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BEHAVIOURAL AND SENSORY ASPECTS OF PREDATION IN MUSTELIDS

Studies on the sensory capabilities of the weasel, *Mustela nivalis* L. and the polecat, *Mustela putorius* L., with particular reference to predatory behaviour.

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This is to certify that this thesis is the result of the candidate's own investigations. No part of it has been submitted in candidature for any other degree.

M. J. Murphy......

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ABSTRACT

The relative importance of vision, audition and olfaction to weasels and polecats was determined by training the predators to find a mouse located in a predator-proof container within a small arena. The diversity of sensory information available to the predators had an effect on the time taken to find the mouse with this being shorter when three senses could be used compared to when one sensory modality was available. Vision and olfaction (air-borne scent) were equivalent, with audition being less important. The mouse was found quicker using substrate-scent cues than with air-borne olfactory cues. There was no difference in the relative importance of the senses between the predators. The removal of movement cues had a significant effect on the behaviour of the weasels.

The visual movement discrimination ability of both species was investigated using a horizontally-moving spot on a cathode-ray oscilloscope screen. Thresholds were determined for the discrimination of the direction of a fast-moving stimulus and were equivalent in the polecat and weasel. The mean threshold for polecats was 292cms^{-1} and for weasels was 267cms^{-1}. The movement detection ability of the weasel was consistent over a range of stimulus radiant intensities (35.4-2.0x10^{5} µWsteradian^{-1}) and discrimination distances (10-50cm), although there was a slight decrease in threshold at the furthest distance used and when the distance traversed by the stimulus was short.

A relative velocity discrimination task was devised in which polecats were trained to discriminate differences in speed between identical objects moving in opposite directions in the horizontal plane. They could detect velocity differences of 20% and showed a tendency to select the slower-moving of the two stimuli.

Polecats and weasels do not specialize in the use of a particular distance sense to locate potential prey. In terms of their movement detection ability and the relative importance of vision they are intermediate between strictly nocturnal and diurnal species, which is probably attributable to their predominately crepuscular activity pattern.

CONTENTS

CHAPTER ONE INTRODUCTION

Whilst a considerable amount of research has been conducted on the behavioural mechanisms involved in predation, the sensory control of predatory behaviour has been little studied. This study investigates some sensory capabilities likely to be of importance to hunting predators.

Predator species differ in the relative importance of the different senses. The use an animal makes of its senses can be related to its relationship with the environment. The habitat frequented, type of food eaten and the timing of activity (i.e. whether nocturnal or diurnal) are the main ecological factors that can be correlated with a predator's sensory biology. The present study was conducted to widen the range of species so far investigated and to provide comparative data on two closely related species, the weasel (*Mustela nivalis* L.) and the polecat (*M. putorius* L.). A comparative approach is useful as it is then possible to examine the interrelationships between the ecology, behaviour and sensory systems of related species which occupy different ecological niches. The mammals so far studied have been either nocturnal or diurnal in habits and it is therefore of interest to investigate the sensory capabilities of species such as the polecat and weasel which are predominately crepuscular.

The relative importance of the distance senses, vision, audition and olfaction, are determined in a prey location task. The importance of substrate-scent cues compared to air-borne olfactory information and the use of prey movement cues are also evaluated.

The visual perception of movement by these animals has been selected for detailed study as it is important in the elicitation of predatory behaviour (Eisenberg and Leyhausen, 1972). Movement cues can provide the spatio-temporal information necessary for the location, pursuit and capture of prey. Furthermore, movement is more readily quantifiable than other sensory cues.

In addition to perceiving that movement has taken place, a predator also needs to determine the direction of that movement. Experiments are conducted to determine the thresholds of polecats and weasels for the discrimination of the direction of a fast-moving stimulus. Comparative movement discrimination experiments have most often been conducted using slow-moving stimuli (e.g. Berkley *et al*., 1978), but the present experiments concern high-speed movement as this has more relevance to a predator. The effect of varying discrimination distance and stimulus radiant intensity on movement detection are examined. These experiments are an extension of previous studies on the visual capability of the American mink, *Mustela vison* Schreber, (Dunstone and Clements, 1979; Clements and Dunstone, 1984).

An ability to discriminate between objects moving at different velocities would also be useful to a predator, for example when selecting single prey from groups. This capability is investigated by training animals to discriminate

between identical objects moving at different speeds along a horizontal trackway.

The results of the experiments on the relative importance of the senses and the different movement detection tasks are discussed in relation to the predatory behaviour of the polecat and weasel.

CHAPTER TWO LITERATURE REVIEW

2.1 THE POLECAT *MUSTELA PUTORIUS*

General accounts of the biology of the polecat in Great Britain are given in Poole (1970), Corbet and Southern (1977) and Boyle (1981), while Herter (1959) has reviewed continental work. Walton (1968) provided information on morphometrics, the reproductive cycle, age determination and population structure of Welsh polecats.

Considerable debate has been concerned with the origin of the ferret, *Mustela furo*, and its relationship with the two species of polecat, *M. putorius* and *M. eversmanni* (Pocock, 1936; Tetley, 1945; Ashton and Thomson, 1955). It is quite possible that both species are ancestors to the ferret, but it is not clear whether differences between *M. furo* and *M. putorius* are consequences of domestication (including inbreeding) or due to a closer relationship with *M. eversmanni*.

Previous authors have not always distinguished between polecats and ferrets, for example, Poole (1972b, 1973, 1974) used wild-caught polecats, ferrets and "hybrids" in his studies of polecat behaviour. Poole (1972a) did demonstrate differences in exploratory behaviour between true polecats and ferrets. Consequences of domestication include reduced reluctance to explore new areas and ferrets are less nervous and easier to handle, making them more suitable than polecats for behavioural studies.

Ecology of the Polecat

Polecats occupy a variety of habitats including woodland, farmland, marshes and river-banks (Novikov, 1956; Nilsson, 1978). Distribution and abundance are related to prey availability (Kalela, 1940; Danilov and Rusakov, 1969).

Movements and Activity

Polecats are generally considered to be solitary, occupying a home-range to the exclusion of members of the same sex (Poole, 1970). Nilsson (1978) and Herrenschmidt (1982) found the home-range to be unevenly exploited with activity being concentrated in areas of high prey density.

After a period of inactivity within a den, locomotory and foraging activity may occur for a period of up to 2.5 hours (Herrenschmidt, 1982). Polecats may move a distance of 5km at a time (Danilov and Rusakov, 1969), although excursions of approximately 1km or less are probably more typical (Herrenschmidt, 1982).

Various authors have stated that the polecat is active almost exclusively at night (Goethe, 1940; Novikov, 1956; Herter, 1959). Other workers however, have recorded varying amounts of day-time activity. Labhardt (1979) observed day-time as well as nocturnal activity in a female polecat bringing food to her young. Diurnal activity was also recorded by Herrenschmidt (1982), although peaks of activity occurred at dawn and dusk. Seasonal variation in activity has also been recorded, with polecats being less active during cold weather (Danilov and Rusakov, 1969; Nilsson, 1978).

Food Habits

Polecats take a wide variety of prey, according to its availability, with the most important category being mammals. The frequency of occurrence of different types of prey in the diet range from mammals, 35-71%; birds, 6-14%; amphibians and reptiles, 9-26%; fish, 0-14% and invertebrates, 0-24% (see Poole, 1970).

The main prey species taken include voles (*Microtus* sp. and *Clethrionomys* sp.), rats (*Rattus norvegicus*) and water voles (*Arvicola terrestris*) (Novikov, 1956; Danilov and Rusakov, 1969). Other mammals such as ground squirrels (*Spermophilus citellus*), hamsters (*Cricetus cricetus*), lagomorphs and insectivores are also taken (Novikov, 1956; Walton, 1968). Polecats take relatively more larger prey such as lagomorphs than stoats and weasels (Brugge, 1977). Frogs have a secondary importance in the diet, particularly when rodents are scarce (Kalela, 1940). Polecats in captivity show a preference for warm-blooded vertebrates over frogs, although in the wild they can be an important dietary constituent (Herter, 1959). Toads, lizards and snakes are occasionally recorded in the diet (Poole, 1970). Birds are also taken, with the greatest proportion occurring in spring when juveniles are available (Kratochvil, 1952; Ognev, 1962; Danilov and Rusakov, 1969).

Occasionally invertebrates such as insects, slugs and earthworms are taken, but never in any great quantity (Kratochvil, 1952). Even fish have been recorded, probably taken as carrion (Kalela, 1940; Ognev, 1962). Carrion (e.g. ungulates) appears to be important in winter if live prey is scarce (Danilov and Rusakov, 1969).

Dietary studies of feral ferrets in New Zealand also found that mammals occurred most frequently in the diet (Gibb and Flux, 1973; Roser and Lavers, 1976).

Studies of polecat and ferret behaviour in the laboratory

Social Behaviour

Poole has investigated the social behaviour of the polecat in captivity, with particular emphasis placed on aggression. Aggressive play is described by Poole (1966) and a description of different categories of aggressive behaviour is given in Poole (1967). Factors affecting aggressive behaviour, such as the familiarity of the opponent have also been investigated (Poole, 1972b, 1973) and the effect of oestrous condition on behaviour between male and female polecats was examined in Poole (1974).

Poole (1978) and Diener (1985) descibed social play in polecats and Biben (1982) noted sex-related differences in the play of young ferrets, which reflected differences in adult behaviour. Other workers have investigated the effect of early experience on learning abilities and exploratory behaviour (e.g. Bunnell, 1979; Weiss-Burger, 1981; Chivers and Einon, 1982). Lazar et al. (1973) investigated dyadic interactions between young ferrets and Lazar and Beckhorn (1974) discussed the nature of play in ferrets.

Investigations of play are pertinent to studies of predatory behaviour as it is possible that the behaviour patterns used in the capture of prey are perfected during play with siblings. The animals used in the present study were not deprived of the opportunity to play, therefore there should not have been any behavioural abnormalities as a result of play-deprivation.

Learning

Ferrets and polecats have rarely been used in behavioural experiments by comparative psychologists, although they are readily trainable animals. Doty and Combs (1969) found that mink and ferrets show comparable performance to some primates in learning-set formation. Doty and Jones (1967) showed that in reversal learning, mustelids respond more to object cues, unlike cats which are more responsive to positional cues.

Ferrets have been successfully trained on spatial discrimination problems (e.g. Hughes, 1964a), but Haddad et al. (1976) noted a learning deficit in young ferrets. Although juveniles were not inferior to adults in learning a left-right discrimination, they were slow in learning to reverse this discrimination.

Ferrets show spontaneous alternation in a Y-maze (Hughes, 1965). They have been shown to have a high exploratory drive, as they alternated more frequently following a confinement in a chosen arm, and they respond to stimulus novelty (Hughes, 1964b, 1967; Eastment and Hughes, 1968).

Performance of ferrets in complex mazes has been judged to be poor by some workers, as the subjects tended to explore rather than find the direct route to the reward. However, Pollard and Lewis (1969) were successful in training ferrets to negotiate complex mazes, and performance was equivalent to that of rats and cats. Pollard et al. (1971) compared the performance of ferrets in a closed-field test with other species and found that although they had an equivalent learning rate to cats, they were less reliant on visual cues.

Experimental Studies on the Use of the Senses

Early psychophysical studies on the polecat include those of Muller (1930) and Gewalt (1959). These studies concentrated on investigation of colour vision and it was concluded that brightness cues are more important to the polecat than colour information.

Poole (1972a) investigated behavioural differences between ferrets and polecats. Consequences of domestication include differences in exploratory behaviour and reduced fear. The behaviour of the animals towards a sound source was measured. It was found that although polecats made attention responses more frequently than ferrets when exploring novel environments, they habituated more readily to a sound source.

Foraging Behaviour

There have been few experimental investigations of foraging behaviour conducted in the laboratory. The ferret was used as a subject by Cott (1953) in an investigation of the palatability of eggs of different bird species. Behaviour toward eggs has also been recorded by Wustehube (1960).

An operant-type procedure was used by Kaufman (1980) to investigate the responses of ferrets to changes in the cost of obtaining food. As cost increased (the number of bar presses needed to gain access to food), meal frequency declined and meal size increased. Unlike social feeders such as chickens, bar pressing and food consumption rates remained the same regardless of cost.

2.2 THE WEASEL, MUSTELA NIVALIS

General accounts of the weasel are given in Linn (1962), Corbet and Southern (1977) and Boyle (1981).

Ecology of the Weasel

Weasels do not appear to have any distinct habitat preferences, with their distribution being related to prey availability (Erlinge, 1974). An extreme example of this is given by Rubina (1960) where high densities of weasels were found frequenting mouse-ridden hay stacks.

Social Organisation

The social organisation of weasels has been described by Lockie (1966), Erlinge (1974), King (1975) and Pounds (1981). Weasels are solitary, with males occupying intrasexually-defended territories, within which one or more females may have a home-range. Home-range sizes vary between 1 and 34ha, although usually they are less than 10ha in size. The spatial pattern is maintained mainly by mutual avoidance and scent marking (King, 1975), although overt aggression also occurs.

Activity and Movements

Early studies assumed that weasel activity is arhythmic (Gewalt, 1959; Heptner, 1967). These authors did not detect any clear activity rhythm, but found the weasel to be most active during twilight hours and at night, although day-time activity also occurred. Kavanau (1969) and Kavanau and Ramos (1975) found weasels to be active both by day and by night, with a tendency toward nocturnal activity. Kavanau suggested that the "weasel′s retina is evolving from a nocturnal one in the diurnal direction".

However, Buckingham (1979) used spectral analysis to show a cyclical pattern of activity. There were considerable individual differences, but despite this there were consistent seasonal variations in activity. Daily cycles of activity also occurred, with activity bouts often coinciding with dawn and dusk. Short-period activity cycles of 20-50 minutes duration were followed by rest, with weasels only being active for 20% of the day.

Musgrove (1951) reported _M_. _frenata_ travelling around the home-range in a cyclical manner, but Pounds (1981) found the movement patterns of weasels to be very variable. He classified movements into two types; short foraging movements in the vicinity of a den corresponding to the short-period activity cycle reported by Buckingham (1979), and occasional long excursions. Weasels are capable of travelling the total length of their home-range during a period of activity (Pounds, 1981).

Food Habits

Most studies on the diet of weasels have been concerned with populations from restricted geographical areas, but an exception is the work of Day (1968), whose samples were obtained from various parts of Britain. He found that weasels predate small rodents, lagomorphs and birds, but that over half of their food is small rodents. The most frequent prey animal was the field vole, *Microtus agrestis*. Birds constituted 14.5% (frequency of occurrence) of the diet and lagomorphs made up 19%, while insectivores were taken rarely.

Where populations from a limited geographical area have been studied, different proportions of prey are taken according to availability. For example, Moors (1975) and Pounds (1981) working in an area of farmland, found a predominance of *Microtus agrestis* in the diet, while in a woodland area, *Clethrionomys glareolus* was most frequently taken (King, 1980). Walker (1972) recorded the diet of a sample of weasels from estates in Hertfordshire to be dominated by *Apodemus* sp. at a time when ground cover was limited.

Erlinge *et al*. (1973) and Erlinge (1975) showed that weasel diet in Southern Sweden was similar to that in Britain. Voles predominated, the species taken varying according to habitat, although there appeared to be a preference for field voles. Water voles (*Arvicola terrestris*) and lagomorphs had a secondary importance, with males switching to this type of prey when voles became scarce. Lagomorphs were not taken by females, and shrews were rarely included in the diet of either sex.

Other accounts of weasel ecology have recorded a high proportion of mice and voles in the diet (e.g. Novikov, 1956; Rubina, 1960; Linn, 1962; Parovschikov, 1963; Heptner, 1967). A wide variety of other prey species are occasionally taken including crayfish (*Astacus astacus*) and insects (Linn, 1962), amphibians and reptiles (Howes, 1977) and larger mammals such as hares (*Lepus capensis*) and squirrels (*Sciurus vulgaris*) (Heptner, 1967).

Predation on birds has often been recorded, including attacks on nesting birds and their broods (Sherrell, 1953; Ferns, 1974). Dunn (1977) related predation by weasels on tits to the relative density of nesting birds and rodents. Tapper (1976) investigated weasel predation on game-birds and found that although game-bird chicks are occasionally taken, the main bird prey are passerines.

Invertebrate remains are occasionally recorded in the diet, but they may be taken incidentally (Day, 1968). However, Osgood (1936) observed a weasel feeding earthworms to her young. Invertebrates may be important when other prey are scarce. In New Zealand, mustelids take more insect prey than their European counterparts (Gibb and Flux, 1973; Marshall, 1963; King and Moody, 1982).

Studies of Energetics

Early studies emphasised the high food requirements of weasels (e.g. Short, 1961). Price (1971) noted that activity was nearly doubled in response to food deprivation, which he considered adaptive in a small mammal with high metabolic requirements. A more recent study (Gillingham, 1984) investigated meal size and feeding rate in the weasel. He found that weasels cannot eat more than one small meal every few hours and they cannot completely compensate for extreme food deprivation.

More direct evidence for a high metabolic rate has come from experimental studies of metabolism (e.g. Brown and Lasiewski, 1972; Moors, 1977). The elongate body-form of weasels is expensive in terms of energetics, but this is compensated for by an increased ability to obtain prey by being able to enter confined spaces. Investigation of the foraging behaviour of small mustelids is of particular interest owing to the energetic constraints imposed by their body-shape. However their high metabolic rate can cause problems with regards to their maintenance in captivity (see Ch. 3).

Studies of weasel behaviour in the laboratory

The weasel has been used in few experimental studies of behaviour. Buckingham (1979) conducted some preliminary experiments and Velander (1980) has carried out a more detailed study of social interactions between captive weasels. Avoidance of confrontations occurs principally through scent marking. However, during encounters with other weasels, communication occurs through postures and vocalisations, with the establishment of a dominant-subordinate relationship. Therefore, olfaction, audition and vision are all involved in weasel social behaviour.

A complete ethogram for the weasel is given in Velander (1980) and vocalisations are described by Huff and Price (1968) and Gossow (1970). Buckingham (1979) also investigated the exploratory behaviour of the weasel.

2.3 PREDATORY BEHAVIOUR OF MUSTELIDS

Predatory behaviour involves a series of stages, including searching for prey, localisation, pursuit and capture. Searching is directed to microhabitats likely to contain prey (Heptner, 1967; Nams, 1981). Pounds (1981) showed that weasels concentrate their hunting efforts to rodent runways in walls and rough grassland.

Different searching strategies have been recorded between male and female weasels. Females spend more of their hunting effort in rodent tunnel systems, while males hunt more over open ground (Erlinge, 1975; Pounds, 1981). This difference in hunting behaviour, which is a result of the sex-related difference in body-size, and also more direct consequences of the sexual dimorphism, result in male weasels taking a broader spectrum of prey than females. The hunting behaviour of the weasel in a large enclosure is described by Erlinge *et al.* (1974a).

The active pursuing mustelids e.g. the various *Mustela* species, are considered to be more specialized in terms of prey requirements than certain confamilial searchers e.g. skunks, *Mephitis mephitis* (Rosenzweig, 1966). Their killing behaviour is stereotyped and they show a remarkable similarity in killing technique (Heidt, 1970). Weasels and polecats are amongst the most predacious species of mustelid and, in relation to their size, they are formidable efficient killers (Ewer, 1973). Adult lagomorphs appear to be the upper size limit of prey that stoats and weasels are capable of killing efficiently (Allen, 1938).

Once within striking distance, the typical method of attack is to leap onto the prey, clutching its body with the fore-limbs. The killing-bite is delivered to the occipital region (Ewer, 1973), with death resulting from damage to the hind-brain or spinal cord (Hewson and Healing, 1971). Preliminary bites may be made on any part of the body before the prey is secured, particularly if the prey animal is large (Allen, 1938). Byrne _et_ _al_. (1978) recorded the use of a throat-bite by _Mustela_ _frenata_ on ground squirrels (_Spermophilus_ _richardsoni_) underground. This alternative method of killing prey may be used when prey are cornered in confined spaces.

Comparative studies of predatory behaviour include investigations on polecats, stoats and weasels by Wustehube (1960) and stoats and weasels by Gossow (1970). The predatory behaviour of the polecat was described by Goethe (1940) and Eibl-Eibesfeldt (1956). The killing behaviour of weasels has been described by Llewellyn (1942) and Heidt (1972). These authors also described feeding behaviour and comments were made on surplus killing by this animal. Caching of food by weasels has been described by Rubina (1960), Linn (1962) and Sueur (1980) and in polecats by Danilov and Rusakov (1969) and Poole (1970).

There has been considerable debate over whether the killing behaviour of mustelids is innate or learned. Goethe (1940) and Wustehube (1960) assumed that prey-catching in polecats is innate. Eibl-Eibesfeldt (1956, 1963) however, stated that the proper orientation of the killing bite has to be learned, although the other prey-catching movements are innate. Apfelbach and Wester (1977) supported this conclusion. Polecats may learn the advantage of the neck-bite during play with siblings, and this may also occur in stoats (Gillingham, 1978). Heidt (1972) and East and Lockie (1964, 1965) suggested that killing behaviour in the weasel appears to be innate, but killing attempts improve with practice. The two sources disagreed on whether or not the mother plays a role in the development of predatory behaviour.

2.4 COMPARATIVE ASPECTS OF THE SENSORY CONTROL OF PREDATORY BEHAVIOUR : BEHAVIOURAL INVESTIGATIONS ON TERRESTRIAL VERTEBRATES

Amphibians

Amphibian predatory behaviour has long been considered to be visually-guided. Early studies stressed that predatory behaviour can only be elicited by moving stimuli (e.g. Honigmann, 1944; Ewert, 1974). Prey can be represented by abstract stimuli such as moving stripes elongated in the direction of motion, i.e "worm-like" or horizontal stimuli, (Ingle and McKinley, 1978; Ewert et al., 1979a). The preference for this configuration is independent of direction, speed and type of movement (whether continuous or stepwise). Frogs and toads snap at the leading edge of prey stimuli (Ingle, 1968; Ingle and McKinley, 1978; Burghagen and Ewert, 1982) and respond better to a withdrawing edge than an advancing one (Beck and Ewert, 1979). The discrimination abilities of a wide variety of anurans have similar components, but there are species differences in preferred absolute prey size (Ewert and Burghagen, 1979).

Prey catching in urodeles is influenced more by the nature of stimulus movement than in other amphibians, with the preference for horizontal stimuli not being invariant with respect to changes in stimulus velocity (Roth, 1978; Luthardt and Roth, 1979a).

In early studies it was assumed that amphibian predatory behaviour could not be elicited by stationary prey objects, but recent experiments have shown that it is possible to train toads to respond with prey-catching behaviour to motionless stimuli (e.g. Brzoska and Schneider, 1979; Roth and Wiggers, 1983). Prey-catching behaviour in salamanders can also be considerably modified by experience; salamanders reared on dead prey are significantly better in responding to stationary prey than those with only experience of moving prey (Luthardt and Roth, 1979b, 1983; Roth and Luthardt, 1980).

Although emphasis has been placed on the role of visual stimuli, the use of the other senses in prey catching has also been investigated. In most amphibian species, olfactory cues are less informative than visual cues, but a combination of cues is more effective (Martin et al., 1974; Sternthal, 1974; Lindquist and Bachmann, 1982). Olfactory stimuli increase in importance when prey location occurs during darkness (Roth, 1976). Auditory stimuli do not appear to be important, as Brzoska and Schneider (1979) were unsuccessful in training toads to make prey catching movements in response to an auditory tone.

Amphibians have been more completely studied than any of the other vertebrate groups. They are useful models for understanding the sensory systems of vertebrates in general, but there are some differences between amphibians and higher vertebrates. In lower vertebrates, there is a rigid selectivity of particular stimulus configurations, but in most vertebrates, availability and palatability appear to be more important factors governing prey selection.

Reptiles

Compared to amphibians, little is known about the relative importance of the senses to reptiles. Conclusions on the use of the senses have often been derived from anatomical studies. It was assumed that olfaction was the most important sense to skinks and was less important to the iguanids until a behavioural study by Burghardt (1964) showed that both groups of lizard used mainly visual cues when searching for food. Iguanids do not appear to use olfactory cues at all (Curio and Mobius, 1978), and even skinks, with their well-developed olfactory apparatus, use visual cues to guide their predatory attack (Cooper, 1981).

Snakes respond to visual, thermal and chemical cues. In an early study on the garter snake (_Thamnophis_ sp.), Burghardt (1966) concluded that olfactory cues were more important than vision. Later, Burghardt and Denny (1983) showed that prey movement is an important stimulus for the elicitation of predatory behaviour in these snakes and is enhanced if odour is also present. Water snakes (_Nerodia sipedon_) were also found to respond to and to integrate visual and chemical cues (Drummond, 1979).

Birds

Vision is the most important sense used by birds searching for food, olfaction has not been widely implicated. Blackbirds (_Turdus merula_) utilise movement cues, and experienced birds can intercept moving prey, seizing it by the anterior end (Schlee, 1983).

Predatory birds utilise both vision and hearing when hunting, (e.g. owls, Kaufman, 1974). Payne (1961) has shown that the barn owl, *Tyto alba*, can detect prey using auditory cues alone, but owls which hunt under conditions of dim illumination such as *Bubo virginianus*, probably rely more on vision than hearing (Fite, 1973).

Several authors have investigated the stimulus control of predatory behaviour in diurnal birds of prey. Mueller (1974) did not consider that learning played a major role in the development of predatory behaviour in the American kestrel, *Falco sparverius*, as naive birds ignored models, while attacks on live mice were rapid and well orientated. Smith (1973) considered predatory behaviour in the loggerhead shrike, *Lanius ludovicianus*, also to be innate.

However, other authors have implicated learning in the development of predatory behaviour of raptors. Ruggiero *et al*. (1979) found that kestrels preferred non-moving unfamiliar prey to moving unfamiliar prey, but that the highest rates of attack were elicited by moving familiar prey. The acceptability of familiar prey was enhanced when accompanied by aberrant movement. Snyder (1975), working with red-tailed hawks, *Buteo jamaicensis*, found an interaction between prey size and movement. When given a choice between prey of the same size, moving animals were preferred when the prey size was small. If the prey animals were large, less active animals were selected, as such prey is probably sick or injured, thereby being easier to capture and also less likely to cause damage to the predator.

In conclusion, it appears that although movement cues are important to predatory birds, they are not essential for the elicitation of predatory behaviour, even in naive avian predators.

Mammals

Mammals are probably less specialised in the use of their senses than other vertebrate groups. The stimuli most useful to a predator depends on the characteristics of the prey species, the habitat, and time of day at which hunting occurs.

However, movement of the prey is one of the most important cues for the elicitation of predatory behaviour. Movement cues appear to be particularly important to naive mammalian predators, e.g. canids (Fox, 1969) and polecats (Eibl-Eibesfeldt, 1956). Eisenberg and Leyhausen (1972) observed the prey capture techniques of a wide range of mammalian predators and concluded that the movement of the prey was the most important stimulus. Prey movement can, of course, be detected by the visual sense or by hearing.

Of the limited number of mammalian species that have been investigated experimentally, the trend appears to be for vision to be used by diurnal hunters whilst audition is more important to nocturnal predators. The methods used to investigate sensory capability of predators can be divided into three main types, the least satisfactory being observation of animals during predatory encounters. Some authors have used choice tests (e.g. Slobodchikoff, 1978), while in other tests, various combinations of sensory input were deprived and the search-time or attack latencies were measured (Wells and Lehner, 1978). Osterholm (1964) used a series of choice tests to show that the red fox, Vulpes vulpes, is most reliant on auditory cues when hunting. Although visual cues were preferred to a sound source under daylight conditions, auditory cues were utilised at night, at which time the fox does most of its foraging. Auditory stimuli were always preferred to olfactory stimuli. Isley and Gysel (1975) further investigated auditory location by the red fox, examining the ability to detect a wide range of sound frequencies.

The use of visual and auditory cues by skunks, Mephitis mephitis and opossums, Didelphis marsupialis, in capturing prey was investigated by Langley (1979). Both of these nocturnal predators had shorter attack latencies when auditory stimuli were available. However, Slobodchikoff (1978) showed that skunks find prey by smell and that naive skunks require the presence of odour in order to recognise a beetle as prey.

A more recent study by Langley (1983a) on grasshopper mice (Onychomys leucogaster) showed all three distance senses contributed to the location of an active prey, but that audition was the most important. When searching for stationary prey, the mice used vision and olfaction interchangeably. Once an active prey is subdued, the feeding sequence is controlled by olfactory cues, although tactile cues are also important (Langley, 1983b). Herbivorous small mammals appear to use primarily olfaction to locate food (e.g. *Peromyscus*, Drickhamer, 1972).

While the feeding and predatory behaviour of small nocturnal mammals is under auditory and olfactory control, the diurnal coyote (*Canis latrans*) places considerable emphasis on vision. Wells and Lehner (1978) measured the time taken by coyotes to locate rabbits in an enclosed room. The least important sense was olfaction. When the procedure was repeated in a large outdoor enclosure, olfaction assumed the second position in the sensory hierachy (Wells, 1978).

The mongoose, *Helogale undulata*, also appears to use vision to recognise prey (Rasa, 1972). In an elegant series of experiments, Rasa determined the hierachy of stimuli involved in the precise orientation of the killing bite. The most important stimulus was prey movement, with vision being used to aim a bite at the anterior end of a moving stimulus. The position of the eyes and the physical end of a body were additional cues. Olfactory and tactile cues were of lesser importance.

Sensory Control of the Predatory Behaviour of Mustelids

The roles of the senses have often been discussed in observational studies of the predatory behaviour of various mustelid species. Several authors (e.g. Eibl-Eibesfeldt, 1956; Wustehube, 1960) have realised that movement is an important stimulus for prey detection in these animals.

Moving objects are more effective in eliciting prey catching reactions than stationary ones. Heidt (1972) concluded that the stimulus for attack was prey movement, as weasels were observed to pass within inches of a motionless mouse without appearing to detect it.

Wustehube (1960) and Muller (1970) state that location of prey by both stoats and weasels is by vision, although weasels are also attracted by prey scent. The visual stimulus involved is movement rather than shape, although the eyes and ears are used to orient the bite to the nape (Wustehube, 1960). Wustehube believes the polecat responds more to the scent of the prey than do stoats and weasels.

Raber (1944) determined the role of the senses in the predatory behaviour of the beech marten, Martes foina, and polecat, Mustela putorius. Both species use vision to detect prey, while the manipulation of the prey is under olfactory control.

Speed of movement may be a decisive factor in predatory encounters (Curio, 1976). While many authors stress the importance of prey movement only Apfelbach and Wester (1977) have investigated experimentally the role of prey speed. Apfelbach and Wester (1977) examined the visual and tactile characteristics of stimuli that elicit prey-catching reactions in ferrets, Mustela furo. Prey dummies of up to the size of a ferret elicit hunting reactions if they are moving at 25-45cms^{-1}. They found no influence of shape on "prey-catching" and agreed with Muller (1930) and Raber (1944) that ferrets react to brightness cues when hunting.

Apfelbach (1973a) concluded that olfaction is more important than vision to ferrets and polecats. Ferrets learn to recognise the odour of prey animals (Apfelbach, 1973b, 1978). When a novel smell is fanned toward a ferret, it shows no observable reaction, whereas it shows searching behaviour toward a known odour. There is a sensitive phase for learning prey odours at two-three months of age. Apfelbach's experiments were concerned with air-borne scent, but experimental investigation of the use of substrate-borne olfactory cues by weasels has been undertaken by Herman (1973).

Little investigation of the role of auditory stimuli in the predatory behaviour of mustelids has been carried out. Muller (1970) believed hearing could be important for locating prey moving under vegetation and Willey (1970) observed M. erminea, pursuing the flight sounds of grasshoppers.

There is clearly a need for a complete experimental evaluation of the relative importance of the senses to mustelids, as previous workers have not always reached the same conclusions. The vertebrate classes show different sensory specialisations with birds relying mostly on vision while mammals use all senses almost equally. A disproportionate amount of research effort has been directed at amphibians while mammals have been poorly studied. Therefore an investigation of the relative importance of the senses in some mustelid species will also extend the range of mammalian species so far examined in experimental studies of sensory capability.

2.5 THE MUSTELID VISUAL SYSTEM

Descriptions of the eye of various mustelids, including the polecat, were first given in Lindsay Johnson (1901). The visual field was found to vary between 26^{0} and 48^{0} according to species. Mustelids have fronto-lateral eyes with a binocular field of 60^{0}-80^{0}, compared to 130^{0} in the cat (Walls, 1942).

While the proportions of rods and cones vary, there is a general consensus that mustelids have a duplex retina, with rods or rod-like photoreceptors predominating. Polecat rod: cone ratios of 14: 1 (Gewalt, 1959), have been measured while values for the ferret range from 20: 1 (Baumeister, 1974) to 50: 1 (Braekevelt, 1983). The ratio in the American mink, _Mustela vison_, is 20: 1 (Herter and Klaunig, 1956).

Details of photoreceptor structure in the retina of the ferret has been reported by Braekevelt (1983), and the most detailed description of a mustelid's retina (_M. vison_) is given by Dubin and Turner (1977). Mustelid retinas resemble those of other predatory mammals which often hunt under conditions of low light intensities (e.g. harbour seal, _Phoca vitulina_, Jamieson and Fisher, 1971, and cat, Steinberg _et al_., 1973), with a well-developed tapetum being present (Baumeister, 1975).

Abnormal retino-geniculate pathways are found in mustelids with reduced visual pigment. Lack of pigment in the fur of the mink is often linked with reduced amounts of retinal pigment (Sanderson _et al_., 1974). Albino ferrets also possess abnormal retino-geniculate projections (Guillery, 1971). In addition, both pigmented and albino ferrets have a poorly developed lateral geniculate nucleus (LGN). As both the weasel and mink possess a well developed LGN, there is the possibility that the reduction in lamination is a consequence of domestication (Sanderson, 1974).

Psychophysical studies of visual acuity have been conducted. The species examined include the Asian clawless otter, Amblonyx cineraria (Balliet and Schusterman, 1971; Schusterman and Barrett, 1973), the American mink, M. vison (Sinclair et al., 1974; Dunstone and Sinclair, 1978a) and the ferret (Neumann and Schmidt, 1959; Pontenagel and Schmidt, 1980). The visual acuity of these species are similar, approximately 15min. The acuity measurement however, depends on the method used. Neumann and Schmidt (1959) used a size discrimination method rather than grating stimuli. A more recent study (Pontenagel and Schmidt, 1980) showed the ferret to have a higher resolution ability of up to 8.5min at high luminances.

The effect of various environmental parameters on the visual acuity of the American mink was investigated by Sinclair et al. (1974) and Dunstone and Sinclair (1978a, b). Thresholds were estimated in air and underwater and the effects of varying discrimination distance and stimulus luminance were investigated.

High-speed movement detection capability was investigated in the mink (Dunstone and Clements, 1979) in air and underwater over a range of stimulus radiant intensities and discrimination distances (Clements, 1980; Clements and Dunstone, 1984). Simple pattern discrimination experiments have been conducted using the ferret, (Pollard et al., 1967), but many aspects of the visual abilities of mustelids remain uninvestigated.

Of these abilities, movement detection is probably the most relevant to predatory behaviour. Previous studies on the American mink (Sinclair et al., 1974; Poole and Dunstone, 1976) have suggested that movement detection may be more important than visual acuity to hunting mustelids and Apfelbach and Wester (1977) believe that movement is a more important than stimulus configuration for the elicitation of a chasing reaction by ferrets. Information on the movement detection ability of the American mink is already available, therefore comparative data on additional mustelid species would be useful.

2.6 VISUAL MOVEMENT PERCEPTION

The significance of movement to all animals is best summarised by the statement of Johansson (1975) "that the concept of a world without movement has no biological significance". The ability to perceive movement is particularly important to many predators for the recognition and capture of prey.

General Theories

Early theories suggested that the visual perception of movement arises from the successive stimulation of adjacent retinal loci (Kennedy, 1936; Spigel, 1965). The nervous system codes successive changes across the retina as movement and there is some neurophysiological evidence for this type of mechanism (see below).

Gibson (1968) developed a model encompassing all aspects of visual perception, where perception results from distortions of the optical array. Moving objects are detected because they cause changes in, rather than of, the optical pattern and motion is perceived when there is a relative transformation in the retinal projection, not as a result of displacement on the retina. A full discussion of Gibson's theories of visual perception are given in Gibson (1966, 1979). Theories concerned with the geometry of the transformations which result from movement of stimuli are further discussed in Johansson (1973, 1975), Caelli et al.

(1971) and Kalveram and Ritter (1979).

The above theories do not fully explain the ability to discriminate between movements of objects and movement of the subject. For this to occur, non-optic information is also necessary (Haber and Hershenson, 1973). Research has been conducted on the perception of self-movement, involving interactions between the vestibular apparatus and vision (e.g. Dichgans and Brandt, 1972; Bairstow and Laszlo, 1978).

Psychophysical Studies on Human Subjects

The greatest number of psychophysical studies of movement perception have been conducted on man. Research on other animals has been mainly neurophysiological, although some comparative behavioural studies have been conducted. Therefore, in order to obtain the most complete picture of how movement is perceived, the experimental work on man and animals needs to be synthesised.

Many authors have concentrated on developing models which imply the presence of a two-feature analysing system. Leibowitz (1955) and Brown (1955) proposed that one system analyses the spatial and stationary components of a moving stimulus, while movement information, i.e. velocity, is processed by another system. The phenomenon of two channels for the analysis of motion and pattern was first defined in the spatial frequency/ temporal frequency domain by Tolhurst (1973) and Kulikowski and Tolhurst (1973). Sekuler and Levinson (1977) and von Grunau (1978, 1979) provided further evidence for a two-channel system. The two channels are consistent with the X-Y classification of nerve cells in higher mammals (see p. 42). Thompson (1983) confirmed the existence of two channels, but suggested there may be a third channel which is concerned with high temporal rates (i.e. flicker).

Sekuler et al. (1982) stressed that motion perception is not a single function, but a heterogenous collection of diverse functions. There are differences in responses to moving targets mediated by central and peripheral vision. The peripheral retina has often been described as being specialized for motion detection (Walls, 1942; Hood and Leech, 1974). Peripheral vision contributes to the control of normal eye movements and serves to bring stimuli of interest to the fovea. A review of the control of eye movements is given in Wallach (1982).

There are two limits between which movement perception can occur. The upper limit, sometimes called the fusion threshold, has received little attention; most threshold determinations have been concerned with slow movement. Threshold measurement consists of defining the zero point of motion sensation in terms of the stimulus dimensions. Both the upper and lower thresholds are a function of a number of variables (see p.37).

Several procedures can be used to determine thresholds, for example, the exposure time can remain constant while velocity and amplitude (angular extent) vary, or a constant amplitude procedure can be used. In a constant velocity procedure, exposure time and amplitude vary yielding displacement thresholds (Graham, 1965). Another procedure involves changing the luminance of the target (Van den Brink and Bouman, 1957; Remole, 1974).

The human threshold for slow movement is less than $1^{\circ}sec^{-1}$ (Bouman and Van den Brink, 1953; Carpenter and Carpenter, 1958), with an optimal sensitivity to speed of around 3°-$6^{\circ}sec^{-1}$ (Richards, 1971). Thresholds vary according to stimulus conditions and other authors measured values as low as $0.05^{\circ}sec^{-1}$ (Pasternak and Merigan, 1980), thus the minimum threshold approaches visual acuity (Haber and Hershenson, 1973).

