 fixes)

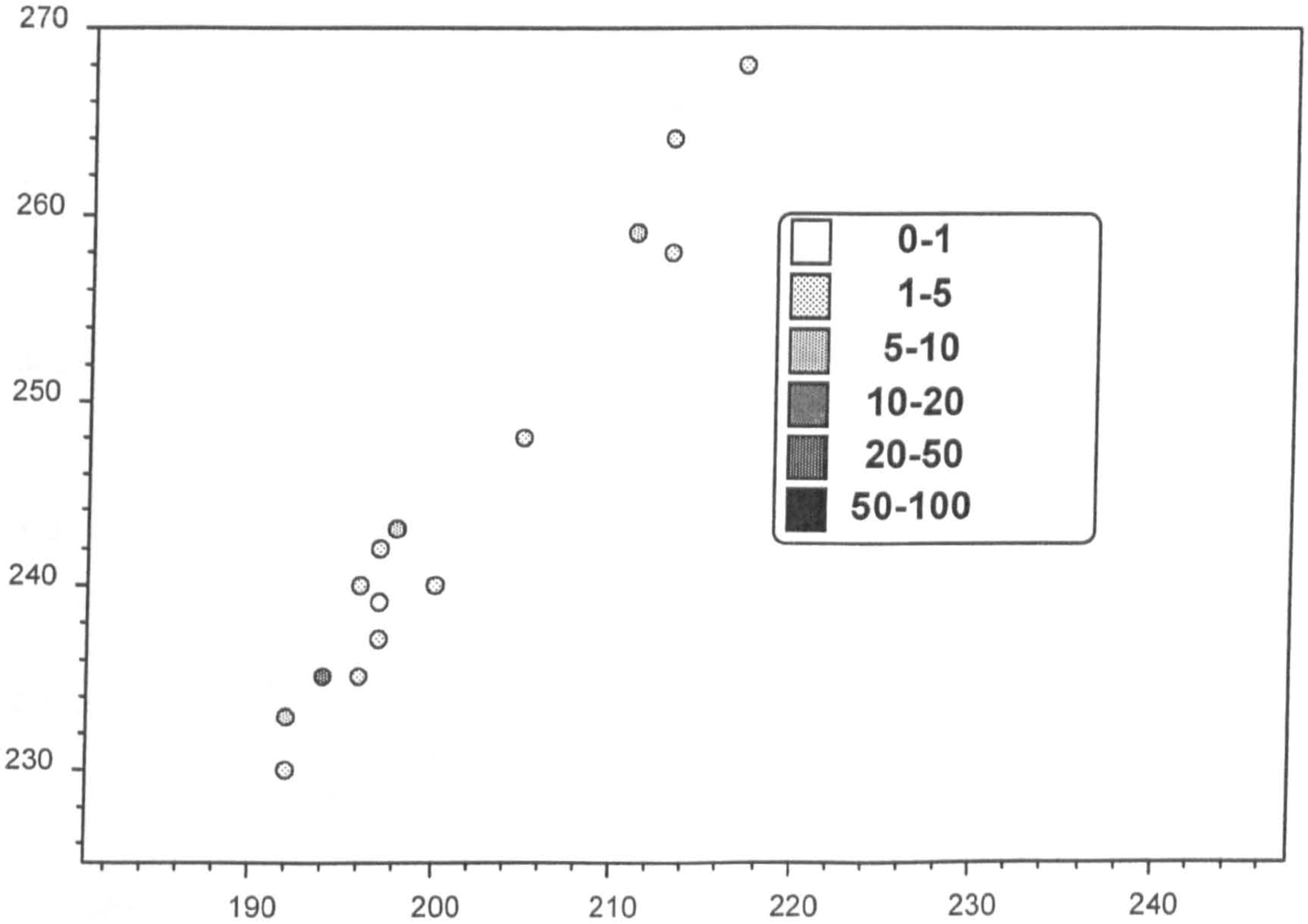

Figure A3.10 Grid Cell Plot (1m cells) for **Vole E♂ 15 April 2000** (N=96 fixes)

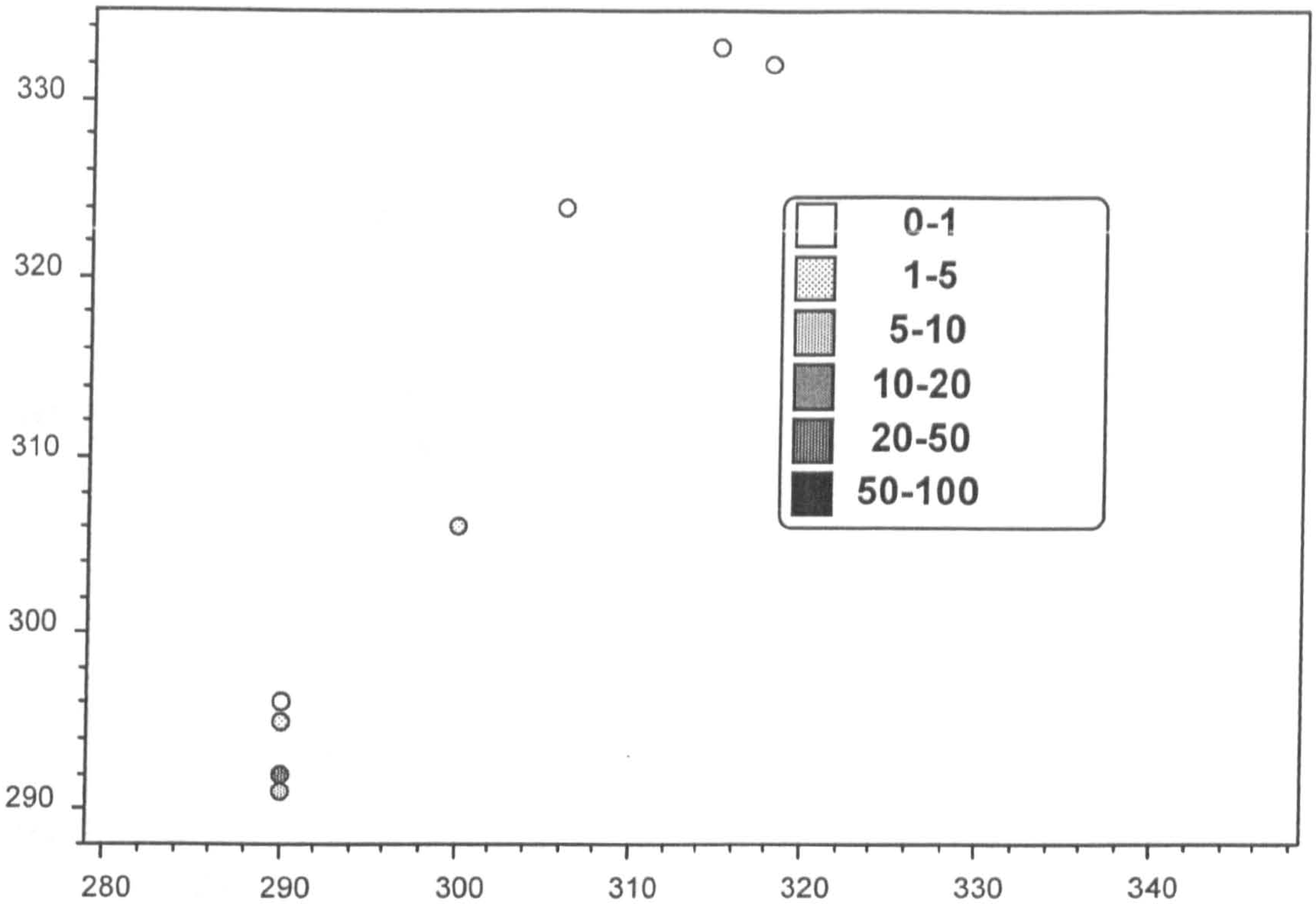

Figure A3.11 Grid Cell Plot (1m cells) for **Vole F♂ 12 January 2000** (N=48 fixes)