Investigations of high-speed movement detection by human subjects include threshold values of $50^{\circ}sec^{-1}$ (Pollock, 1953; Caelli _et al_., 1978) and $35^{\circ}sec^{-1}$ (Brown, 1957, 1958). Definitions of the high-speed threshold vary; Pollock (1953) defined it as that above which subjects could not tell the direction of motion, while De Silva (1929) described it as when a moving light source appeared as a stationary sheet of light.

Kaufman _et al_. (1971) investigated the perception of fast movement in detail. A moving object is perceived clearly at about $10^{\circ}sec^{-1}$, but above this value, the image becomes blurred, and is replaced by an undifferentiated or fused blinking stimulus. The values of approximately $10^{\circ}sec^{-1}$ and 20°-$30^{\circ}sec^{-1}$ were values for the perception of blur and fusion respectively.

Investigations of the perception of flicker involve measurement of the critical flicker-fusion frequency (CFF), which is essentially the fusion threshold determined by Kaufman et al. (1971). CFF is the rate of flicker at which a flickering stimulus ceases to be discriminated from a steady stimulus of the same brightness. The critical flicker-fusion frequency of man has been determined in some early studies, including Hecht and Verrijp (1933) and Brecher (1935).

The stimulus for perception of motion can be produced by several mechanisms; the movement of a real object, movement of the eyes with the object being stationary, or movement of several points or contours relative to each other (e.g. Johansson, 1975).

The contribution of eye and head movements to the ability to resolve detail of moving objects has been investigated in studies of dynamic visual acuity (DVA). Reading (1972a, b) found no significant correlations between dynamic and static acuity because the former is limited by the subject's ability to track stimuli. Brown (1972b) found that DVA deteriorated with increasing angular velocity of the stimulus. Successful tracking involves fixation on the retina, and this observed deterioration was produced by increasing position errors of the image on the retina (Brown, 1972a).

The above mechanisms are concerned with real image movement, but perception of movement can be achieved by a sequential displacement of an image without continuous movement of the object having taken place; this is known as apparent movement (the "phi" phenomenon). This phenemenon points out the importance of the temporal characteristics of the visual system. Time (e.g. latency, persistence) is an important parameter. The amount of time taken to process the image influences the limit of movement perception (Ripps and Weale, 1976). Traditionally, real and apparent motion have been considered as parallel processes (e.g. Kolers, 1963), but this view has been questioned by Kaufman et al. (1971).

Various authors have investigated the effect of different stimulus variables. Kennedy (1936) reviewed the importance of velocity, form and size of stimulus, characteristics of the path of movement, illumination, distance from the stimulus and the duration of the observation period.

Cohen and Bonnet (1972) measured movement detection thresholds for varying durations of stimulus presentation and found there was a trade-off in which an increase in duration (T) was offset by a decrease in the velocity (V) required for detection. The observed VxT constancy was interpreted as evidence for the direct detection of movement, with rate of motion being regarded as an intensity measure.

The visual perception of moving objects depends on a high photon flux (Lythgoe, 1979). Various studies have stressed the importance of luminance for motion perception. Brown (1955, 1957, 1958) also believed motion perception to be an energy-based mechanism. He implied a luminance-time reciprocity function whereby motion is signalled upon the accumulation of a critical energy quantity in the retina. Henderson (1971, 1973) however, argued against an energy explanation, perceived motion being the result of the retina being able to discriminate successive events. Henderson

(1973) criticised Brown's hypothesis as it implied that motion will be detected regardless of its velocity as long as the stimulus is sufficiently bright.

Not only are the luminance properties of the stimulus important, but also the relationship between stimulus brightness and ambient illumination. Thompson (1982) showed that the perceived rate of movement depends on contrast.

Additional factors that have been investigated include the relationship between the stimulus and background (Wallach, 1959), the effect of monocular or binocular viewing (McGolgin, 1960), and the input of colour information (Ramachandran and Gregory, 1978).

Sekuler _et al_. (1982) reviewed responses to direction of motion. Discrimination between a moving and a non-moving field is different from the perception of the direction of a moving stimulus (Ball _et al_., 1983). Thompson (1984) suggested that a velocity threshold must be exceeded before the direction of a grating can be identified. The mechanisms behind perception of direction were investigated by Ball and Sekuler (1980).

Comparative Animal Psychophysics

As in studies of human visual perception, emphasis has been placed on detecion of slow movement. One of the earliest studies was that of Kennedy and Smith (1935) on the cat. More recent work on cats includes that of Berkley (1970), where cats were trained to discriminate between a slowly moving spot and an adjacent stationary stimulus. Such a task appears to be a more difficult problem than brightness discrimination. The slow movement threshold of the cat ranges from 0.6°-$2.3^{\circ}sec^{-1}$ (Pasternak and Merigan, 1980) to $3.3^{\circ}sec^{-1}$ (Berkley et al., 1978). Similar thresholds are obtained using a variety of stimuli ranging from spots and lines (Berkley et al., 1978) to more complex stimuli such as random dot patterns and square-wave gratings (Pasternak and Merigan, 1980). Pasternak and Merigan did not find any directional asymmetry for motion detection, but Camisa et al. (1977) demonstrated directional selectivity in the visual system of the cat.

Slow-detection thresholds have been determined in monkeys (Ross, 1943), chimpanzees, Pan troglodytes (Carpenter and Carpenter, 1958), pigeons (Hodos et al., 1976) and rats (Hawley and Munn, 1933). Although slow movement thresholds are well above resolution thresholds, there is a correlation between movement detection and acuity thresholds in a number of species (Berkley et al., 1978). Primates have a well developed motion detection capability, with diurnal species having thresholds similar to that of man (Carpenter and Carpenter, 1958).

The pigeon does not have such a well developed movement detection ability as that of some primates. The minimum detection threshold was determined as 4°-$6^{\circ}sec^{-1}$ by Hodos et al. (1976). Siegel (1970, 1971) found that pigeons generalized between apparent and real movement.

Some behavioural investigations have related movement detection to the natural behaviour of the animal. For example, Ingle *et al*. (1979) and Ingle (1981) investigated tracking of moving visual stimuli (food items) in the gerbil. Orientation to stimuli presented in the frontal visual field, indicated that gerbils could predict the pathway of a target. Prediction of pathways need not imply that coordination of movements is under the control of central mechanisms. Prediction of pathways by the teleost fish, *Acantholuteres spilomelanurus*, could be accounted for by the alignment of eye and body during pursuit of moving food (Lanchester and Mark, 1975).

The perception of fast movement has probably the most biological relevance to animals. The ability to detect fast-moving prey is necessary to predators, and similarly, good movement perception capability may aid the detection of predators by prey. Measurements of high-speed movement thresholds as such are lacking, but measurements of critical flicker-fusion frequency have been made in several species. The perception of flicker and of the fast movement of directional stimuli are related, since at threshold both phenomena give rise to fusion. The faster an animal's CFF, the shorter the persistence time, and therefore at high speeds the less likely the perception of a moving object will be blurred, making the determination of its nature, direction, and velocity easier (Walls, 1942).

The classic study on critical flicker frequency is that by Crozier *et al*. (1936). The critical flicker frequency of a variety of animals has been measured including budgerigar, *Melopsittacus undulatus*, (Ginsberg and Nilsson, 1971), rat

(Goldzband and Clark, 1955), and ground squirrel *Spermophilus beecheyi* (Jacobs *et al*., 1980). There is a trend for diurnal animals to have higher CFF values than nocturnal ones. Crozier and Wolf (1941) found that the horned lizard, *Phyrynosoma cornutum*, has a higher critical flicker frequency than the gecko (*Sphaerodactylus inaguae*). The CFF of the nocturnal gecko drops slowly with decreasing illumination, resulting in it having a higher CFF than the horned lizard under dim light conditions. The CFF of closely related species of *Anolis* correlated with the degree of insolation experienced in the natural habitat of the species concerned (Jenssen and Swenson, 1974). However, the CFF of animals with cone-retinas are not necessarily higher than those with a predominance of rods. Critical flicker-fusion frequency may be related to an animal's ability to negotiate a complex habitat and identify and catch swift prey. For example, Protasov (1970) found that fish with high CFF values fed on moving organisms and were themselves potential prey of fast-moving predators.

Neurophysiological Studies of Movement Perception

The neural substrates of visual movement perception in higher vertebrates are reviewed by Berkley (1982). Other major reviews include Grusser and Grusser-Cornehls (1973) and Sekuler *et al*. (1978). Movement perception is not localised within one neural structure; movement-sensitive cells are present for example in the retina, lateral geniculate nucleus, superior colliculus and cortex.

Different classes of cells in the cat's retina and also at higher levels of the visual system have different temporal response properties. The X-cell class responds better to stationary or slow-moving patterns, while Y-cells respond to faster moving stimuli (Enroth-Cugell and Robson, 1966; Lee and Willshaw, 1978; Cohen et al., 1980).

Although some neurons in the lateral geniculate nucleus respond to movement and appear to signal stimulus velocity (Hess and Wolters, 1979), they are not directionally selective (see below). However, in the superior colliculus, there are movement-sensitive cells which are directionally selective and which also respond to variations in background illumination (Harutiunian-Kozak et al., 1975).

There are cells in the cortex of the cat which are sensitive to stimulus movement (Hubel and Wiesel, 1962; Hamilton and Lund, 1970), some of which are directionally selective (Pettigrew et al., 1968). Movshon (1974) found that simple cortical cells responded best to slow movement, while complex cells prefer more rapid rates. Complex cells receiving Y-cell input may be the neural substrate of movement sensitivity (Kulikowski and Tolhurst, 1973).

A common explanation for the ability to distinguish between real and self movement is the production of a corollary discharge in the superior colliculus whenever there are eye movements. However, Collin and Cowey (1980) found that after removal of the superior colliculi, there was no evidence for rhesus monkeys confusing real movement with self movement. Palka (1972) suggested that there is no need to propose a central mechanism to distinguish between the two types of movement as an inhibition is generated whenever large areas of the receptive fields of movement-sensitive cells are stimulated.

A major topic of interest has been the investigation of directionally selective units. These units respond to movement of a stimulus in one direction, and not to movement in the opposite direction. One of the earliest studies to demonstrate the existence of directionally selective units in the retina of the rabbit, was that of Barlow and Hill (1963). The mechanism underlying this phenomenon was investigated by Barlow and Levick (1965) and Oyster (1968).

Directional selectivity has also been found to exist in the retinas of goldfish, *Carassius auratus* (Cronly-Dillon, 1964), pigeon (Maturana and Frenk, 1963), grey squirrel, *Sciurus carolinensis* (Cooper and Robson, 1966), ground squirrel, *Citellus mexicanus* (Michael, 1966) and in the superior colliculus of the golden hamster, *Mesocricetus auratus* (Rhoades and Chalupa, 1976).

Neurophysiological studies using the same configurational stimuli used in behavioural studes of prey recognition have been conducted on amphibians, allowing behaviour and neuronal activities to be correlated. Maturana *et al*. (1960) established that four of the five main classes of ganglion cells in the retina of the frog, respond to moving stimuli. Grusser-Cornehls *et al*. (1963) investigated the nature of movement detecting units both in the retina and in the tectum.

The responses of the cells led to the suggestion that it is successive positions of a stimulus that stimulate the motion detectors and not movement itself (c.f. Kennedy, 1936; Spigel, 1965). Finkelstein and Grusser (1965) found that the neuronal discharge rate of retinal ganglion cells could be related to the angular velocity of a stimulus by a power function. Grusser *et al*. (1967) showed that neuronal responses were determined by the following main parameters: angular velocity, stimulus size and contrast.

Retinal ganglion cells have also been found in the toad, *Bufo bufo*, which show an increase in activity with increasing velocity and stimulus size (Ewert and Hock, 1972). Borchers and Ewert (1979) investigated the distribution of movement-sensitive cells within the visual pathway and Ewert *et al*. (1978) used correlation methods to analyse responses of neurons from different levels of the pathway, to stimuli of particular configurations. No neurons were found with specific responses to prey stimuli, although some neurons did show sensitivity to a stimulus of a certain configuration. Most discrimination of configuration appears to occur in the tectum (von Wietersheim and Ewert, 1978; Ewert *et al*., 1979c) although general properties concerning discrimination of moving stimuli are already present in the retina (Ewert *et al*., 1979b). There is no correlation between the types of response shown by a neuron and its anatomical position within the optic tectum (Roth and Jordan, 1982).

The response patterns of tectal neurons in *Hydromantes italicus* show differences from those known in other amphibia, corresponding well to the differences in prey-catching behaviour (Roth, 1982). The organisation and properties of neurons in different parts of the visual pathway of <u>Salamandra salamandra</u> were first described by Grusser-Cornehls and Himstedt (1973). Himstedt and Roth (1980) studied responses of neurons in the optic tectum of this species. Although there were partial similarities between behaviour and neuronal activity, correlations were not as good as with other amphibian species, therefore none of the neuron types could be called a prey detector.

The neurophysiological basis of movement perception has been well studied, but comparative behavioural studies have been neglected. Most studies have used slow-moving stimuli, therefore there is a need for perception of fast movement to be investigated. The determination of upper movement thresholds is of particular relevance when using predators as subjects as movement of prey is widely acknowledged to be an important stimulus for the elicitation of killing behaviour (Eisenberg and Leyhausen, 1972).

Since fast-moving stimuli may have both an absolute velocity and a relative velocity in relation to other moving objects, a complete study of movement perception needs to examine both absolute and relative movement detection. An investigation of movement perception in a predator has only biological relevance if it is known how important vision is and under what circumstances movement perception may be used. To this end, the importance of vision relative to the other distance senses will be evaluated.

CHAPTER THREE GENERAL MANAGEMENT OF POLECATS AND WEASELS

3.1 Polecats

The colony was established in January 1981, as a pair of related individuals obtained from a wildlife park. These captive-bred animals were said to be descended from wild caught polecats. The colony consisted of the offspring of these two animals, and in addition, a wild-caught polecat bred with a female from the colony in spring 1982. The exact ancestry of the animals was unknown, but judging from external appearances there was some *Mustela furo*, as well as *M. putorius* ancestry. The animals were more nervous and difficult to handle than typical ferrets (pers. obs.) and showed a great reluctance to explore novel open areas, characteristics ascribed to polecats by Poole (1972a). Therefore I will refer to the animals used in the present study as polecats, although they are not 100% *M. putorius*.

The polecats were maintained communally, except during the breeding season (March - June), when the sexes were kept separate. They were housed in a large room, dimensions 2.9m x 1.8m. There was no heating and a natural day-night illumination cycle was provided. The floor was covered in wood shavings and hay was available as additional bedding during the winter. A large wooden nest box was provided and various objects e.g. tubes, balls, were strewn around the floor for the animals to play with. They were cleaned out twice weekly. Water was available *ad libitum* and they were fed once a day in the evening. Food consisted of dead laboratory rats (on average half a rat each) or dead day-old chicks (two or three per animal).

During the breeding season, the males were kept in a separate enclosure of dimensions 1.3m x 1.8m. During this period there was the problem of aggression between male polecats, but there were no serious injuries as a result of any fighting.

No problems were experienced with breeding the animals, a male and an oestrous female polecat were kept together in a small enclosure until the vulval swelling of the female began to diminish. Pregnant females were isolated from the rest of the colony and, once the litter was born, were disturbed as little as possible until the young were aged four weeks old. The young polecats were then handled daily to familiarise them with the author. Surplus food was available for the mother and litter at all times. Litters of seven and six respectively were reared successfully in 1981 and 1982.

It was possible to handle the adult polecats, but as they occasionally protested at this, they were trained to enter travelling cages within which they were transported to the laboratory.

3.2 Weasels

Weasels were housed individually in weldmesh cages (93x58x30cm), of 10mm diameter mesh or in metal cages (90x57x20cm) with weldmesh lids (10mm mesh). Each cage possessed a wooden nest box. The aluminium floors of the cages were covered in wood shavings and hay was available as additional bedding during the winter. The animals were kept under natural illumination conditions and the room was heated during cold weather to a temperature of 16-18 ^{o} C.

They were fed once a day, in the evening, with male weasels receiving two or three, and females receiving one or two dead day-old chicks per day. Occasionally they were given mice or young rats, when these were available. Water was provided _ad libitum_.

Except when in oestrous, female weasels are extremely aggressive towards males. At first, to avoid any serious fighting, breeding was achieved by connecting two metal-based cages with a tube of diameter sufficiently wide to allow the passage of a female weasel, but not a male. Success was achieved with this method of breeding weasels as, when in oestrous, the female would enter the male′s cage, but this method was abandoned when a male animal became trapped in the connecting tube and died. Thereafter, breeding was achieved by placing the female directly into a male′s cage, in her own nest box. If on introduction to a male, the female was aggressive, she was returned to her home cage. If not, the two animals were left together until the female began to reject the advances of the male. Usually mating took place several times over two to three days.

Two litters a year per female were possible, as reported by Linn (1962), with females being fecund between March and September. Pregnant weasels were disturbed as little as possible and were given surplus food after the birth of the litter. Once the young emerged from the nest, they were handled daily, until they were aged between twelve and fourteen weeks, when they became too lively. The young animals were separated and housed individually when aged about sixteen weeks. Weasels were then trained to enter travelling cages, within which they were transported to the laboratory.

Health problems were few, except for the occurrence of what appeared to be a stress-related condition. Apparently healthy animals would suddenly lose weight over a few hours and die. Animals particularly prone to this condition were young males aged between four months and one year old. Symptoms were excessive activity and weight loss. If the condition was detected in time and the animal given extra food it was not always fatal. Loss of weight can have serious consequences in these animals due to their high metabolic rate (Moors, 1977), and their inability to completely compensate for food deprivation (Gillingham, 1984).

The experimental history of individual animals is illustrated in Table 1.

<u>TABLE 1</u> Experimental history of animals.

	Sex	Date of birth	A	B	C	D	E	F	G	Order of presentation of experimental treatments for distance senses experiments
POLECATS										
Morin	M	04 81	/	/			/	/	/	VAO VAOd V O A VO VA AO NONE
Marny	M	04 81	/	/						
Midge	F	04 81	/	/						
Memla	F	04 81	/	/			/	/		VAO O A V AO VO VA VAOd NONE
Mira	F	04 81					/			
Mona	F	04 81						/	/	VAO VA VO VAOd AO V A O NONE
Merril	F	04 81	/							
Hunk	M	05 82					/			
Herman	M	05 82					/			
Horace	M	05 82						/		VAO VO VA AO VAOd V A O NONE
Hazel	F	05 82					/			
WEASELS										
Loopy	M	08 79	/	/	/	/				
Henry	M	08 79	/							
Sophie	F	08 79						/		VAO VO AO VAOd VA O V A NONE
Nero	M	11 79	/	/	/	/		/		VAO AO VA VO VAOd V O A NONE
Tiny	F	11 79	/					/		VAO VAOd A O V VA AO VO NONE
Tulip	F	11 79						/		VAO VA VAOd VO AO A O V NONE
Alex	M	11 79	/	/	/					
Charley	M	11 79	/							
Brinn	M	05 81						/	/	VAO V A O VA VO AO VAOd NONE
Tonia	F	05 81	/							
Roger	M	04 82						/	/	VAO A O V VO AO VAOd VA NONE
Lucy	F	04 82	/							

KEY:
A-D Directional movement detection (Chapter 5)
    A Training
    B Threshold estimation under standard conditions
    C Effect of discrimination distance
    D Effect of stimulus radiant intensity
E Relative movement detection (Chapter 6)
F-G Relative importance of distance senses (Chapter 4)
    F Experiments on the use of the distance senses
    G Scent trail experiments
Key for experimental treatments is in Chapter 4.

CHAPTER FOUR THE RELATIVE IMPORTANCE OF THE DISTANCE SENSES TO THE POLECAT AND WEASEL DURING A PREY LOCATION TASK

4.0 INTRODUCTION

The relative importance of the distance senses has been evaluated in only a small number of mammalian species. Those studied so far have usually been large diurnal predators such as the coyote (Wells and Lehner, 1978) or relatively unspecialised nocturnal predators (e.g. Langley, 1979). In order to widen the range of species examined and to provide comparative data on species which are neither strictly nocturnal nor diurnal it was decided to determine the relative importance of the senses to the polecat and weasel. Many of the mammals previously studied have not been highly predacious carnivores therefore it is pertinent to study species which are. Mustelids are considered by Eisenberg and Leyhausen (1972) to be specialised predators as they use a precisely-aimed killing-bite.

Polecats and weasels are also suitable subjects as their predatory behaviour has been particularly well documented (see p. 17). The relative importance of vision and olfaction will be determined as they have been ascribed a different relative importance by previous authors. The use of audition and of substrate scent cues is investigated as they have been neglected in previous studies. The experiments were designed to model a predatory encounter which only involved the predator searching for prey.

4.1 MATERIALS AND METHODS

Subjects

The subjects were six weasels, (3 males: 3 females) and four polecats, (2 males: 2 females), which were completely naive of live prey at the beginning of the experiments.

Arena

Experiments were conducted in an arena of dimensions 3.0m x 3.5m. The walls of the enclosure were 1.2m high and were surmounted by a 41cm wide aluminium baffle which prevented escapes. Three walls were constructed of hardboard and one was of transparent perspex through which observations could be made. A sliding perspex door gave access to the arena. The floor was sealed in clear plastic sheeting and marked out as a grid with 60cm x 50cm rectangles.

Collection of data

The behaviour of the experimental animals was recorded using a monochrome "Sony" video camera (model AVC 3450CE), mounted on an overhead beam so that the field of view covered the entire arena. A spoken commentary of each experimental trial was recorded simultaneously on the video-tape recording.

Presentation of Stimuli

Subjects were required to locate the position of a mouse within the experimental arena. Owing to ethical considerations direct contact between the predator and the mouse was prevented by presenting the mouse inside a glass container (23cm x 11cm) which could be fitted with either a wire mesh or an airtight lid. There were a total of eight identical containers, all equidistant (1.1m) from the release-point (see Fig. 1). The position of the container holding the mouse was varied in a random fashion, within the constraints of approximately equal numbers of presentations at each location per experimental treatment. An adult male laboratory mouse, either dead or living, weighing approximately 40g, was placed in a container along with a small quantity of wood shavings as bedding. All experiments requiring live prey, involved the use of the same mouse, controlling for individual variation in body scent and behaviour.

The experimental design entailed altering the type of sensory information available to the predator. Visual information was available when the experimental animal could see the mouse inside the container; vision could be occluded by covering the container with opaque black paper. Olfactory information was permitted by fitting the container with a lid of 2mm mesh, or was eliminated by an airtight lid. Auditory

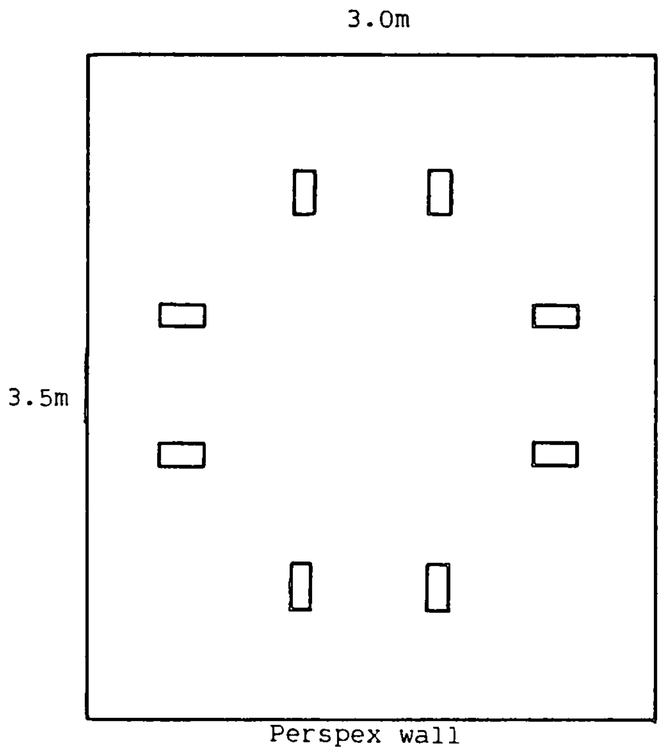


FIGURE 1. Plan diagram of arena showing arrangement of containers.

stimuli were available when a live mouse was present. It was felt that the noise made by a mouse inside a glass container was rather limited, so to supplement the information available to the predator a small 8ohm speaker, mounted inside a wooden box, was placed on top of the container. The speaker was connected to a portable tape recorder situated outside the arena and played a sound recording of a mouse digging and scratching. The other containers were provided with "dummy" speakers and leads. Auditory stimuli were eliminated by replacing the live mouse with a dead one and by not playing the recording.

Preliminary Trials

The experimental animals were allowed to become familiar with the empty arena and then with eight empty containers present.

Experimental Procedure

The procedure for all trials involved the release of a predator from a central carrying box and allowing it to search for the container holding the mouse. Subjects were trained to search for the mouse and then return to the release-point where they received a food reward, a small quantity of "Heinz" strained baby food, "Beef and Oxtail Dinner". The predators received a verbal signal from the experimenter, which was associated with a food reward, after they arrived at the mouse container. A trial was continued until the predator found the mouse (usually within 5 minutes) and subsequently returned to the release point. The criterion for finding the mouse was the active investigation of the container holding the mouse. Each subject was given up to five trials per day. The arena was wiped clean with dilute alcohol between trials to remove scent marks. There were approximately twenty trials for each experimental treatment. The number of trials was reduced if the mean time taken to find the mouse began to increase rather than showing a decreasing trend, or if the mean time reached a plateau. This was considered to have occurred when the mean time to find the mouse in a block of five trials did not increase by more than five percent of the mean time for the previous block of five trials. Six series of experiments were conducted.

Experiment I

Information available to three sensory modalities.
Animals were required to locate the mouse with visual, auditory and olfactory information available (VAO). A live mouse was presented in a container fitted with a wire mesh lid and the sound recording was played.

Experiment II

Stimuli available to two senses.
Animals were tested by eliminating the prey stimuli for one

sensory modality at a time. There were three experimental treatments, with the following sensory cues available:

Vision + Audition (VA):

Live mouse, airtight lid, recording played.

Vision + Olfaction (VO):

Dead mouse, wire mesh lid.

Audition + Olfaction (AO):

Live mouse, wire mesh lid, covered container, recording played.

Experiment III

An experiment to investigate the ability to locate prey with only one sensory modality available.
The treatments were achieved as follows:

Vision only (V):

Dead mouse, airtight lid.

Audition only (A):

Live mouse, airtight lid, covered container, recording played.

Olfaction only (O):

Dead mouse, wire mesh lid, covered container.

Experiment IV

An experimental treatment to investigate the importance of movement cues during prey location (VAOd).
A dead mouse was placed within a container, all other sensory information was available, including the sound recording.

Experiment V

A control treatment to test the effectiveness of the experimental manipulations, particularly the air-seal of the containers.
The animals were tested with all three classes of stimuli eliminated. The treatment was achieved as follows:

"No senses" (-):

Airtight lid, dead mouse, no sound recording, covered container.

Experiment VI

An additional experiment was designed to investigate the role of substrate-borne olfactory cues in prey localisation. The body of a dead mouse was smeared along the floor of the arena, from the release-point to the container holding the mouse. Two subjects of each species were used and there were five trials of each of three experimental treatments:

VAO + substrate odour
Olfaction + substrate odour
"No senses" + substate odour

The floor of the arena was cleaned thoroughly between trials.

Order of Presentation of Experiments

The order of presentation of the treatments within Experiments II and III was different for each animal. Also, some animals took part in Experiment III before Experiment II (and vice versa). The positions of Experiments IV and VI within the series were randomised. Experiment V was always conducted last. The order in which the different treatments were presented to each subject is given in Table 1, Chapter Three, which contains the full experimental history of all animals used.

Data Analysis

The video-tapes were analysed using a custom-built real-time digitiser connected to an "Apple II" microcomputer. The behaviour of the animals was analysed using the microcomputer, programmed in Basic, as a real-time event recorder. The data were stored as behaviour codes along with their onset-times and durations. Preliminary analysis of these data was achieved using a program written in Pascal on the Durham facility of Numac (Northumbrian Universities

Multiple Access Computer). Use of statistical packages was made in the analysis of both the event recorder and digitiser data.

The search-path of an experimental animal was followed accurately using the digitiser. The video-image could be followed using a pointer attached to a drawing-board arm (see Plate 1). The angular displacements of the two elements of the arm were measured by two potentiometers and were recorded by the microcomputer at pre-set intervals. The x,y coordinates of the pointer were therefore registered as voltages. A momentary-action switch mounted on the arm allowed the operator to define either a slow or a fast sampling rate of the animal's position. The sampling rates selected were every 0.87s (slow) or 0.42s (fast).

A program written in Basic (Behpath) was available which stored the voltage values on floppy disk. During the digitised transcription of video-tapes, behaviour codes were entered which corresponded to different phases of the trial (e.g. search, with prey etc.). The data were checked using another program (List/plot) which printed out the voltages and associated behaviour codes for each trial and gave a graphic representation of the arena and the searchpath the animal followed.

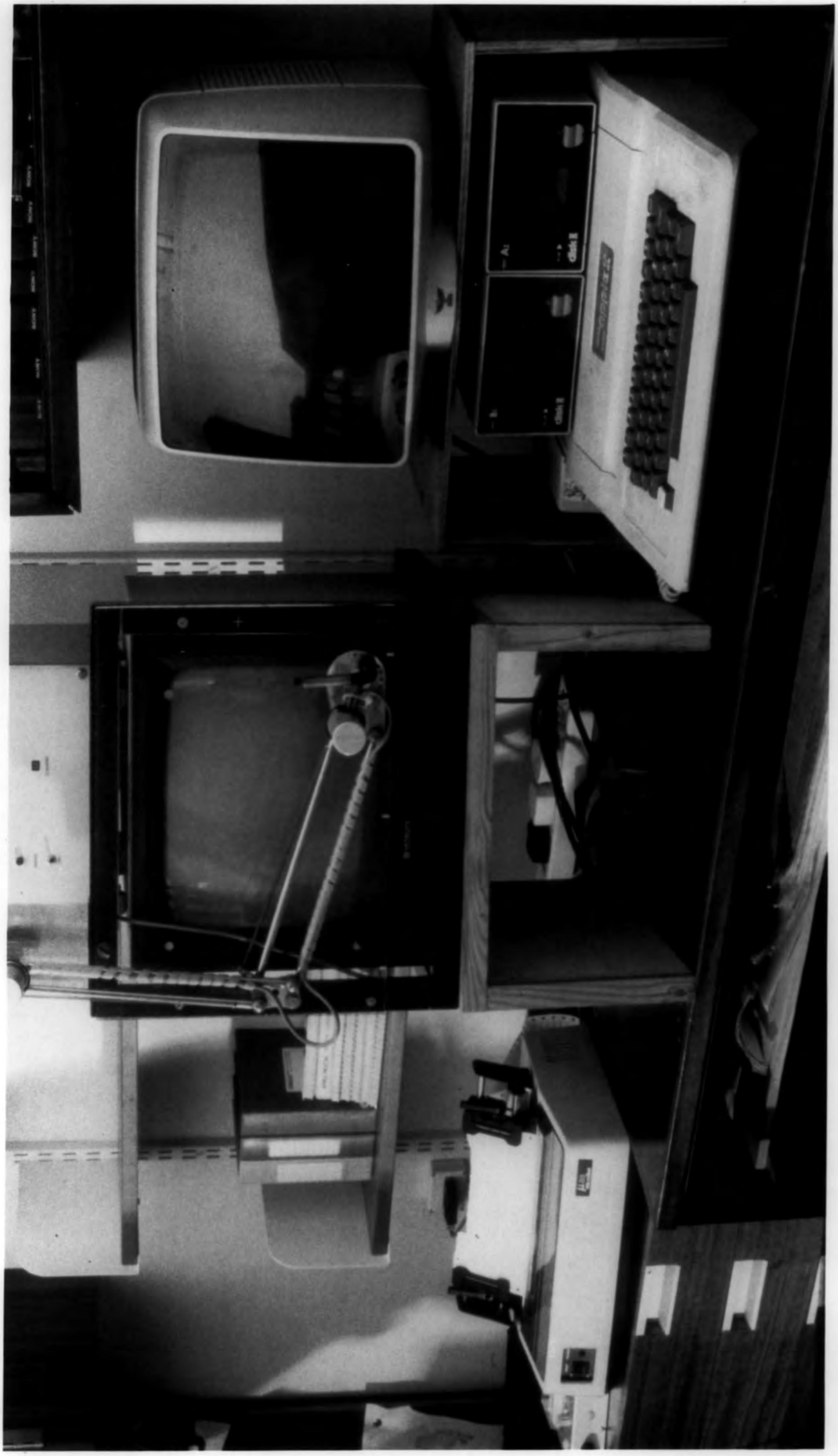
Data collected in this way were analysed on the mainframe computer using a program written in Fortran which converted the voltages into corresponding x,y coordinate values. The program incorporated a scaling factor to convert successive coordinate values into absolute distances. The dimensions of

PLATE 1. Apparatus used for the transcription of video-tapes.

Left; printer.

Centre; black and white television monitor with tracking arm.

Right; Apple II microcomputer.


disk II
disk II

the video-image of the experimental arena was 2300 x 1700 coordinate units, approximately six coordinates for each centimetre of arena. Various searchpath parameters were calculated including distance travelled, speed of movement, and pause frequency. A hard-copy diagrammatic representation of each searchpath was obtained.

Detailed records were made only of the behaviour of the weasels. The variables search-time, and the number of containers visited, were felt to reflect the difficulty of the task and hence the relative importance of the senses. A comparison was made between the polecats and weasels using these variables. A more detailed comparison of the behaviour of the two species was made in experiment VI (substrate scent trials).

A wide variety of behavioural measures were taken to build up a complete picture of the weasel's searching behaviour. In addition to search-time, other parameters were accurately quantified including speed of movement, pause and turn rates. Attention responses were also recorded to investigate whether they were in response to particular sensory cues. The time spent near the prey animal (prey-time) was taken as a measure of the importance of (or the interest shown in) different sensory cues when in close proximity to prey.

4.2 RESULTS OF EXPERIMENTS I-V

4.2.1 Predator species: Weasel

Search-time

Search-time was defined as the time from the release of the predator until it arrived at the container holding the mouse. The mean time taken to locate the mouse according to experimental treatment is shown in Fig. 2. Results of a two-way analysis of variance of search-time according to treatment and subject is given in Table 2a and according to treatment and sex in Table 2b. The type of sensory information available significantly affected search-time. A 't' test analysis showed that mean search-times for vision only, olfaction only, audition only and "no senses" were significantly longer than the baseline condition (VAO) (see Fig. 2). The time taken to find the mouse depended on the amount of sensory information available. The mean search-time in the control "no senses" treatment was significantly greater than all the other conditions except audition only (A).

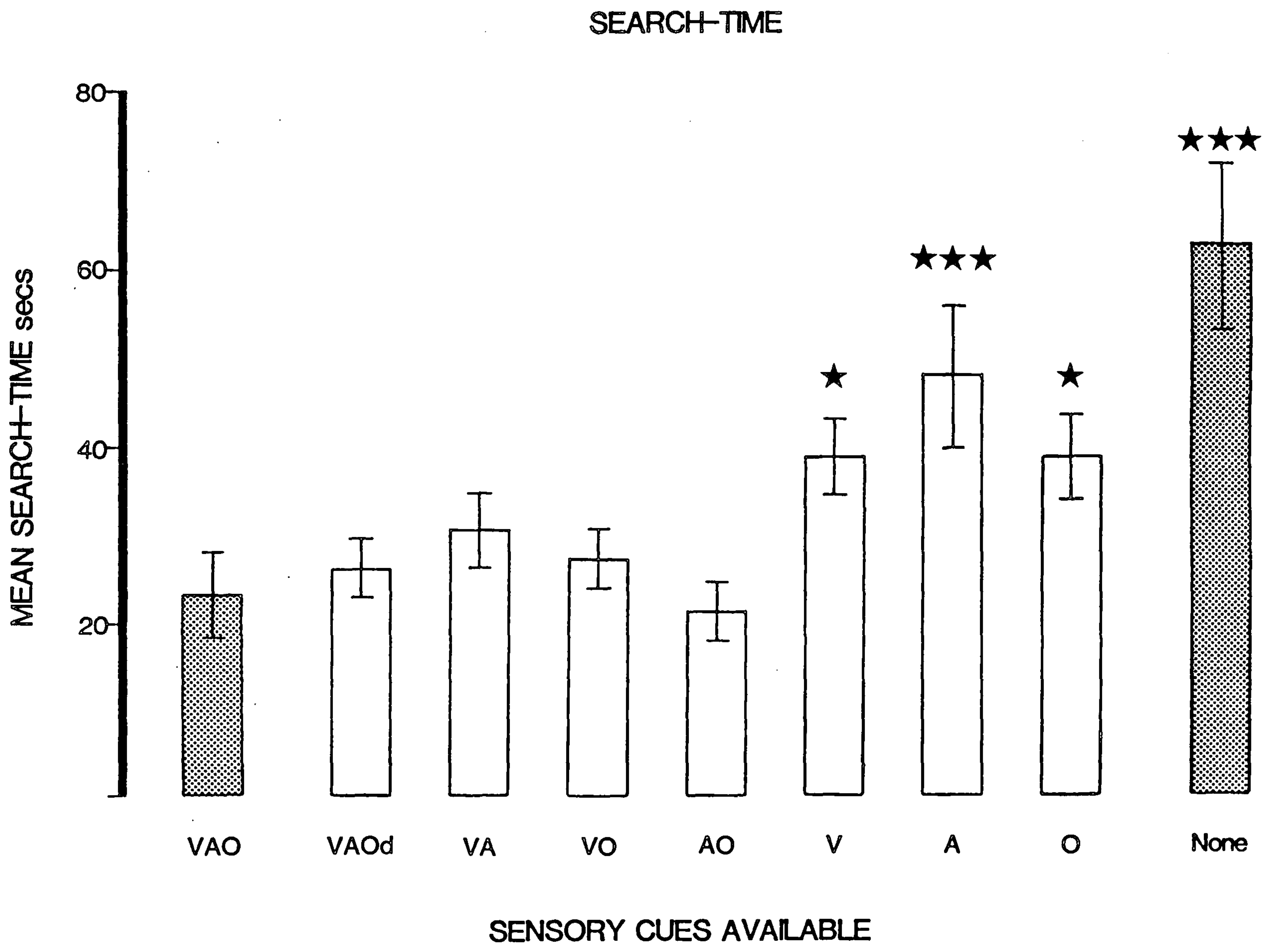
There was no difference in mean search-time between male and female weasels (see Table 2b), but individual variation was apparent (Table 2a). There were no significant two-way interactions between treatments and individual subjects. Tulip (♀), Brinn (♂), and Roger (♂) found the mouse more quickly than the other subjects.

The first five to ten trials were usually characterised

FIGURE 2. Mean time taken to locate mouse according to experimental treatment. Predator species: Weasel.

Standard error bars and the treatments significantly different from the three senses control (VAO) are indicated. The control treatments (VAO and "no senses") are indicated by shading.

KEY: VAO, visual + auditory + olfactory cues;
VAOd, visual + auditory + olfactory cues, dead mouse;
VA, visual + auditory cues;
VO, visual + olfactory cues;
AO, auditory + olfactory cues;
V, visual cues;
A, auditory cues;
O, olfactory cues,
None, "No senses" available.


SEARCH-TIME
MEAN SEARCH-TIME secs
80
60
40
20
★
★★★
★
★★★
VAO
VAOd
VA
VO
AO
V
A
O
None
SENSORY CUES AVAILABLE

<u>TABLE</u> <u>2a</u> Two-way analysis of variance of search-time: Weasels.

Analysis of variance of time taken to find the mouse between experimental treatments (Experiments I-V) and between subjects. All trials are included in the analysis.

Source of variation	SSq.	d.f.	MS.	F	Significance
Main effects	170245.8	13	13095.8	4.7	<0.001
Treatment	126686.5	8	15835.2	5.7	<0.001
Subject	39376.3	5	7875.2	2.8	0.015
Two-way interaction					
Treatment x subject	136941.3	40	3423.5	1.2	0.16
Explained	307188.0	53			
Residual	2378149.0	855			
Total	2685337.0	908			

<u>TABLE</u> <u>2b</u> Two-way analysis of variance of search-time: Weasels.

Analysis of variance of search-time between experimental treatments and between the sexes. All trials are included in the analysis.

Source of variation	SSq.	d.f.	MS.	F	Significance
Main effects	132426.1	9	14714.0	5.2	<0.001
Treatment	129769.2	8	16221.2	5.7	<0.001
Sex	1556.5	1	1556.5	0.6	0.46
Two-way interactions					
Treatment x sex	21876.0	8	2734.5	3.2	0.46
Explained	154303.2	17			
Residual	2531034.0	891			
Total	2685337.0	908			

by long, highly variable search-times, but less variation occurred subsequently. An analysis of variance using only the final five trials of each treatment revealed a significant difference in search-time according to experimental treatment, but no variation between subjects (Table 3).

The relative importance of the senses can be examined by subtracting the mean search-time for the control conditions (VAO or "no senses") from the mean search-time of each experimental treatment (Table 4). Treating the results in this way suggests that the presence of either visual or olfactory cues appears to be equally useful for prey location, whilst audition is less important. When information relevant to only one modality is removed, there is a trend for the removal of visual cues to have the least effect, while removal of only olfactory cues prolongs search-time.

Prey-Time

Figure 3 shows the mean time spent with the container holding the mouse (prey-time) during Experiments I to V (all trials are considered). Table 5 shows the results of a two-way analysis of variance on these data. Prey-time varied according to the amount of sensory information available and showed a similar but inverse trend to search-time. Prey-time during the single sense (vision, olfaction or audition only) and "no senses" treatments was significantly shorter than the base-line VAO condition. There was significant variation (see Table 5), due to a sex difference. Female weasels spent more

TABLE 3 Two-way analysis of variance of search-time: Weasels.

Analysis of variance of search-time between experimental treatments and individual subjects. Only the final five trials of each treatment were included in the analysis.

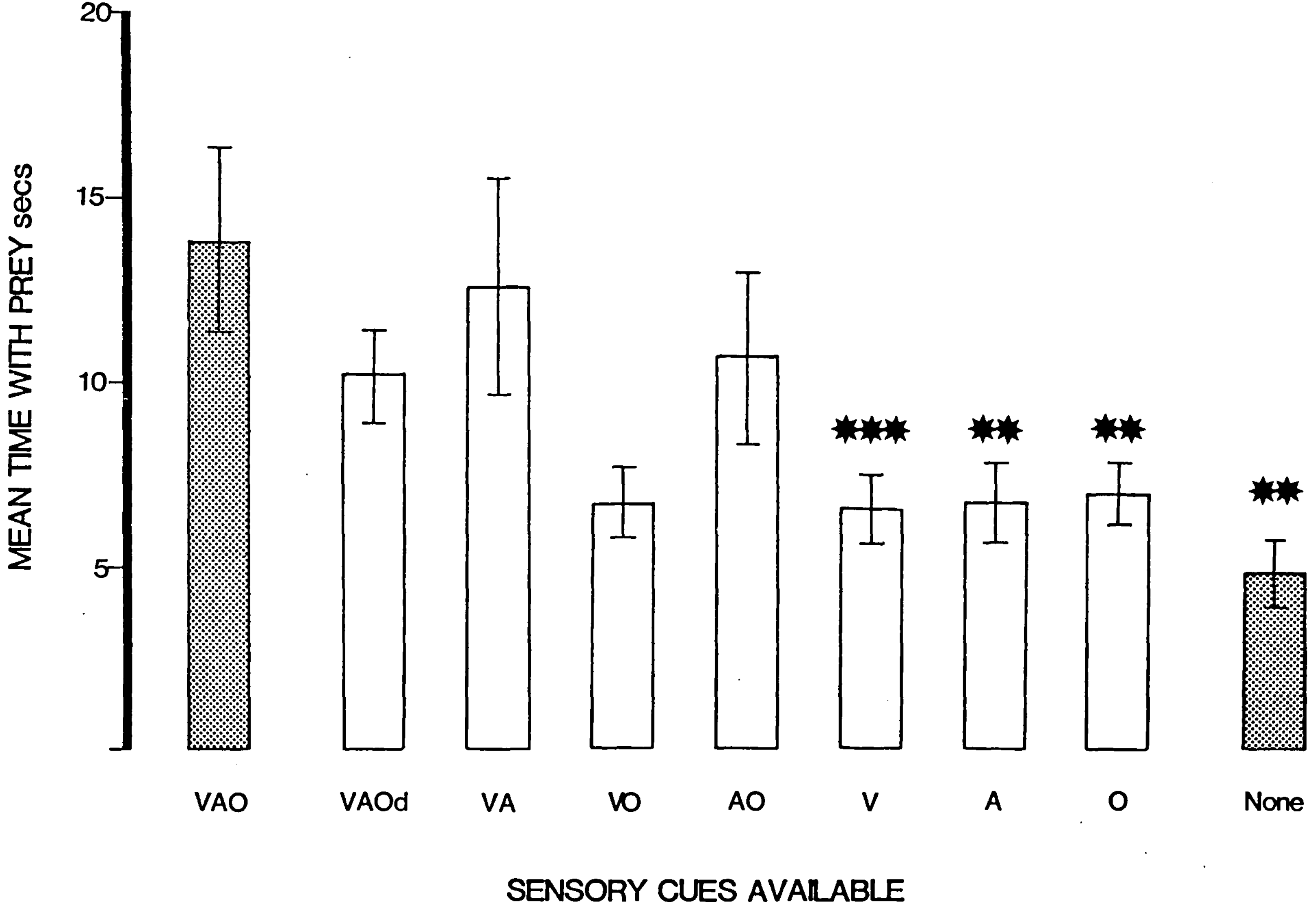
Source of variation	SSq.	d.f.	MS.	F	Significance
Main effects	100119.1	13	7701.5	5.0	<0.001
Treatment	87834.7	8	10979.3	7.1	<0.001
Subject	12284.3	5	2456.9	1.6	0.16
Two-way interactions					
Treatment x subject	18288.6	40	457.2	0.3	1.0
Explained	118407.6	53			
Residual	332336.4	216			
Total	450744.0	269			

TABLE 4 Differences in mean search-time (s) between the experimental treatments and controls.

Presence of	Difference between		Absence of	Difference between	
Vision	NONE-V	24.1	Vision	VAO-AO	-2.0
Audition	NONE-A	14.6	Audition	VAO-VO	2.9
Olfaction	NONE-O	24.0	Olfaction	VAO-VA	7.4
Vision + Audition	NONE-VA	32.4	Vision + Audition	VAO-O	15.8
Vision + Olfaction	NONE-VO	36.9	Vision + Olfaction	VAO-A	25.2
Audition + Olfaction	NONE-AO	41.8	Audition + Olfaction	VAO-V	15.7

The mean search-time for each treatment is subtracted from that of the controls.

FIGURE 3. Mean time spent near the prey according to experimental treatment. Predator species: Weasel. Conventions as in Fig. 2.



time near the prey animal than did males (Female mean = 10.4s ± 0.9 (S.E.); Male mean = 6.6s ± 0.6 (S.E.). There was also considerable individual variation which could not be accounted for by the sex-related difference.

Table 6 shows the effect of the presence or absence of different sensory cues on the time spent with the prey animal. There was a trend for the removal of auditory cues to have the most detrimental effect on prey-time, while the removal of olfactory cues had relatively little effect. There was no correlation between search-time and prey-time ($r=0.05$, $n=246$, $p=0.16$).

Number of Containers Visited

A major factor affecting search-time was the number of containers visited before the mouse was located. On average, the number of empty containers visited is a reflection of the difficulty of the task. A significantly greater number of containers were visited during VO, single sense and "no senses" experiments compared to the baseline condition (VAO) (Fig. 4). The VAOd, VA and AO treatments had low frequencies of container visits. Individual variation was also significant, but this was not due to a sex-related difference (Table 7). Tulip, Roger and Nero visited fewer containers than did the other subjects.

Table 8 shows the effect of the presence or absence of sensory cues on the mean number of containers visited per trial. There was a trend for a greater number of container

TABLE 5 Two-way analysis of variance of prey-time: Weasels.

Analysis of variance of time spent near the prey animal, between experimental treatments and between the sexes. All trials are included in the analysis.

Source of variation	SSq.	d.f.	MS.	F	Significance
Main effects	8573.3	9	952.6	3.7	<0.001
Treatment	5924.9	8	740.6	2.9	0.004
Sex	2722.5	1	2722.5	10.6	<0.001
Two-way interactions					
Treatment x sex	2713.6	8	339.2	1.3	0.23
Explained	11286.9	17			
Residual	199543.1	773			
Total	210830.1	790			

TABLE 6 Differences in mean prey-time (s) between the experimental treatments and controls.

Presence of	Difference between		Absence of	Difference between	
Vision	NONE-V	0.2	Vision	VAO-AO	3.1
Audition	NONE-A	0.4	Audition	VAO-VO	5.0
Olfaction	NONE-O	0.6	Olfaction	VAO-VA	1.3
Vision + Audition	NONE-VA	6.2	Vision + Audition	VAO-O	6.9
Vision + Olfaction	NONE-VO	2.5	Vision + Olfaction	VAO-A	7.1
Audition + Olfaction	NONE-AO	4.4	Audition + Olfaction	VAO-V	7.3

FIGURE 4. Mean number of empty containers visited before the mouse was located according to experimental treatment. Predator species: Weasel. Conventions as in Fig. 2.

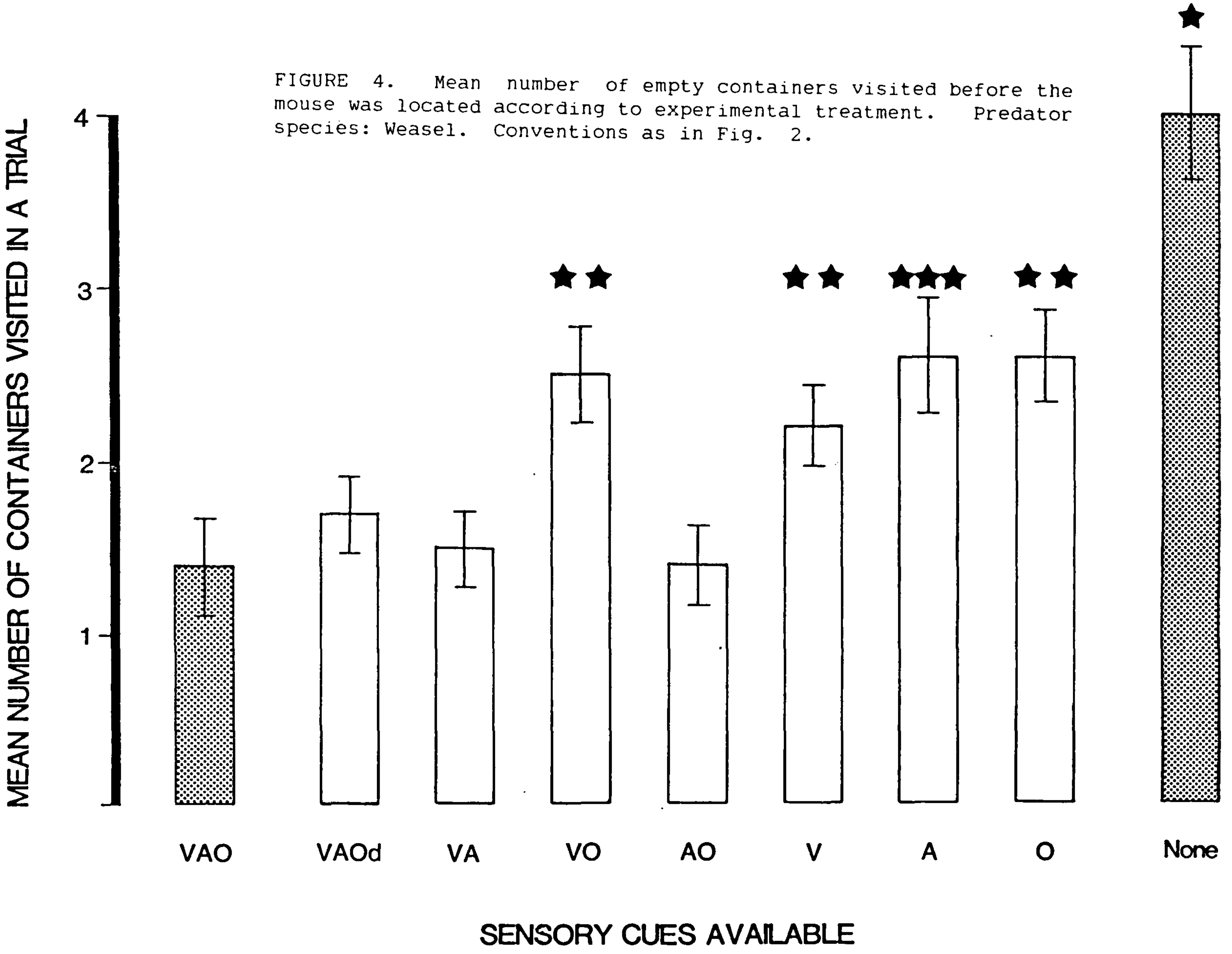


TABLE 7 Two-way analysis of variance of total number of containers visited: Weasels.

Analysis of variance of total number of empty containers visited in a trial between experimental treatments and individual subjects.

Source of variation	SSq.	d.f.	MS.	F	Significance
Main effects	582.4	13	44.8	6.8	<0.001
Treatment	427.2	8	53.4	8.1	<0.001
Subject	161.3	5	32.3	4.9	<0.001
Two-way interactions					
Treatment x subject	190.2	40	4.8	0.7	0.9
Explained	772.5	53			
Residual	4881.5	738			
Total	5654.0	791			

TABLE 8 Differences in mean number of containers visited between the experimental treatments and controls.

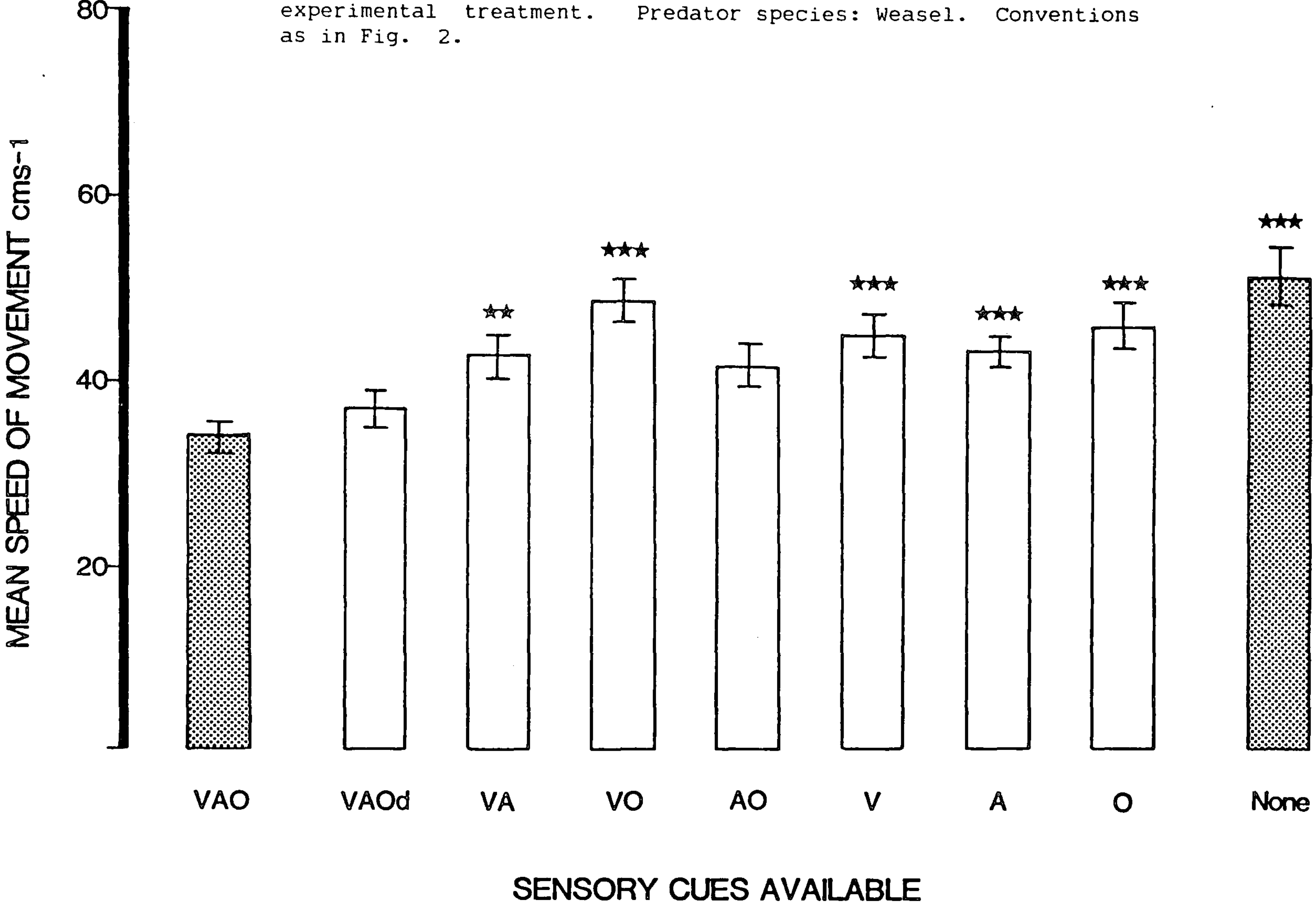
Presence of	Difference between		Absence of	Difference between	
Vision	NONE-V	1.8	Vision	VAO-AO	0.3
Audition	NONE-A	1.4	Audition	VAO-VO	1.1
Olfaction	NONE-O	1.4	Olfaction	VAO-VA	0.1
Vision + Audition	NONE-VA	2.6	Vision + Audition	VAO-O	1.2
Vision + Olfaction	NONE-VO	1.4	Vision + Olfaction	VAO-A	1.2
Audition + Olfaction	NONE-AO	2.3	Audition + Olfaction	VAO-V	0.8

visits when auditory cues were removed. When stimuli were available to only one sense, fewer visits were made when visual cues were available.

Mean Speed of Movement During a Trial

The mean speed of movement was calculated from total distance travelled during a trial (cm) divided by total trial length in seconds. Therefore, periods when the animals were not moving were included in the calculation, so this value is not a measure of the actual velocity of the moving animal. A measure of how long the animal remained stationary in a trial is given by pause duration, which is discussed below. The mean speed for each experimental treatment is shown in Fig. 5 and Table 9 shows the results of a two-way analysis of variance. Although speed varied according to experimental treatment, individual variation also occurred. Speed of movement was slow during VAO, VAOd and AO, when in fact search-time was short and was significantly higher than the baseline results in the other treatments (see Fig. 5). The sexes differed in mean speed and individual variation was also considerable, although differences were not always consistent (Table 9). Male weasels on average moved $10cms^{-1}$ faster than females (Male mean = $49.3cms^{-1} \pm 1.3$ (S.E.), Female mean = $39.2cms^{-1} \pm 0.9$). The sex difference in speed was related to the difference in size between the sexes; male weasels are on average 4cm longer than females. Conversion of these speeds to body-lengths/ second gave mean speeds of approximately 1.9

FIGURE 5. Mean speed of movement during a trial according to experimental treatment. Predator species: Weasel. Conventions as in Fig. 2.



and 1.8 body-lengths/ second, for male and female weasels respectively. Table 10 shows that there was a trend for a reduction in mean speed when auditory cues were present.

To investigate the variation in speed of movement that occurred during a trial, each trial was divided into four sections: Search, orientation/approach, find and after find. The search phase was defined as the period from when the animal was released until it detected the presence of the mouse, at which point the orientation/approach phase began. The weasel was judged to have orientated to the prey animal at the point where it changed direction to that of a direct approach to the mouse. Orientation was identified by a brief pause, often associated with an attention response (see p. 67 for a definition of this behaviour). The speed of the animal was recorded from the point of orientation until it arrived at the prey container. The speed of the weasel as it investigated the container was recorded separately (find phase). The final part of the trial was from when the weasel left the prey animal until it returned to the carrying box.

The mean speeds for all treatments for the different phases are shown in Fig. 6. Mean speed was fastest during the approach to the prey animal, and after the weasels had left the mouse, with males and females showing a similar trend. The speeds given in Fig. 6 are mean values and do not reflect the high running speeds recorded for short periods of time, e.g. up to 200cms^{-1}. The slowest speeds recorded were during the Find phase, whereby a long prey-time resulted in the lowering of the mean speed for a trial.

TABLE 9 Two-way analysis of variance of mean speed of movement: Weasels.

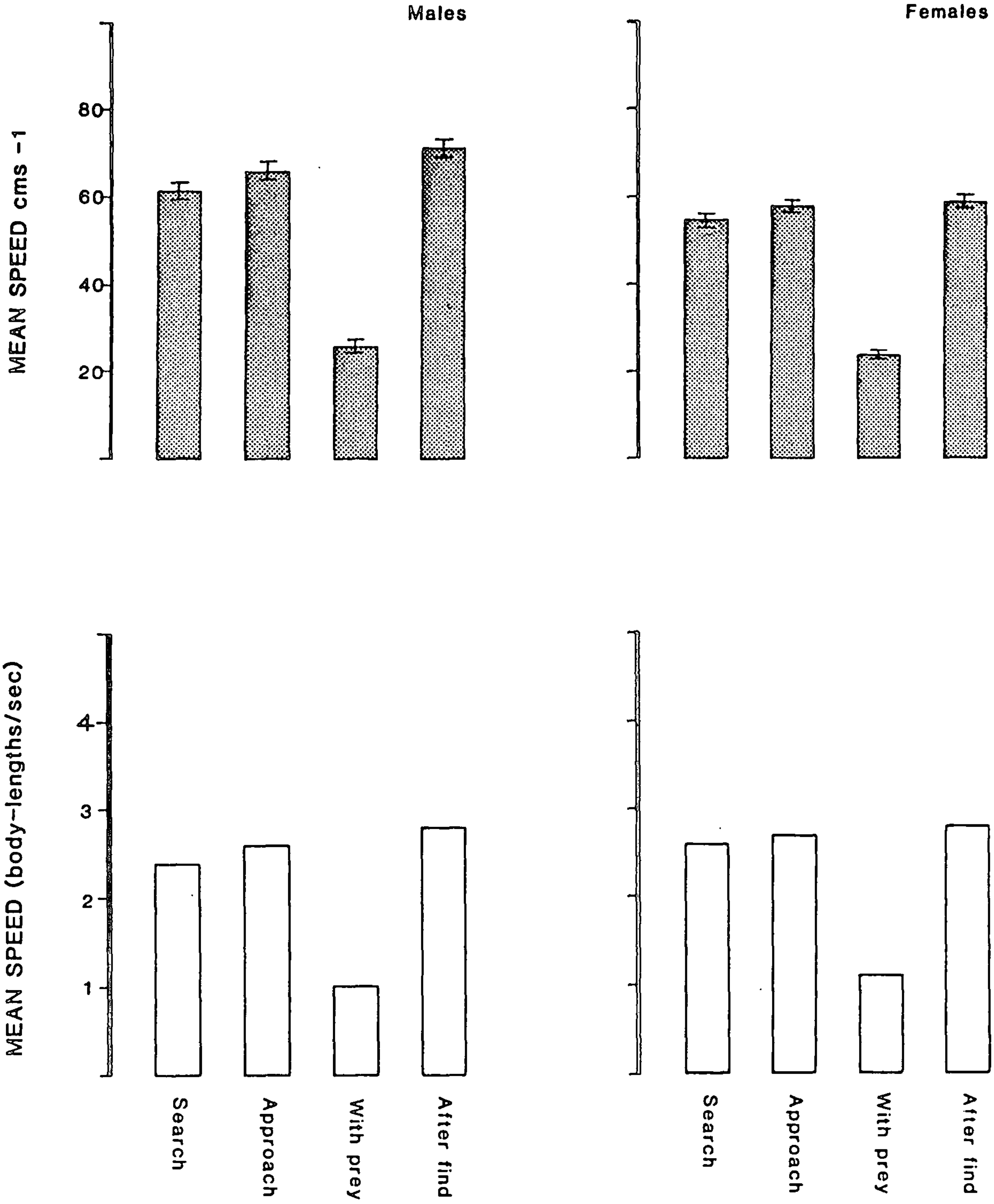
Analysis of variance between experimental treatments and the sexes.

Source of variation	SSq.	d.f.	MS.	F	Significance
Main effects	39619.4	9	4402.2	11.3	<0.001
Treatment	20806.9	8	2600.9	6.7	<0.001
Sex	18536.0	1	18536.0	47.5	<0.001
Two-way effects					
Treatment x sex	7361.7	8	920.2	2.4	0.02
Explained	46981.2	17			
Residual	305165.0	782			
Total	352146.2	799			

TABLE 10 Differences in mean speed of movement (cms^{-1}) between the experimental treatments and controls.

Presence of	Difference between		Absence of	Difference between	
Vision	NONE-V	6.2	Vision	VAO-AO	4.3
Audition	NONE-A	8.1	Audition	VAO-VO	14.5
Olfaction	NONE-O	5.4	Olfaction	VAO-VA	8.7
Vision + Audition	NONE-VA	8.6	Vision + Audition	VAO-O	11.9
Vision + Olfaction	NONE-VO	2.8	Vision + Olfaction	VAO-A	9.2
Audition + Olfaction	NONE-AO	13.0	Audition + Olfaction	VAO-V	11.1

FIGURE 6. Mean speeds of movement overall (all treatments are included) for different phases of the trial. Predator species: Weasel. Standard error bars are indicated.



Mean Speed During Search Phase

The mean searching speeds of the weasels are shown in Fig. 7, and the results of a two-way analysis of variance are presented in Table 11. The weasels moved faster in the two senses (VA, VO, AO) and "no senses" experiments than in the baseline VAO condition. There was a negative correlation between the number of containers visited and search speed ($r=-0.22$, $n=774$, $p<0.01$), with speed being higher when fewer containers were visited. However, the correlation is weak and this may have been partly due to the results for the three senses treatments, where speed of movement was slow, even though few containers were visited. In the "no senses" experiments, the weasels moved quickly but took longer to find the mouse, an indication of the difficulty of the task under these conditions.

A greater variation was found between individuals than between treatments (Table 11). There was a trend for the mean speed of males to be greater than that of females, but this trend was not always noted. Individual variation was also considerable, within the sexes.

Mean Approach Speed

Mean approach speed did not vary significantly according to treatment (Table 12), although individuals varied in their speed. A sex-related difference (Male mean = $66 cms^{-1} \pm 1.8$, Female mean = $58 cms^{-1} \pm 1.5$) was apparent. Two types of

FIGURE 7. Mean speed of movement during the search phase according to experimental treatment. Predator species: Weasel. Conventions as in Fig. 2.

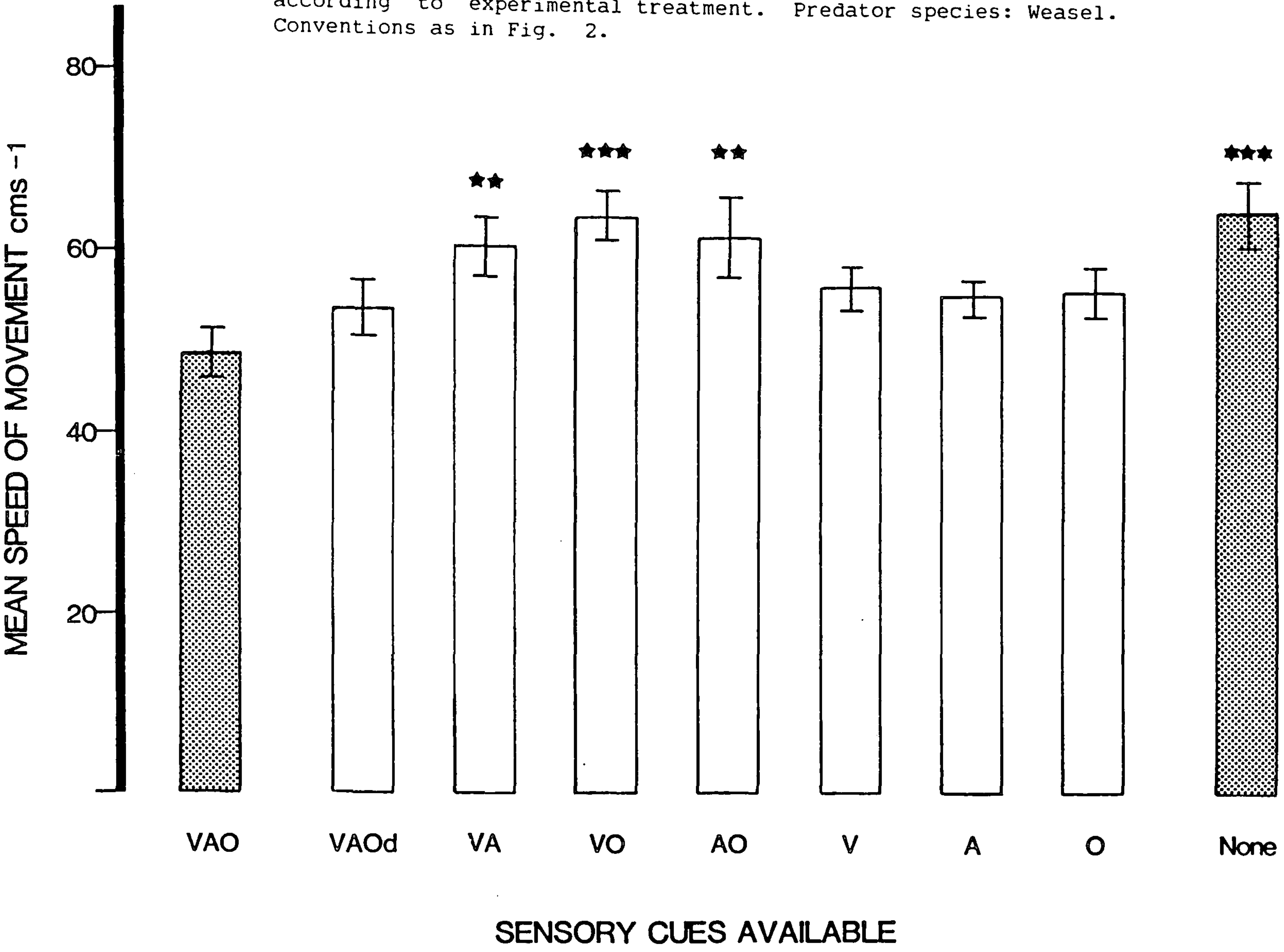


TABLE 11 Two-way analysis of variance of searching-speed: Weasels.

Analysis of variance of mean speed of movement while searching.

Variation between experimental treatments and subjects.

Source of variation	SSq.	d.f.	MS.	F	Significance
Main effects	26489.3	9	2943.3	3.7	<0.001
Treatment	18672.4	8	2334.1	2.9	0.003
Sex of subject	8622.8	1	8622.8	10.8	0.001
Two-way interactions					
Treatment x sex	13309.3	8	1663.7	2.1	0.04
Explained	39798.6	17			
Residual	618588.8	773			
Total	658387.4	790			

TABLE 12 Two-way analysis of variance of mean speed of movement during approach to mouse: Weasels.

Variation between experimental treatments and subjects.

Source of variation	SSq.	d.f.	MS.	F	Significance
Main effects	18855.9	9	2095.1	2.3	0.02
Treatment	8134.1	8	1016.8	1.1	0.4
Sex of Subject	8831.8	1	8831.8	9.5	0.002
Two-way interactions					
Treatment x sex	6735.6	8	842.0	0.9	0.5
Explained	25591.5	17	1505.4		
Residual	651306.2	702	927.8		
Total	676897.7	719	941.4		

approach were recognised: occasionally a "slow stalk" occurred when the animal walked on "tip-toe", at a speed less than 40cms^{-1}; more often, the approach to the mouse was indistinguishable from normal movement. A high incidence of slow approaches occurred in the three senses treatments, e.g. 40.9% of VAOd approaches were of this type, compared to approximately 20% in the one sense treatments.

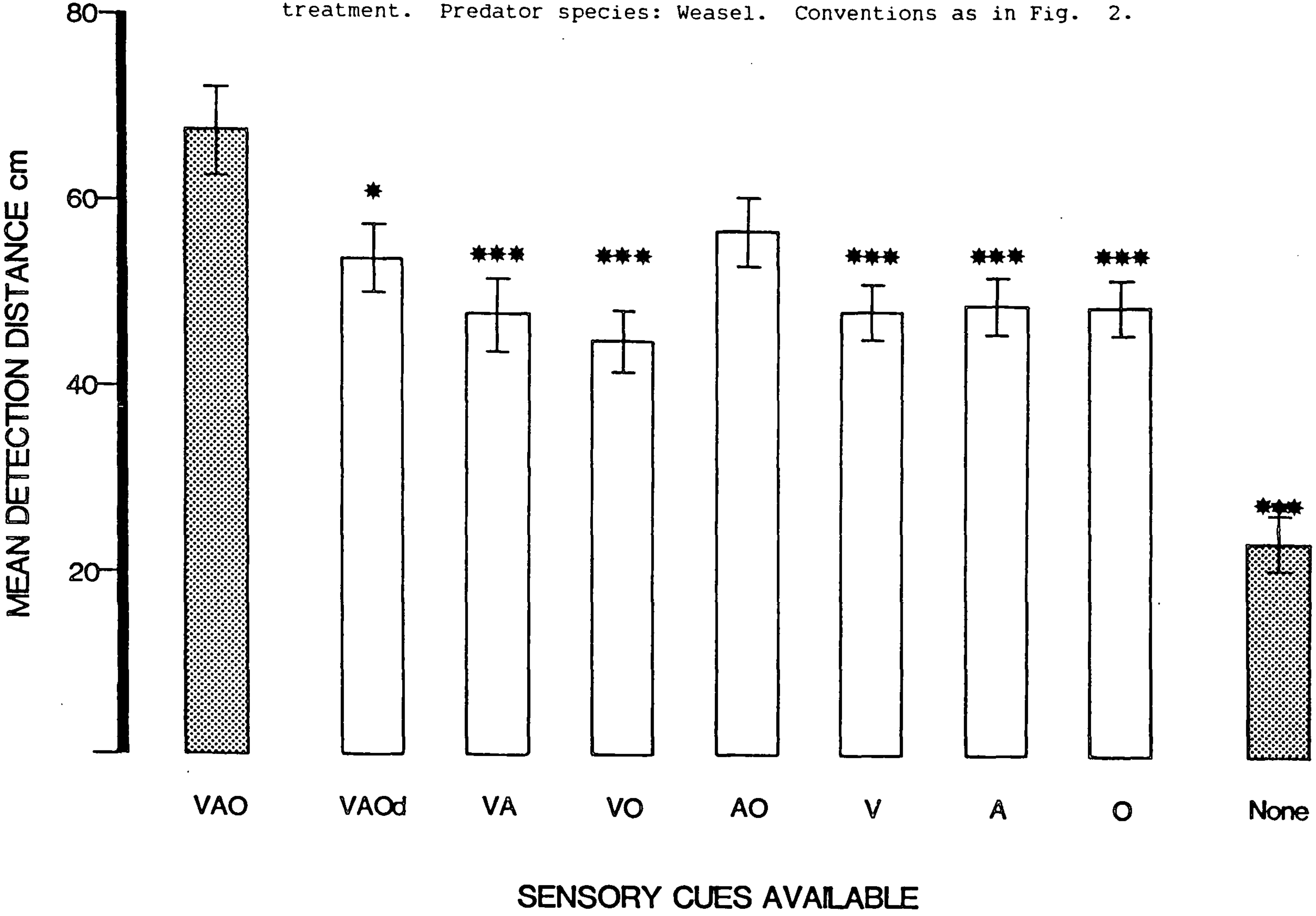
Detection Distance

This was determined as the distance between the point at which the weasel orientated to the mouse and the container holding the mouse. The mean detection distances for the various experimental treatments are shown in Fig. 8. Detection distance varied with treatment and between individuals (Table 13). The longest mean detection distances were in VAO and AO conditions, the former was significantly greater than all other treatments except AO.

The mouse was detected at the closest distance from the container under the "no senses" condition ('t' test). Male weasels detected the mouse at a greater distance than females with a mean of 54.7cm ± 2.1 (S.E.) compared to 45.9cm ± 1.5 (S.E.), although this sex-related difference was not consistent for all experimental treatments.

Table 14 shows the percentage frequency of occurrence of orientation to the mouse. Orientation was not recorded in every trial and only those instances where orientation was

FIGURE 8. Mean detection distance according to experimental treatment. Predator species: Weasel. Conventions as in Fig. 2.



obvious to the observer are included in the analyses. Orientation movements were recorded in 90% of trials during most experimental treatments, exceptions were VA and "no senses". The low frequency recorded for "no senses" reflects the difficulty the weasels had in locating the mouse under these conditions.

Table 15 shows the effect of the presence or absence of sensory modalities on detection distance. There was a trend for detection distance to be longest whenever auditory cues were available, with the removal of visual cues having the least effect on this variable.

Pauses

A pause was recorded when the x,y coordinates of the animal's position did not change between successive digitised samples of the searchpath. The number of pauses and the total pause duration were recorded for each trial. The rate of pausing (frequency per second) was then calculated from the number of pauses/ length of trial in seconds. Pause-rate differed according to treatment (Table 16), but individual results were more variable (Table 17). Weasels paused more often in VA and audition only trials than in the VAO control.

Male weasels tended to pause more often than females (Male mean pause-rate = 0.18 ± 0.009 pauses per second, Female mean = 0.12 ± 0.005 pauses per second). Variation between the sexes only accounted for a small amount of the total variance; differences between individual subjects must also have been

TABLE 13 Two-way analysis of variance of detection distance: Weasels. Variation between experimental treatments and subjects.

Source of variation	SSq.	d.f.	MS.	F	Significance
Main effects	99371.5	9	11041.3	10.0	<0.001
Treatment	84932.5	8	10616.6	9.6	<0.001
Sex of subject	11784.5	1	11784.5	10.6	0.001
Two-way interactions					
Treatment x sex	22151.6	8	2769.0	2.5	0.01
Explained	12523.1	17			
Residual	863268.1	780			
Total	984791.2	797			

TABLE 14 Percentage frequency of occurrence of orientation phase.

Treatment	VAO	VAOd	VA	VO	AO	V	A	O	"No senses"
% Trials with orientation	93.1	94.7	81.0	91.7	95.0	95.7	93.6	95.6	69.3

TABLE 15 Differences in mean detection distance (cm) between the experimental treatments and controls.