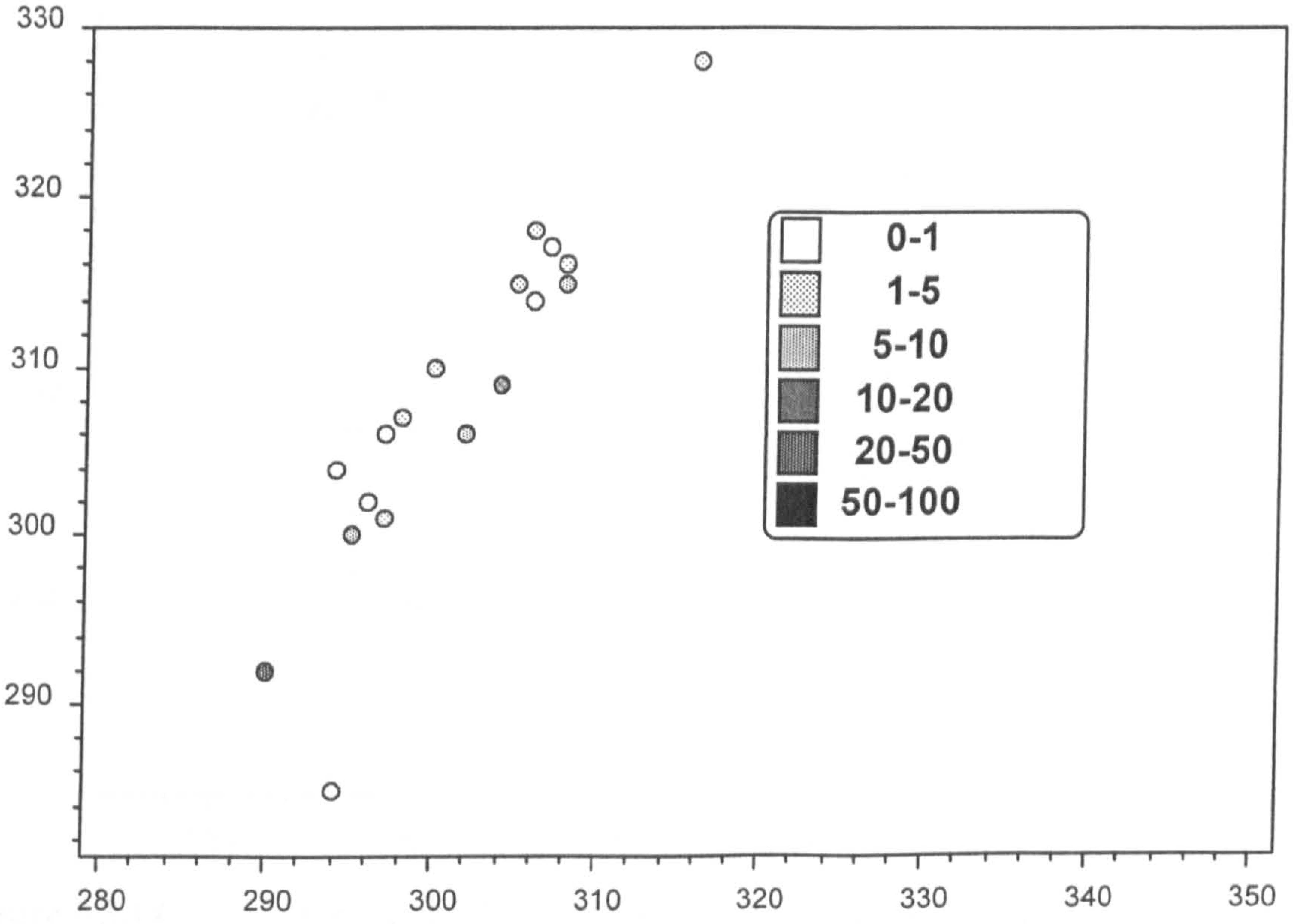

Figure A3.12 Grid Cell Plot (1m cells) for **Vole F♂ 18 January 2000** (N=96 fixes)

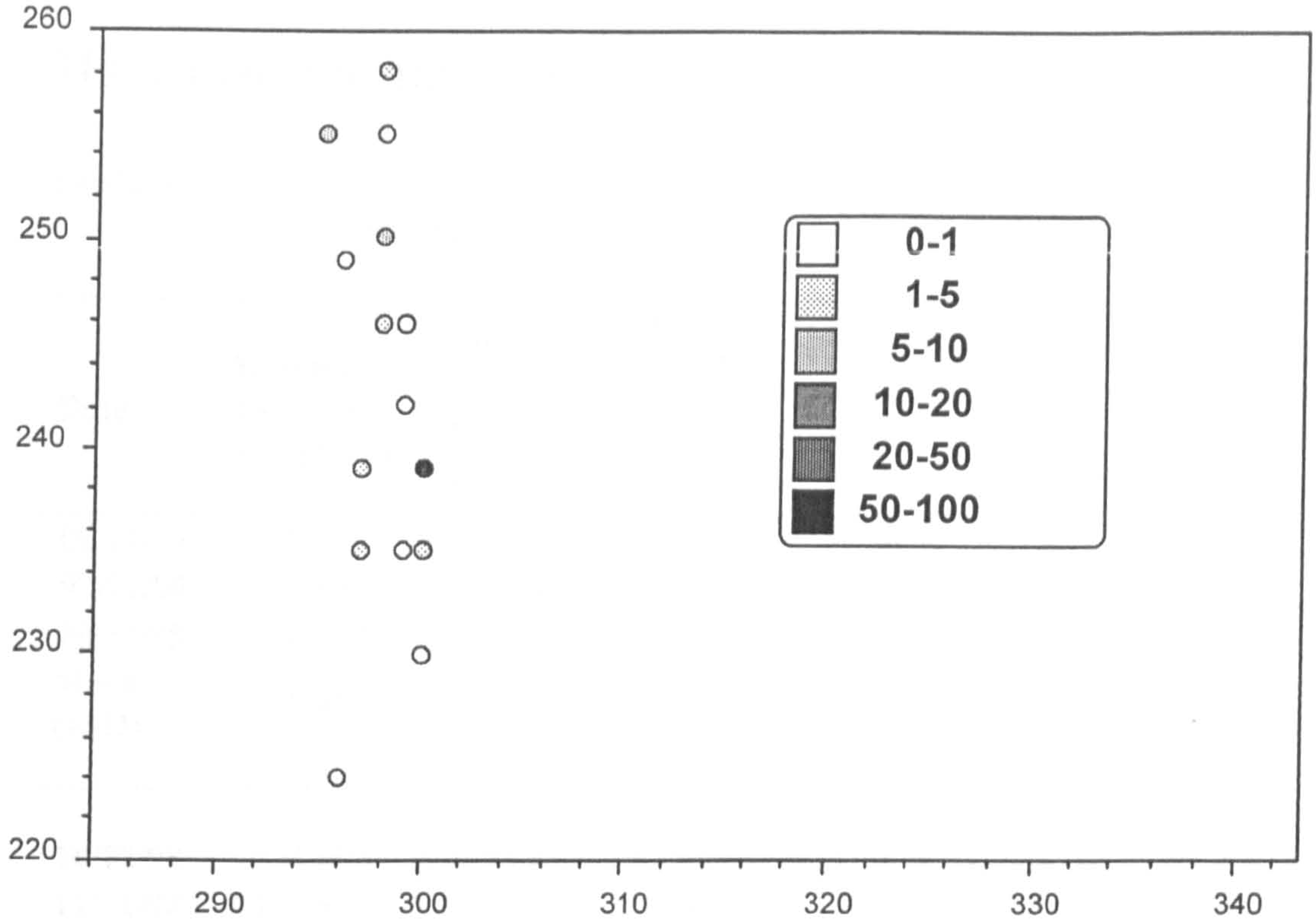

Figure A3.13 Grid Cell Plot (1m cells) for **Vole G♀ 16 February 2000** (N=96 fixes)