Presence of	Difference between		Absence of	Difference between	
Vision	NONE-V	24.7	Vision	VAO-AO	10.9
Audition	NONE-A	25.4	Audition	VAO-VO	22.7
Olfaction	NONE-O	25.3	Olfaction	VAO-VA	19.9
Vision + Audition	NONE-VA	24.3	Vision + Audition	VAO-O	18.9
Vision + Olfaction	NONE-VO	21.5	Vision + Olfaction	VAO-A	18.8
Audition + Olfaction	NONE-AO	33.3	Audition + Olfaction	VAO-V	19.5

TABLE 16 Mean pause-rate (frequency of pauses/second) according to experimental treatment: Weasels.

Treatment	VAO	VAOd	VA	VO	AO	V	A	O	"No senses"
Mean pause-rate	0.13	0.13	0.18	0.15	0.11	0.14	0.17	0.16	0.12
Treatments different from VAO control			*				*		

TABLE 17 Two-way analysis of variance of pause-rate.

Analysis of variance of frequency of pauses/second, between experimental treatments and individual subjects.

Source of variation	SSq.	d.f.	MS.	F	Significance
Main effects	2.5	13	0.2	13.5	<0.001
Treatment	0.3	8	0.03	2.3	0.02
Subject	2.1	5	0.4	29.2	<0.001
Two-way interactions					
Treatment x subject	1.9	40	0.05	3.3	<0.001
Explained	4.4	53			
Residual	10.6	746			
Total	14.9	799			

important.

Several different categories of behaviour could have been registered as a pause including the following variables which showed a significant correlation with pause duration during a trial; time spent investigating containers ($r=0.64$, $n=783$, $p < 0.001$), duration of sniffing the floor whilst stationary ($r=0.61$, $n=246$, $p<0.001$) and the time spent around the release-point ($r=0.34$, $n=783$, $p<0.001$). The time spent near the release-point may have occasionally registered as a pause when the animals stood on or around the carrying box whilst surveying the arena.

Attention Responses

Two classes of attention responses were distinguished:

a) Peer

This attention response was recorded when the animal stood with all four feet placed in contact with the ground and with the head raised as far as possible above the substrate. This behaviour was usually of a short duration (<1.0s) and was distinguished by a momentary pause in movement. The total duration and number of peers made in each trial were recorded.

The number of peers per second (peering-rate) varied according to treatment and individual, but there was no difference according to the sex of the subject. (Table 18). Significant two-way interactions occurred between treatments and subjects. Variation of peering-rate according to experimental conditions is illustrated in Fig. 9. The rate of peering during the "no senses" control was lower than all treatments except VAO and VA (see Fig. 9). There was considerable individual variation in peering-rate, e.g. Roger had a peering-rate of 0.14 ± 0.06 peers per second compared to 0.07 ± 0.01 peers per second in Brinn and Tiny. Some individuals had a particularly high peering-rate during certain treatments (e.g. Roger, olfaction mean = 0.56 ± 0.4 peers per second). There was no significant correlation between the duration of "peer" attention responses and pauses ($r=0.09$, $n=246$, $p=0.08$), due to the short duration of attention responses.

Peering-rate was highest when olfactory cues were present and lowest when visual cues were available (see Table 19). The high peering-rate in relation to olfactory cues was however, mainly attributable to the abnormally high result of one individual.

b) Rear

In this attention response the whole body was lifted vertically with the weight resting on the hind limbs. The animals often appeared to be actively sniffing the air as well as being visually alert. The weasels often used the wall of the arena or the release-box as a support by leaning onto the surface with one fore-paw.

FIGURE 9. Mean peering-rate (frequency of peers/second) according to experimental treatment. Predator species: Weasel. Conventions as in Fig. 2.

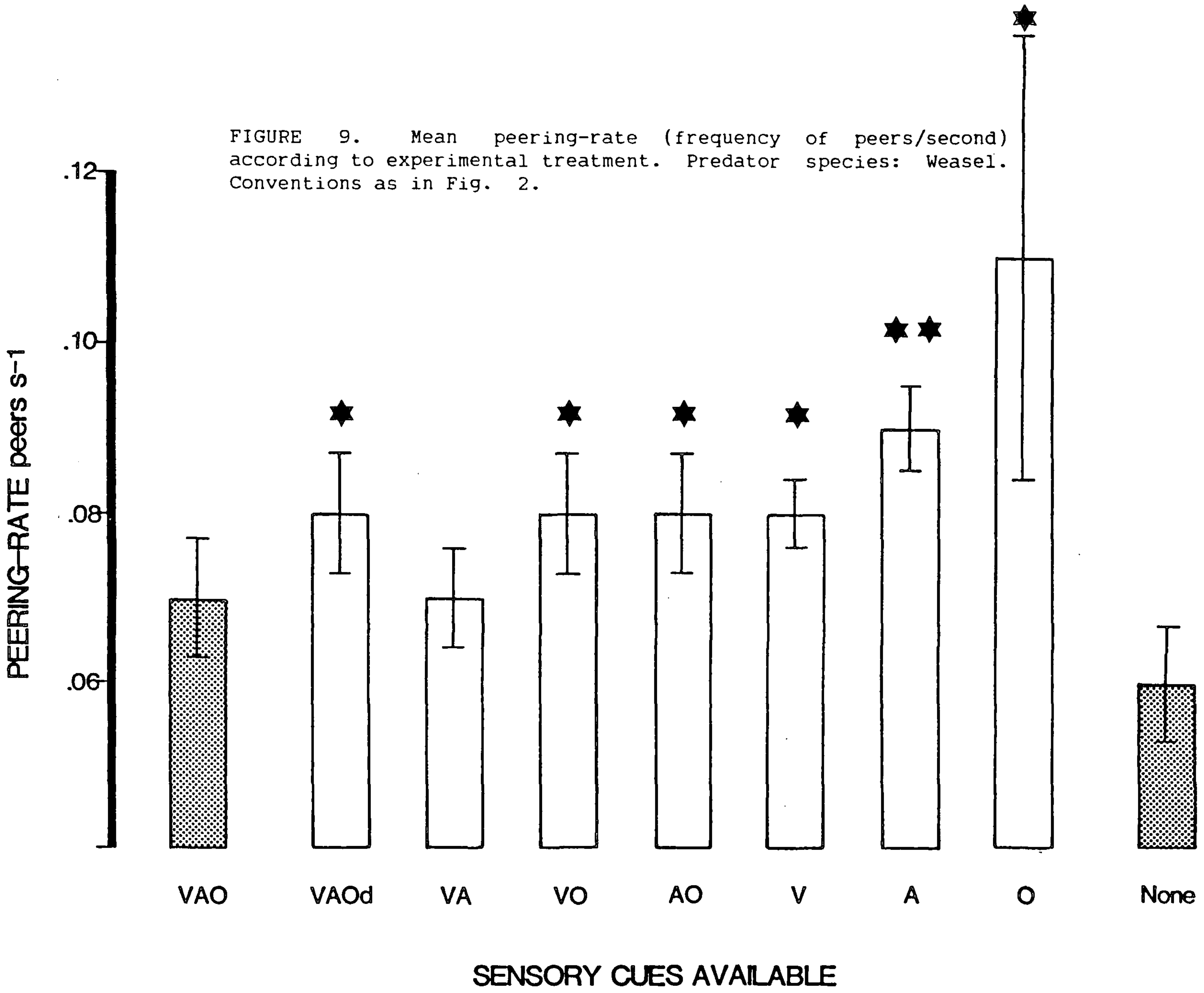


TABLE 18 Two-way analysis of variance of peering-rate: Weasels.

Analysis of variance of frequency of peer attention responses/second, between experimental treatments and individual subjects.

Source of variation	SSq.	d.f.	MS.	F	Significance
Main effects	0.4	13	0.03	3.6	<0.001
Treatment	0.2	8	0.02	2.4	0.02
Subject	0.2	5	0.05	5.7	<0.001
Two-way interactions					
Treatment x subject	1.3	40	0.03	3.9	<0.001
Explained	1.7	53			
Residual	6.0	729			
Total	7.7	782			

TABLE 19 Differences in peering-rate (peers/second) between the experimental treatments and controls.

Presence of	Difference between		Absence of	Difference between	
Vision	NONE-V	0.02	Vision	VAO-AO	-0.01
Audition	NONE-A	0.03	Audition	VAO-VO	-0.01
Olfaction	NONE-O	0.05	Olfaction	VAO-VA	0.0
Vision + Audition	NONE-VA	0.01	Vision + Audition	VAO-O	-0.04
Vision + Olfaction	NONE-VO	0.02	Vision + Olfaction	VAO-A	-0.02
Audition + Olfaction	NONE-AO	0.02	Audition + Olfaction	VAO-V	-0.01

Results of a two-way analysis of variance of rearing-rate (frequency per second) are given in Table 20. The rate of rearing varied according to treatment and subject (Table 21). Rearing-rate was highest in the "no senses" experiments and was also significantly higher than the baseline condition in VA and vision only trials. Individual differences could be partly attributed to a sex-related difference, with males rearing more often than females. Subjects occasionally showed high rates of rearing in certain treatments, e.g. Tulip had a high frequency of this behaviour in VA experiments. Again, there was not a significant correlation between duration of attention responses and pauses (r=0.007, n=246, p=0.5) in a trial.

Turns

Turns were recorded from the searchpath plots. A turn occurred when the path followed by the animal deviated more than 10^{o} from the on-going direction. A turn was only noted if an abrupt change in direction occurred; if the searchpath followed a curve, it was not counted as a turn. Turning-rate did not vary according to treatment, but did vary according to the individual, with males turning more often than females (Table 22). Males turned more often in proportion to their speed of movement, than females.

The number of turns made while each subject searched for the mouse was recorded separately and the mean results for turning-rate according to treatment are shown in Fig. 10.

TABLE 20 Two-way analysis of variance of rearing-rate: Weasels

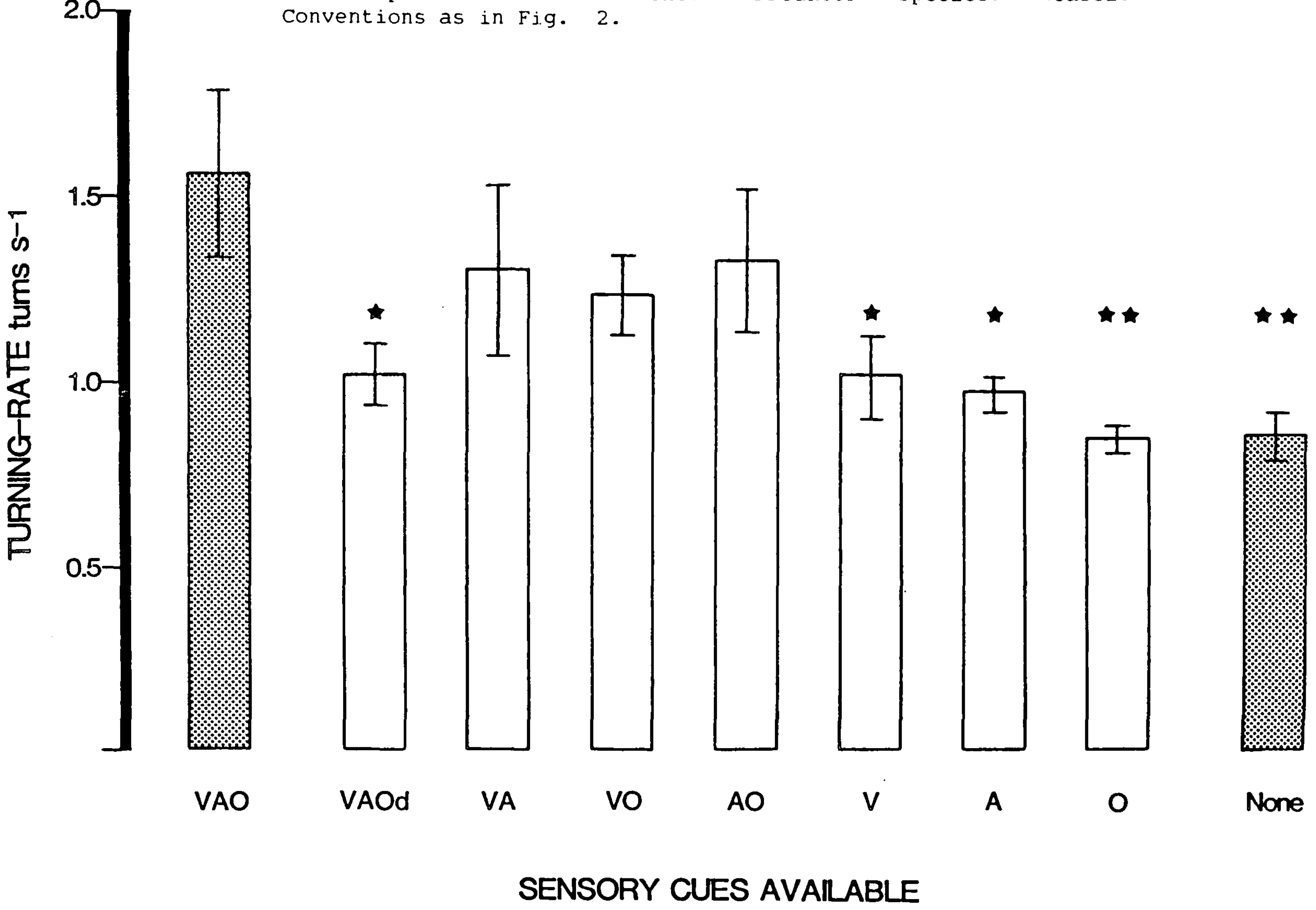
Analysis of variance of frequency of rear attention responses/second, between experimental treatments and individual subjects.

Source of variation	SSq.	d.f.	MS.	F	Significance
Main effects	0.04	13	0.003	8.4	<0.001
Treatment	0.10	8	0.001	3.1	0.002
Subject	0.03	5	0.007	16.6	<0.001
Two-way interactions					
Treatment x subject	0.06	40	0.001	3.6	<0.001
Explained	0.10	53			
Residual	0.29	729			
Total	0.39	782			

TABLE 21 Rearing-rate (rears/second) according to experimental treatment.

Treatment	VAO	VAOd	VA	VO	AO	V	A	O	"No senses"
Rearing-rate	0.002	0.004	0.008	0.003	0.005	0.008	0.005	0.008	0.02
Treatments different from VAO control			*			*			**

FIGURE 10. Mean turning-rate during the search phase according to experimental treatment. Predator species: Weasel. Conventions as in Fig. 2.



The results of a two-way analysis of variance are given in Table 23. Turning-rate was significantly lower in the single sense and "no senses" treatments than in the VAO control experiment. Individual variation was significant, with males turning more often than females. Turning-rate was greatest when visual cues were available, while removal of auditory cues caused the greatest reduction in turning-rate from the base-line condition (see Table 24). In general, turning-rate while searching was higher than the overall turning-rate for the trial, with the turning-rate for the period after the predator had left the mouse container being particularly low.

Although there was a correlation between turning-rate for the whole trial and mean speed ($r=0.46$, $n=196$, $p<0.001$), there was no relationship between speed and turning-rate while searching ($r=0.02$, $n=193$, $p=0.4$). There was a negative correlation between turning-rate and number of containers visited ($r=-0.37$, $n=38$, $p=0.012$).

Searching Strategies

a) Use of Spatial Memory

It is possible that the weasels were using their spatial memory to locate the container holding the prey animal rather than using sensory cues. If sensory cues were not being used at all, the optimum strategy would be to make one visit to each container until the mouse was found, and not to repeat visits to containers within one trial. The experimental

TABLE 22 Two-way analysis of variance of turning-rate: Weasels.

Analysis of variance of frequency of turns/second, over the whole trial, between experimental subjects and between the sexes.

Source of variation	SSq.	d.f.	MS.	F	Significance
Main effects	13.5	9	1.5	1.6	0.1
Treatment	7.4	8	0.9	1.0	0.5
Sex	5.7	1	5.7	6.1	0.01
Two-way interactions					
Treatment x sex	13.7	8	1.7	1.8	0.07
Explained	27.2	17			
Residual	564.1	601			
Total	591.2	618			

TABLE 23 Two-way analysis of variance of turning-rate during the search phase: Weasels.

Analysis of variance of frequency of turns/second while weasels searched for the mouse, between experimental subjects and the sexes.

Source of variation	SSq.	d.f.	MS.	F	Significance
Main effects	48.5	9	5.4	3.5	<0.001
Treatment	31.9	8	4.0	2.6	0.009
Sex	15.9	1	15.9	10.4	0.001
Two-way interactions					
Treatment x sex	40.9	8	5.1	3.3	0.001
Explained	89.4	17			
Residual	921.6	600			
Total	1010.0	617			

TABLE 24 Differences in turning-rate (turns/second) during the search phase between the experimental treatments and controls.

Presence of	Difference between		Absence of	Difference between	
Vision	NONE-V	0.16	Vision	VAO-AO	0.23
Audition	NONE-A	0.12	Audition	VAO-VO	0.32
Olfaction	NONE-O	-0.01	Olfaction	VAO-VA	0.25
Vision + Audition	NONE-VA	0.45	Vision + Audition	VAO-O	0.71
Vision + Olfaction	NONE-VO	0.38	Vision + Olfaction	VAO-A	0.58
Audition + Olfaction	NONE-AO	0.47	Audition + Olfaction	VAO-V	0.54

paradigm is roughly analagous to radial-arm maze experiments (e.g. Olton and Samuelson, 1976; Walker and Olton, 1979), as an animal's ability to remember places where it has been recently is being measured.

A new choice was recorded as a visit to a previously unvisited container. The results were subdivided according to the total number of containers visited in a trial and the mean number of new choices per trial were plotted as a function of total number of visits (Fig. 11). Complete sets of data were only available for four subjects.

The mean number of new choices made was compared to that expected if the weasels had selected locations randomly. Data for chance performance were obtained from Spetch and Wilkie (1980) (see Fig. 11). The animals performed better than would be expected by chance, but when more than six containers were visited in a trial, the animals' performance approached the chance level. The mean number of new choices made when eight containers was visited in a trial was 6.2 (S.D.± 0.95). There was very little variation in the number of new choices according to the sensory cues available (Table 25). There was a trend for higher scores to be recorded when the number of visits to containers in a trial was low (e.g. in AO trials), as errors increased with the number of visits.

Selection of previously unvisited containers did not always occur, the weasels appeared to have preferences for particular locations to which they often returned in a trial. Table 26 shows the total number of visits made to each container (positions 1-8) by four weasels. A significantly

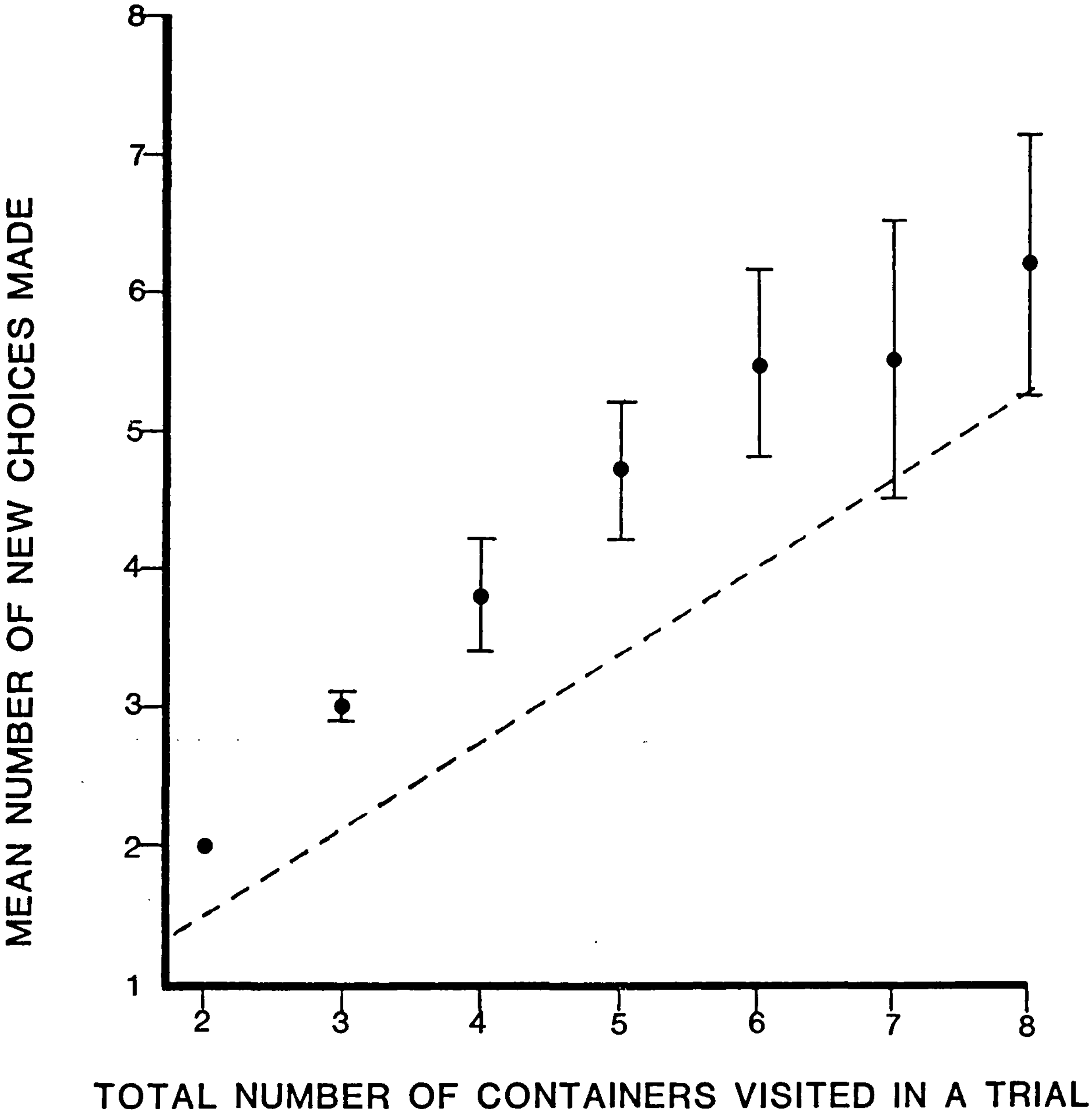


FIGURE 11. Mean number of new choices (visits to previously unvisited locations) as a function of the total number of containers visited in a trial. Predator species: Weasel. Standard deviations are indicated and the broken line represents chance performance.

TABLE 25 Percentage new choices for each experimental treatment. Number of new choices are expressed as a percentage of the total number of containers visited. Trials in which a direct approach to the mouse occurred are not included.

Treatment	VAO	VAOd	VA	VO	AO	V	A	O	"No senses"
%	83.9	88.8	88.4	86.5	91.4	91.0	88.5	89.4	83.2
N visits	112	161	147	193	140	233	226	216	262

TABLE 26 Number of visits to each container location.

a) Total number of visits to each container

Location	1	2	3	4	5	6	7	8	Expected	chi-sq.	p
Brinn	87	62	63	39	39	46	59	60	56.9	30.6	**
Nero	54	41	77	72	54	53	48	72	58.9	20.2	**
Sophie	87	77	70	60	55	62	96	79	73.3	14.7	**
Tiny	84	40	59	67	81	93	90	81	74.4	29.6	**
TOTAL	312	220	269	238	229	254	293	292			

b) Location of first container visited

Location	1	2	3	4	5	6	7	8
Total N visits	143	58	84	53	36	38	67	100
N trials mouse presented at location	73	76	67	79	67	68	79	70

different number of visits were made to particular locations by the individual weasels. Preferences were shown for particular spatial locations both in terms of the total number of visits made and for the first container visited. Preferences were not always consistent between the container first visited and the container most frequently visited.

b) Specific Searching Strategies

Table 27 shows the number of occasions where the first container location investigated was that in which the mouse had been presented in the previous trial. The weasels used this strategy in 11% of total trials. Individual differences in performance were slight, but there was some variation according to treatment.

The weasels may have adopted strategies such as visiting adjacent containers or moving in a constant direction around the arena (e.g. anticlockwise or clockwise). To investigate this, each searchpath plot was broadly classified into one of eight categories. An example of each category is given in Fig. 12.

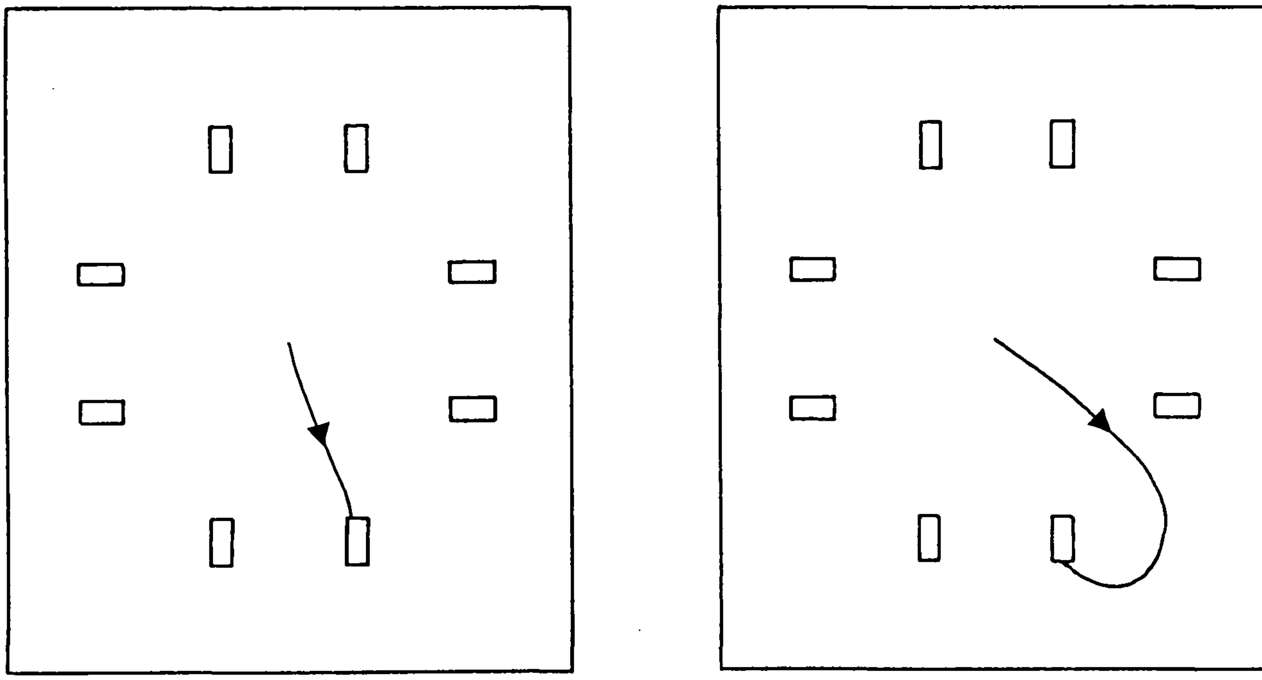
1. Direct Approach. The animal left the release-point and went directly to the container holding the mouse, taking the bee-line distance. No other containers were visited.

2. Circuitous Approach. The predator approached the mouse, without investigating any other containers, as in 1., but the

TABLE 27 Number of trials in which the first container visited was the location of the mouse in the previous trial.

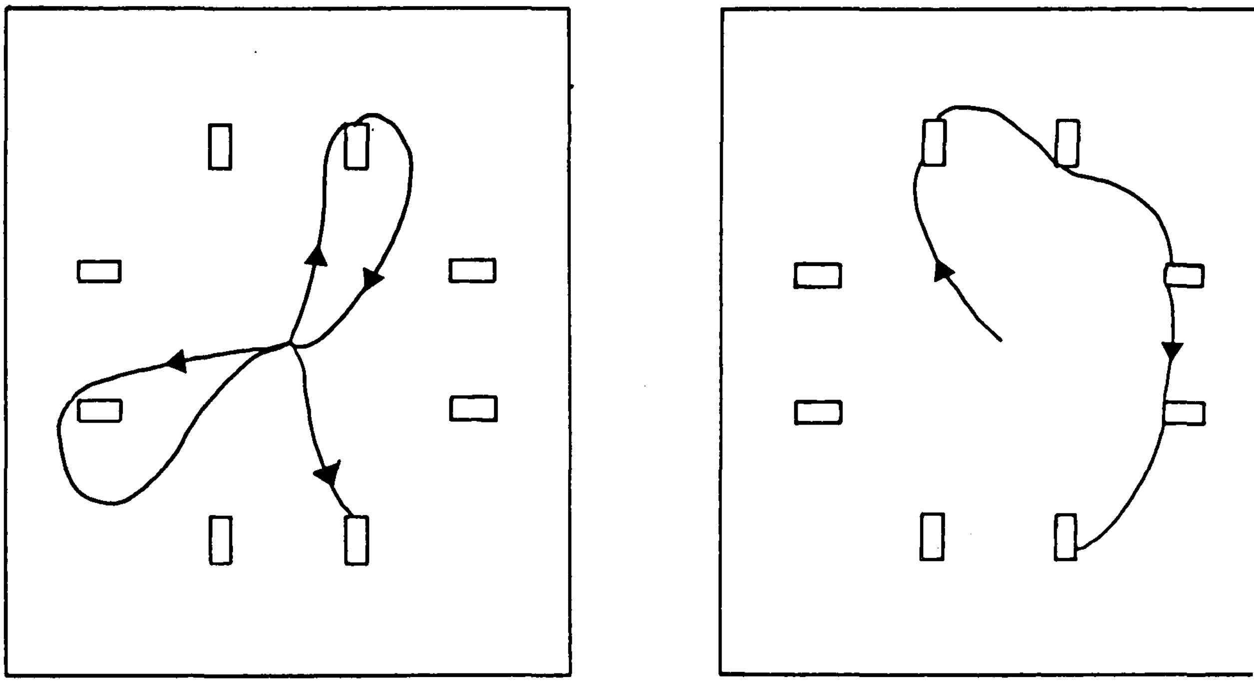
Treatment	N	N trials	Percentage
VAO	67	10	14.9
VAOd	63	11	17.5
VA	70	4	5.7
VO	59	10	16.9
AO	47	1	2.1
V	73	8	11.0
A	69	9	13.0
O	60	2	3.3
"No senses"	52	7	13.5

FIGURE 12. Diagrammatic representations of each search-path category.



Direct Approach

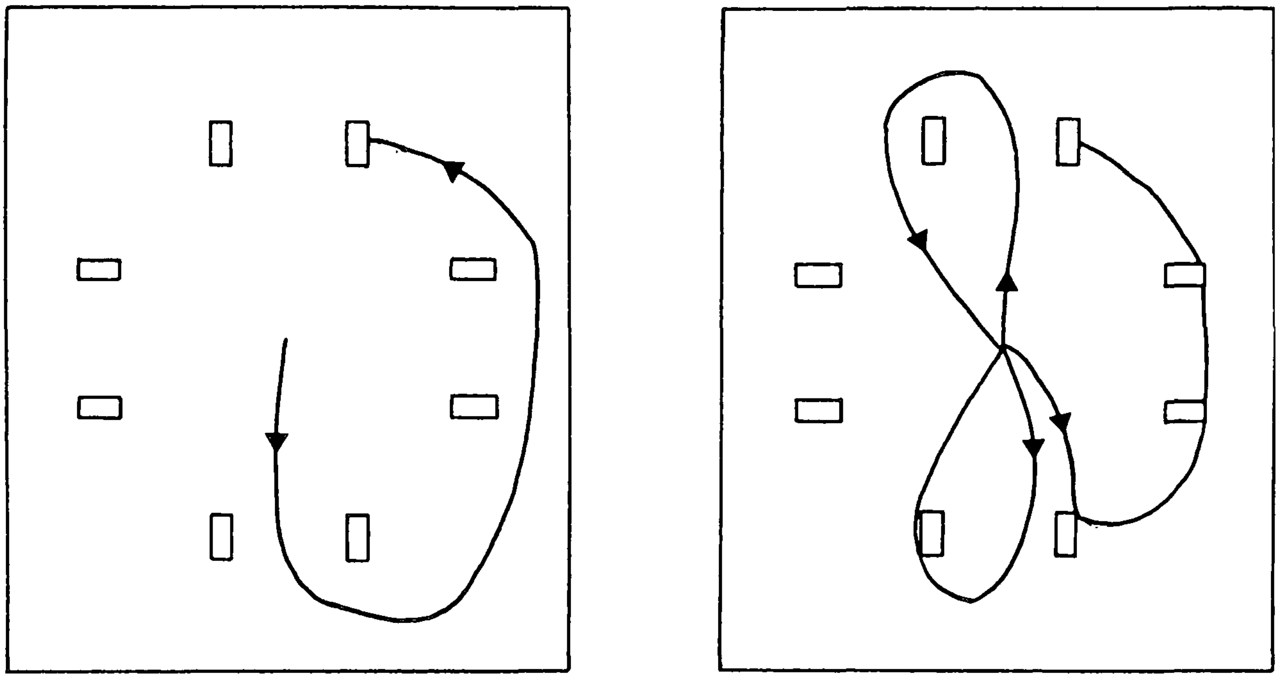
Circuitous Approach



Excursion

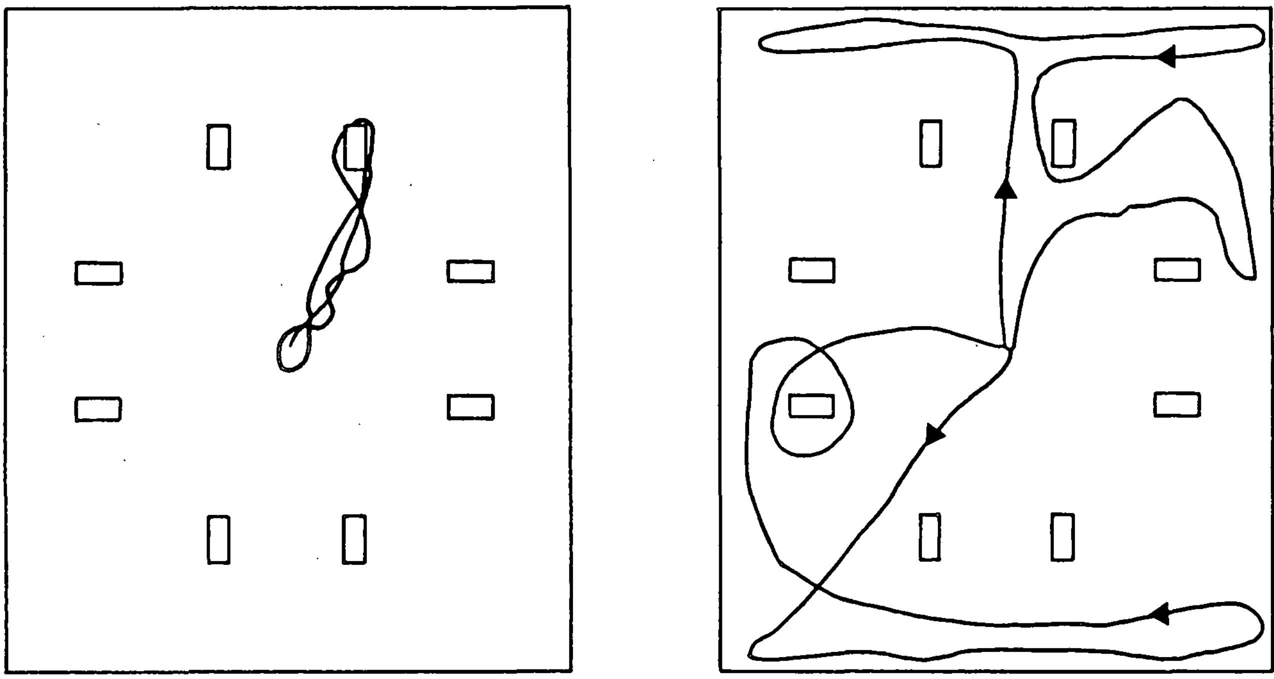
Adjacent Container Search

FIGURE 12 Continued.



Circular Movement

Combination



Area-restricted

"Random"

shortest route was not taken.

3. Excursion. The predator visited one part of the arena and then returned to the central carrying box before moving on to another area. Often one, occasionally more, containers would be visited before the animal returned to the carrying box.

4. Adjacent Container Search. The weasel moved around the arena in a continuous clockwise or anticlockwise direction, visiting each container in turn, occasionally missing a container out.

5. Circular Movement. The weasel moved around the arena in a continuous anticlockwise or clockwise direction, not visiting containers or only occasionally doing so.

6. Combination. More than one of the above categories occurring in a trial.

7. Area-restricted. The animal spent most of the trial in a small part of the arena.

8. "Random". The searchpath did not fit into any of the above categories; no obvious pattern of movement.

Table 28 shows the percentage frequency of the use of each strategy according to experimental treatment. 23.8% of

TABLE 28 Percentage frequency of search-path categories according to experimental treatment.

		Searchpath Category (see Key)							
Treatment	N	A	B	C	D	E	F	G	H
VAO	88	23.8	12.3	8.2	4.4	8.2	6.4	40.0	1.9
VAOd	91	14.3	9.2	10.2	11.0	14.8	9.0	-	13.5
VA	93	16.4	13.8	10.2	5.9	11.5	12.8	-	15.4
VO	83	6.3	12.3	10.2	14.7	9.8	15.4	20.0	7.7
AO	80	15.3	13.8	6.1	12.5	6.6	10.3	-	1.9
V	93	7.4	6.2	12.2	12.5	18.0	20.5	20.0	11.5
A	94	9.5	13.8	12.8	14.7	8.2	9.0	-	19.2
O	85	4.8	15.4	11.2	14.0	16.4	9.0	-	15.4
"No senses"	75	2.1	3.1	18.9	10.3	6.6	7.7	20.0	13.5
N of each category		189	65	196	136	61	78	5	52
%frequency of occurrence		24.2	8.3	25.1	17.4	7.8	10.0	0.6	6.6

Key:

A	Direct Approach	E	Circular Movement
B	Circuitous Approach	F	Combination
C	Excursion	G	Area-Restricted
D	Adjacent Container Search	H	Random

all "direct approaches" observed occurred in the VAO experiments, the fewest (2.1%) occurred in the "no senses" experiments. More direct approaches occurred during the two and three senses treatments than in the one or "no senses" treatments. The treatment resulting in the most "circuitous approaches" was olfaction only, probably a result of the weasels detecting the scent coming from the opening of the container. Strategies such as movement around the containers were few during VAO trials, their frequency increased in the single sense trials.

Table 29 gives the results for individual weasels; some individuals showed a preponderance for a particular type of movement pattern e.g. Sophie and Tiny tended to use the "adjacent container" strategy more often than other subjects. The mean percentage frequency for this strategy in females was 11.2% compared to 4.7% in males. Males and females did not differ in overall frequency of direct approaches (Male = 22.0%, Female = 21.6%), but there was a difference in frequency of excursion searchpaths (Male = 41.7%, Female = 18.9%).

In conclusion, the many variables measured supported the search-time results. Three sensory modalities provided the best information for prey localisation, whilst the "no senses" condition was always the worst. It was not felt necessary to investigate the behaviour of the polecats in such detail, a comparison between species was made only using two variables.

TABLE 29 Percentage frequency of search-path categories for individual weasels.

Search-path	Brinn	Nero	Roger	Sophie	Tiny	Tulip
Direct Approach	24.4	36.2	5.3	20.1	17.3	27.4
Circuitous Approach	5.9	7.1	13.2	8.2	9.4	9.1
Excursion	28.6	33.3	63.2	7.6	25.9	23.1
Container Search	15.1	7.8	5.3	34.0	23.0	10.2
Circular movement	9.2	3.6	5.3	6.3	9.4	10.8
Combination	12.6	8.5	7.9	11.3	11.5	7.5
Area-Restricted	-	-	-	1.9	1.4	-
Random	4.2	3.6	-	10.7	2.2	11.8

4.2.2 Predator Species: Polecat

Search-time

The mean time to find the mouse varied according to the experimental treatment (Fig. 13); when VAOd stimuli were present search-time was significantly lower than the baseline condition (VAO) whereas in the audition only and "no senses" treatments, search-times were significantly higher. Individual performance was also variable (see Table 30). This could not be accounted for by a difference between the sexes. In general, one animal (Morin) tended to find the prey animal faster than the other subjects (Morin mean search-time = 20s compared to 32s for other subjects). Individual variation in performance was not significant during the final five trials (Table 31).

Table 32 shows the effect of the presence or absence of sensory cues on search-time. Search-times were equivalent when visual or olfactory cues were present and slightly greater with auditory cues. The removal of auditory cues had the most detrimental effect on search-time, while the removal of visual cues had the least effect.

Number of Containers Visited

The mean number of containers visited in a trial was significantly different between treatments, but individual performance was consistent (Table 33). The mean number of

FIGURE 13. Mean time taken to locate mouse according to experimental treatment. Predator species: Polecat. Conventions as in Fig. 2.

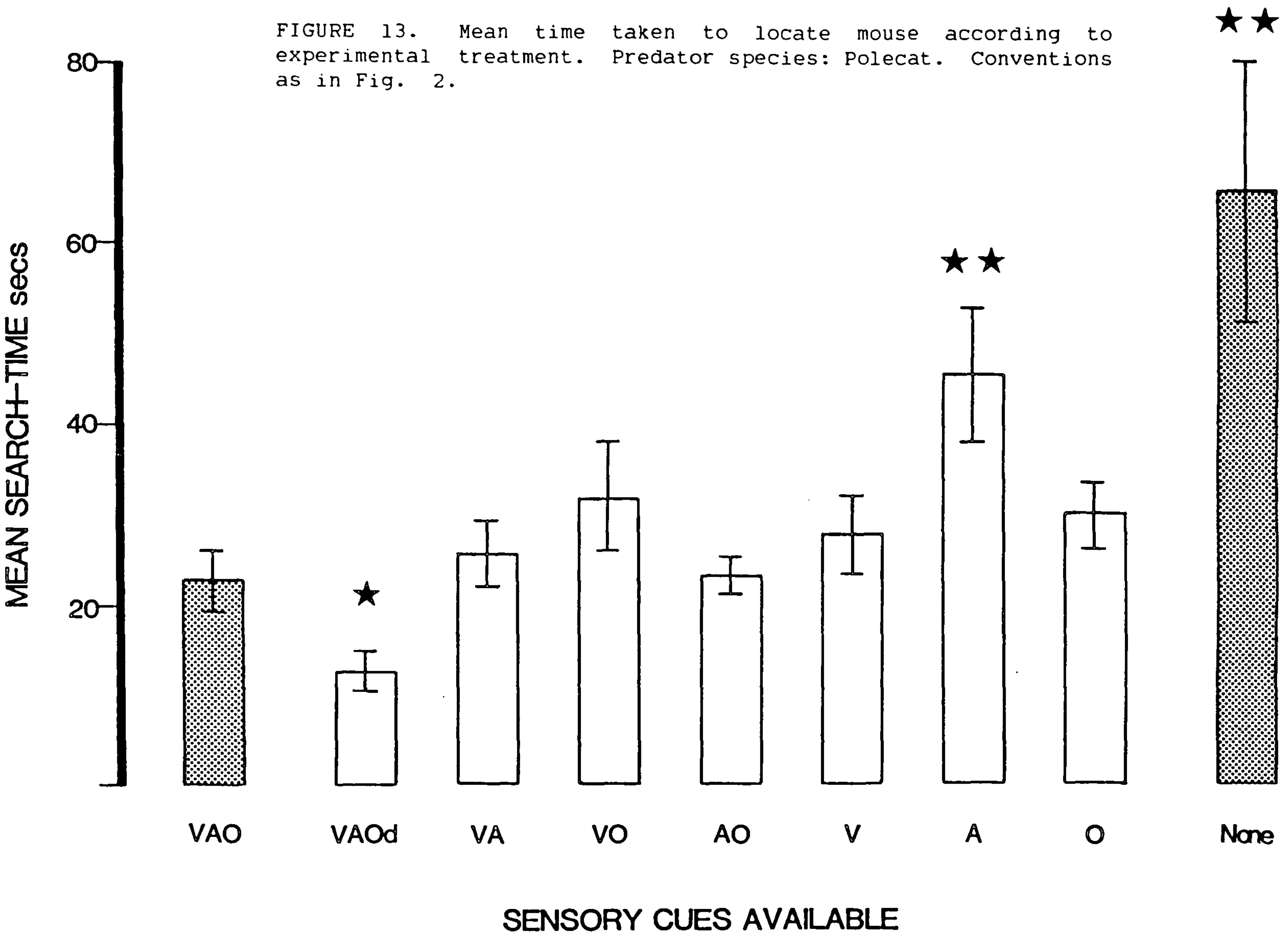


TABLE 30a Two-way analysis of variance of search-time: Polecats.

Analysis of variance of time taken to find the mouse between experimental treatments and between subjects. All trials are included in the analysis.

Source of variation	SSq.	d.f.	MS.	F	Significance
Main effects	63114.0	11	5737.6	5.32	<0.001
Treatment	52948.9	8	6618.6	6.14	<0.001
Subject	10045.1	3	3348.4	3.11	0.03
Two-way interactions					
Treatment x subject	18680.3	24	778.3	0.72	0.83
Explained	81794.3	35			
Residual	390190.9	362			
Total	471985.1	397			

TABLE 30b Two-way analysis of variance of search-time: Polecats.

Analysis of variance of search-time between experimental treatments and between the sexes. All trials are included in the analysis.

Source of variation	SSq.	d.f.	MS.	F	Significance
Main effects	56021.1	9	6224.6	5.79	<0.001
Treatment	52421.7	8	6552.7	6.10	<0.001
Sex	2952.2	1	2952.2	2.75	0.10
Two-way interactions					
Treatment x sex	7519.9	8	940.0	0.88	0.54
Explained	63541.0	17			
Residual	408444.1	380			
Total	471985.1	397			

TABLE 31 Two-way analysis of variance of search-time: Polecats.

Analysis of variance of search-time between experimental treatments and individual subjects. Only the final five trials of each treatment were included in the analysis.

Source of variation	SSq.	d.f.	MS.	F	Significance
Main effects	64955.3	11	5905.0	6.51	<0.001
Treatment	62955.6	8	7869.5	8.68	<0.001
Subject	1999.7	3	666.6	0.74	0.53
Two-way interactions					
Treatment x subject	5893.4	24	245.6	0.27	1.00
Explained	70848.8	35			
Residual	130575.6	144			
Total	201424.3	179			

TABLE 32 Differences in mean search-time (s) between the experimental treatments and controls: Polecats.

Presence of	Difference between		Absence of	Difference between	
Vision	NONE-V	37.8	Vision	VAO-AO	0.6
Audition	NONE-A	20.2	Audition	VAO-VO	9.2
Olfaction	NONE-O	35.7	Olfaction	VAO-VA	3.1
Vision + Audition	NONE-VA	39.9	Vision + Audition	VAO-O	7.3
Vision + Olfaction	NONE-VO	33.8	Vision + Olfaction	VAO-A	22.8
Audition + Olfaction	NONE-AO	42.4	Audition + Olfaction	VAO-V	5.2

containers visited was lower during the VAOd condition than in the VAO control, and more containers were visited during audition only and "no senses" experiments (Fig. 14). Table 34 shows the effect of presence or absence of sensory cues on the number of containers visited in a trial. The number of visits were fewer when vision could be used.

4.2.3 Comparison of Weasel and Polecat Results

The search-times for the two predators were subjected to a two-way analysis of variance which showed that although there was a significant difference between experimental treatments, there was no difference according to species (Table 35). The mean search-time for all experiments was 34.9 seconds for weasels and 29.1 seconds for polecats.

Although the analysis of variance did not reveal any significant differences, the predators did appear to behave differently in some experiments. A 't' test analysis showed there was a trend for the polecats to find the prey animal faster than the weasels during VAOd experiments ('t'=2.5, p=0.015), while weasels were quicker during AO conditions ('t'=2.5, p=0.015).

The two predators differed in the mean number of containers visited in a trial (Table 36). The weasels visited fewer containers than the polecats in AO trials (weasel mean=1.7, polecat mean=2.8; 't'=2.9, p=0.004). During vision only experiments, the polecats visited fewer containers in a trial (weasel mean=2.2, polecat mean=1.4; 't'=2.3, p=0.02).

FIGURE 14. Mean number of empty containers visited before the mouse was located according to treatment. Predator species: Polecat. Conventions as in Fig. 2.

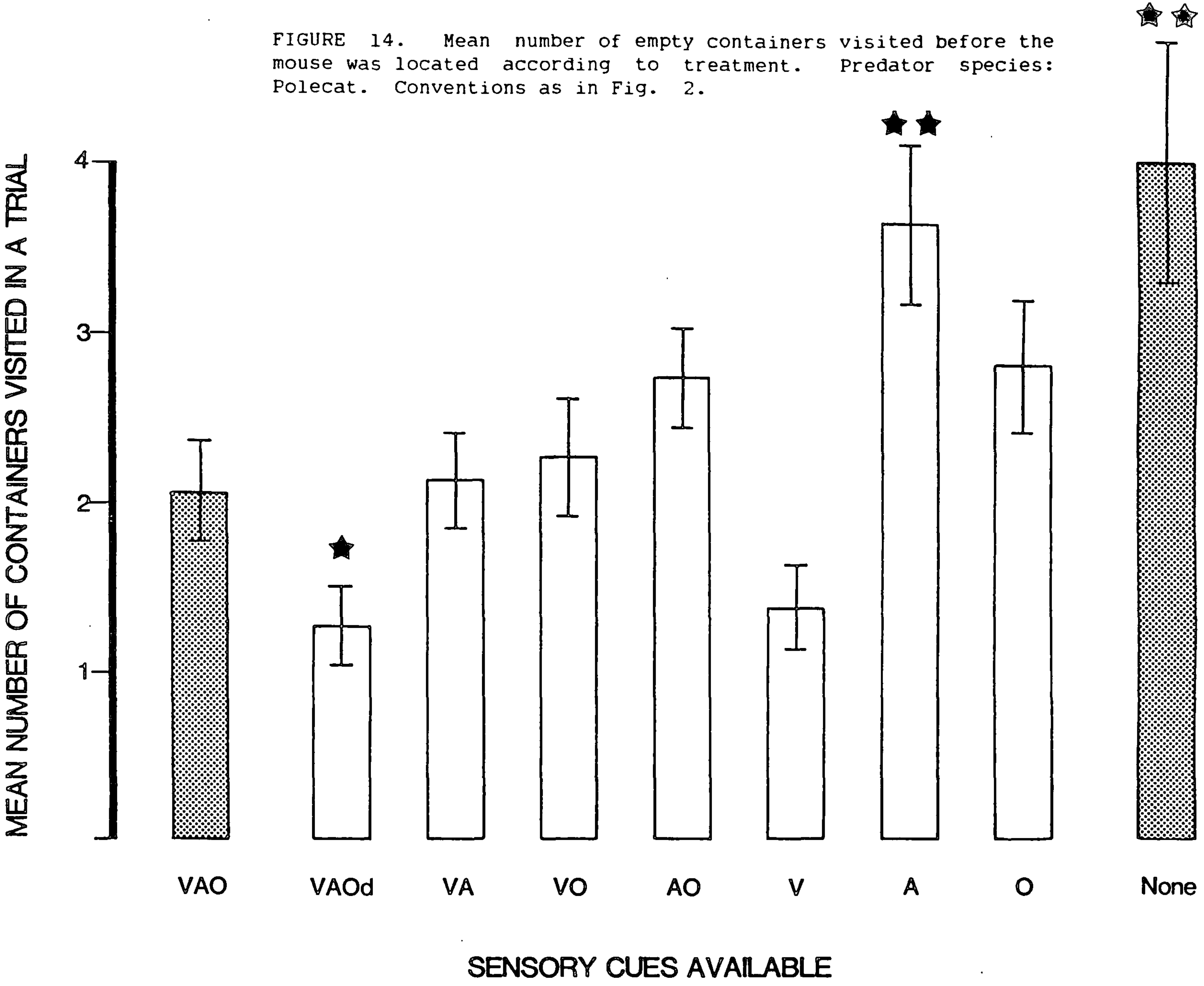


TABLE 33 Two-way analysis of variance of total number of containers visited: Polecats. Analysis of variance of total number of empty containers visited in a trial between experimental treatments and individual subjects.

Source of variation	SSq.	d.f.	MS.	F	Significance
Main effects	226.4	11	20.6	4.10	<0.001
Treatment	215.8	8	27.0	5.38	<0.001
Subject	13.1	3	4.4	0.87	0.457
Two-way interactions					
Treatment x subject	161.2	24	6.7	1.34	0.135
Explained	387.6	35			
Residual	1696.0	338			
Total	2083.6	373			

TABLE 34 Differences in the mean number of containers visited between the experimental treatments and controls: Polecats.

Presence of	Difference between		Absence of	Difference between	
Vision	NONE-V	2.6	Vision	VAO-AO	0.8
Audition	NONE-A	0.3	Audition	VAO-VO	0.3
Olfaction	NONE-O	1.2	Olfaction	VAO-VA	0.1
Vision + Audition	NONE-VA	1.9	Vision + Audition	VAO-O	0.8
Vision + Olfaction	NONE-VO	1.7	Vision + Olfaction	VAO-A	1.7
Audition + Olfaction	NONE-AO	1.2	Audition + Olfaction	VAO-V	0.6

TABLE 35 Two-way analysis of variance of search-time according to species of predator.

Source of variation	SSq.	d.f.	MS.	F	Significance
Main effects	183582.8	9	20398.1	8.84	<0.001
Treatment	174336.7	8	21792.1	9.44	<0.001
Predator species	3008.5	1	3008.5	1.30	0.25
Two-way interactions					
Treatment x species	9065.8	8	1200.7	0.52	0.84
Explained	193189.0	17			
Residual	2973187.0	1289			
Total	3166376.0	1306			

Analysis of variance between experimental treatments and between weasels and polecats.

TABLE 36 Two-way analysis of variance of number of empty containers visited according to species of predator.

Source of variation	SSq.	d.f.	MS.	F	Significance
Main effects	541.9	9	60.2	9.7	<0.001
Treatment	533.8	8	66.7	10.8	<0.001
Predator Species	24.5	1	24.5	4.0	0.05
Two-way interactions					
Treatment x Species	100.5	8	12.6	2.0	0.04
Explained	642.4	17			
Residual	7102.6	1148			
Total	7745.0	1165			

4.3 RESULTS OF EXPERIMENT VI

This experiment investigated the importance of substrate scent cues during prey location. A scent trail was available in addition to the following sensory cues: Three senses (VAO), olfaction only and with the "no senses" control. Only five trials of each treatment were conducted.

The search-time results are presented in Table 37. There were no significant differences in the times taken to find the mouse between the scent trail treatments (paired 't' tests) and there was no difference between the two species. The search-times for Experiment VI were equivalent to that for VAO (paired 't' test).

The search-times for the scent trail treatments were compared to those of five trials of the corresponding treatments from experiments I to V, i.e. VAO, olfaction and "no senses". The results of a series of paired 't' tests are given in Table 38. Although search-times for VAO and VAO + scent were equivalent, the search-times for olfaction + scent and "no senses" + scent were significantly shorter than those for olfaction and "no senses" respectively.

The use of the scent trail was only recorded when the animal precisely followed the trail with its nose to the ground. The trail was usually followed from the release-point to the container holding the mouse, but if the trail was not followed for its entire length it was recorded as being part followed. Table 37 shows the incidence of scent trail use; the scent trail was seen to be followed in 60% of trials.

TABLE 37 Mean search-times for substrate-scent experiments.

WEASELS	VAO +scent	OLFACTION +scent	"NO SENSES" +scent
Mean search-time (s)	13.9	9.9	9.5
%Use of scent trail	50.0	60.0	70.0
POLECATS			
Mean search-time (s)	10.7	13.4	15.9
%Use of scent trail	70.0	60.0	50.0

TABLE 38 Results of paired 't' tests between the search-times of the substrate-scent trials and those of 10 trials of the corresponding treatment without a scent trail.

	Polecat		Weasel	
Treatment Comparison	t	p	t	p
VAO v VAO+scent	1.1	N.S	0.6	N.S
OLFACTION v OLFACTION+scent	3.0	*	3.5	**
"NO SENSES" v "NO SENSES"+scent	2.2	N.S	4.5	**

There was no difference between subjects, species or treatments for the number of occasions in which the scent trail was followed.

The two species did differ in their behaviour towards the scent trail. The polecats often followed the scent trail for part of its length, sniffing the substrate at intervals. The weasels tended to sniff the trail intently, often whilst stationary, and occasionally the trail was part followed before the weasel back-tracked and followed the trail in the other direction.

There was a trend for the time spent with the prey to be longer in the substrate scent experiments than in the main experiments. Overall speed of movement was slower when a scent trail was present, e.g. polecat approach speed was slower in VAO + scent than in VAO (paired 't' test $t = 2.6$, $p=0.03$). There was also a trend for fewer attention responses to be made during substrate scent experiments than during the corresponding treatments without a scent trail (see Table 39). Fewer containers were visited during substrate scent experiments, since following the scent trail usually involved a direct approach to the mouse (see Table 40).

Searchpath Description

Table 40 shows the incidence of different searchpath types recorded during the substrate scent experiments. Area restricted searchpaths occurred more frequently than during experiments I-V. In these trials, a considerable amount cf

TABLE 39 Frequency of attention responses in 10 trials. A comparison between substrate-scent trials and the corresponding treatments without a scent trail.

POLECAT					WEASEL				
Treatment	N "peers"		N "peers"	chi sq.	Treatment	N "peers"		N "peers"	chi sq.
VAO	14	+scent	7	N.S	VAO	24	+scent	5	***
OLFACTION	13		11	N.S	OLFACTION	57		24	***
"NO SENSES"	15		15	N.S	"NO SENSES"	22		11	*

TABLE 40 Search-path descriptions for substrate-scent trials.

	WEASELS	POLECATS
Search-path	N	N
Direct Approach	6	11
Area-Restricted	9	-
Excursion	2	3
Circular Movement	2	8
Circuitous Approach	4	2
Excursion + Scent Trail	7	3
Combination	-	3

time was spent moving along the scent trail in both directions. This type of searchpath commonly occurred in the weasels, but was never shown by the polecats.

The incidence of direct approaches to the mouse, which involved following the scent trail, was also considerably higher, 43% of the weasel searchpaths were of this type. This figure includes direct approaches of the standard type but also searchpaths where the subject moved over a small part of the arena before the scent trail was located (excursion + scent trail).

4.4 DISCUSSION

Until the present study, there has been no complete experimental investigation of the underlying sensory basis of the predatory behaviour of mustelids. Information is available from observations of predator-prey interactions and from some preliminary experiments with prey models. As conclusions on the the role of the senses has usually been speculative, it is perhaps not surprising that authors are not in agreement.

It is apparent from the results that both the weasels and polecats found the task of finding the mouse of varying difficulty according to the type of sensory information available. As most of the results were obtained from the weasels, much of the discussion will be concerned with this species, with a short discussion of the comparative results. Discussion of olfactory stimuli will be concerned with air-borne olfactory cues and any discussion of substrate scent cues involves mention of this specifically.

Sense Hierachy of Weasels

The difficulty encountered in finding the mouse was reflected in the search-time. The results of Experiments I to V (Fig. 2) show that it is the diversity of sensory information available that has a significant effect on search-time. If information is available to three senses, a potential food item is located faster than if only one sense can be used. When information is only available to one sense, it appears that all three distance senses are broadly equivalent, although audition may be the least important. However, the different senses appeared to interact when in combination, for example search-times for treatments with auditory cues available were not always the longest, e.g. the short mean search-time for audition + olfaction (AO).

Conclusions based on the substrate-scent experiments can only be tentative, owing to the small number of trials conducted, but it appears that substrate scent cues are as important as visual, auditory and olfactory (air-scent) cues in combination (VAO).

Although search-time probably gives the best indication of the relative importance of the senses, other behavioural measures can be used to give a more complete picture. The presence or absence of particular sensory cues had different effects on the behaviours measured. For example, there was a trend for the presence of visual cues to reduce the mean number of containers visited in a trial, while the prey was detected at greater distances using auditory cues. There was a trend for the absence of auditory cues to have the greatest effect on a variety of behavioural measures such as decreasing detection distance, decreasing "preytime" and increasing the number of containers visited in a trial (Tables 8 and 15).

It is impossible to tell whether the removal of auditory cues is important or that it is visual and olfactory cues in combination that are unsatisfactory. The apparent detrimental effect of the removal of auditory cues may be partially a response to the replacement of a live mouse with a dead one, which includes the removal of visual movement cues (see discussion on importance of prey movement, p. 88).

The time spent near the prey animal, in particular, confirmed the results for search-time, although there was a trend for prolonged "prey-times" to be associated with the presence of a live mouse in the container. Many of the other behaviours measured confirmed the search-time results, but when they did not, this was taken into account in order to arrange the sensory combinations in a hierachy. Treatments having more features in common with VAO were placed higher than those with similarities to the "no senses" treatment. The behaviour of the experimental animals during the "no senses" experiments was the antithesis of that during VAO experiments. The sense hierachy is illustrated in Fig. 15. The treatments are arranged according to the sensory cues available, but any reduction in search-time etc. may be attributable to the negative effect of the removal of a particular sensory cue.

Although mean search-time was equivalent in vision + olfaction (VO) experiments and vision + audition (VA) conditions, the latter is given a higher rank as, in the former case, many more containers were visited, the detection distance was shorter and the mean time spent with the prey was of a short duration.

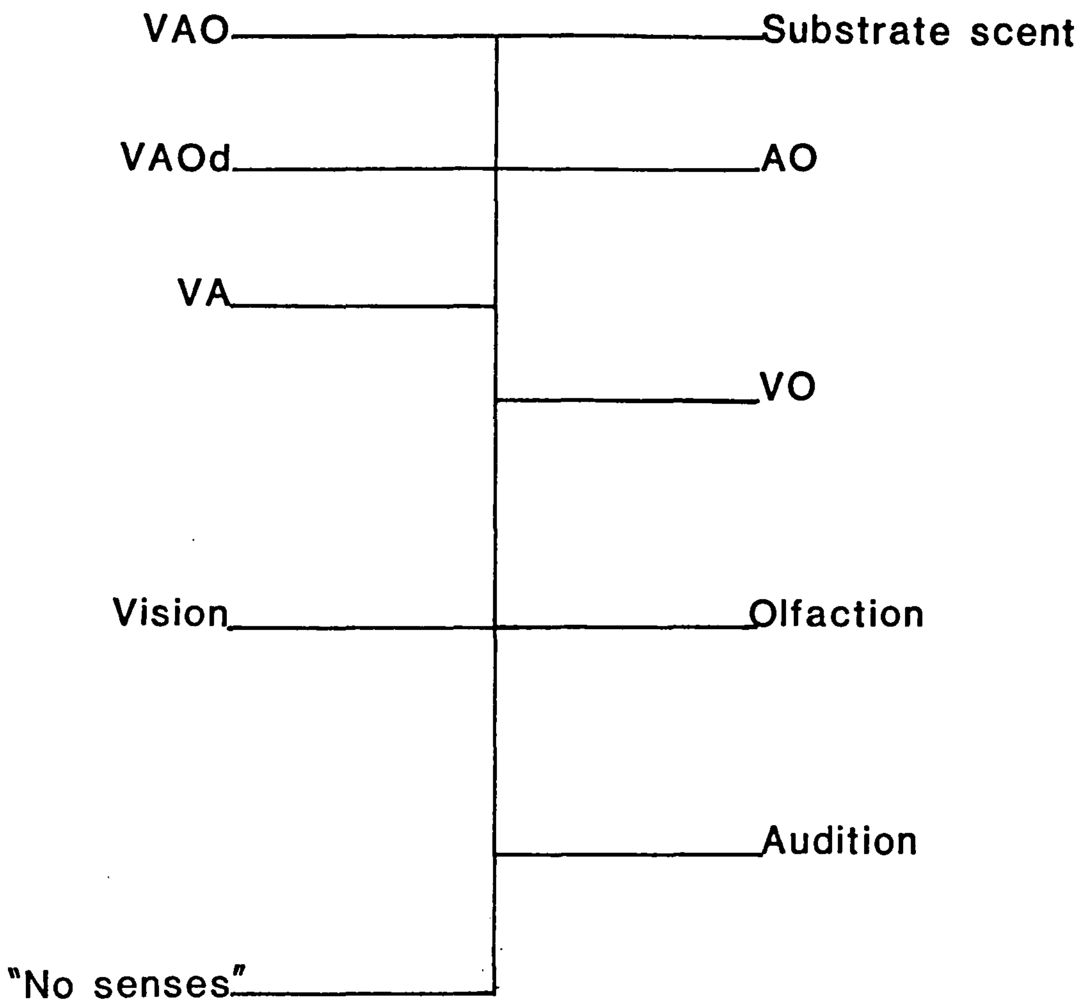


FIGURE 15. Sense Hierachy of Weasels.

Factors Affecting Search-time

Variation in search-time could have been due to individuals differing in the time taken to learn the stimulus features of the "mouse" under different treatments. Evidence for individual subjects having differential rates of learning includes the absence of significant variation at the performance ceiling (final five trials), although individual variation was significant during the experiments as a whole. It may have been preferable to confine the statistical analysis to the final five trials, but analysis of such a small sample may not have been valid. Individual variations in behaviour, not related to learning, may have had more spurious effects on the results than with a larger sample.

This variation between individuals may have been a consequence of the order of presentation of each experimental treatment. However, the search-times for the single sense treatments were always consistently longer than for the two or three senses treatments, regardless of the order of presentation, making this explanation unlikely. Within experiments II and III there did not appear to be any consistent decreasing or increasing trend in search-time according to the order of presentation.

An obvious factor affecting search-time is the speed of movement of the animal. As would be expected, the mean searching speeds were faster during the two senses treatments than in the single sense treatments. However, although search-times were short when three sensory modalities were available, speed of movement in fact was slow, therefore other factors such as searching strategies must have caused the reduction in search-time. These experiments had a high frequency of "direct approaches", which appears to be a more important factor affecting search-time than speed of movement.

When the mouse was not approached directly, the time spent investigating containers had an important influence on search-time. However, an increase in the number of containers visited did not always cause an increase in search-time. For example, in vision + olfaction (VO) conditions, many containers were visited, yet search-time was short. Speed of movement between the containers must have been particularly quick in this treatment.

Although the long search-times recorded in the single sense treatments may have been mainly due to the number of containers visited, they may have been directly a result of an actual slow speed of movement. The increased frequency of pausing and attention responses in some of these treatments, could have been responsible for the decrease in mean speed.

Measurement of turning-rate gave a quantitative measure of an animal′s searching behaviour. Turning-rate was negatively correlated with the number of containers visited; fewer turns were made when the animals directed their searching to the containers, as they tended to move in straight lines between the containers. A high turning-rate was associated with trials characterised by a short search-time, in which active searching for the mouse may have occurred.

Attention Responses

It is generally recognised that there are two main types of attention response shown by weasels (Pounds, 1981). Previous authors (e.g. Poole, 1972a), have assumed that attention responses of the polecat are in response to auditory stimulation as they are elicited by rustling and scratching noises. The results of the present study confirm this; peering-rate was higher than in the baseline condition during audition only trials. However, attention responses were not particularly frequent when auditory cues were available in combination with other senses (Fig. 9). Sampling of olfactory information probably also occurs.

The "rear" attention response appeared to occur in response to a shortage of stimuli, as the highest frequency of this behaviour occurred in the "no senses" experiments. It could be a method of scanning for stimuli, when none are readily apparent.

The possibility exists that attention responses may have been made in response to stimuli not related to the experiment, as it was impossible to exclude noises coming from other areas of the building, a sound-proof room not being available. This is a possible explanation for the occasional high individual frequency in certain treatments, e.g Tulip in VA conditions and Roger in olfaction only experiments. Attention responses were extremely variable in occurrence with respect to both time and the individual so it is difficult to make definite conclusions about their function.

Scent Trail Experiments

In many previous studies of the sensory control of predatory behaviour (e.g. Osterholm, 1964; Wells and Lehner, 1978; Langley, 1983a), investigation of the role of olfaction was confined to the odour of the prey animal carried by air. However, an animal also leaves its odour on the ground over which it walks. Previous authors either overlooked the importance of substrate scent or it was not examined in studies on distance senses as it was not considered a "distance sense". Substrate scent cues may be of considerable importance in finding prey, therefore were investigated in the present study.

As it was not possible to ensure that the scent trail from a previous trial had been adequately removed, only a small number of trials were conducted, allowing a time-interval between trials. Although the substrate was not ideal for the experiment, it was felt necessary to conduct it under identical conditions to experiments I to V in order to provide comparative data. Ideally, a study of this capability should be conducted under conditions where flooring can be removed between trials (e.g. Herman, 1973).

The search-time results for all the scent trail treatments were equivalent, despite the different amounts of sensory information associated with the container holding the prey. Therefore the predators were mainly responding to the scent trails and not to the stimulus cues associated with the container. There is the possibility that selective attention to particular stimuli may have occurred. While paying full attention to substrate scent, other sensory cues may not need to be used. Differences in the behaviour of the predators between the substrate-scent trials and the main experiments were mainly due to the time spent sniffing the scent trail, e.g. the slower speed of movement and lower frequency of attention responses.

There did not appear to be any difference between the weasel and polecat in the time taken to find the mouse using substrate scent, but there were subtle differences in their searching behaviour. The polecats appeared to be more efficient at following the trail than were the weasels. They rarely followed it in the wrong direction and did not need to sniff it intently in order to follow it.

The observed infrequent use of the scent trail by the predators may have been an artefact of the experimental conditions, as the stimulus was an unnatural one and the animals had already learned to direct their searching to the containers.

There is some evidence that mustelids can use scent trails when hunting in the wild. A weasel (_Mustela frenata_) was observed by Murie (1935) to precisely follow a hare's trail, although at times it was followed in the wrong direction. A notable feature of the weasel's behaviour was that at one point it passed within a few feet of the hare it was tracking without apparently detecting it. This confirms the difficulty that weasels have in detecting prey using only visual (without movement) and olfactory cues. Also, Smith

(1978) observed a stoat, *M. erminea*, follow scent trails of mice in an enclosure.

Experimental investigation of the use of substrate-borne olfactory cues by weasels has already been conducted by Herman (1973). A potential prey animal was allowed to run through a Y-maze, and then a weasel was allowed to run the maze. His finding that substrate-scent is more important to weasels than air-borne scent, is supported by the present study.

Olfaction based on substrate scent may be the most important sense for finding prey to both polecats and weasels. Apfelbach (1973a, b) also believes olfaction to be the most important sense to hunting polecats, but his experiments were concerned with air-borne olfactory cues, and this is not supported by my results.

Importance of Prey Movement

The movement of the prey also appeared to be an important stimulus. When visual movement cues were available, search-time was generally reduced. Visual movement cues were not available in the single sense treatments and this may have been important in causing the observed increase in search-time (Fig. 2). A moving mouse is also emmitting auditory cues and unfortunately it was difficult to distinguish clearly between auditory and visual movement cues. However, as search-time was prolonged in audition only experiments, it appears that visual cues are more important.

The importance of prey movement is best illustrated by the results for the two senses treatments. The behaviour of the animals during vision + olfaction (VO) conditions, (the treatment without a moving prey), was significantly different from the control (VAO), although mean search-times were equivalent. It is interesting that visual and air-borne olfactory stimuli are those associated with a motionless mouse. Many small rodents e.g. Apodemus, freeze when they detect the presence of a predator (Erlinge et al., 1974a). The success of this anti-predator strategy is borne out by the observations of Heidt (1972), Erlinge et al. (1974a) and Pounds (1981) where weasels were observed to pass close to stationary rodents without apparently detecting them.

Movement cues were particularly important when the predators were near the mouse. The longest times spent with prey were recorded when there was a live moving mouse inside the container. However, in this study, it may not always have been the movement cues that were important, rather it was the difference between a live prey and dead food item that may have influenced the behaviour of the weasels.

Individual Variation

There were different degrees of motivation for the task, with the performance of individuals varying on a day to day basis. Occasionally, the predators showed no inclination to look for the mouse until they had dug up the floor, slept for a few minutes or engaged in other diversionary behaviour! Apart from fluctuations in motivation there were some consistent individual differences in performance. This frequently occurred between the sexes, and much of this variation could be accounted for by the relatively faster speed of the males. Male weasels moved faster than the females due mainly to their larger size.

The faster speed of the males was reflected in other behaviours; e.g. rates of turning, pausing and rearing. Velander (1980) noted that female weasels were more active and moved quicker than the males. I disagree with this observation; although female weasels can give the impression of being faster, they in fact are not. Male weasels detected the mouse from a greater distance than the females, possibly due to differences in searching behaviour (see p. 93). Erlinge et al. (1974a) stated that male weasels are more efficient predators as they catch more prey animals in a given time than females. In the present study, female weasels appeared to be more efficient as they found the prey as quickly as the males, even though they moved slower. Erlinge's result could be explained by the males being more successful in killing prey than females, possibly by virtue of their larger size.

Weasels appear to be individualists, often adopting their own specific strategies for solving problems. While this individuality may be an artefact of the experimental conditions, there is evidence from free-living populations of considerable individual variation in behaviour. Pounds (1981) noted that there was as much variation in habitat preferences and foraging strategies between individual weasels as between stoats and weasels.

Searching Strategies

There is the possibility that the weasels were not responding to sensory stimuli but were using searching strategies involving spatial memory to find the prey. There is some evidence that the weasels were investigating unvisited containers while trying to find the mouse (see Fig. 11). The mean number of new choices of 6.2 out of eight, though, is a much poorer performance than that of the rat in the eight-arm radial maze (Olton and Samuelson, 1976; Einon, 1980; Suzuki et al., 1980), but is comparable to the mean performance of the weasel in the radial maze (mean correct = 6.6, Pratt and Howard, 1981, Meadows and Jackson, 1982). The low correct score in the present experiments suggests that either the weasels were forgetting where they had been previously or were not using spatial memory to find the mouse. It is unlikely that the weasel has a poor memory for different spatial locations, as it would be expected to have a good memory for the distribution of resources within its home range.

The radial-arm maze is believed to investigate foraging strategies (Olton et al., 1981) with win-shift foragers such as the rat being particularly good at the task. The results of the present experiments can also be related to the weasel's foraging behaviour. However, the experiments are not strictly comparable as all of the eight locations in the present experiments were not rewarded in each trial, and the weasels had freedom to move around the whole arena.

Evidence from studies of foraging movements of weasels (Musgrove, 1951; Pounds, 1981) suggests that the weasel may be a win-shift forager. After a time spent foraging in one of the hunting areas of its home-range it moves to another. However, one aspect of the weasel's foraging behaviour that causes it to return to sites is its habit of caching food (Rubina, 1960; Sueur, 1981). Hunting weasels probably show neither strong win-shift nor win-stay searching strategies.

It is possible that the weasels' memory extended further than one trial. If this was the case, the mouse would occasionally appear in places that had been recently investigated, therefore it would pay to occasionally re-check containers. There were no great penalties incurred by the weasels if they returned to a container. The reasons why weasels showed preferences for particular locations is unclear. The containers visited most often were neither the ones nearest or furthest away from the experimenter, but some of the preferred containers were in an area favoured for scent marking.

The relation between the tendency to show a shift strategy and foraging behaviour has been questioned by some authors. It has been ascribed to the degree of spontaneous alternation shown by the species (Gaffan and Davies, 1981). This explanation has been used by Sheri et al. (1982) for the failure of mice to equal the performance of the rat in the radial maze, although the foraging behaviour of the two species is similar. However, there does not appear to be any difference in alternation behaviour between ferrets and rats (Sutherland, 1957; Hughes, 1967).

Visiting adjacent containers would have been an aid to the strategy of investigating previously unvisited containers. It is also an energetically more efficient strategy than searching at random or the excursion type of searchpath, since the latter may involve crossing the same area several times. However, this latter strategy may have its advantages, as the animals occasionally used the release-box as a vantage-point, standing on or near it, before moving off again in a particular direction. Also, animals learn spatial relationships better, if they can travel in both directions between locations (Maier, 1932; Stahl and Ellen, 1974).

The female weasels tended to use the adjacent container strategy more often than the males, and this was reflected in male-female differences in certain behaviours, i.e. turning rate was lower and detection distance was significantly shorter in female weasels.

Obvious orientation to the mouse only occurred when the weasel was close to the container holding the mouse when searching was directed to the containers. Rather than detecting the mouse using distant sensory cues, it occurred at close quarters.

Comparative Results

There did not appear to be any significant difference between polecats and weasels in terms of the relative importance of the distance senses. There was no difference in mean search-time, despite the difference in body-size. There were some minor differences in behaviour however.

The species differed in their behaviour toward auditory and olfactory cues in combination (AO) and visual cues. Polecats certainly appeared to detect visual cues (when prey movement cues were not present) more successfully than weasels. It should be noted that a mouse presented in auditory and olfactory conditions was a particularly potent stimulus for the weasels. There was no significant difference between vision or olfaction only search-times and the three senses control in the polecat subjects. Polecats may be more able to locate prey with reduced sensory information available than weasels.

In both species, search-time was long in the audition only experiments. The use of audition by hunting mustelids is rarely mentioned by authors, which also implies that this sense is little used. However, this study shows that auditory cues become important when in combination with cues from other senses. Indirect evidence for the low importance of audition lies with the morphology of the animals. The pinnae are small and inconspicuous compared to those of predators known to rely on audition when hunting, e.g. red fox, Vulpes vulpes (Osterholm, 1964).

Previous workers appear to disagree on the relative importance of vision and olfaction to polecats. Raber (1944) and Eibl-Eibesfeldt (1956) believe the polecat detects prey using vision while Apfelbach (1973b) and Apfelbach and Wester

(1977) believe that olfactory stimuli are more important than visual stimuli for eliciting hunting behaviour. However this latter conclusion was reached without investigating the use of olfaction and vision under the same experimental conditions.

Wustehube (1960) believed that the key stimuli for predatory behaviour are both visually perceived movements and the scent of the prey, with polecats responding more to the latter than stoats and weasels. However, I did not find any evidence for polecats responding more to olfactory cues than weasels.

Experiments on the predatory behaviour of South African species of mustelid provide an interesting comparison to the present study (Rowe-Rowe, 1978). The striped polecat, Ictonyx striatus, a generalist predator, was observed to use vision to detect rats, while the African weasel, Poecilogale albinucha, a small-mammal specialist, used scent to locate prey until it was visually fixated.

The olfactory sense is thought to be not particularly acute in the Mustelidae compared to other Carnivora (Novikov, 1956; Korytin, 1977). It would be perhaps surprising if olfaction, using air-borne scent cues, could play the dominant role in predatory behaviour that some authors suggest.