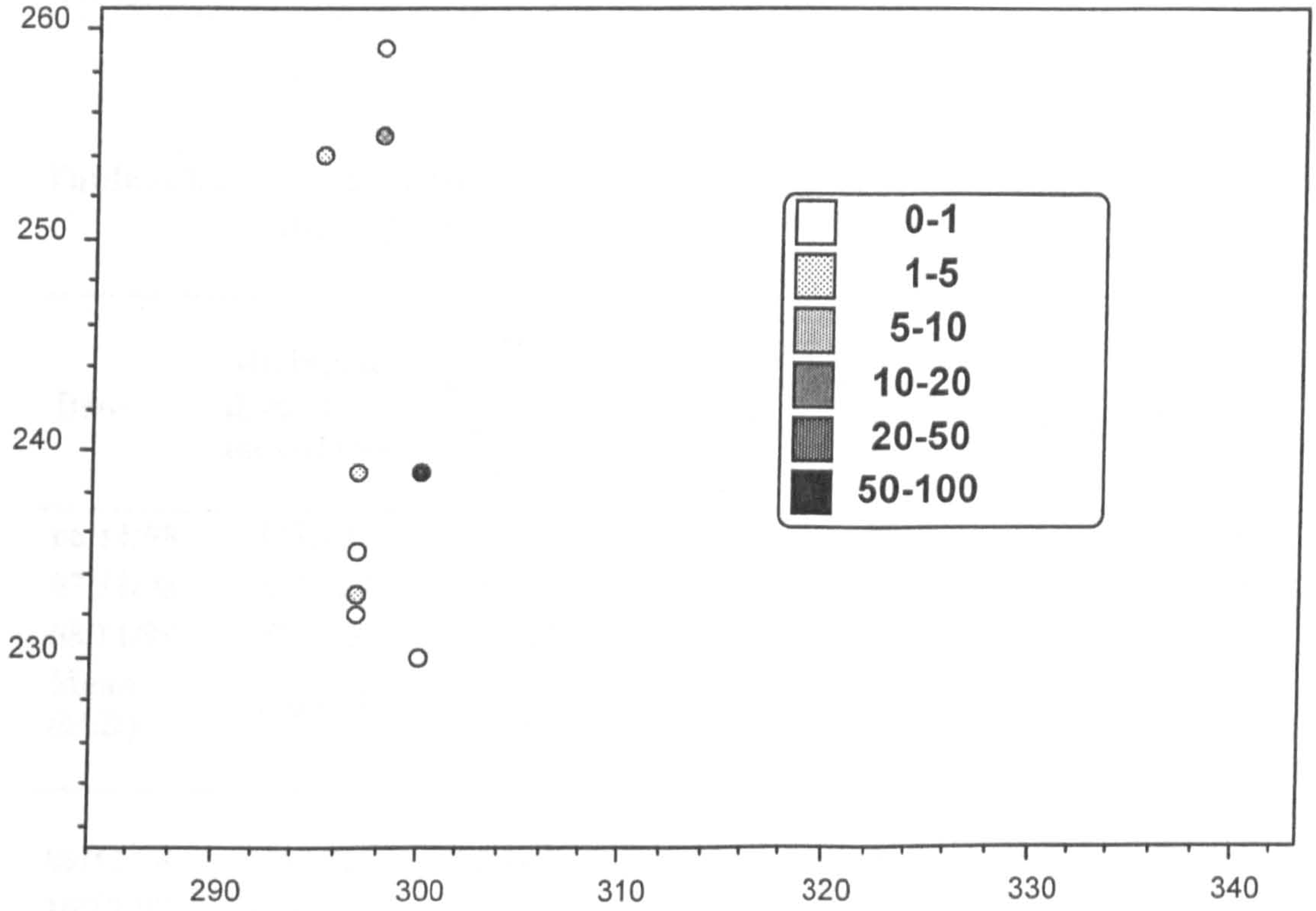

Figure A3.14 Grid Cell Plot (1m cells) for **Vole G♀ 1 March 2000** (N=96 fixes)

APPENDIX 4

Movement Parameters

Table A4.1 Distance and speed parameters for Vole A♀ based on fixes out of the nest site

Date	Minimum distance moved (m)	Mean speed (all fixes; m/min)	Mean speed (moving fixes; m/min)	Fixes (all)	Fixes (moving)	Percentage moving fixes
06/11/98	88.56	0.155	0.311	38	19	50
07/11/98	97.898	0.081	0.176	82	38	46
08/11/98	38.277	0.048	0.106	42	17	40
Mean (±SD)	74.912	0.087 (±0.068)	0.187 (±0.099)	162	74	46
10/12/98	171.995	0.122	0.28	78	27	35
11/12/98	177.818	0.126	0.269	82	32	39
12/12/98	82.312	0.062	0.289	90	20	22
13/12/98	32.986	0.105	0.367	22	7	32
Mean (±SD)	116.278	0.104 (±0.101)	0.282 (±0.166)	272	86	32

Table A4.2 Distance and speed parameters for Vole B♀ based on fixes out of the nest site

Date	Minimum distance moved (m)	Mean speed (all fixes; m/min)	Mean speed (moving fixes; m/min)	Fixes (all)	Fixes (moving)	Percentage moving fixes
06/11/98	113.093	0.193	0.279	39	27	69
07/11/98	241.627	0.173	0.322	94	51	54
08/11/98	67.115	0.081	0.166	44	18	41
Mean (±SD)	140.612	0.15 (±0.096)	0.27 (±0.129)	177	96	54
09/12/98	53.586	0.143	0.51	25	8	32
10/12/98	220.193	0.156	0.341	77	33	43
11/12/98	144.462	0.113	0.438	73	23	32
Mean (±SD)	139.414	0.137 (±0.155)	0.387 (±0.260)	175	64	37

Table A4.3 Distance and speed parameters for Vole C♀ based on fixes out of the nest site

Date	Minimum distance moved (m)	Mean speed (all fixes; m/min)	Mean speed (moving fixes; m/min)	Fixes (all)	Fixes (moving)	Percentage moving fixes
06/11/98	93.256	0.168	0.249	38	26	68
07/11/98	165.244	0.117	0.234	95	48	51
08/11/98	36.419	0.056	0.27	31	9	29
Mean (±SD)	98.306	0.113 (±0.077)	0.243 (±0.113)	164	83	51

Table A4.4 Distance and speed parameters for Vole E♂ based on fixes out of the nest site