Differences in the relative importance of vision and olfaction to polecats may be due to some authors using polecats, Mustela putorius (e.g. Raber, 1944) and others ferrets, M. furo (e.g. Apfelbach, 1978). Differences in the brain (Schumacher, 1963), behaviour (Poole, 1972a) and visual abilities (Gewalt, 1959) have been demonstrated between the two forms. There is evidence for albino animals having abnormal visual pathways (Sanderson *et al.*, 1974), therefore some ferrets may not have the visual abilities of their wild counterparts.

Sense hierachies vary according to environmental conditions. The relative importance of the distance senses in a hunting coyote (*Canis latrans*) was different in an outdoor enclosure compared to a small indoor arena (Wells, 1978; Wells and Lehner, 1978). It is possible that in the variable environmental conditions in the wild, the relative importance of the senses to polecats and weasels may change from that reported in the present experiments. For example, wind conditions may favour the use of air-borne scent. There is scope for further investigation of the effect of environmental conditions such as illumination, prey type etc. on the sense hierachies of predators. Apart from factors in the environment affecting the above result, differences in methodology could have been responsible for the reported difference. In the indoor arena, olfactory stimuli were blocked by a masking odour, while in the outdoor enclosure an injection of zinc sulphate was given to the predators to induce anosmia.

Although the main experiments were confined to the distance senses, (apart from substrate scent cues), other senses e.g. tactile and taste, are involved in predatory behaviour. Tactile stimuli are important regarding placement of bites and the consumption of prey. Kemble and Lewis (1982) showed that vibrissal amputation disrupts the timing of the pounce in grasshopper mice, Onychomys leucogaster, and vibrissae are important to otters and seals hunting in turbid waters (Green, 1977; Renouf, 1980).

According to optimisation models of predatory behaviour, a predator should respond selectively to the stimuli that maximise its effectiveness to find and capture prey. Eisenberg and Leyhausen (1972) hypothesised that primitive or small nocturnal predatory mammals should rely on audition and olfaction to find prey and this has been supported by work on opossums (Didelphis marsupialis) and grasshopper mice (Langley, 1979, 1983a). Conversely, diurnal predators hunting in more open habitats for relatively more conspicuous prey should be more visually orientated, e.g. the African hunting dog, Lycaon pictus, (Estes and Goddard, 1967) and the coyote (Wells and Lehner,1978).

Although polecats and weasels are mainly crepuscular, they can be active at night or during the day, this being particularly the case with the latter species. The polecat can be considered a generalist predator, but the weasel is often classified as a specialist, as it feeds mainly on microtine rodents, however, it does take other prey according to availability. Therefore, these two predators can be described as generalists in terms of activity rhythm, habitat selection, prey selection, and as this study shows, also in terms of the use of their senses.

The results of this experiment are discussed in more general terms in Ch. 7, with particular reference to how they may be related to the animals' predatory behaviour.

CHAPTER FIVE DIRECTIONAL MOVEMENT DETECTION CAPABILITY OF POLECATS AND WEASELS

5.0 INTRODUCTION

It appears that polecats and weasels are sensory generalists with all the senses contributing to the finding of prey. While movement cues are not the most important sensory cues overall for prey localisation they do appear to be important when the predators are close to prey. The visual perception of movement rather than other sensory cues was selected for more detailed study for several reasons. Stimulus parameters such as speed and direction are readily quantifiable and techniques were already available (Dunstone and Clements, 1979) to estimate movement detection capability of mustelids. Many authors have stressed that movement cues are very important to hunting mustelids (Eibl-Eibesfeldt, 1956; Heidt, 1972). It is possible that the importance of movement cues was underestimated in the previous experiments due to the method of stimulus presentation. However, the movement detection abilities of the polecat and weasel are estimated under conditions of a short viewing distance, when movement cues are particularly relevant to these predators.

Predators not only need to detect fast movement, they also have to determine its direction. Therefore thresholds for directional movement detection were determined. Various factors such as viewing distance, illumination and distance of traverse have been found to limit movement perception (Kennedy, 1936; Cohen and Bonnet, 1972; Thompson, 1982), therefore the influence of such factors on movement perception by the weasel is investigated.

5.1 MOVEMENT DETECTION THRESHOLDS OF POLECATS AND WEASELS UNDER STANDARD CONDITIONS

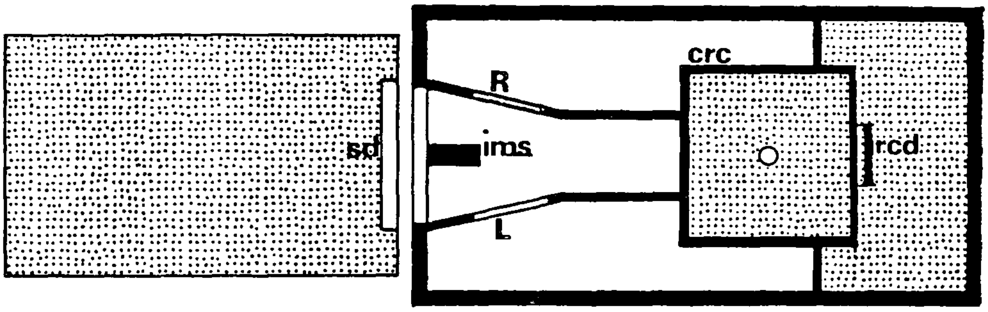
5.1.1 Materials and Methods

Apparatus

Experiments were conducted in a discrimination apparatus adapted from that developed by Dunstone and Clements (1979) and Clements (1980) for the estimation of the directional motion detection capability of the American mink. This consisted of a clear perspex box (39x28x105cm) enclosing a central discrimination chamber constructed of opaque perspex, bounded by two one-way doors, which gave access to a central, raised food reward chamber (39x18x31cm). The apparatus is illustrated in Fig. 16 and Plates 2 and 3.

The stimulus was a moving defocussed phosphor spot of light, 4mm in diameter, of known radiant intensity, provided by a cathode-ray oscilloscope situated at one end of the apparatus. The spectral characteristics of the stimulus are described on page 115. The stimulus spot travelled across the whole width of a 20cm dark screen and could be projected over a wide range of horizontal velocities (1.0 - 3000cms^{-1}) in either a left or right direction.

Plan elevation.



Side elevation.

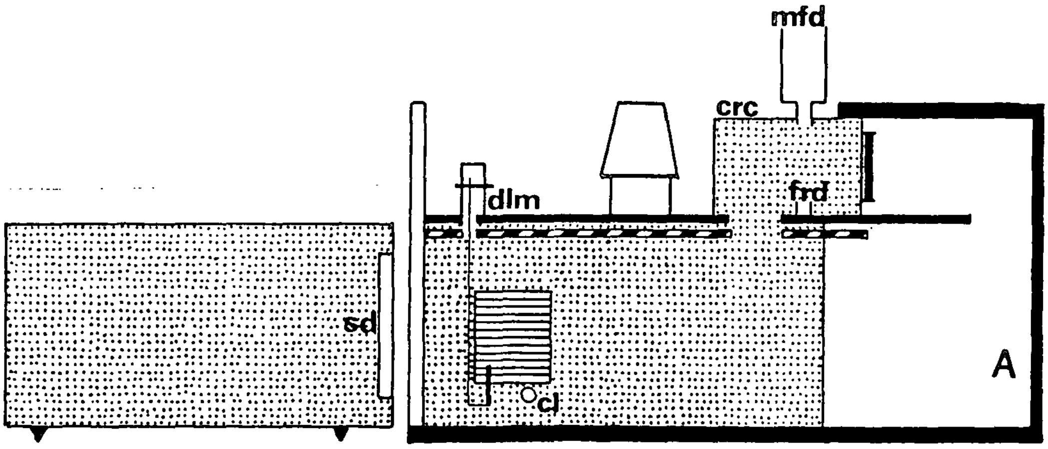
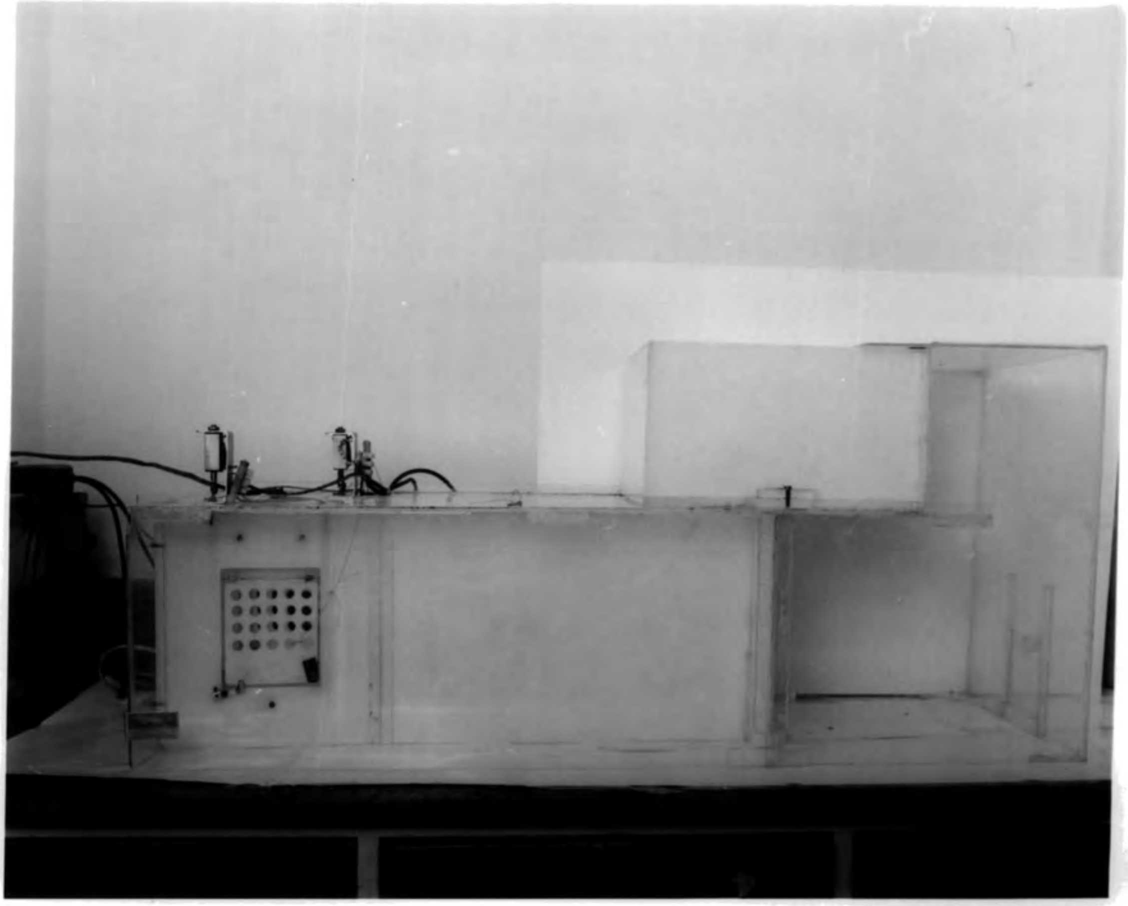


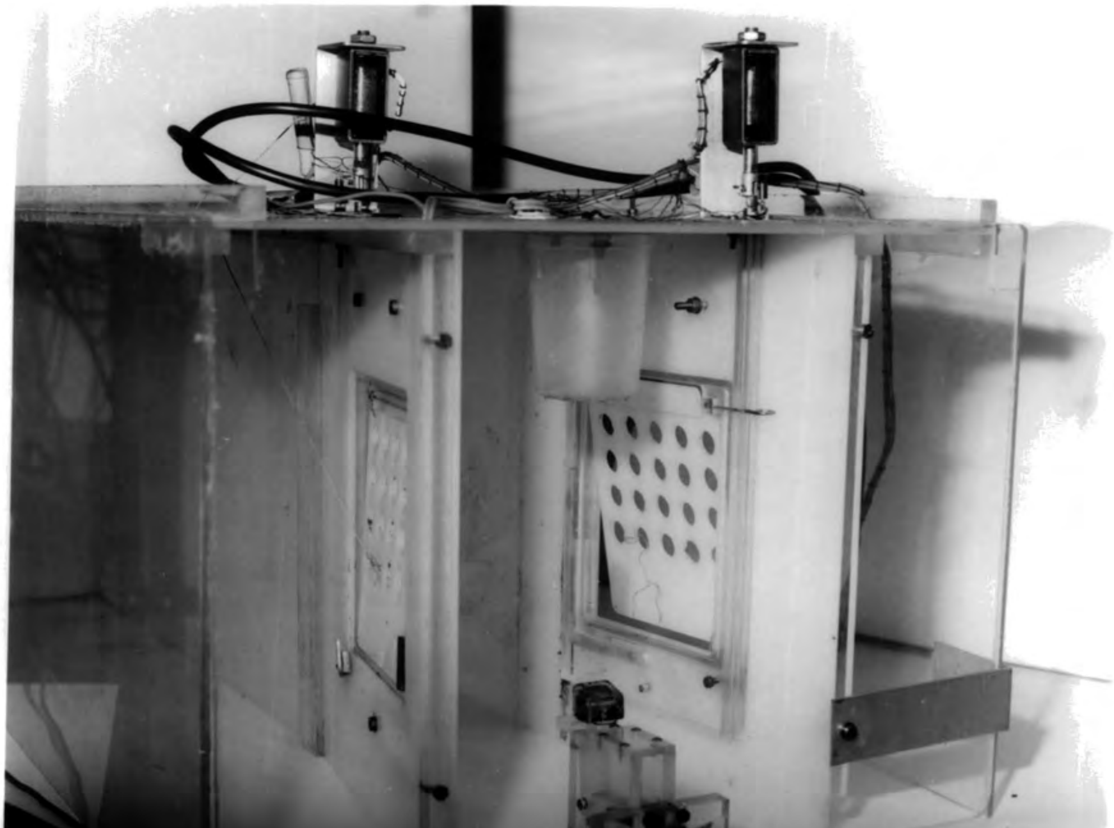
FIGURE 16. Side and Plan Elevations of Movement Discrimination Apparatus

Key: cl, cue light; crc, central food reward chamber; dlm, door locking mechanism; frd, food reward dish: ims, initiation microswitch; L, left response door; mfd, food dispenser; R, right response door; rcd, reward compartment door; sd, stimulus display;

PLATE 2. Side View of Movement Discrimination Apparatus
(Upper Plate)
The stimulus display screen (CRO) is to the left.

PLATE 3. Front View of Movement Discrimination Apparatus
showing initiation microswitch (Lower Plate)





Experimental Procedure

Individual animals were introduced into the apparatus at end A, (see Fig. 16) and were trained to run into the discrimination chamber, and there initiate the stimulus display by pressing forward a microswitch button (ims) with their nose (Plate 4). The switch produced an audible click when operated. It was situated at a measured distance from the stimulus display, 6cm above the floor and required $20gcm^{-1}$ pressure for its operation.

After pressing the switch each animal was then trained to turn either to the right or left, according to the horizontal movement of the stimulus. It could then gain access to the food reward compartment (crc) via one of the one-way doors (R or L) (see Plates 5, 6). Access back to the discrimination chamber was through a one-way door at the rear of the food reward compartment (rcd). The experimental design was such that the animals were allowed free movement within the apparatus and were not restrained or handled in any way, as this would have been unsatisfactory with such intractable animals.

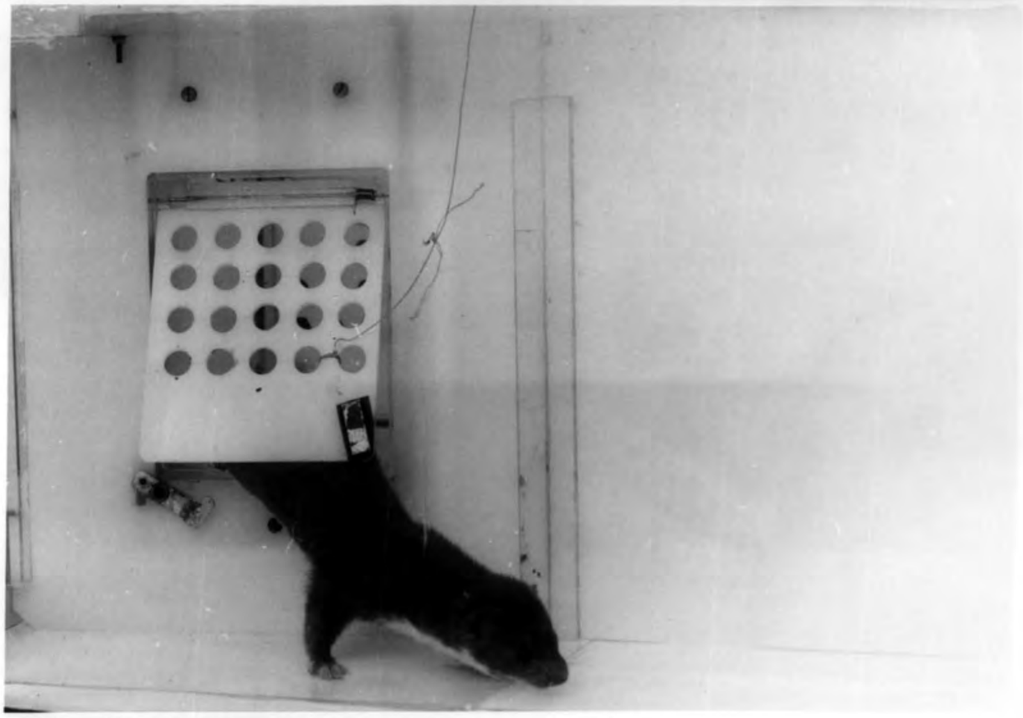
The food reward used was "Heinz" strained baby food, "Beef and Oxtail Dinner" variety. It was delivered by the operator in 1ml quantities from a calibrated syringe into a small dish situated in the centre of the food reward compartment.

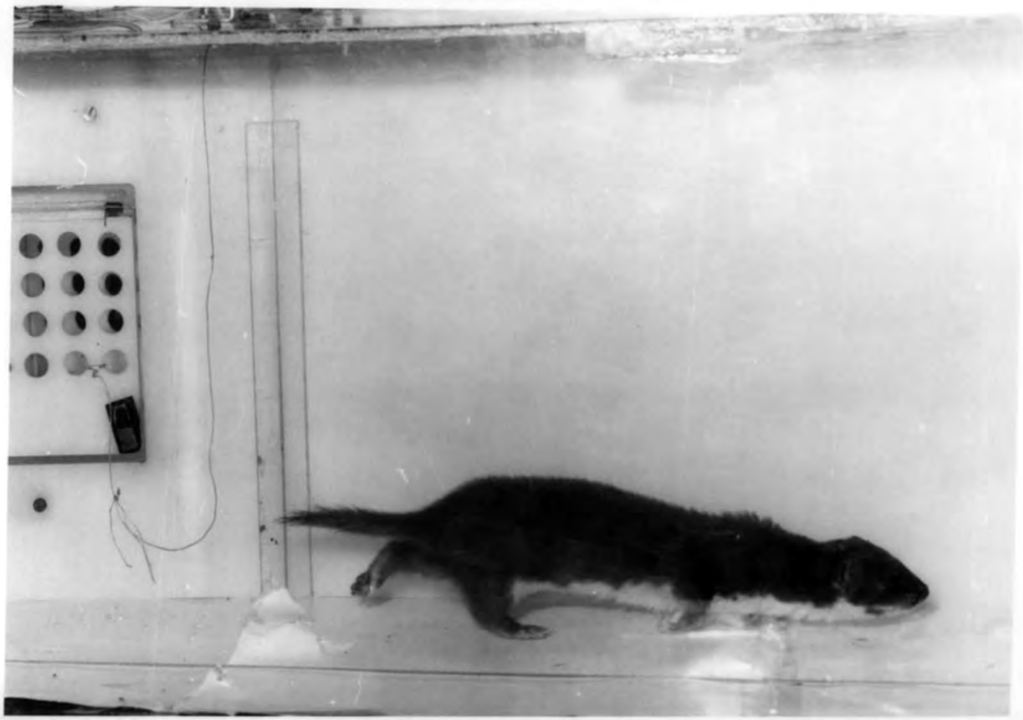
Animals only gained access to the food reward if they pressed against the door corresponding to the direction of

PLATE 4. Weasel pressing forward the switch. (Upper Plate)

PLATE 5. Weasel moving through response door. (Middle Plate)

PLATE 6. Weasel on the way to the food reward compartment. (Lower Plate)





movement of the stimulus. When a correct choice was made, the door was unlocked, giving an audible click, and a cue light on the door signalled to the animal that it had made a correct choice. If an incorrect choice was made, the door remained locked, and the animal was subjected to an eight second time-delay before it could initiate the stimulus display again.

Stimulus speed and direction, and the locking and unlocking of doors were controlled by a specially designed electronic logic system (see Plate 7). The direction of travel of the stimulus was varied in accordance with a Gellerman series, (Gellerman, 1933) a semi-random series of left and right presentations pre-programmed into this stimulus control unit.

Training Procedure

Polecats

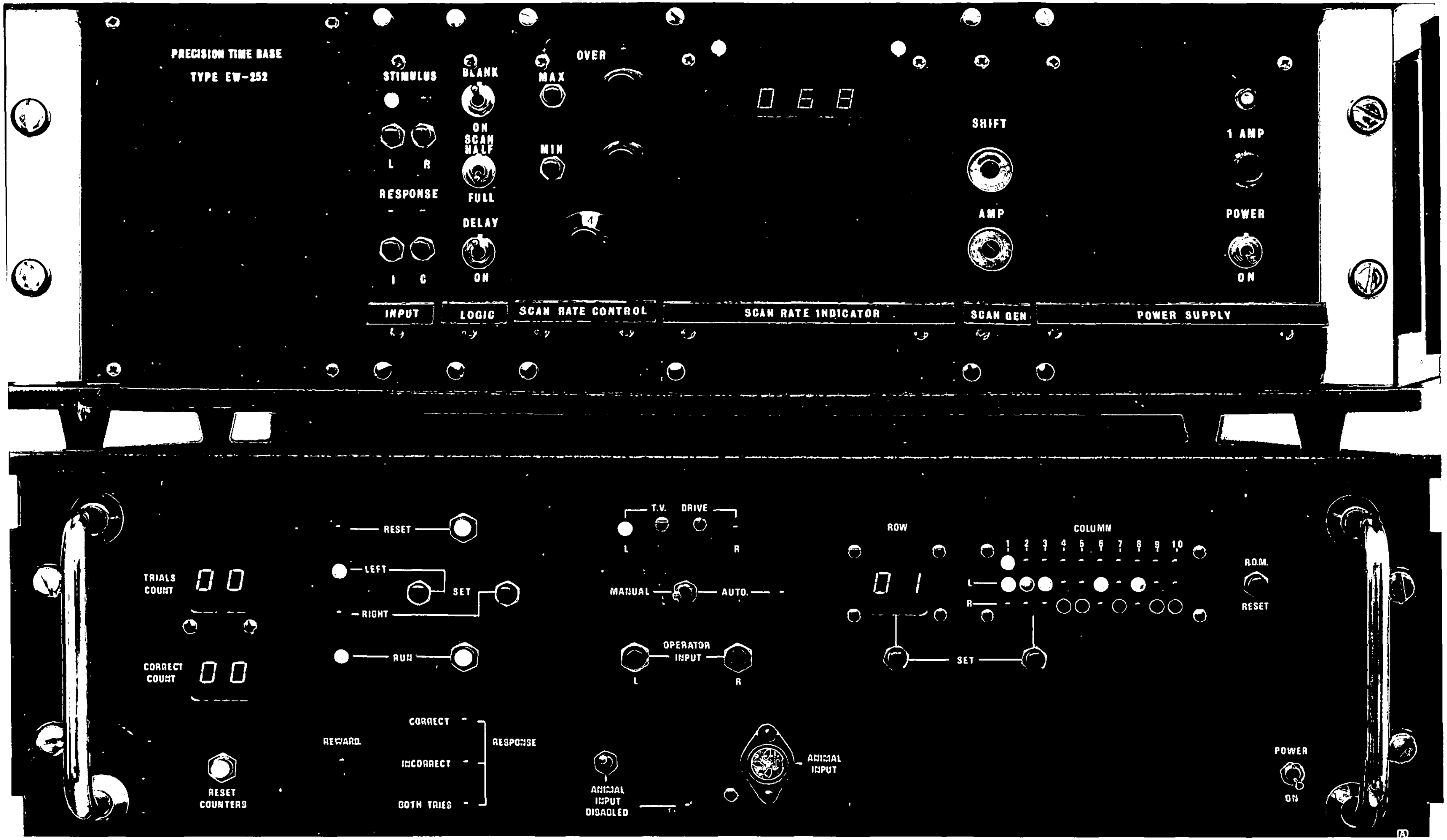
The subjects were two male and two female polecats, aged six months at the commencement of training. The animals were not food-deprived, but were fed daily after the experimental sessions.

The first objective was to train the subject to press the initiation microswitch with its nose whilst looking forward towards the stimulus display screen. Food was placed on the switch, and the animal would occasionally press the switch while licking the food off. Subsequently, the polecat was

PLATE 7. Front view of stimulus control unit.

Top section: Stimulus speed control.

Bottom section: Gellerman series and trials count display.


PRECISION TIME BASE
TYPE EW-252
STIMULUS
L
R
RESPONSE
I
C
BLANK
ON
SCAN
HALF
FULL
DELAY
ON
OVER
MAX
MIN
4
0 6 8
SHIFT
AMP
1 AMP
POWER
ON
INPUT
LOGIC
SCAN RATE CONTROL
SCAN RATE INDICATOR
SCAN GEN
POWER SUPPLY
TRIALS COUNT
0 0
CORRECT COUNT
0 0
RESET COUNTERS
RESET
LEFT
SET
RIGHT
RUN
REWARD
CORRECT
INCORRECT
BOTH TRIES
RESPONSE
T.V.
DRIVE
L
R
MANUAL
AUTO.
OPERATOR INPUT
L
R
ANIMAL INPUT DISABLED
ANIMAL INPUT
ROW
0 1
COLUMN
1 2 3 4 5 6 7 8 9 10
L
R
SET
R.O.M.
RESET
POWER
ON

only rewarded with food when it pressed the switch forward. Over several days, this regime of positive reinforcement allowed a gradual association between pressing the switch and gaining a food reward. Once the animal consistently pressed the switch during a training session the food reward was gradually transferred to the central reward compartment. This involved a series of stages.

At first, food was delivered to the right or left of the microswitch button rather than on to the switch itself. The subject was then trained to negotiate the response doors to obtain food in either of the side-passages leading to the reward box, the doors initially being held open by the operator. Both left and right sides of the apparatus were used in a random fashion in order to avoid the development of a position or alternation tendency by the animal. The final stage of training entailed the animal moving to the reward compartment for reinforcement. Again, the subject′s use of the one-way door at the rear of the box was aided by holding it open until the animal became proficient at opening the door itself.

Once a polecat had learned the sequence of pressing the switch, pushing open a response door unaided, and moving to the reward compartment for a food reward, the stimulus was introduced. The animal was then only allowed access to the right or left side-passage corresponding to the direction of movement of the stimulus. Trials were then run so that the animal learned to associate the direction of movement with the route of access to the food reward. Learning curves for the discrimination habit were compiled.

Weasels

The training procedure for weasels was identical to that for polecats except for the initial stage of training the animal to press the switch. A considerable problem was experienced with this species, primarily due to the relatively small size in relation to the switch. This was a particular problem with female weasels, and although attempts were made to train three different individuals, I was unsuccessful in training female weasels to consistently press forward the switch. As a result, only male weasels could be used, with three individuals aged between four and seven months old being trained.

A consequence of the small head size of the male weasels was that they rarely pressed the switch accidentally while licking off the food reward, so the training method for larger mustelids could not be used. A perspex shelf was mounted below and behind the microswitch button, onto which the food reward was placed. A weasel was trained to lick food off this shelf, which was in such a position that the animal's head was in the correct orientation for pressing the switch with its nose. While the animal was feeding, the switch was triggered by the operator, thereby causing an association of the audible click with the food reward. The animal was encouraged to press the switch by reinforcing approximations of the desired behaviour in a series of steps, gradually only providing reward when the switch was pressed fully.

Establishment of Learning Curves

There were twenty stimulus presentations, or trials, in each learning session, stimulus direction being varied using two ten-trial blocks of Gellerman elements. Only legal combinations were used, within the constraints put forward by Gellerman (1933). There were three sessions per day.

The stimulus traversed the screen at a constant velocity of 50cms^{-1} during each trial. Stimulus radiant intensity and ambient illumination were kept constant at 3.4×10^4 µWsteradian^{-1} and 1.26×10^{-2} mLambert respectively. Illumination (a tungsten lamp) provided the minimum amount of light for the animals to see the main parts of the apparatus. Details of measurement of the light levels are given on page 114. The switch was situated 10cm from the display screen. During each session the following were recorded:

The number of correct responses:

A correct response was defined as when the animal pressed against and opened the door corresponding to the direction of movement of the stimulus, gaining access to the food reward compartment.

The number of incorrect responses:

An incorrect response occurred when the animal pressed against the incorrect door and as a result was confined to the discrimination chamber without a food reward.

The number of cancelled responses:

A cancelled response occurred when the animal made no response.

Orienting Responses

The manner in which the animals orientated to the stimulus was divided into three main categories; quick response, tracking movement, and "guess".

A tracking response was defined as when the animal paid close attention to the stimulus display screen, appeared to fixate the stimulus spot and followed it across the screen with a visible head movement, the speed of which closely corresponded to that of the stimulus. A quick response occurred when an animal chose a door before the complete passage of the stimulus across the screen. A "guess" took place when the animal pressed against the door after the stimulus had traversed the screen.

Training for the learning curves was continued until the animal reached the criterion for learning to associate the direction of movement with the door giving access to the food reward. This criterion was established as when the individual's performance was consistently higher than 72.4% correct over each of five consecutive sessions; this value being that of the upper 5% chance limit calculated using the formula:

$$2\sigma = 2\sqrt{\frac{p.q}{N}}\ \%$$

Where σ = standard deviation

p = probability of a correct response

q = probability of an incorrect response

N = number of trials

For any one trial $p = q = 0.5$

2σ = 5% chance zone limits. (see Krechevsky, 1932)
Cancelled responses were excluded from the calculation.

Movement Perception Threshold Procedure

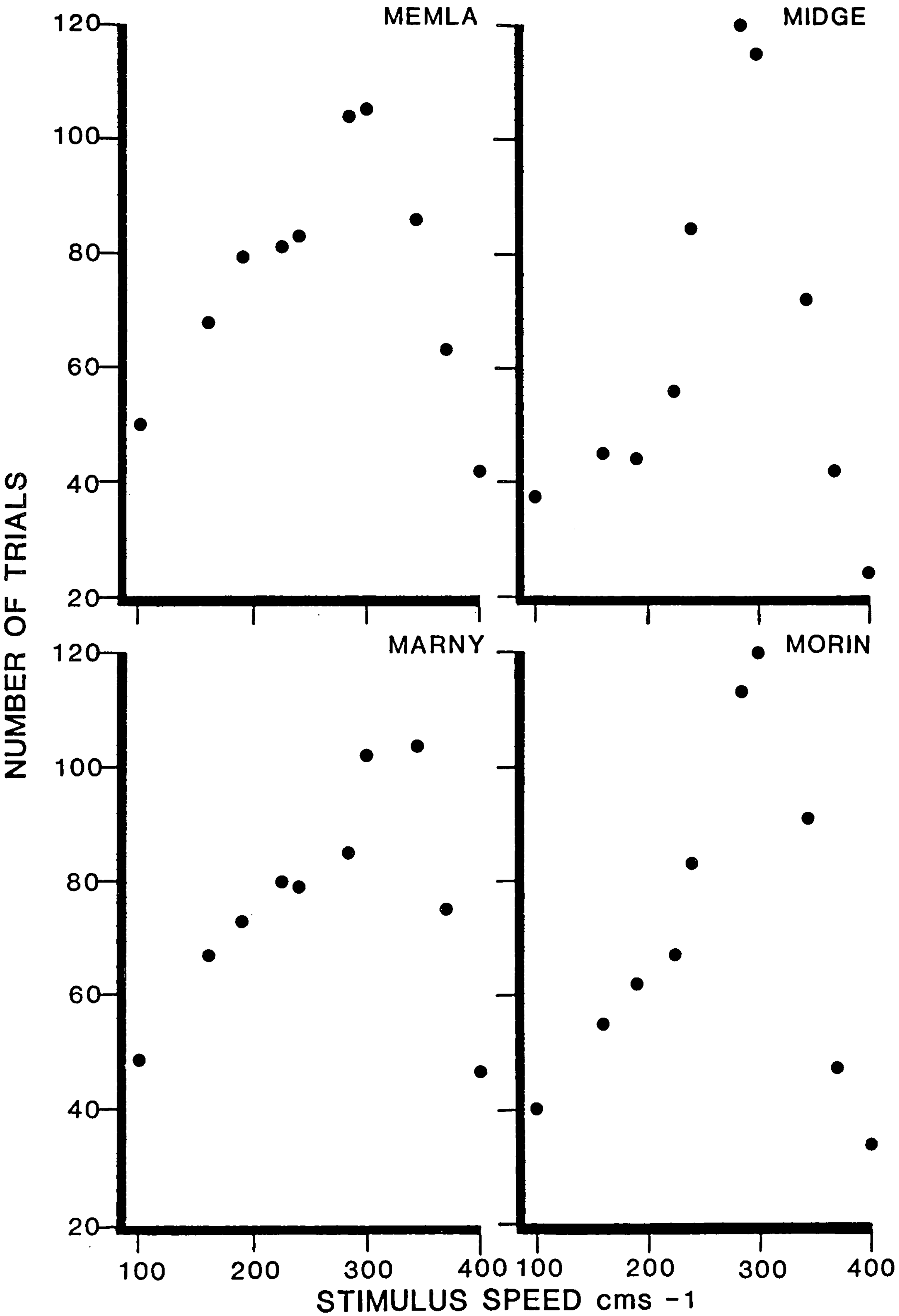
Once the animals consistently performed at or above the learning criterion over five consecutive sessions their motion perception capability was estimated. The stimulus radiant intensity and illumination conditions were maintained at $3.4\text{x}10^4$ µWsteradian^{-1} and $1.26\text{x}10^{-2}$ mLambert, with the stimulus traversing a screen width of 20cm. The initiation microswitch was 15cm from the stimulus display, the stimulus therefore gave an angular subtense of 79.6^0 at the subject's head. There were twenty stimulus presentations (trials) per session.

Stimulus speed was controlled by the stimulus control unit. During threshold estimation experiments the speed of the stimulus varied between pre-set upper and lower limiting values. A pilot experiment was carried out in order to estimate roughly the threshold value for the animals, over a stimulus speed range from 100 to 900cms^{-1}.

The movement perception thresholds were then more precisely estimated with the lower and upper stimulus speeds (the speed window) set at values lower and higher than the rough estimate of the threshold. These values were 100 and 330cms^{-1} for weasels and 100 and 400cms^{-1} for polecats. Within the speed window, stimulus speed was divided into ten steps of constant ratio.

If the animal made a correct choice at a particular stimulus speed, the speed was incremented by one step in the next trial. If an incorrect response occurred, the stimulus speed was reduced by one step in the subsequent trial. This resulted in the animal regulating its performance in a self-tracking manner (analagous to Cornsweet's staircase method (1962)). This economical method of stimulus presentation resulted in a peak of presentations of speeds around the threshold value. This is shown diagramatically for polecats in Fig. 17. Near threshold speeds were presented more than 100 times, with most of the other speeds presented for at least 60 trials. The first stimulus speed presented in each session was not always the minimum value (100cms^{-1}), but was varied randomly to control for temporal variations in performance.

FIGURE 17. Frequency of speed presentations for four polecats.



5.1.2 Results

Learning Curves

The results for polecats are shown in Fig. 18 and for weasels in Fig. 19. The results are expressed as the percentage correct responses per experimental session (consisting of twenty trials). The 50% chance level is indicated, as are the 5% chance zone limits. Since all sessions were of constant length the chance level is indicated by a constant width zone; the zone limits being 50% ± 22.4%. The number of sessions taken by each animal in reaching criterion is shown in Table 41. There was no significant difference between polecats and weasels with four polecats taking a mean of 30.3 ± 15.7 (S.D.) sessions to solve the problem, and three weasels, taking a mean of 39 ± 4.6 (S.D.) sessions before the learning criterion was reached (Mann-Whitney U Test, "U"=3, p=0.2).

Where the two species′ abilities did differ was in the way in which they learned the discrimination problem. Weasels and polecats gave an similar mean percentage correct score over the learning period as a whole, with polecats on average scoring 63.0% and weasels 60.0%. When the first and last ten sessions were examined, polecats made more correct choices than the weasels during the first part of the learning period, (χ^2=6.8, d.f.=1, p=0.01) but there was no difference between the species during the last ten trials (χ^2=2.8, d.f.=1, p=0.1)

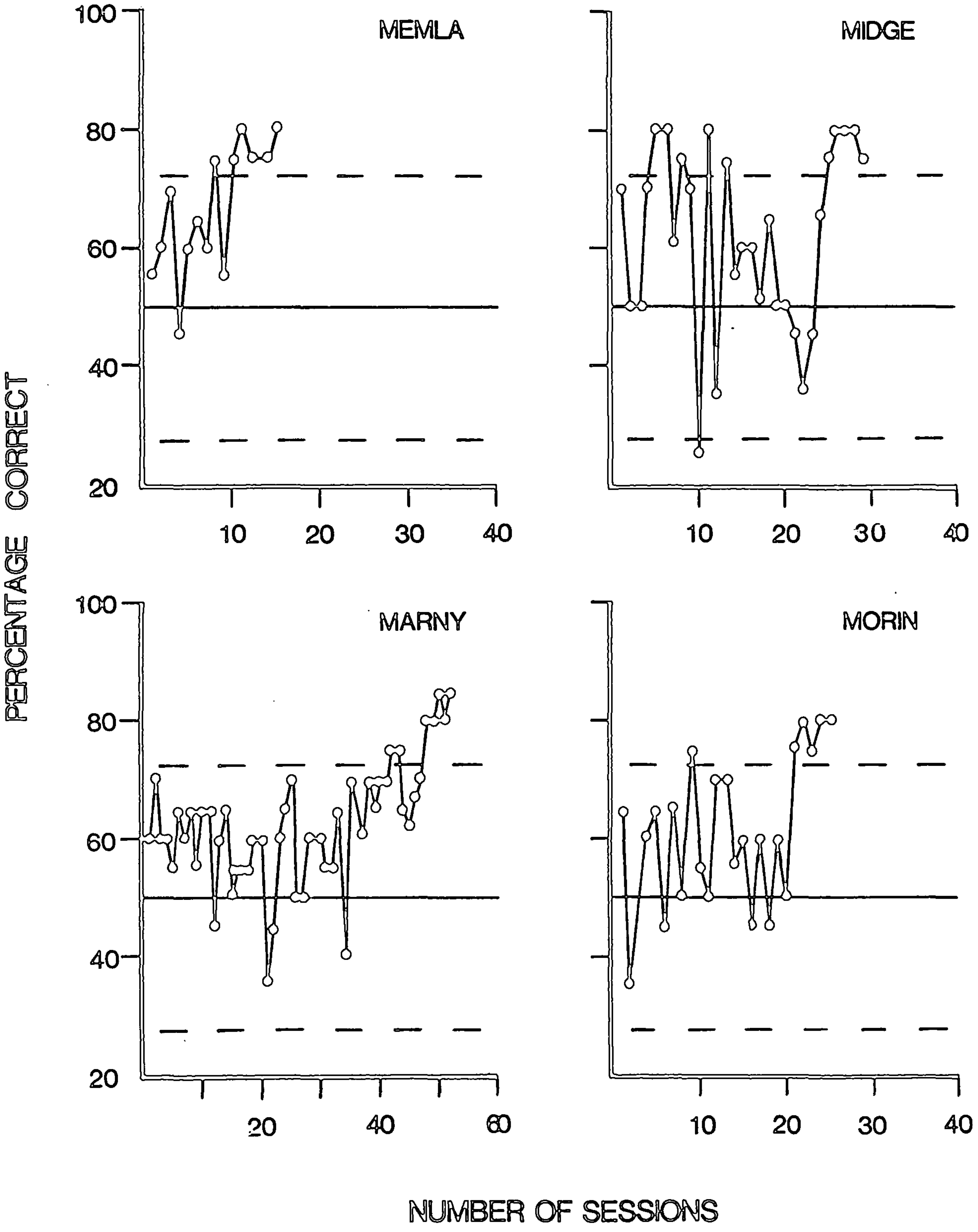


FIGURE 18. Discrimination learning curves for four polecats. The 50% chance level is indicated by an unbroken line and the 5% chance zone limits are shown by dotted lines.

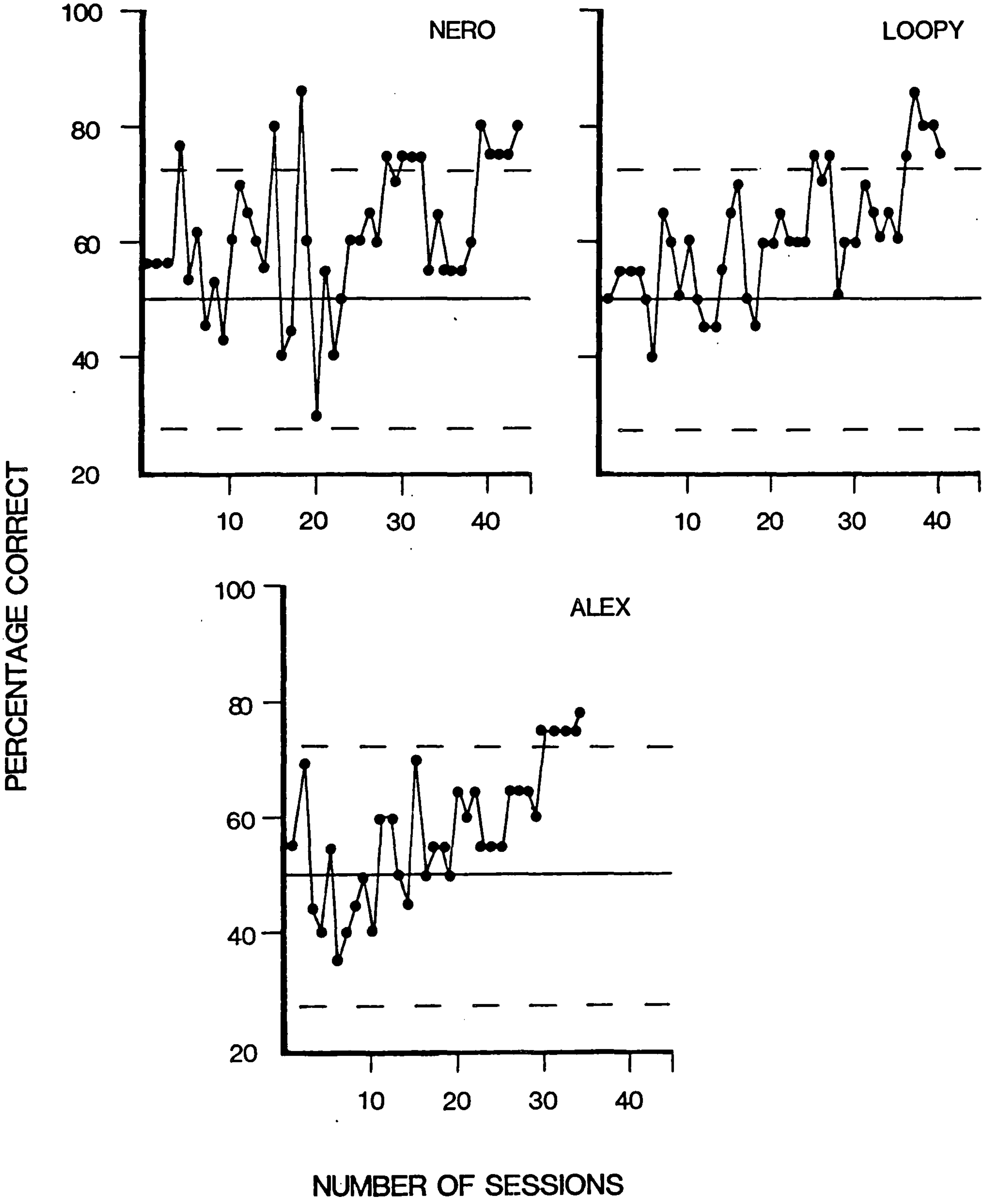


FIGURE 19. Discrimination learning curves for three weasels with conventions as in Fig. 18.

TABLE 41 The number of sessions taken to learn the movement discrimination task. Each session consisted of twenty trials.

POLECATS		WEASELS	
Subject	N sessions	Subject	N sessions
Memla	15	Loopy	40
Midge	29	Nero	43
Marny	25	Alex	34
Morin	52		
MEAN	30.3	MEAN	39.0
S.D±	15.7	S.D±	4.6

Movement Perception Thresholds

Psychophysical functions for four polecats and three weasels are shown in Figs. 20 and 21 respectively. The percentage correct responses are plotted for the stimulus speeds presented. A decline in performance occurred when the animals were no longer able to identify the direction of movement of the stimulus. Above the threshold the percentage correct score falls to within the chance zone. The threshold is defined as the point at which the psychophysical function crosses the 75% correct line (Schusterman and Balliet, 1971; Schusterman, 1972). At each of the stimulus speeds presented, 5% chance limit bars are indicated (calculated using the formula on p. 105).

The movement perception thresholds for four polecats and three weasels are expressed in both linear and angular terms in Table 42. The mean value for the polecats was 292cms^{-1} (S.D.$\pm$ 8.9), equivalent to 1162^{o}s^{-1} in relation to the visual field of the animals (see Clements, 1980), and for the weasels was 267cms^{-1} (S.D.$\pm$ 34.4), equivalent to 1061^{o}s^{-1}. Although the weasel thresholds were lower than the values for the polecats, there was no significant difference between the species (Mann Whitney U Test, "U"=3, p=0.2).

Orienting Responses

Percentage tracking responses expressed as a function of stimulus speed are plotted for polecats in Fig. 22 and for

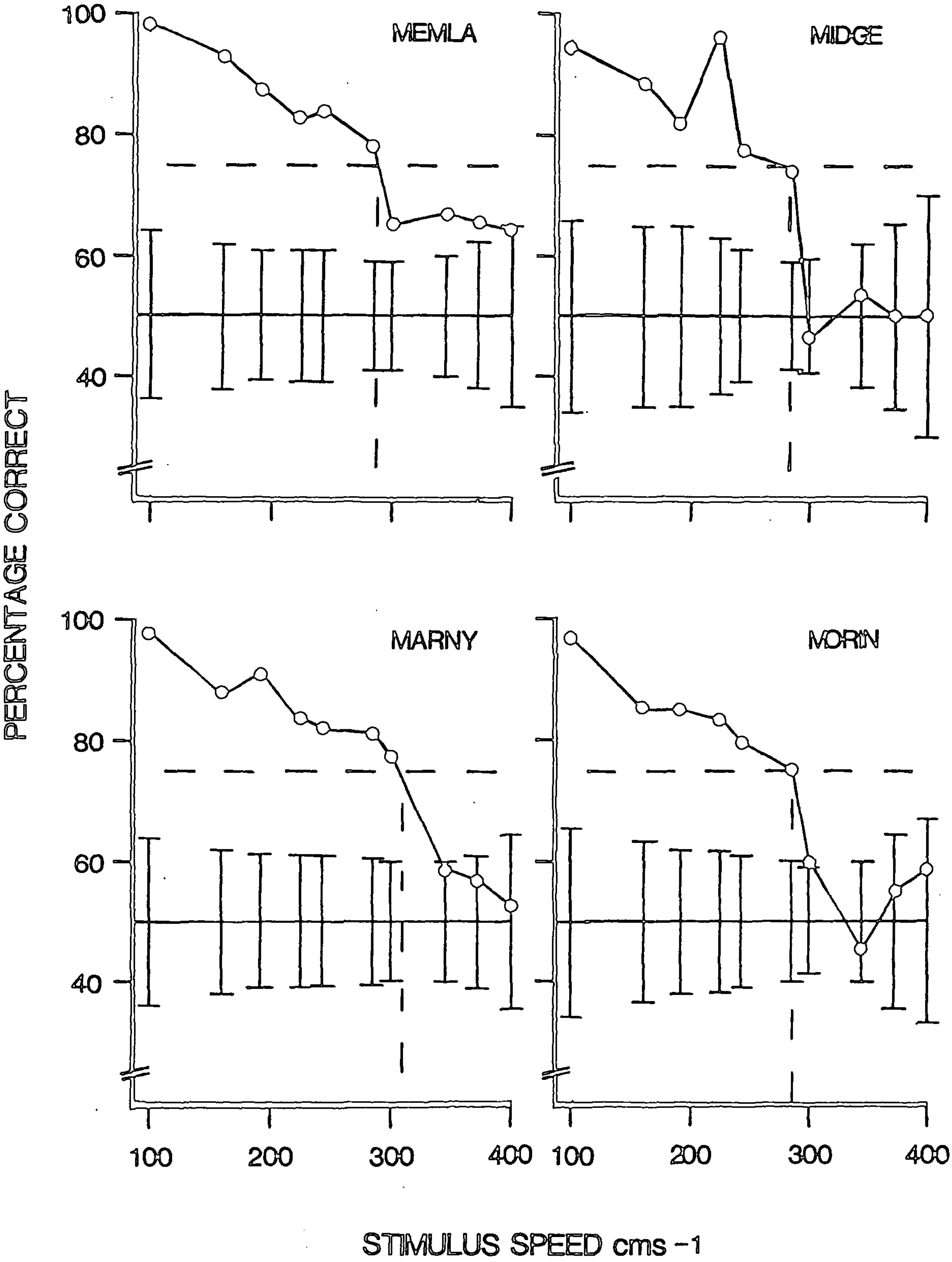


FIGURE 20. Psychophysical functions for four polecats. The threshold is indicated by the vertical broken line and 5% chance limit bars are shown.

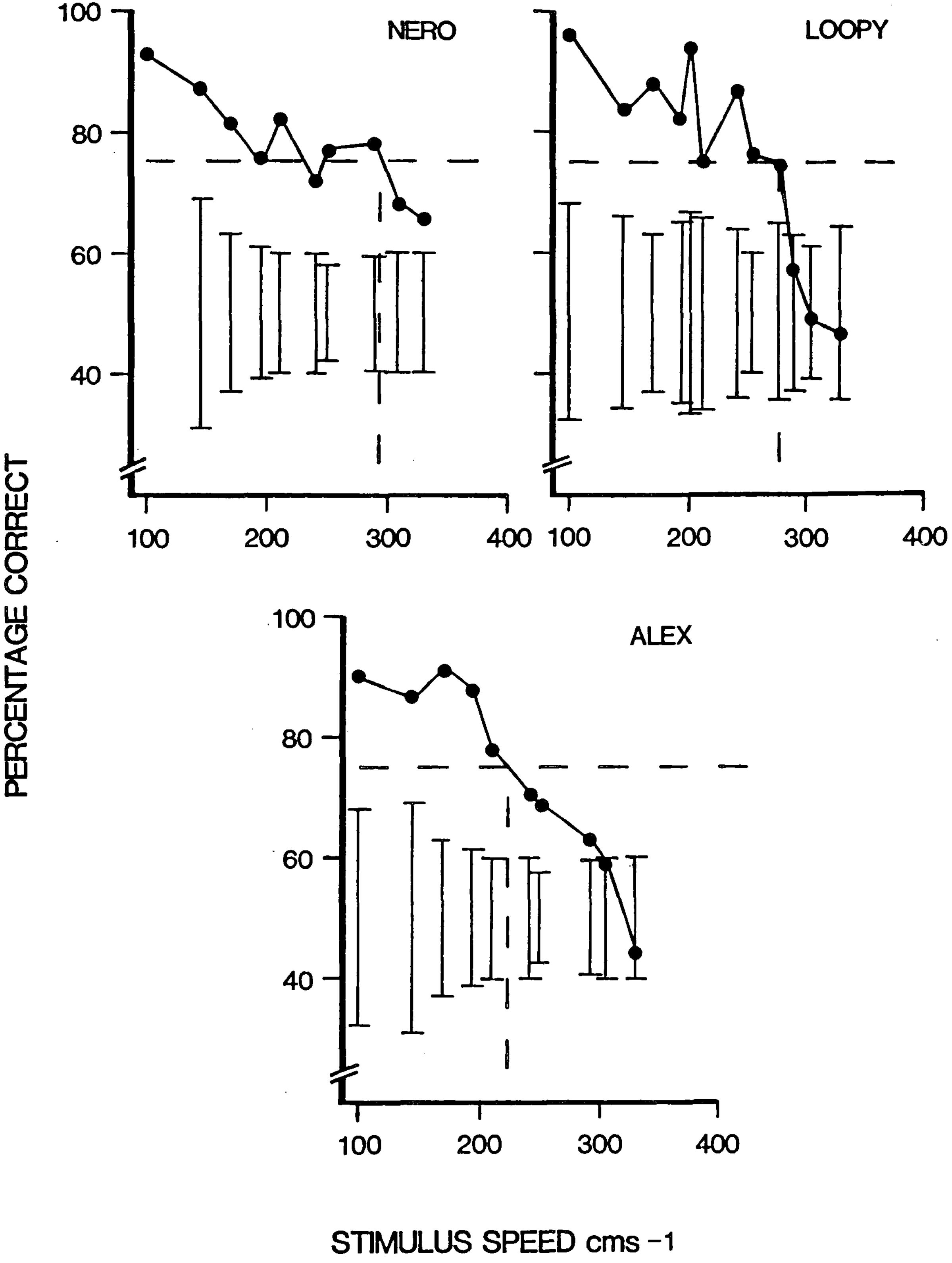


FIGURE 21. Psychophysical functions for three weasels with conventions as in Fig. 20.

TABLE 42 Movement detection thresholds under standard conditions.

	Linear Threshold (cms^{-1})	Stimulus Duration (s)	Angular Thresholds ($^{o}s^{-1}$) (visual field)	(retina)
POLECATS				
Memla	290	0.069	1154.2	22.1
Midge	285	0.070	1134.3	21.8
Marny	305	0.066	1213.9	23.1
Morin	288	0.069	1146.2	22.1
MEAN	292		1162.0	22.3
S.D.±	8.9		35.5	0.6
WEASELS				
Loopy	294	0.068	1170.1	22.5
Nero	278	0.072	1106.4	21.2
Alex	228	0.088	907.4	17.4
MEAN	267		1061.0	20.4
S.D.±	4.4		137.0	2.7

weasels in Fig. 23. In all cases there was a peak in tracking behaviour at stimulus speeds near the threshold value. There was some variation in the frequency of tracking responses between individuals, the lower values for the two male polecats may have been partly due to the fact that tracking responses were not so obvious to the observer in these animals as their larger heads filled a greater proportion of the discrimination chamber. The mean percentage tracking responses over all speeds for polecats was 31.2% and for weasels was 28.1%. The number of tracking responses observed in 300 trials was not significantly different between the two species (Mann Whitney U Test "U"=1.0, p=0.06).

Table 43 shows the mean percentage correct scores for the different types of orienting response, for four polecats, over the threshold estimation period. It is interesting to note that nearly all tracking responses were associated with a correct response. The success rate of the quick response was similar to the mean percentage correct score for the entire threshold estimation period. This is because quick responses were numerically the most frequent type of orienting response observed.

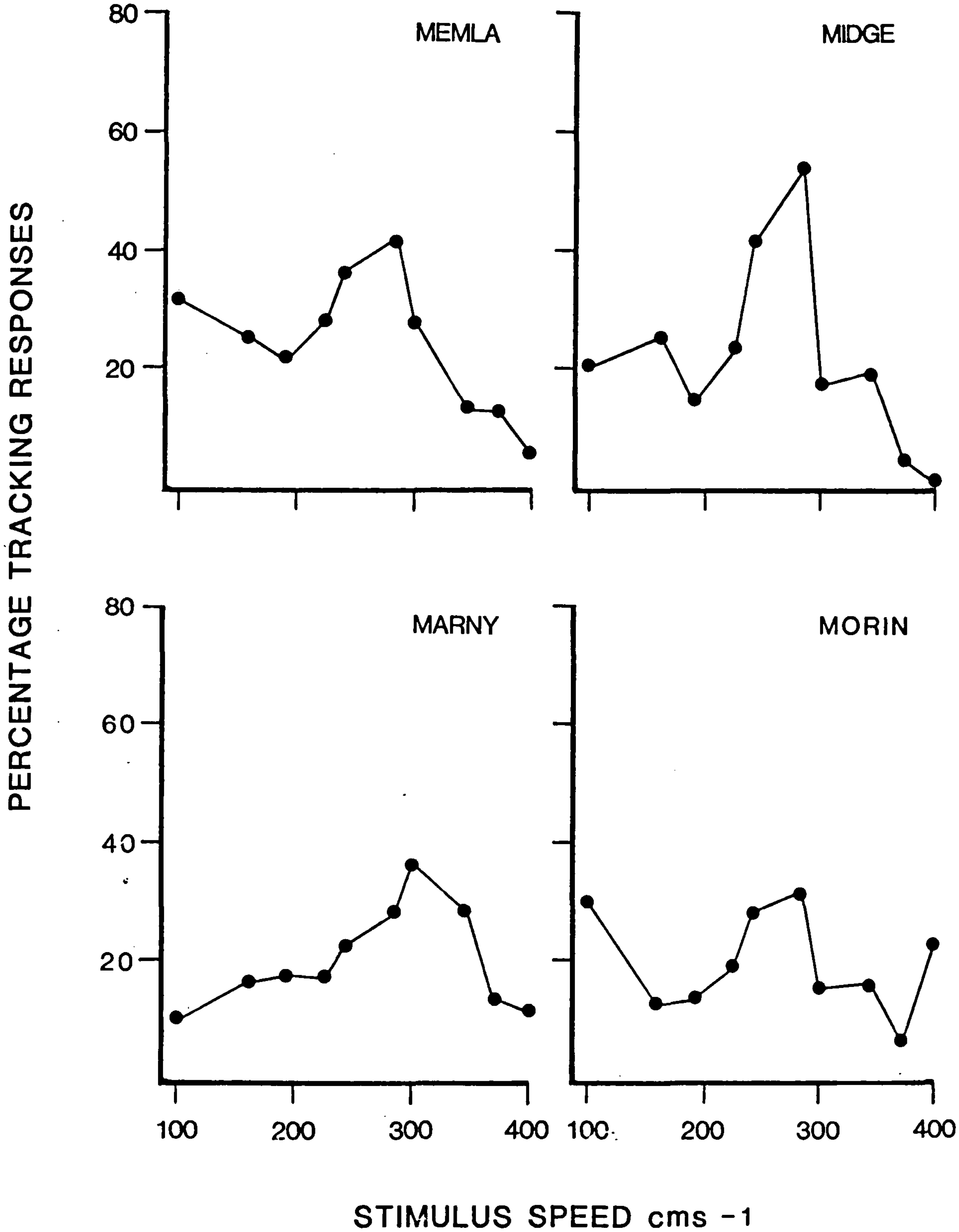


FIGURE 22. Percentage frequency of tracking responses as a function of stimulus speed for four polecats.

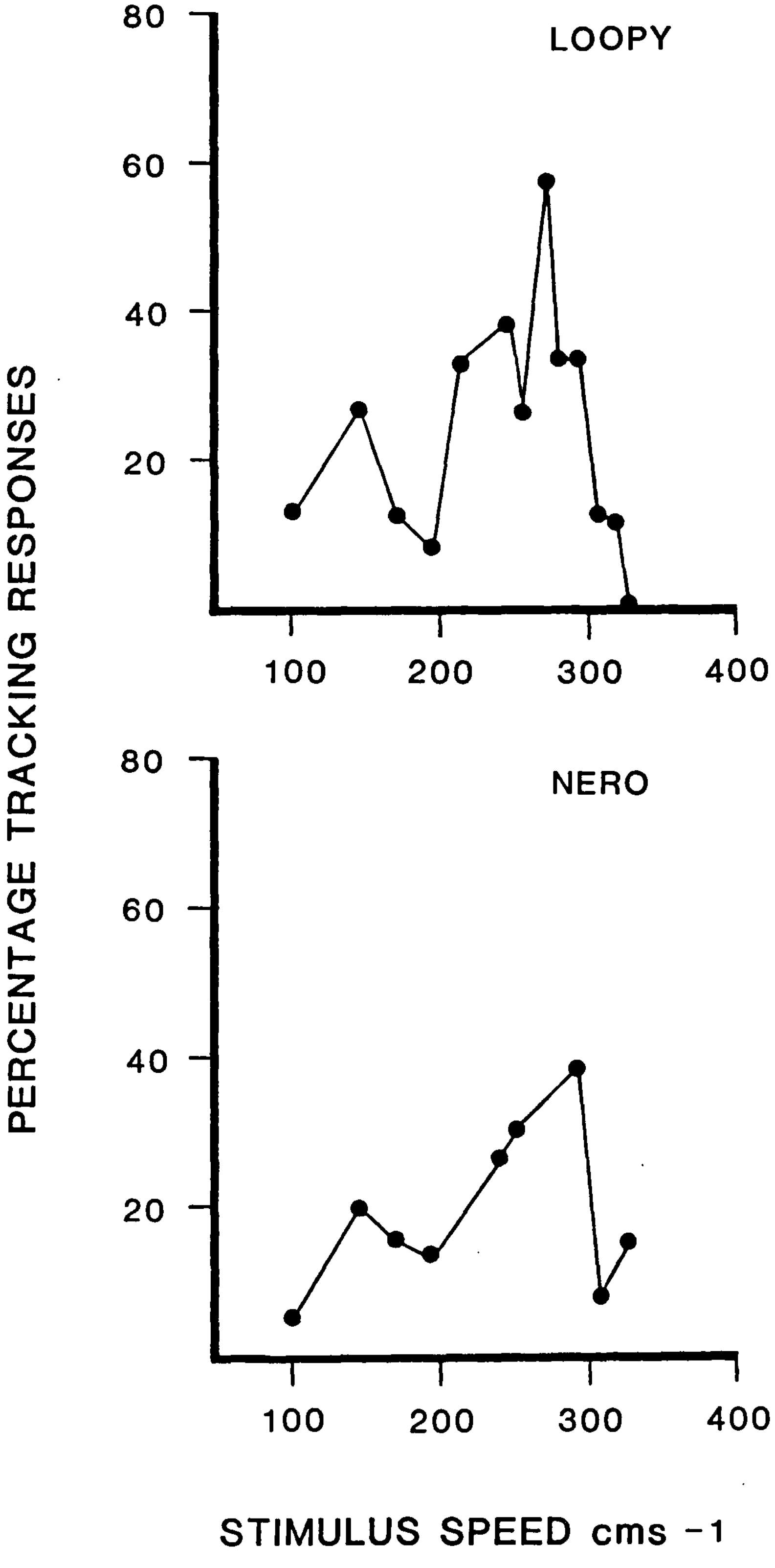


FIGURE 23. Percentage frequency of tracking responses as a function of stimulus speed for three weasels.

TABLE 43 Mean percentage correct scores of orienting responses.

	Memla		Midge		Marny		Morin	
	%correct	N	%correct	N	%correct	N	%correct	N
Tracking response	100.0	196	97.3	111	99.4	166	99.0	96
Quick response	70.0	550	57.4	272	70.4	575	64.3	367
"Guess"	93.3	15	80.8	26	77.8	18	100.0	16

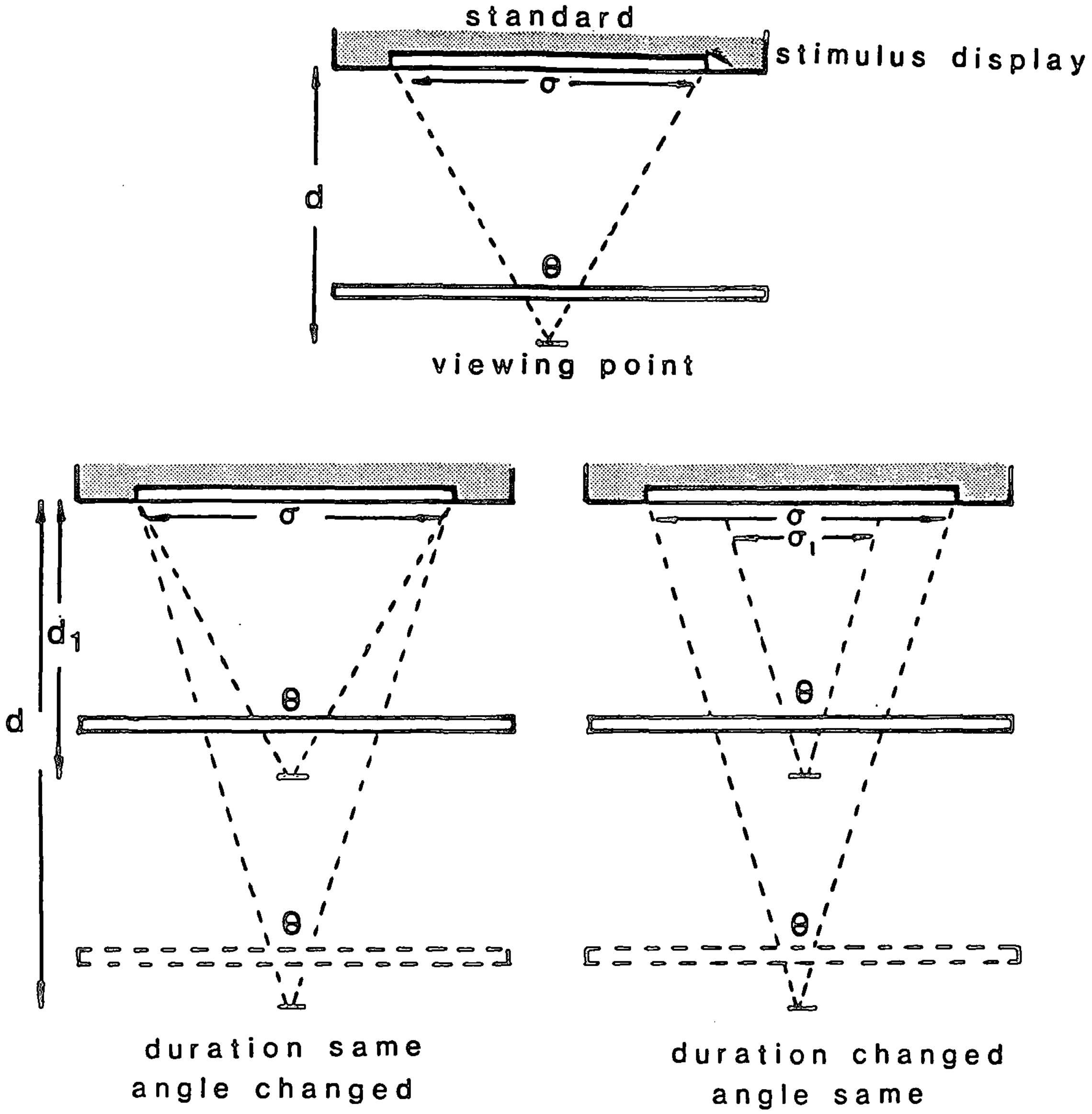
5.2 MOVEMENT DETECTION IN THE WEASEL AS A FUNCTION OF DISCRIMINATION DISTANCE

5.2.1 Introduction

At any given distance, the stimulus has an angular velocity relative to the visual field of the subject as well as having a linear velocity across the screen of the stimulus display. Changing the distance between the stimulus display and the animal therefore changes the proportion of the visual field traversed by the stimulus. In order to keep the discrimination angle constant, with changing distance, the width of the screen must be varied. This however, results in the stimulus spot being visible for different amounts of time (see Fig. 24). The two variables, discrimination angle and screen width, can be controlled for by conducting two series of experiments. In one, the screen width is kept constant; the "Traverse same: Angle changed" series, and one in which the discrimination angle (the angular portion of the animal′s visual field over which the stimulus travels) is kept constant; the "Angle same: Traverse changed" series.

5.2.2 Method

Three animals were used in the experiments, Nero and Loopy for the "Traverse same: Angle changed" series and Nero and Alex for the "Angle same: Traverse changed" series. The five discrimination distances tested were 10, 20, 30, 40 and



duration same
angle changed

duration changed
angle same

FIGURE 24. Effect of varying discrimination distance on discrimination angle and the distance traversed by the stimulus. KEY: d, Discrimination distance; θ, discrimination angle, σ, screen width.

50cm. Distances greater than 50cm could not be used owing to constraints imposed by apparatus design and the amount of space available. The ambient illumination was 1.26×10^{-2} mLambert, and the radiant intensity of the stimulus spot was 3.4×10^{4} µWsteradian^{-1}. For each series, one animal was tested with the farthest distance first and the nearest last (descending), while the second animal was given the opposite treatment (ascending). Each animal was tested at each distance until there had been over one hundred stimulus presentations of near threshold speeds. Every few days, the animals were tested with a simple motion detection task (stimulus speed 50cms^{-1}) for twenty stimulus presentations to check constancy of performance. Illumination, stimulus radiant intensity and discrimination distance were the same as the standard conditions (Section 5.1), in these sessions.

5.2.3 Results

Movement Perception Thresholds

The psychophysical functions for the two experimental series are shown in Figs. 25 and 26 and the linear thresholds as a function of discrimination distance are presented in Fig. 27. The values for the linear and angular movement detection thresholds are shown in Table 44.

The relationship between discrimination distance and movement detection threshold differed according to the parameter varied, although thresholds were fairly consistent

FIGURE 25. Psychophysical functions for two weasels as a function of discrimination distance.

Traverse same: Angle changed series.

Experimental conditions are given as;
viewing distance: screen width: discrimination angle.
Other conventions as in Fig. 20.

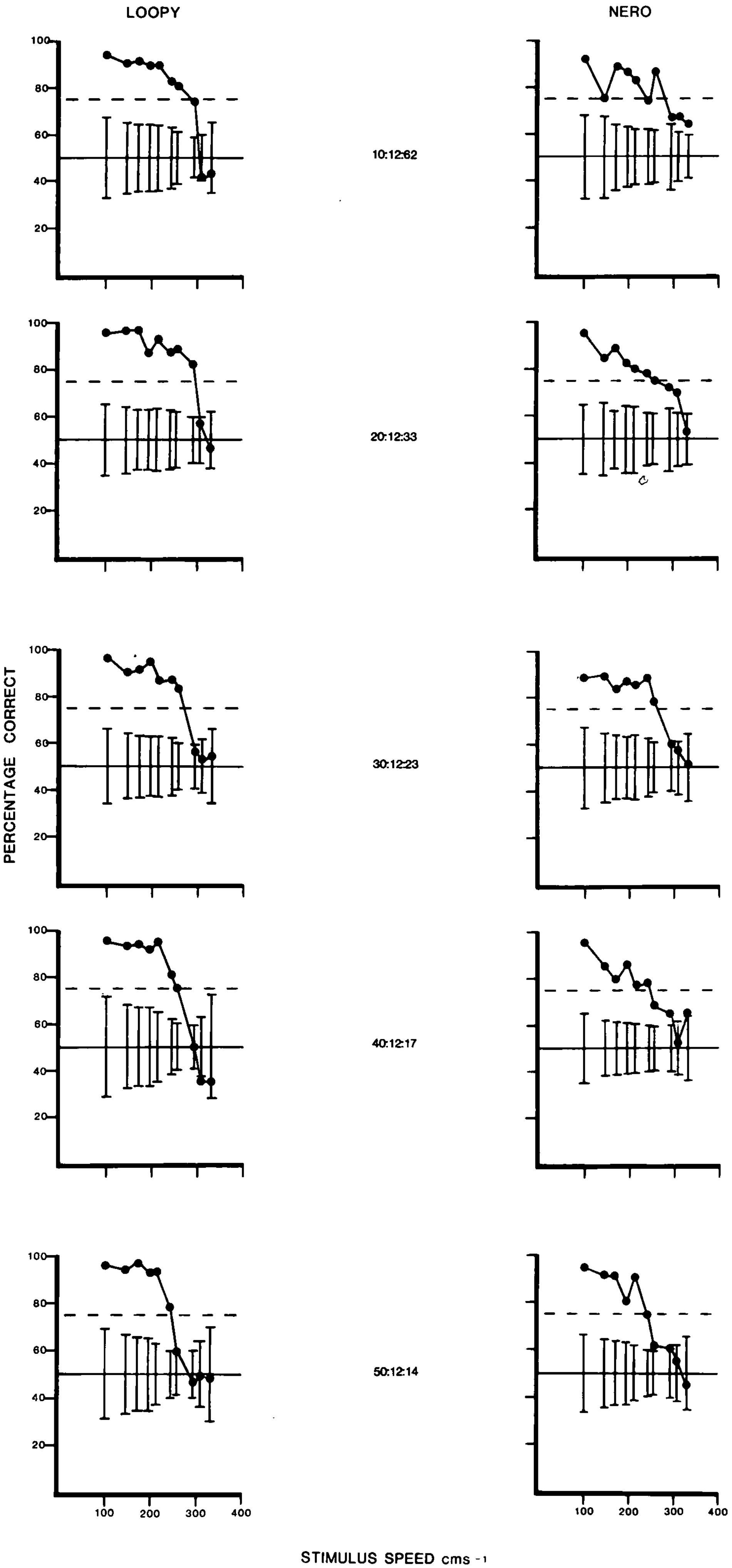
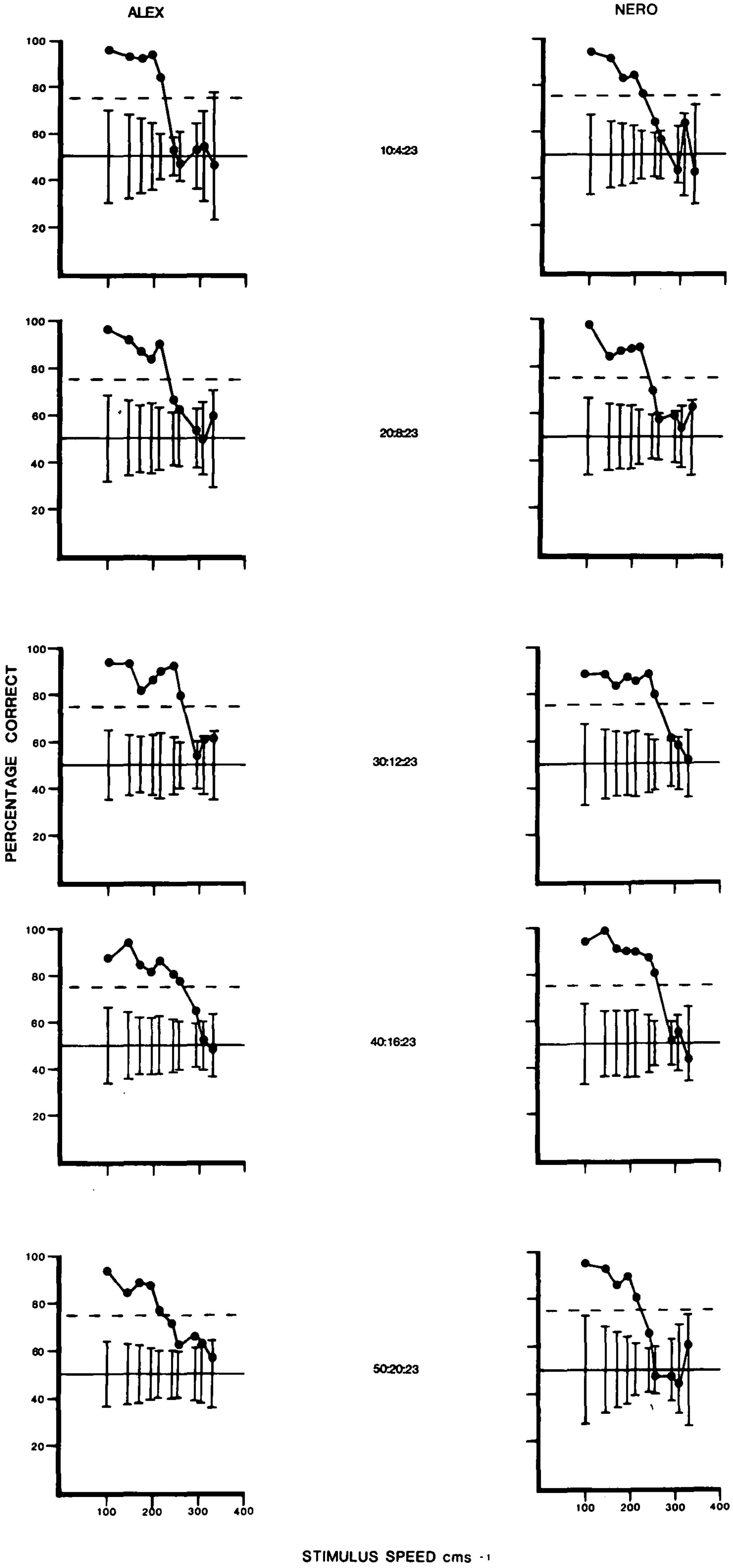

LOOPY
NERO
100
80
60
40
20
10:12:62
20:12:33
30:12:23
40:12:17
50:12:14
PERCENTAGE CORRECT
100
200
300
400
STIMULUS SPEED cms -1

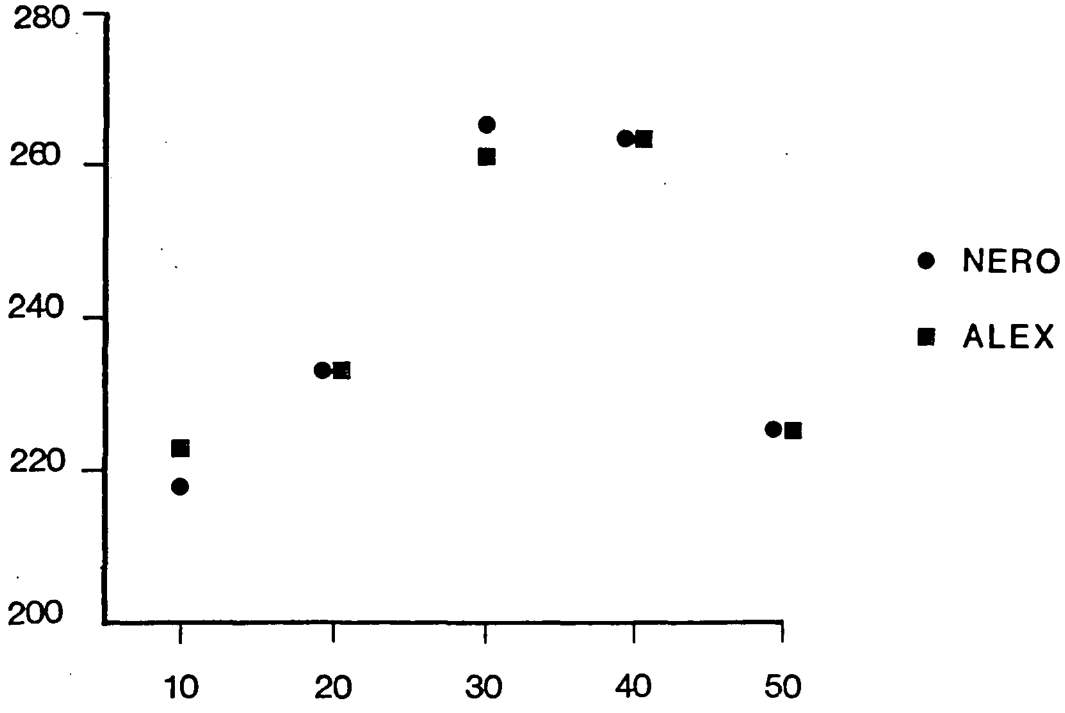
FIGURE 26. Psychophysical functions for two weasels as a function of discrimination distance.