Date	Minimum distance moved (m)	Mean speed (all fixes; m/min)	Mean speed (moving fixes; m/min)	Fixes (all)	Fixes (moving)	Percentage moving fixes
01/03/00	86.077	0.191	0.638	31	10	32
02/03/00	639.333	0.609	1.705	71	26	37
Mean (±SD)	362.705	0.484 (±0.441)	1.422 (±0.757)	102	36	35
12/03/00	92.202	0.137	1.024	46	7	15
Mean (±SD)	92.202	0.137 (±0.206)	1.024 (±0.567)	46	7	15
21/03/00	118.02	0.197	0.983	41	9	22
22/03/00	148.54	0.211	0.582	48	18	38
23/03/00	77.882	0.236	0.577	23	10	43
24/03/00	252.519	0.24	0.802	71	22	31
Mean (±SD)	149.24	0.222 (±0.199)	0.724 (±0.359)	183	59	32
15/04/00	67.546	0.1	0.5	46	10	22
16/04/00	65.071	0.167	0.362	27	13	48
Mean (±SD)	66.308	0.125 (±0.110)	0.421 (±0.202)	73	23	32

Table A4.5 Distance and speed parameters for Vole F♂ based on fixes out of the nest site

Date	Minimum distance moved (m)	Mean speed (all fixes; m/min)	Mean speed (moving fixes; m/min)	Fixes (all)	Fixes (moving)	Percentage moving fixes
12/01/00	213.577	0.324	1.294	45	12	27
Mean (±SD)	213.577	0.324 (±0.340)	1.294 (±0.681)	45	12	27
19/01/00	244.419	0.214	0.708	77	24	31
Mean (±SD)	244.419	0.214 (±0.198)	0.708 (±0.360)	77	24	31

Table A4.6 Distance and speed parameters for Vole G♀ based on fixes out of the nest site

Date	Minimum distance moved (m)	Mean speed (all fixes; m/min)	Mean speed (moving fixes; m/min)	Fixes (all)	Fixes (moving)	Percentage moving fixes
16/02/00	169.291	0.125	0.491	91	24	26
Mean (±SD)	169.291	0.125 (±0.116)	0.491 (±0.230)	91	24	26
02/03/00	279.475	0.296	1.694	64	12	19
Mean (±SD)	279.475	0.296 (±0.465)	1.694 (±1.116)	64	12	19
12/03/00	234.422	0.233	0.579	67	27	40
Mean (±SD)	148.54	0.211 (±0.182)	0.582 (±0.288)	48	18	38
22/03/00	14.489	0.027	0.193	37	6	16
24/03/00	166.956	0.161	0.655	68	18	26
Mean (±SD)	90.722	0.115 (±0.153)	0.55 (±0.335)	105	24	23
15/04/00	102.196	0.145	0.619	47	12	26
16/04/00	174.327	0.27	0.894	44	14	32
Mean (±SD)	138.262	0.205 (±0.299)	0.768 (±0.580)	91	26	29

Table A4.7 Distance and speed parameters for Vole H♂ based on fixes out of the nest site

Date	Minimum distance moved (m)	Mean speed (all fixes; m/min)	Mean speed (moving fixes; m/min)	Fixes (all)	Fixes (moving)	Percentage moving fixes
16/02/00	186.168	0.214	0.887	58	14	24
Mean (±SD)	186.168	0.214 (±0.234)	0.887 (±0.477)	58	14	24
01/03/00	37.324	0.083	0.276	31	10	32
02/03/00	77.719	0.084	0.432	63	13	21
Mean (±SD)	57.521	0.083 (±0.076)	0.365 (±0.166)	94	23	24
12/03/00	121.013	0.155	0.576	53	15	28
Mean (±SD)	121.013	0.155 (±0.184)	0.576 (±0.355)	53	15	28
21/03/00	98.047	0.327	0.726	21	10	48
22/03/00	833.557	1.292	2.315	44	25	57
23/03/00	218.305	0.728	1.455	21	11	52
24/03/00	446.157	0.419	0.875	72	35	49
Mean (±SD)	399.016	0.691 (±0.613)	1.382 (±0.868)	158	81	51
15/04/00	108.401	0.151	0.516	49	15	31
16/04/00	308.98	0.49	1.212	43	18	42
Mean (±SD)	208.691	0.309 (±0.309)	0.898 (±0.528)	92	33	36

Table A4.8 Distance and speed parameters for Vole D♂ based on fixes out of the nest site

Date	Minimum distance moved (m)	Mean speed (all fixes; m/min)	Mean speed (moving fixes; m/min)	Fixes (all)	Fixes (moving)	Percentage moving fixes
16/11/99	215.117	0.448	1.195	33	13	39
17/11/99	75.338	0.129	0.558	40	10	25
Mean (±SD)	145.228	0.273 (±0.240)	0.922 (±0.442)	73	23	32
23/11/99	266.016	0.211	0.493	81	33	41
24/11/99	179.034	0.217	0.519	56	24	43
Mean (±SD)	222.525	0.213 (±0.162)	0.503 (±0.248)	137	57	42
30/11/99	206.723	0.27	0.689	52	21	40
01/12/99	53.72	0.128	0.256	29	15	52
Mean (±SD)	130.222	0.22 (±0.273)	0.511 (±0.417)	81	36	44

Table A4.9 Distance and speed parameters for Vole EM♀ based on fixes out of the nest site

Date	Minimum distance moved (m)	Mean speed (all fixes; m/min)	Mean speed (moving fixes; m/min)	Fixes (all)	Fixes (moving)	Percentage moving fixes
16/11/99	176.219	0.287	0.979	37	13	35
17/11/99	169.583	0.269	0.628	43	19	44
Mean (±SD)	172.901	0.278 (±0.228)	0.768 (±0.379)	80	32	40
23/11/99	250.572	0.176	0.491	96	35	36
24/11/99	249.612	0.287	0.489	59	35	59
Mean (±SD)	250.092	0.218 (±0.189)	0.49 (±0.284)	155	70	45
14/12/99	90.903	0.289	1.01	16	7	44
Mean (±SD)	90.903	0.289 (±0.378)	1.01 (±0.710)	16	7	44

Table A4.10 Distance and speed parameters for Vole J♂ based on fixes out of the nest site

Date	Minimum distance moved (m)	Mean speed (all fixes; m/min)	Mean speed (moving fixes; m/min)	Fixes (all)	Fixes (moving)	Percentage moving fixes
22/02/00	170.069	0.344	0.945	34	13	38
23/02/00	319.986	0.41	0.97	53	23	43
Mean (±SD)	245.027	0.384 (±0.310)	0.961 (±0.490)	87	36	41

Table A4.11 Distance and speed parameters for Vole K♂ based on fixes out of the nest site

Date	Minimum distance moved (m)	Mean speed (all fixes; m/min)	Mean speed (moving fixes; m/min)	Fixes (all)	Fixes (moving)	Percentage moving fixes
22/02/00	170.418	0.316	0.812	37	15	41
23/02/00	351.972	0.469	1.235	51	20	39
Mean (±SD)	261.195	0.405 (±0.297)	1.055 (±0.480)	88	35	40
07/03/00	576.735	0.493	1.479	79	27	34
08/03/00	408.251	0.698	1.814	40	16	40
Mean (±SD)	492.493	0.561 (±0.426)	1.602 (±0.721)	119	43	36

Table A4.12 Distance and speed parameters for Vole L♂ based on fixes out of the nest site

Date	Minimum distance moved (m)	Mean speed (all fixes; m/min)	Mean speed (moving fixes; m/min)	Fixes (all)	Fixes (moving)	Percentage moving fixes
22/02/00	104.376	0.303	0.633	24	12	50
23/02/00	334.095	0.378	0.928	60	25	42
Mean (±SD)	219.235	0.356 (±0.272)	0.835 (±0.417)	84	37	44
07/03/00	761.676	0.619	1.154	83	45	54
Mean (±SD)	761.676	0.619 (±0.639)	1.154 (±0.873)	83	45	54

Table A4.13 Distance and speed parameters for Vole FR♂ based on fixes out of the nest site

Date	Minimum distance moved (m)	Mean speed (all fixes; m/min)	Mean speed (moving fixes; m/min)	Fixes (all)	Fixes (moving)	Percentage moving fixes
17/11/99	47.782	0.06	0.187	54	18	33
Mean (±SD)	47.782	0.06 (±0.060)	0.187 (±0.105)	54	18	33
23/11/99	193.354	0.172	0.586	76	23	30
24/11/99	37.614	0.043	0.148	59	18	30
Mean (±SD)	115.484	0.116 (±0.214)	0.395 (±0.396)	135	41	30

Table A4.14 Distance and speed parameters for Vole HE♀ based on fixes out of the nest site

Date	Minimum distance moved (m)	Mean speed (all fixes; m/min)	Mean speed (moving fixes; m/min)	Fixes (all)	Fixes (moving)	Percentage moving fixes
16/11/99	143.653	0.383	0.798	26	13	50
17/11/99	136.912	0.277	1.304	34	8	24
Mean (±SD)	140.282	0.322 (±0.271)	0.984 (±0.473)	60	21	35
23/11/99	410.853	0.365	1.442	76	20	26
24/11/99	63.161	0.105	0.526	41	9	22
Mean (±SD)	237.007	0.275 (±0.307)	1.17 (±0.634)	117	29	25

Table A4.15 Distance and speed parameters for Vole I♂ based on fixes out of the nest site

Date	Minimum distance moved (m)	Mean speed (all fixes; m/min)	Mean speed (moving fixes; m/min)	Fixes (all)	Fixes (moving)	Percentage moving fixes
14/12/99	17.43	0.073	0.097	11	7	64
15/12/99	14.786	0.043	0.246	16	5	31
Mean (±SD)	16.108	0.055 (±0.045)	0.134 (±0.070)	27	12	44

Table A4.16 Distance and speed parameters for Vole MO♂ based on fixes out of the nest site

Date	Minimum distance moved (m)	Mean speed (all fixes; m/min)	Mean speed (moving fixes; m/min)	Fixes (all)	Fixes (moving)	Percentage moving fixes
22/02/00	150.044	0.278	0.769	37	14	38
23/02/03	152.13	0.203	0.845	51	13	25
Mean (±SD)	151.087	0.234 (±0.239)	0.806 (±0.443)	88	27	31
07/03/00	488.628	0.459	2.715	72	13	18
Mean (±SD)	488.628	0.459 (±0.791)	2.715 (±1.928)	72	13	18

Table A4.17 Distance and speed parameters for Vole N♂ based on fixes out of the nest site

Date	Minimum distance moved (m)	Mean speed (all fixes; m/min)	Mean speed (moving fixes; m/min)	Fixes (all)	Fixes (moving)	Percentage moving fixes
19/08/00	158.911	0.183	0.279	59	39	66
20/08/00	73.755	0.145	0.214	35	24	69
Mean (±SD)	116.333	0.169 (±0.112)	0.254 (±0.138)	94	63	67
02/09/00	93.521	0.102	0.164	62	39	63
03/09/00	114.029	0.23	0.507	34	16	47
Mean (±SD)	103.775	0.147 (±0.162)	0.261 (±0.215)	96	55	57

Table A4.18 Distance and speed parameters for Vole O♀ based on fixes out of the nest site

Date	Minimum distance moved (m)	Mean speed (all fixes; m/min)	Mean speed (moving fixes; m/min)	Fixes (all)	Fixes (moving)	Percentage moving fixes
19/08/00	335.574	0.386	0.533	59	43	73
20/08/00	169.122	0.332	0.434	35	27	77
Mean (±SD)	252.348	0.366 (±0.222)	0.495 (±0.258)	94	70	74

Table A4.19 Distance and speed parameters for Vole Q♀ based on fixes out of the nest site

Date	Minimum distance moved (m)	Mean speed (all fixes; m/min)	Mean speed (moving fixes; m/min)	Fixes (all)	Fixes (moving)	Percentage moving fixes
09/09/00	145.963	0.191	0.336	52	30	58
10/09/00	69.281	0.14	0.308	34	16	47
Mean (±SD)	107.622	0.171 (±0.130)	0.326 (±0.179)	86	46	53

APPENDIX 5

Static Interactions

Table A5.1 Static interaction analysis between **Vole EM♀ and Vole D♂ 16 November 1999**

File name	Fixes used	Fixes total	Range cells	Range area (ha)	Overlap cells	Overlap area (ha)	% range shared
Vole EM♀ 16 Nov 99	91	91	10	0	3	0	30
Vole D♂ 16 Nov 99	96	96	10	0	3	0	30
Both			17	0	3	0	17.6

Spearman's rank correlation coefficient=0.0242
Grid cell side length (m.) = 1
Independence interval (mins.) =15
No influences.

Table A5.2 Static interaction analysis between **Vole EM♀ and Vole D♂ 23 November 1999**

File name	Fixes used	Fixes total	Range cells	Range area (ha)	Overlap cells	Overlap area (ha)	% range shared
Vole D♂ 23 Nov 99	157	157	24	0	9	0	37.5
Vole EM♀ 23 Nov 99	161	161	26	0	9	0	34.6
Both			41	0	9	0	22

Spearman's rank correlation coefficient=-.1677
Grid cell side length (m.) = 1
Independence interval (mins.) =15
No influences.

Table A5.3 Static interaction analysis between **Vole EM♀ and Vole D♂ 23 November 1999**

File name	Fixes used	Fixes total	Range cells	Range area (ha)	Overlap cells	Overlap area (ha)	% range shared
Vole D♂ 30 Nov 99	96	96	16	0	8	0	50
Vole EM♀ 30 Nov 99	96	96	23	0	8	0	34.8
Both			31	0	8	0	25.8

Spearman's rank correlation coefficient=-.0717
Grid cell side length (m.) = 1
Independence interval (mins.) =15
No influences.

Table A5.4 Static interaction analysis between **Vole G♀ and Vole H♂**
16 February 2000

File name	Fixes used	Fixes total	Range cells	Range area (ha)	Overlap cells	Overlap area (ha)	% range shared
Vole G♀ 16 Feb 00	96	96	15	0	1	0	6.7
Vole H♂ 16 Feb 00	86	86	11	0	1	0	9.1
Both			25	0	1	0	4

Spearman's rank correlation coefficient=-.7697
Grid cell side length (m.) = 1
Independence interval (mins.) =15
No influences.

Table A5.5 Static interaction analysis between **Vole G♀ and Vole H♂**
1 March 2000

File name	Fixes used	Fixes total	Range cells	Range area (ha)	Overlap cells	Overlap area (ha)	% range shared
Vole G♀ 1 Mar 00	96	96	10	0	0	0	0
Vole H♂ 1 Mar 00	111	111	12	0	0	0	0
Both			22	0	0	0	0

Spearman's rank correlation coefficient=-.8641
Grid cell side length (m.) = 1
Independence interval (mins.) =15
No influences.

Table A5.6 Static interaction analysis between **Vole G♀ and Vole H♂**
11 March 2000

File name	Fixes used	Fixes total	Range cells	Range area (ha)	Overlap cells	Overlap area (ha)	% range shared
Vole G♀ 11 Mar 00	95	95	14	0	2	0	14.3
Vole H♂ 11 Mar 00	96	96	18	0	2	0	11.1
Both			30	0	2	0	6.7

Spearman's rank correlation coefficient=-.6448
Grid cell side length (m.) = 1
Independence interval (mins.) =15
No influences.

Table A5.7 Static interaction analysis between **Vole G♀ and Vole H♂**
21 March 2000

File name	Fixes used	Fixes total	Range cells	Range area (ha)	Overlap cells	Overlap area (ha)	% range shared
Vole G♀ 21 Mar 00	190	190	17	0	7	0	41.2
Vole H♂ 21 Mar 00	192	192	55	0.01	7	0	12.7
Both			65	0.01	7	0	10.8

Spearman's rank correlation coefficient=-.3616
Grid cell side length (m.) = 1
Independence interval (mins.) =15
No influences.

Table A5.8 Static interaction analysis between **Vole G♀ and Vole H♂ 15 April 2000**

File name	Fixes used	Fixes total	Range cells	Range area (ha)	Overlap cells	Overlap area (ha)	% range shared
Vole G♀ 15 Apr 00	95	95	20	0	6	0	30
Vole H♂ 15 Apr 00	96	96	26	0	6	0	23.1
Both			40	0	6	0	15

Spearman's rank correlation coefficient=-.5232
Grid cell side length (m.) = 1
Independence interval (mins.) =15
No influences.

Table A5.9 Static interaction analysis between **Vole N♂ and Vole O♀ 19/20 August 2000**

File name	Fixes used	Fixes total	Range cells	Range area (ha)	Overlap cells	Overlap area (ha)	% range shared
Vole N♂ 20 Aug 00	96	96	32	0	8	0	25
Vole O♀ 19 Aug 00	96	96	38	0	8	0	21.1
Both			62	0.01	8	0	12.9

Spearman's rank correlation coefficient=-.5116
Grid cell side length (m.) = 1
Independence interval (mins.) =15
No influences.

Table A5.10 Static interaction analysis between **Vole N♂ and Vole O♀ 19/20 August 2000**

File name	Fixes used	Fixes total	Range cells	Range area (ha)	Overlap cells	Overlap area (ha)	% range shared
Vole N♂ 2 Sep 00	96	96	20	0	9	0	45
Vole O♀ 2 Sep 00	96	96	23	0	9	0	39.1
Both			34	0	9	0	26.5

Spearman's rank correlation coefficient=-.1596
Grid cell side length (m.) = 1
Independence interval (mins.) =15
No influences.

Table A5.11 Static interaction analysis between **Vole N♂ and Vole Q♀ 19/20 August 2000**

File name	Fixes used	Fixes total	Range cells	Range area (ha)	Overlap cells	Overlap area (ha)	% range shared
Vole N♂ 9 Sep 00	63	96	10	0	0	0	0
Vole Q♀ 9 Sep 00	96	96	22	0	0	0	0
Both			32	0	0	0	0

Spearman's rank correlation coefficient=-.8027
Grid cell side length (m.) = 1
Independence interval (mins.) =15
No influences.

Table A5.12 Static interaction analysis between **Vole K♂ and Vole J♂ 22 February 2000**

File name	Fixes used	Fixes total	Range cells	Range area (ha)	Overlap cells	Overlap area (ha)	% range shared
Vole K♂ 22 Feb 00	112	112	22	0	8	0	36.4
Vole J♂ 22 Feb 00	112	112	21	0	8	0	38.1
Both			35	0	8	0	25.8

Spearman's rank correlation coefficient=-.443
Grid cell side length (m.) = 1
Independence interval (mins.) =15
No influences.

APPENDIX 6

Dynamic Interactions

Table A6.1 The proportion of paired (observed) and paired plus unpaired (expected) at given separation intervals of **Vole D♂ and Vole EM♀ 16 November 1999.** Probabilities that the excess or deficit of paired fixes may result from random variation are obtained from two-tailed binomial distribution

Files used: Vole D♂ 16 Nov 99 Vole EM♀16 Nov 99				
Separation (m)	**Observed**	**Expected**	**Difference**	**P**
19-20	0	0.0024	-0.0024	1
18-19	0	0.0097	-0.0097	1
17-18	0	0.0091	-0.0091	1
16-17	0.033	0.0161	0.0169	0.1805
15-16	0.033	0.0116	0.0214	0.0896
14-15	0	0.0002	-0.0002	1
13-14	0.0659	0.1508	-0.0849	0.019
12-13	0.022	0.085	-0.063	0.0235
11-12	0	0.0338	-0.0338	1
10-11	0.0879	0.0372	0.0507	0.0202
9-10	0	0.0077	-0.0077	1
8-9	0	0.0059	-0.0059	1
7-8	0	0.0117	-0.0117	1
6-7	0.022	0.0086	0.0134	0.1838
5-6	0	0.0023	-0.0023	1
4-5	0.011	0.01	0.001	0.6002
3-4	0	0.0035	-0.0035	1
2-3	0	0.0016	-0.0016	1
1-2	0	0.0174	-0.0174	1
0-1	0.0989	0.2314	-0.1325	0.0017
0	0.5604	0.2773	0.2832	0
	<= 1 m.	> 1 m.	Totals	
Paired	60	31	91	
Unpaired	4152	4038	8190	
Totals	4212	4069	8281	

Table A6.2 The proportion of paired (observed) and paired plus unpaired (expected) at given separation intervals of **Vole D♂ and Vole EM♀ 23 November 1999.** Probabilities that the excess or deficit of paired fixes may result from random variation are obtained from two-tailed binomial distribution

Files used: Vole D♂ 23 Nov 99 Vole EM♀23 Nov 99				
Separation (m)	**Observed**	**Expected**	**Difference**	**P**
19-20	0	0.0082	-0.0082	0
18-19	0	0.0043	-0.0043	1
17-18	0	0.0047	-0.0047	1
16-17	0	0.0033	-0.0033	1
15-16	0.0892	0.1119	-0.0228	0.447
14-15	0.0064	0.0701	-0.0637	0.0002
13-14	0	0.0173	-0.0173	1
12-13	0.0382	0.0575	-0.0193	0.3901
11-12	0.0191	0.0173	0.0018	0.7547
10-11	0.0255	0.0382	-0.0127	0.5331
9-10	0.0764	0.0813	-0.0049	1
8-9	0.0064	0.0202	-0.0139	0.3851
7-8	0.0064	0.0034	0.0029	0.4186
6-7	0.0892	0.0474	0.0418	0.022
5-6	0.0382	0.0463	-0.0081	0.8484
4-5	0.0255	0.0289	-0.0034	1
3-4	0	0.0256	-0.0256	1
2-3	0.0446	0.0539	-0.0093	0.7253
1-2	0.0382	0.0798	-0.0415	0.0547
0-1	0.0764	0.0798	-0.0034	1
0	0.3694	0.1514	0.218	0
	<= 1 m.	> 1 m.	Totals	
Paired	70	87	157	
Unpaired	5631	18861	24492	
Totals	5701	18948	24649	

Table A6.3 The proportion of paired (observed) and paired plus unpaired (expected) at given separation intervals of **Vole D♂ and Vole EM♀ 30 November 1999.** Probabilities that the excess or deficit of paired fixes may result from random variation are obtained from two-tailed binomial distribution

Files used: Vole D♂ 30 Nov 99 Vole EM♀ 30 Nov 99				
Separation (m)	Observed	Expected	Difference	P
19-20	0	0.0014	-0.0014	1
18-19	0	0.0099	-0.0099	1
17-18	0.0104	0.0101	0.0003	0.6223
16-17	0	0.0023	-0.0023	1
15-16	0.0104	0.0039	0.0065	0.3132
14-15	0	0.0084	-0.0084	1
13-14	0.0312	0.0308	0.0004	0.7716
12-13	0	0.0122	-0.0122	1
11-12	0	0.0113	-0.0113	1
10-11	0.0104	0.0319	-0.0215	0.3779
9-10	0	0.0053	-0.0053	1
8-9	0.0104	0.0138	-0.0034	1
7-8	0	0.0149	-0.0149	1
6-7	0	0.0037	-0.0037	1
5-6	0.0104	0.0322	-0.0218	0.3789
4-5	0.0312	0.0421	-0.0108	0.8005
3-4	0.0625	0.0317	0.0308	0.1304
2-3	0.0417	0.031	0.0106	0.5456
1-2	0.0312	0.0299	0.0013	0.7653
0-1	0.1667	0.1994	-0.0328	0.5226
0	0.4271	0.3114	0.1157	0.02
	<= 1 m.	> 1 m.	Totals	
Paired	57	39	96	
Unpaired	4651	4469	9120	
Totals	4708	4508	9216	

Table A6.4) The proportion of paired (observed) and paired plus unpaired (expected) at given separation intervals of **Vole G♀ and Vole H♂ 16 February 2000.** Probabilities that the excess or deficit of paired fixes may result from random variation are obtained from two-tailed binomial distribution

Files used: Vole G♀ 16 Feb 00 Vole H♂ 16 Feb 00				
Separation (m)	**Observed**	**Expected**	**Difference**	**P**
19-20	0.4884	0.4498	0.0385	0.5159
18-19	0	0.0185	-0.0185	1
17-18	0	0.0003	-0.0003	1
16-17	0.0116	0.0023	0.0093	0.1796
15-16	0	0.0127	-0.0127	1
14-15	0	0.0051	-0.0051	1
13-14	0.0581	0.0657	-0.0076	1
12-13	0	0.0085	-0.0085	1
11-12	0.0233	0.0189	0.0043	0.6793
10-11	0	0.005	-0.005	1
9-10	0	0.0069	-0.0069	1
8-9	0.0698	0.0561	0.0137	0.4851
7-8	0.0233	0.0111	0.0122	0.247
6-7	0.0116	0.0026	0.0091	0.1985
5-6	0.0349	0.0041	0.0308	0.0053
4-5	0	0.0015	-0.0015	1
3-4	0.0233	0.0115	0.0118	0.2599
2-3	0.0465	0.0791	-0.0326	0.3217
1-2	0.0116	0.0014	0.0103	0.1098
0-1	0	0	0	0.9999
0	0.0116	0.0077	0.0039	0.4859
	<= 1 m.	> 1 m.	Totals	
Paired	1	85	86	
Unpaired	56	7254	7310	
Totals	57	7339	7396	

Table A6.5 The proportion of paired (observed) and paired plus unpaired (expected) at given separation intervals of **Vole G♂ and Vole H♀ 1 March 2000.** Probabilities that the excess or deficit of paired fixes may result from random variation are obtained from two-tailed binomial distribution

Files used: Vole G♀ 1 Mar 00 Vole H♂ 1 Mar 00				
Separation (m)	**Observed**	**Expected**	**Difference**	**P**
19-20	0.4479	0.4652	-0.0173	0.7598
18-19	0.0312	0.0388	-0.0076	1
17-18	0	0.0117	-0.0117	1
16-17	0	0.0221	-0.0221	1
15-16	0.0208	0.0114	0.0094	0.2989
14-15	0	0.0007	-0.0007	1
13-14	0	0	0	0.9999
12-13	0	0.0005	-0.0005	1
11-12	0	0	0	0.9999
10-11	0	0	0	0.9999
9-10	0.0208	0.0075	0.0133	0.162
8-9	0	0.0085	-0.0085	1
7-8	0	0	0	0.9999
6-7	0	0.0078	-0.0078	1
5-6	0	0.0028	-0.0028	1
4-5	0	0.0064	-0.0064	1
3-4	0.1979	0.1553	0.0426	0.2585
2-3	0.0104	0.0133	-0.0029	1
1-2	0	0	0	0.9999
0-1	0	0.0013	-0.0013	1
0	0	0	0	0.9999
	<= 1 m.	> 1 m.	Totals	
Paired	0	96	96	
Unpaired	12	9108	9120	
Totals	12	9204	9216	

Table A6.6 The proportion of paired (observed) and paired plus unpaired (expected) at given separation intervals of **Vole G♀ and Vole H♂ 11 March 2000.** Probabilities that the excess or deficit of paired fixes may result from random variation are obtained from two-tailed binomial distribution

Files used: Vole G♀ 11 Mar 00 Vole H♂ 11 Mar 00				
Separation (m)	**Observed**	**Expected**	**Difference**	**P**
19-20	0.2105	0.2152	-0.0047	1
18-19	0.0316	0.0113	0.0203	0.0933
17-18	0	0.0071	-0.0071	1
16-17	0.0842	0.0203	0.0639	0.0007
15-16	0.0105	0.0124	-0.0019	1
14-15	0.0105	0.0035	0.007	0.2864
13-14	0.0421	0.0062	0.0359	0.003
12-13	0	0.0049	-0.0049	1
11-12	0	0.0252	-0.0252	1
10-11	0.0526	0.0522	0.0004	1
9-10	0	0.0485	-0.0485	1
8-9	0	0.0052	-0.0052	1
7-8	0.0421	0.054	-0.0119	0.82
6-7	0	0.0212	-0.0212	1
5-6	0.0211	0.025	-0.004	1
4-5	0	0.0127	-0.0127	1
3-4	0.0842	0.0694	0.0148	0.5419
2-3	0.0632	0.0593	0.0039	0.8266
1-2	0	0.0022	-0.0022	1
0-1	0	0.0062	-0.0062	1
0	0.0105	0.0694	-0.0588	0.0146
	<= 1 m.	> 1 m.	Totals	
Paired	1	94	95	
Unpaired	681	8249	8930	
Totals	682	8343	9025	

Table A6.7 The proportion of paired (observed) and paired plus unpaired (expected) at given separation intervals of **Vole G♀ and Vole H♂ 21 March 2000.** Probabilities that the excess or deficit of paired fixes may result from random variation are obtained from two-tailed binomial distribution

Files used: Vole G♀ 21 Mar 00 Vole H♂ 21 Mar 00				
Separation (m)	**Observed**	**Expected**	**Difference**	**P**
19-20	0.1211	0.1204	0.0006	0.9116
18-19	0.0053	0.0079	-0.0026	1
17-18	0.0105	0.007	0.0036	0.381
16-17	0.0158	0.0105	0.0053	0.4565
15-16	0	0.0034	-0.0034	1
14-15	0	0.001	-0.001	1
13-14	0.0263	0.0156	0.0107	0.2283
12-13	0	0.0082	-0.0082	1
11-12	0	0.0021	-0.0021	1
10-11	0.0053	0.003	0.0022	0.44
9-10	0.0105	0.0063	0.0042	0.3395
8-9	0	0.002	-0.002	1
7-8	0.0053	0.0012	0.004	0
6-7	0.0053	0.0089	-0.0036	1
5-6	0.0053	0.0053	-0.0001	1
4-5	0.0053	0.0068	-0.0016	1
3-4	0.0368	0.0348	0.002	0.8417
2-3	0.0368	0.0318	0.005	0.6758
1-2	0.0053	0.0217	-0.0164	0.202
0-1	0	0.0011	-0.0011	1
0	0.0053	0.0034	0.0019	0.4716
	<= 1 m.	> 1 m.	Totals	
Paired	1	189	190	
Unpaired	158	35752	35910	
Totals	159	35941	36100	

Table A6.8 The proportion of paired (observed) and paired plus unpaired (expected) at given separation intervals of **Vole G♀ and Vole H♂ 15 April 2000.** Probabilities that the excess or deficit of paired fixes may result from random variation are obtained from two-tailed binomial distribution

Files used: Vole G♀ 15 Apr 00 Vole H♂ 15 Apr 00				
Separation (m)	**Observed**	**Expected**	**Difference**	**P**
19-20	0.0105	0.0041	0.0064	0.3231
18-19	0	0.0133	-0.0133	1
17-18	0	0.0053	-0.0053	1
16-17	0.0211	0.0236	-0.0025	1
15-16	0	0.0041	-0.0041	1
14-15	0	0.004	-0.004	1
13-14	0	0.0343	-0.0343	1
12-13	0.0105	0.0113	-0.0008	1
11-12	0	0.0096	-0.0096	1
10-11	0.0526	0.0184	0.0342	0.0313
9-10	0	0.0161	-0.0161	1
8-9	0.0632	0.0168	0.0463	0.0055
7-8	0.0421	0.0213	0.0208	0.1448
6-7	0	0.0076	-0.0076	1
5-6	0.0211	0.029	-0.008	1
4-5	0	0.0148	-0.0148	1
3-4	0.0105	0.0172	-0.0066	1
2-3	0.0526	0.0478	0.0049	0.8072
1-2	0.0211	0.0075	0.0135	0.1609
0-1	0	0.0049	-0.0049	1
0	0.0211	0.0143	0.0068	0.3944
	<= 1 m.	> 1 m.	Totals	
Paired	2	93	95	
Unpaired	171	8759	8930	
Totals	173	8852	9025	

Table A6.9 The proportion of paired (observed) and paired plus unpaired (expected) at given separation intervals of **Vole N♂ and Vole O♀ 19/20 August 2000.** Probabilities that the excess or deficit of paired fixes may result from random variation are obtained from two-tailed binomial distribution

Files used: Vole N♂ 20 Aug 00 Vole O♀ 19 Aug 00				
Separation (m)	**Observed**	**Expected**	**Difference**	**P**
19-20	0	0.0178	-0.0178	1
18-19	0.0104	0.0164	-0.006	1
17-18	0.0104	0.0155	-0.0051	1
16-17	0	0.0228	-0.0228	1
15-16	0.0208	0.0234	-0.0026	1
14-15	0.0208	0.0321	-0.0113	0.7726
13-14	0.0938	0.0294	0.0643	0.0021
12-13	0.0312	0.0339	-0.0026	1
11-12	0	0.036	-0.036	1
10-11	0.0104	0.0335	-0.0231	0.3842
9-10	0.0833	0.0317	0.0516	0.0114
8-9	0.0208	0.0284	-0.0076	1
7-8	0	0.0187	-0.0187	1
6-7	0.0104	0.0225	-0.012	0.7281
5-6	0.0208	0.0225	-0.0016	1
4-5	0.0521	0.0377	0.0144	0.4143
3-4	0.0208	0.0432	-0.0224	0.446
2-3	0.0417	0.0361	0.0055	0.7801
1-2	0.0521	0.0301	0.022	0.2165
0-1	0.0312	0.0258	0.0054	0.74
0	0.0104	0.0118	-0.0014	1
	<= 1 m.	> 1 m.	Totals	
Paired	4	92	96	
Unpaired	343	8777	9120	
Totals	347	8869	9216	

Table A6.10 The proportion of paired (observed) and paired plus unpaired (expected) at given separation intervals of **Vole N♂ and Vole O♀ 2 September 2000.** Probabilities that the excess or deficit of paired fixes may result from random variation are obtained from two-tailed binomial distribution

Files used: Vole N♂ 2 Sep 00 Vole O♀ 2 Sep 00				
Separation (m)	**Observed**	**Expected**	**Difference**	**P**
19-20	0	0.0092	-0.0092	1
18-19	0.0312	0.0077	0.0235	0.0385
17-18	0.0208	0.01	0.0108	0.2488
16-17	0	0.017	-0.017	1
15-16	0.0208	0.0215	-0.0007	1
14-15	0.0312	0.0189	0.0124	0.4327
13-14	0	0.0241	-0.0241	1
12-13	0.0104	0.0339	-0.0234	0.3859
11-12	0.0938	0.0531	0.0407	0.103
10-11	0.0521	0.0768	-0.0247	0.4466
9-10	0.0417	0.0702	-0.0285	0.4198
8-9	0.0625	0.0524	0.0101	0.6427
7-8	0.0208	0.0454	-0.0245	0.3301
6-7	0.0104	0.0365	-0.026	0.2697
5-6	0	0.0342	-0.0342	1
4-5	0.0208	0.0458	-0.025	0.3301
3-4	0.0521	0.0497	0.0024	0.8138
2-3	0.0312	0.0476	-0.0164	0.6315
1-2	0.0625	0.0713	-0.0088	1
0-1	0.25	0.0915	0.1585	0
0	0.0417	0.0365	0.0052	0.7811
	<= 1 m.	> 1 m.	Totals	
Paired	28	68	96	
Unpaired	1151	7969	9120	
Totals	1179	8037	9216	

Table A6.11 The proportion of paired (observed) and paired plus unpaired (expected) at given separation intervals of **Vole N♂ and Vole O♀ 9 September 2000.** Probabilities that the excess or deficit of paired fixes may result from random variation are obtained from two-tailed binomial distribution

Files used: Vole N♂ 9 Sep 00 Vole O♀ 9 Sep 00				
Separation (m)	**Observed**	**Expected**	**Difference**	**P**
19-20	0	0.0094	-0.0094	1
18-19	0	0.0027	-0.0027	1
17-18	0	0.0013	-0.0013	1
16-17	0	0.0027	-0.0027	1
15-16	0	0	0	0.9999
14-15	0	0.0013	-0.0013	1
13-14	0	0	0	0.9999
12-13	0	0	0	0.9999
11-12	0	0	0	0.9999
10-11	0	0.0054	-0.0054	1
9-10	0	0	0	0.9999
8-9	0	0.0013	-0.0013	1
7-8	0	0	0	0.9999
6-7	0	0.0013	-0.0013	1
5-6	0	0	0	0.9999
4-5	0	0	0	0.9999
3-4	0	0	0	0.9999
2-3	0	0	0	0.9999
1-2	0	0	0	0.9999
0-1	0	0	0	0.9999
0	0	0	0	0.9999
	<= 1 m.	> 1 m.	Totals	
Paired	0	61	61	
Unpaired	0	3660	3660	
Totals	0	3721	3721	

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