Angle same: Traverse changed series.

Experimental conditions are given as;
viewing distance: screen width: discrimination angle.
Other conventions as in Fig. 20.


ALEX
NERO
100
80
60
40
20
PERCENTAGE CORRECT
10:4:23
20:8:23
30:12:23
40:16:23
50:20:23
100
200
300
400
STIMULUS SPEED cms -1

a) Angle same: Traverse changed series



b) Traverse same: Angle changed series

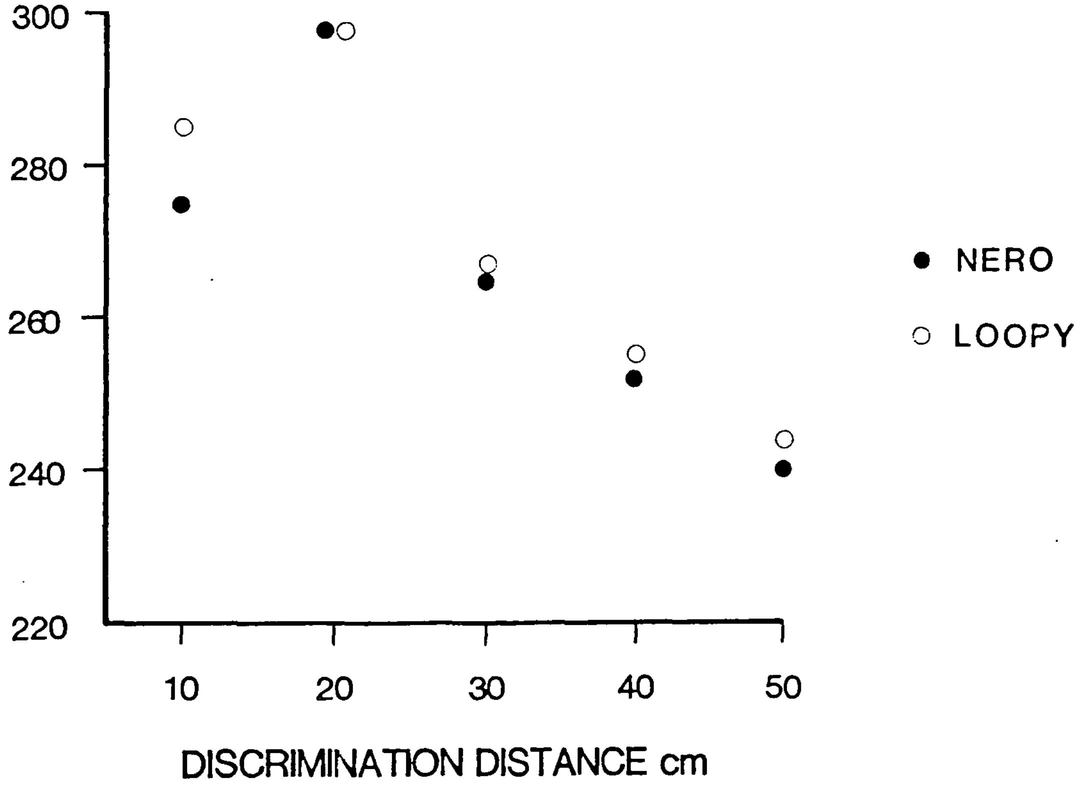


FIGURE 27. Linear movement detection thresholds (cms-1) as a function of discrimination distance.

TABLE 44 Movement detection thresholds of weasels as a function of discrimination distance.

Traverse same: Angle changed series

			Loopy			Nero		
Distance	Traverse	Angle	Linear Threshold (cms^{-1})	Angular Thresholds (^{o}s^{-1})		Linear Threshold (cms^{-1})	Angular Thresholds (^{o}s^{-1})	
				field	retina		field	retina
10	12	62.0	285	1473	54.5	275	1421	52.1
20	12	33.4	298	829	28.6	298	829	28.6
30	12	22.6	267	503	17.0	265	499	17.0
40	12	17.1	255	363	12.2	252	359	11.9
50	12	13.7	244	279	9.4	240	274	9.2

Angle same: Traverse changed series

			Nero			Alex		
10	4	22.6	218	1232	127.3	223	1260	127.3
20	8	22.6	233	658	33.7	233	658	33.7
30	12	22.6	265	499	17.0	261	492	16.6
40	16	22.6	263	372	9.4	263	372	9.4
50	20	22.6	225	254	5.2	225	254	5.2

over the discrimination distances used. When the screen width was varied, there was no clear relationship between threshold and distance (r=0.3, n=10, n.s.). There was a slight increase in threshold between 10 and 30 cm, associated with the increasing screen width, but beyond 40cm, the increased screen width did not appear to have any effect (see Fig. 27a). The greater distance may have resulted in a poorer discriminatory ability, as threshold was low at 50cm in both series. At near distances (10-20cm) in the "Angle same: Traverse changed" series, threshold was reduced under conditions of narrow screen width, compared to the result obtained in the "Traverse same: Angle changed" series (220cms^{-1} compared to 280cms^{-1} at 10cm).

When the screen width was kept constant at 12cm and the discrimination angle was varied, there was a slight decline in the threshold value from 298cms^{-1} at 20cm to 240cms^{-1} at 50cm (Fig. 27b). The threshold was negatively correlated with discrimination distance ($r=-0.86$, $n=10$, $p<0.01$).

Orienting responses

The percentage tracking responses for each viewing distance are shown in Table 45. In the "Traverse same: Angle changed" series, increasing distance from the stimulus may have caused an increase in tracking responses but this trend was only apparent in Nero. As orienting response data were only available for one animal in the "Angle same: Traverse changed" series, the results are inconclusive. It is

TABLE 45 Percentage frequency of tracking responses as a function of discrimination distance.

Discrimination Distance	% Tracking Responses	
	Loopy	Nero
10	13.0	16.5
20	13.7	18.2
30	12.5	17.8
40	13.4	19.2
50	11.7	27.5

noticeable that the frequency of tracking responses overall was lower than in the experiments under standard conditions (10-20% compared to 20-30%).

Using data from the "Traverse same: Angle changed" series, most tracking responses resulted in a correct response (96.6% for Nero and 95.3% for Loopy), with the animals' percentage correct score over the experimental series as a whole being 76.3% and 75.0% respectively.

5.3 MOVEMENT DETECTION IN THE WEASEL AS A FUNCTION OF STIMULUS RADIANT INTENSITY

5.3.1 Introduction

In many psychophysical studies of vision, light levels have been expressed in photometric units. However, photometric measuring instruments use a filter with absorbance properties similar to the human retina, therefore measurements made in these human based units may be inappropriate to animals with different visual systems. Also, photometric detectors measure light of a spectral composition corresponding to tungsten light sources, which have a different spectral composition to the phosphor light source used in the present experiments. As a result of the disadvantages of photometric units, radiometric units were used. Radiometry allows the total quantity of energy emitted by a stimulus to be measured and is expressed as microwatts steradian^{-1} (μWsteradian^{-1}). Unfortunately equipment was not available to measure the ambient illumination in radiometric units, so photometric measurements had to be made.

5.3.2 Method

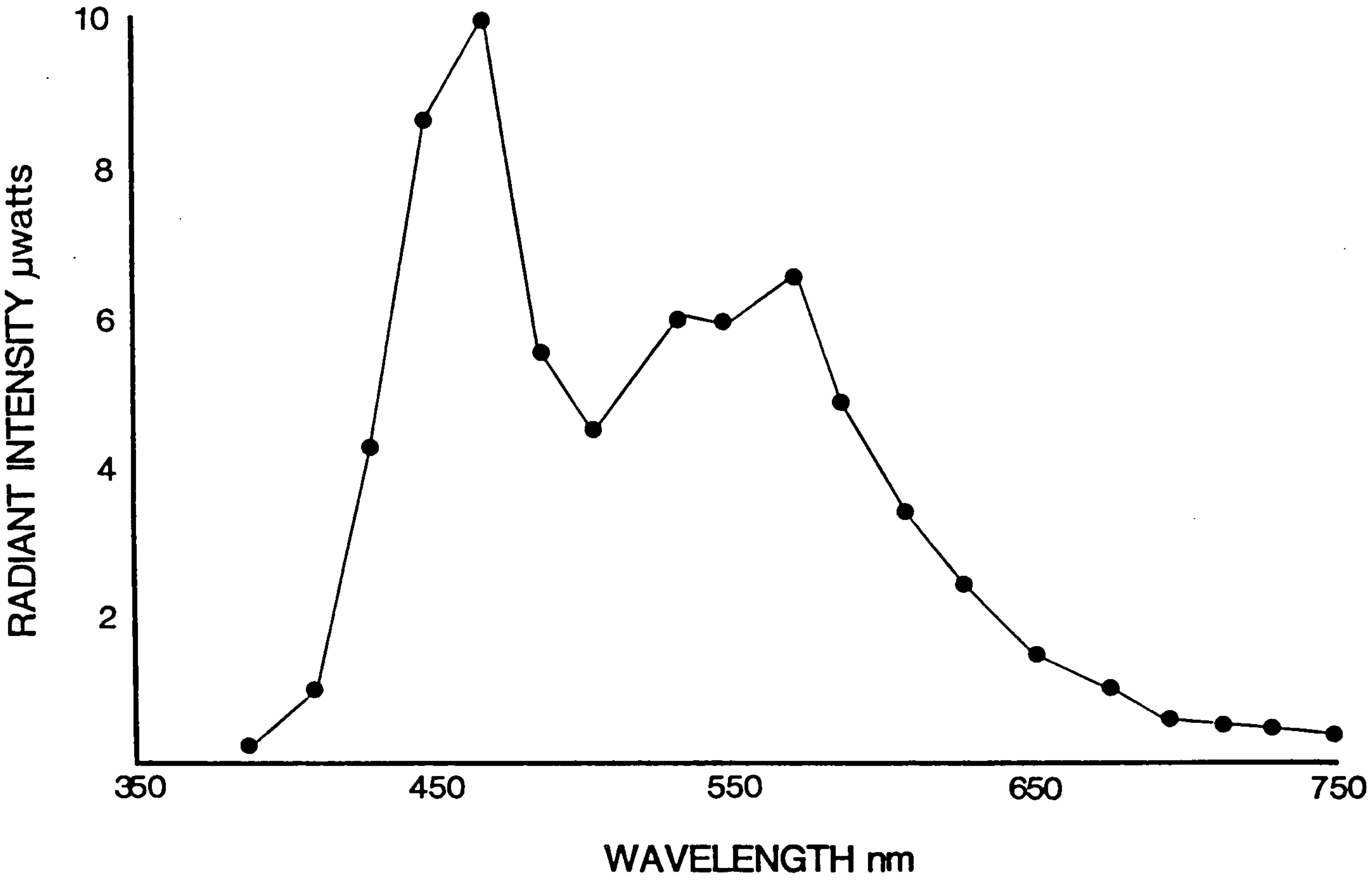
Experiments were carried out at five different stimulus radiant intensities. The radiant energy emitted by the stimulus was measured using a United Detector Technology PIN

10 DF Photodiode fitted to a Pacific Instruments Digital Photometer Amplifier. Measurement of the total radiant energy emitted by the stimulus was expressed in microamps (µA). A reading of 0.1µA was equivalent to 1µwatt (see Clements, 1980 and Clements and Dunstone, 1984). The values of the five radiant intensities are expressed as µWsteradian^{-1} in Table 46. The spectral composition of the stimulus has been measured previously by Clements (1980) and is reproduced in Fig. 28. There were peaks at 475nm and 575nm, i.e. most light was emitted towards the blue end of the spectrum.

The ambient illumination remained at 1.26 x 10^{-2} mLambert. It was measured with a SEI Spot Photometer with a viewing surface of barium sulphate. The discrimination distance remained constant at 30cm, with a screen width of 12cm, resulting in a visual field angle of 22.6^{0}. The order of presentation of the different stimulus conditions was randomised, being 3.4x10^{4}, 9.0x10^{4}, 872, 2x10^{5}, 35.4 µWsteradian^{-1} for Nero and 9.0x10^{4}, 872, 35.4, 3.4x10^{4}, 2.0x10^{5} for Loopy.

Each animal was tested under each stimulus condition until there had been over one hundred presentations of near threshold speeds. Again, there were periodic checks of performance on a simple motion detection problem, with illumination, stimulus radiant intensity and discrimination distance being as in the standard conditions.

FIGURE 28. Spectral emission characteristics of stimulus.



5.3.3 Results

Movement Perception Thresholds

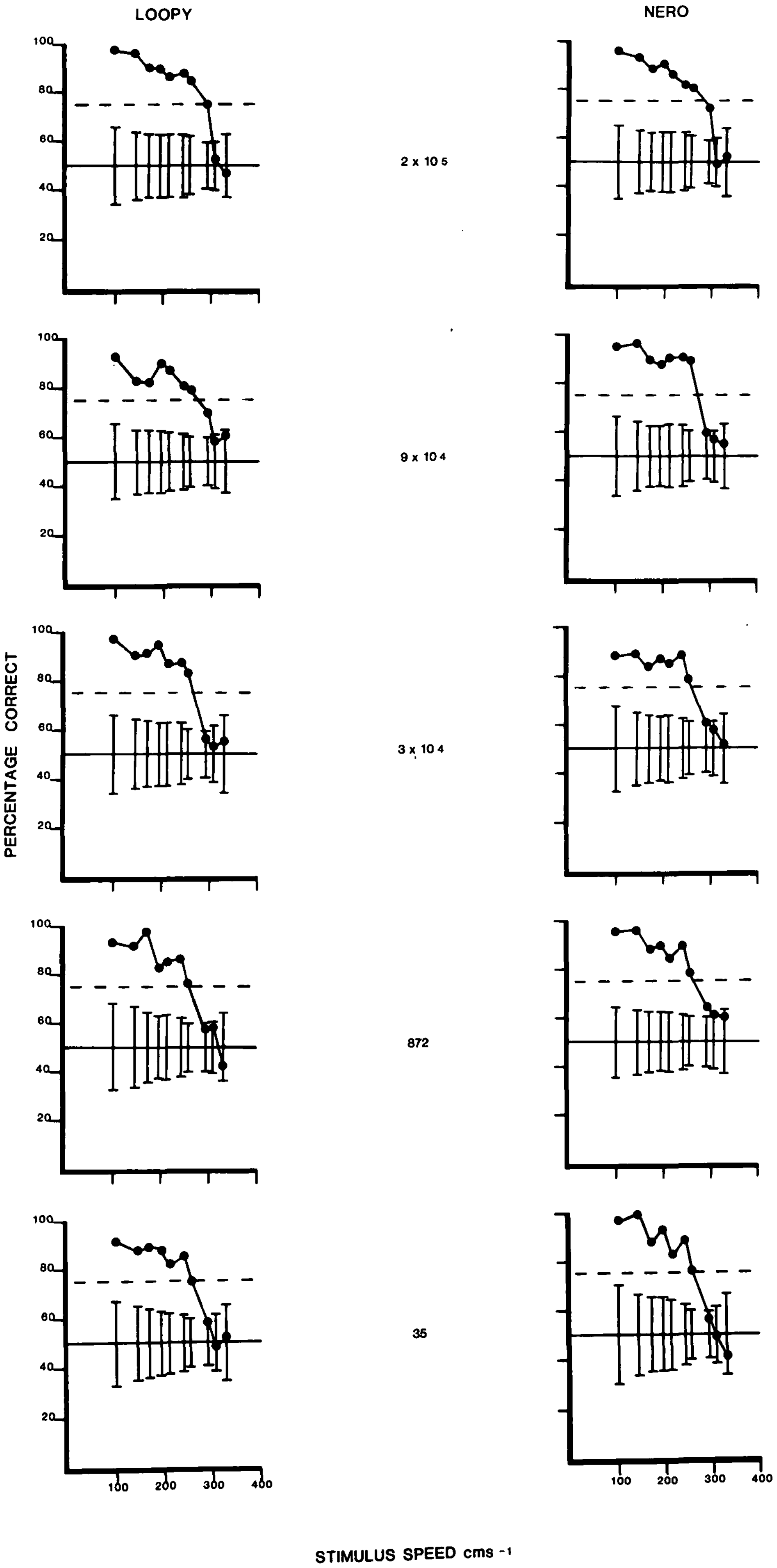
The psychophysical functions for the discrimination task under the five radiant intensity conditions are shown for the two subjects in Fig. 29. The motion detection thresholds in linear units as a function of stimulus radiance are presented in Fig. 30 and the thresholds are expressed in both linear (cms^{-1}) and angular units ($^{o}s^{-1}$) in Table 46. Again, the ability of the weasels to discriminate the direction of movement was fairly consistent but there was a slight decline from approximately $290cms^{-1}$ ($540^{o}s^{-1}$) at $2.0x10^{5}$ $\mu Wsteradian^{-1}$ to $257cms^{-1}$ ($484^{o}s^{-1}$) at 35.4 $\mu Wsteradian^{-1}$. Regression analysis of the log linear threshold data against log stimulus radiant intensity revealed a significant correlation ($r=0.85$, $n=10$, $p<0.01$).

Orienting Responses

Tracking responses were recorded under all stimulus conditions, the total percentage tracking responses for both correct and incorrect responses are shown in Table 47. There was no clear trend and a lower frequency of tracking responses overall were observed compared to the standard conditions (Section 5.1). The percentage correct score for the experimental series was 74.0% for Loopy and 77.3% for Nero. However, 96.6% of the tracking responses were followed by a

FIGURE 29. Psychophysical functions for two weasels as a function of stimulus radiant intensity.

The five conditions of stimulus radiant intensity are indicated.


LOOPY
NERO
PERCENTAGE CORRECT
100
80
60
40
20
2 x 10 5
9 x 10 4
3 x 10 4
872
35
100
200
300
400
STIMULUS SPEED cms -1

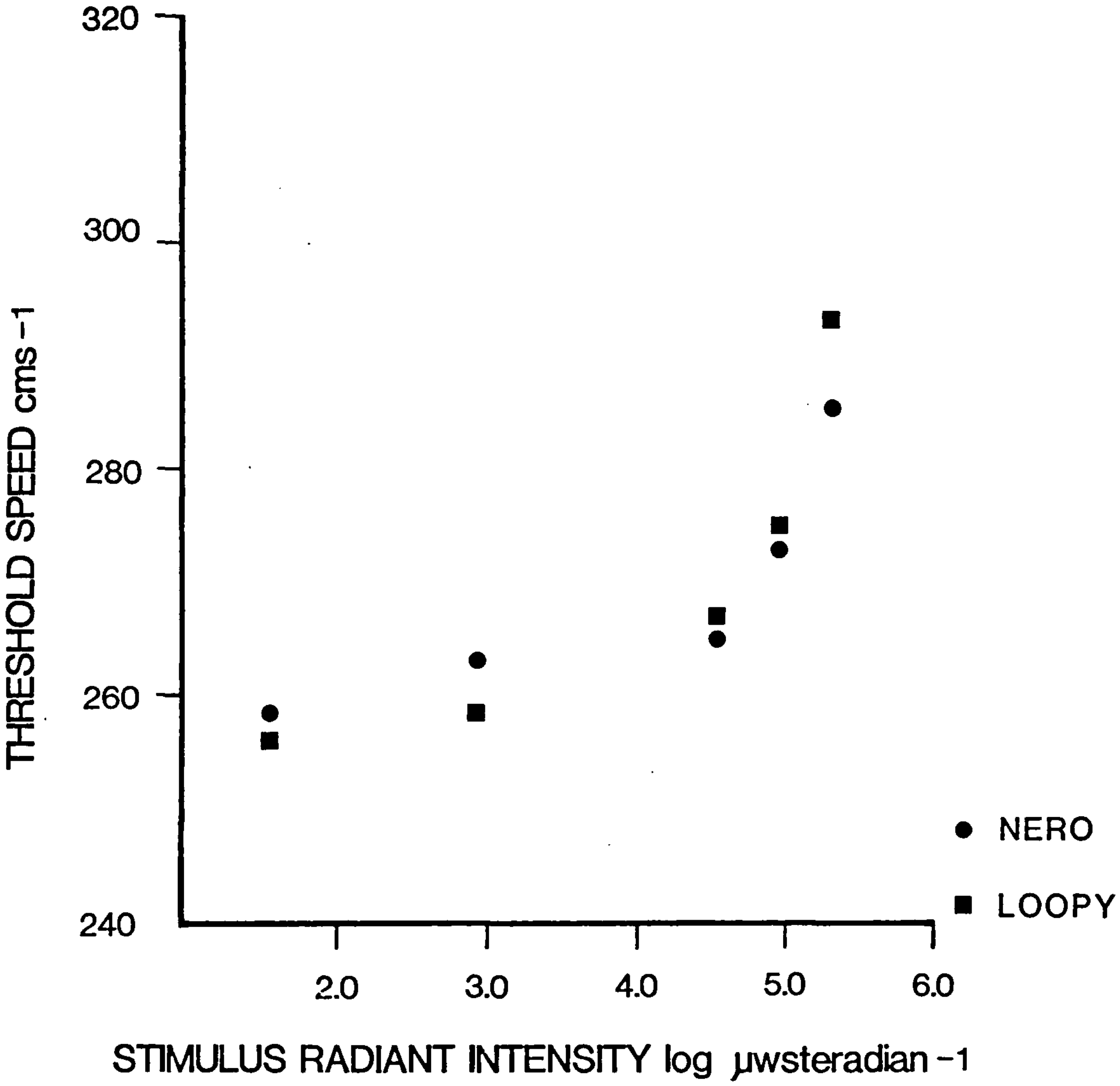


FIGURE 30. Linear movement detection thresholds (cms-1) as a function of stimulus radiant intensity

TABLE 46 Movement detection thresholds of weasels as a function of stimulus radiant intensity.

	Loopy			Nero		
Stimulus Radiant Intensity (μWsteradian^{-1})	Linear Threshold	Angular (field)	Thresholds (retina)	Linear Threshold	Angular (field)	Thresholds (retina)
35.4	256	482	16.3	258	486	16.3
872.0	258	486	16.3	263	495	16.6
3.4×10^4	267	503	17.0	265	499	17.0
9.0×10^4	275	518	17.4	273	514	17.4
2.0×10^5	293	552	18.6	285	537	18.2

<u>TABLE</u> <u>47</u> Percentage frequency of tracking responses as a function of stimulus radiant intensity.

Stimulus Radiant Intensity (μWsteradian^{-1})	% Tracking Responses	
	Loopy	Nero
35.4	13.5	13.7
872.0	15.1	16.1
3.4×10^4	12.5	17.8
9.0×10^4	13.4	16.7
2.0×10^5	12.5	13.9

correct choice. There appears to be a slight increase in the percentage correct score of the tracking responses with increasing stimulus brightness. It is possible that the higher motion perception thresholds attained under conditions of higher stimulus radiance are partly explained by this trend.

5.4 DISCUSSION

Weasels and polecats were successfully trained to perform a complex manipulative task, in response to a small, transient stimulus, and to negotiate the apparatus to obtain reinforcement. There is no significant difference in movement detection ability between the two species, although the weasels thresholds tended to be lower than the polecats.

Owing to the time and labour intensive nature of the procedure only small numbers of animals were used in these experiments. However, Still (1982) maintains that large numbers of animals are not needed if standard psychophysical procedures are used. Even so, there was relatively little variation within species, this being particularly so in the polecats.

The movement detection thresholds obtained for both species ranged from 228 to 305cms^{-1}, which are equivalent to values of 8.2 - 11.0kmhr^{-1}. These values show some correspondence to the typical running speeds of small rodents, 6kmhr^{-1} is quoted as the typical running speed of the mouse (Dagg, 1977), with a maximal speed of 13kmhr^{-1} (Garland, 1983). It might be considered adaptive for a predator to have a discrimination ability within the speed range of its most commonly encountered prey. Although the visual system needs to be "tuned" to the speed of the prey, the size and shape of the stimulus is also important (Kennedy, 1936).

The present experiments investigated directional movement detection, they did not take into account perception of movement for which the direction could not be discriminated. The objective was to investigate movement detection capability with reference to the animals' predatory behaviour, a threshold being determined for the highest speed at which direction could be perceived. It was intended that the presentation of the stimulus could resemble a situation where the predator is a short distance from "prey" which can be seen for only a short time, as for example when a mouse runs between natural obstacles, a likely situation for a hunting mustelid.

Unfortunately there is a notable lack of equivalent work to which the present results can be compared, the only exception being studies on the directional motion detection capability of the American mink, Mustela vison Schreber by Dunstone and Clements (1979), Clements (1980), and Clements and Dunstone (1984). Clements (1980) estimated the high speed movement detection thresholds of four mink to give a mean value of 278cms^{-1}, which does not differ greatly from the thresholds of the polecat and weasel.

It would be expected that these closely related species should possess similar visual capabilities, as they have been shown to possess retinas of similar gross structure (Gewalt, 1959). The two species that most closely resemble each other in terms of appearance, size and ecology are the polecat and mink and they are found to have a similar movement perception threshold, while the weasel possesses a marginally lower threshold.

The slight difference in threshold between the polecat and weasel could be a consequence of the difference in body size. It is possible that the visual acuity of the weasel could be marginally poorer due to the smaller eye-size. Hairston et al. (1982) found that larger sunfish detected planktonic prey that subtended smaller visual angles than smaller fish of the same species, a direct consequence of the higher packing density in larger retinas.

It is likely that the discrimination of moving stimuli is partly dependent on visual acuity, particularly when small stimuli are involved, but Reading (1972a) found no correlation between dynamic and static acuity in human subjects, as dynamic acuity is dependent on eye and head movements. It would not be unreasonable though, to assume that good acuity is necessary for good motion perception.

Although the visual acuity of the weasel is not known, it is likely to be similar to that of the mustelid species so far tested (e.g. Neumann and Schmidt, 1959; Balliet and Schusterman, 1971; Sinclair et al., 1974). The stimulus was likely to be within the acuity range of the weasel; it was bright and conspicuous and did not suffer any marked degradation in brightness over the distances used.

An alternative explanation could be that as weasels are more active, intractable animals than polecats (pers. obs.), they could have been more inattentive during the visual discrimination task.

Motion perception capability is affected by a variety of factors including direction and distance of travel of the stimulus and illumination (Kennedy, 1936). A considerable amount of research has been concerned with how visual abilities are affected by limiting luminance. The results from the present study indicate that movement detection ability in the weasel was reduced when the brightness of the stimulus was lowered, which is in agreement with other studies (e.g. Brown, 1958). The decline in ability could be attributed to the diminished amount of light reaching the retina. Changes in retinal sampling time arising from reduced light levels causes poorer motion perception, since a long retinal memory (persistence time) improves sensitivity at the expense of motion detection (Ripps and Weale, 1976).

The decline in threshold in the weasel may also have been due to the reduced contrast between the stimulus and background illumination at lower stimulus radiant intensities. Static visual acuity (Shlaer, 1937), dynamic acuity (Brown, 1972c) and flicker-fusion frequency (Crozier et al., 1936) all show a decrement in performance when stimulus-background contrast is reduced. Polecats and weasels are predominately crepuscular, (Kavanau, 1969; Corbet and Southern, 1977), so they often hunt under conditions where prey do not contrast greatly with the background. Therefore it is of interest to investigate visual capability at low stimulus-background contrast levels, in terms of the animals' predatory behaviour. Recent work by Thompson (1982) on human subjects has shown how movement perception depends on contrast. Reduced contrast caused observers to overestimate the velocity of fast-moving gratings. It is possible that this effect occurred in the present experiments on the weasel.

It is interesting to compare the performance of weasels with that of mink (Clements, 1980; Clements and Dunstone, 1984). The decline in threshold with decreasing stimulus radiant intensity was less marked in the weasel compared to the mink. Unfortunately, the stimulus brightness levels used in the different experiments on the two species were not the same, although they were similar. Movement perception thresholds of the weasel were lower than the mink under conditions of high stimulus radiant intensity ($2.0-2.5 \times 10^5$ μWsteradian^{-1}), but they were higher with a stimulus of low radiant intensity (35.4-58.0 μWsteradian^{-1}). It is possible that the weasel retina has a marginally shorter memory time than the mink under conditions of low photon flux or the weasel eye may admit more light than that of the mink, i.e. it is better adapted for low light intensities.

The two experimental series concerned with discrimination distance produced different results depending on whether or not the screen width was varied. When the screen width was constant ("Traverse same: Angle changed" series) there was an inverse relationship between viewing distance and threshold. The slight decline in threshold with distance could be explained by a deficiency in the visual system or could have a behavioural explanation. There is the possibility that the weasel is myopic, but this is unlikely as most species so far studied tend to be hypermetropic, with mammals having small eyes showing a higher apparent degree of hypermetropia than those with large eyes (Glickstein and Millodot, 1970). A recent behavioural study on the rat (Dean, 1981) provided no evidence for short-sightedness up to a distance of 160cm and there is no reason to suppose that the weasel is inferior in this respect.

An alternative explanation would be that at greater distances from the stimulus, the weasels became inattentive. The tracking responses were indicative of attention being paid to the stimulus as they were nearly always followed by a correct response. The close correspondence between the tracking response peaks and the threshold value estimated from the psychophysical functions suggest that these responses could be used as a behavioural method of threshold estimation and certainly they confirm the value determined using the percentage correct responses method.

The tracking responses are similar to the orienting responses shown by the Californian sea lion (Schusterman, 1965) and the American mink (Dunstone and Sinclair, 1978b) during other visual discrimination tasks. However, in these previous experiments orienting responses involved hesitant looking back and forth between two stimuli. As only one stimulus was available in the present experiments, this could not occur. While tracking movements peaked near threshold speeds, they did not remain high at speeds above threshold, so in this respect they resemble the orienting responses shown by the mink in visual acuity experiments (Dunstone and Sinclair, 1978b).

Evidence for lack of attention at long viewing distances is inconclusive as there was a reduction in the number of tracking responses at greater distances in one weasel, but not in the other. However, the lower frequency of tracking responses observed in the discrimination distance experiments (Section 5.2), and also when stimulus radiant intensity was varied (Section 5.3), compared to those under standard conditions, suggests that less attention is paid to stimuli at distances greater than 20cm (and also to stimuli travelling across a narrow space).

As tracking responses did not occur very often, it appears the animals were not always giving the stimulus their full attention. The subjects most often made a "quick response", where attention was given to the edges of the display screen. It therefore could be argued that the experiments were not measuring directional movement perception, since the animals were making their discrimination according to which side of the screen the stimulus emerged from. However, as tracking responses also occurred, it is likely that the direction of movement of the stimulus was also discriminated. The problem of how the subjects were responding to the stimulus can only be resolved by conducting further series of experiments.

In the "Angle same: Traverse changed" series the variables discrimination distance and screen width interacted to some degree. Variation in the horizontal distance travelled by the stimulus was found to have an important effect on movement detection ability. Under conditions of short distance and traverse, the narrow screen width caused a decrease in threshold. It is likely that the relatively large spot moving quickly over a small distance would be a difficult discrimination problem. The movement detection threshold increased slightly with increasing screen width up to a viewing distance of 40cm. The distance of traverse of a stimulus has been found by other workers to be an important limiting factor for movement perception (e.g. Cohen and Bonnet, 1972). Henderson (1973) stated that movement discrimination is dependent principally on the time and distance of transit of the stimulus, rather than on the target luminance. Certainly in these experiments there was a relatively greater decrement in threshold when screen width was limiting than with any of the stimulus radiant intensities tested.

Nevertheless it is apparent that the weasel is capable of accurate visual discrimination of the direction of high-speed moving stimuli over a range of stimulus conditions, a capability which this animal shares with its close relatives, the polecat and mink.

CHAPTER SIX RELATIVE MOVEMENT DETECTION

6.0 INTRODUCTION

The previous movement discrimination experiments involved the detection of absolute velocity. However, moving stimuli often have a relative velocity in relation to other moving objects. A single stimulus presented in a controlled environment without additional information to other senses does not have much relevance to predatory behaviour *per se*. Movement cues do not usually occur in isolation, additional stimuli may be available from other prey animals or from other moving stimuli in the environment. Relative movement detection tasks have most often involved a discrimination between a stationary and slow-moving stimulus (e.g. Berkley, 1970). A discrimination between two fast-moving stimuli is of more relevance to a predator, for example, such a discrimination may occur when selecting single prey from groups. Such a discrimination task has not been investigated often, an exception being the work of Thompson (1984). Experiments are conducted to investigate the ability of a predator to discriminate between identical objects moving at different velocities and also between a moving and stationary stimulus.

6.1 MATERIALS AND METHODS

Experiments were designed to investigate the ability of the polecat to discriminate between two identical objects moving at different speeds, in opposite directions. The animals were trained to make a discrimination based on the relative movement of two stimuli, choosing one which was moving slower or faster. The stimuli were moved in the horizontal plane along a purpose-built trackway.

The apparatus used is illustrated in Fig. 31. The trackway consisted of two parallel rails, 1.9m long, mounted on wooden beams. The drive from a "Parvalux A30 F42" DC electric motor was transmitted through a pulley system situated at the end of each track by a nylon cord attached to the stimulus carrier. The movement of the stimulus was controlled by five limit-microswitches on each track. The pulley system and motors were enclosed in boxes (32x31x77cm) to exclude the animals.

The stimulus was a perspex rectangle, (10.5x20.5cm), suspended from a metal strip attached to the stimulus carrier. There were two stimuli, one on each track, 10cm apart. The trackway height was arranged so that each stimulus was at polecat head level, i.e. 6.0cm above the floor. Attached to the rear of the stimulus was a perspex dish into which food reward could be placed. A stimulus card (8.5cmx8.5cm) could be mounted on the front of the stimulus. The electronic

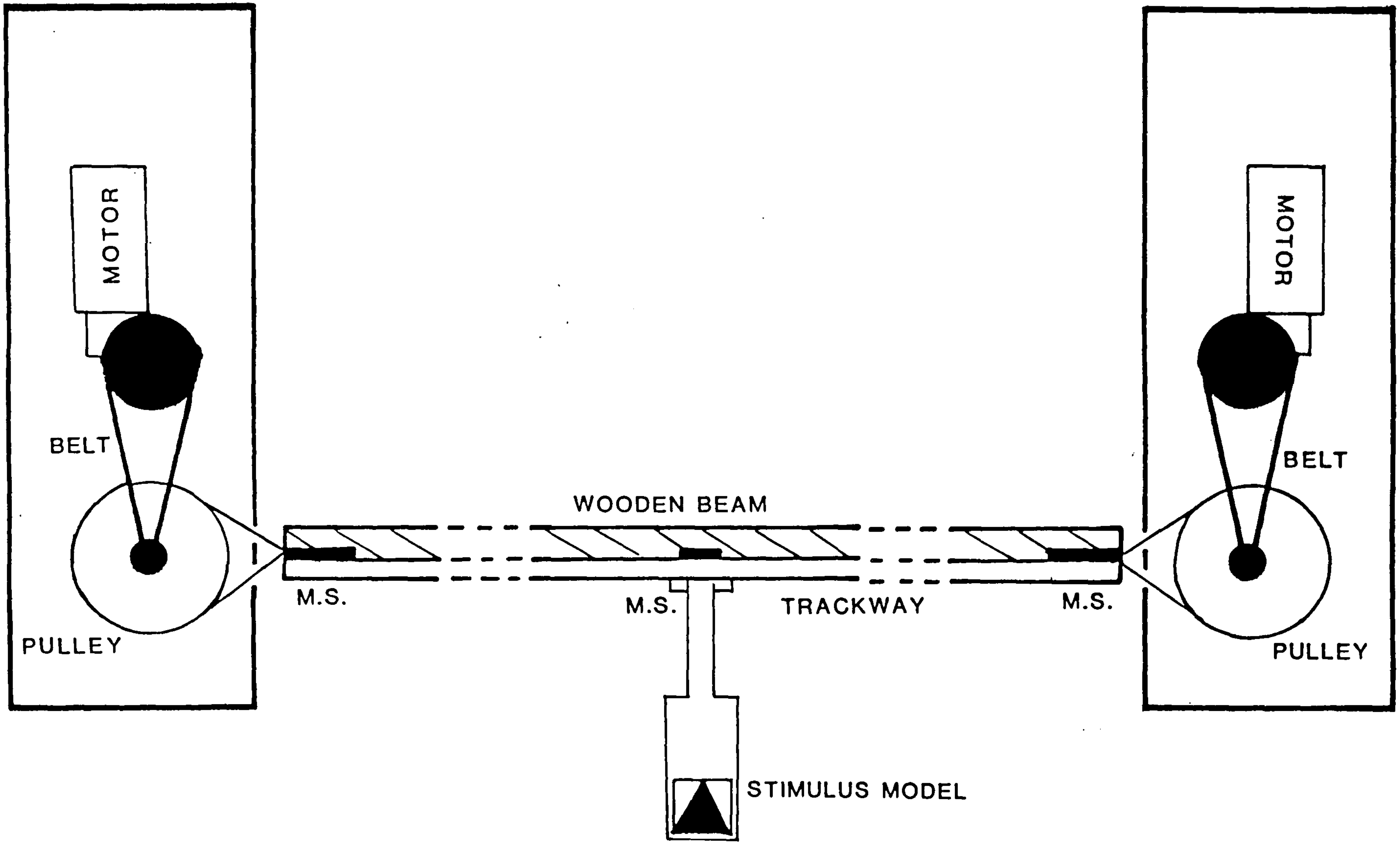


FIGURE 31. Plan diagram (side elevation) of trackway apparatus. One track is illustrated.
Key: M.S.; limit-microswitch.

circuitry involved in moving the stimuli was replicated in each track.

A schematic diagram of the electronic logic system for one track is illustrated in Fig. 32. The movement of the stimulus along the track was powered by a motor which was energised by the choice of one of two relays. The speed of the stimulus was controlled by an oscillator in the speed control unit. The speed could be pre-set before each trial by the operator using the dial on the speed control unit. The minimum and maximum speeds available were 1.0 and 100.5cms^{-1} respectively. The speed of the stimulus was recorded as the mean speed over the entire length of track. An oscillator drove an amplifier which was part of the motor-drive circuitry. There were two amplifiers, one for each direction. The switching on and off of the amplifiers was via a relay; pressing a start button on the hand controller switched a relay on, which was held on until the stimulus reached a limit-microswitch. Of the two microswitches mounted at each end of the track, the one nearest the end prevented "over-run", stopping the stimulus if the first failed to do so.

If the stimulus was initially positioned at one end of the track, pressing the control button (start) caused the stimulus to move towards the centre until it contacted the central limit-microswitch. Pressing the control button again re-initiated the relay and the stimulus moved off in the same direction until it contacted the end-of-track limit-microswitch. The relay was thus switched off and

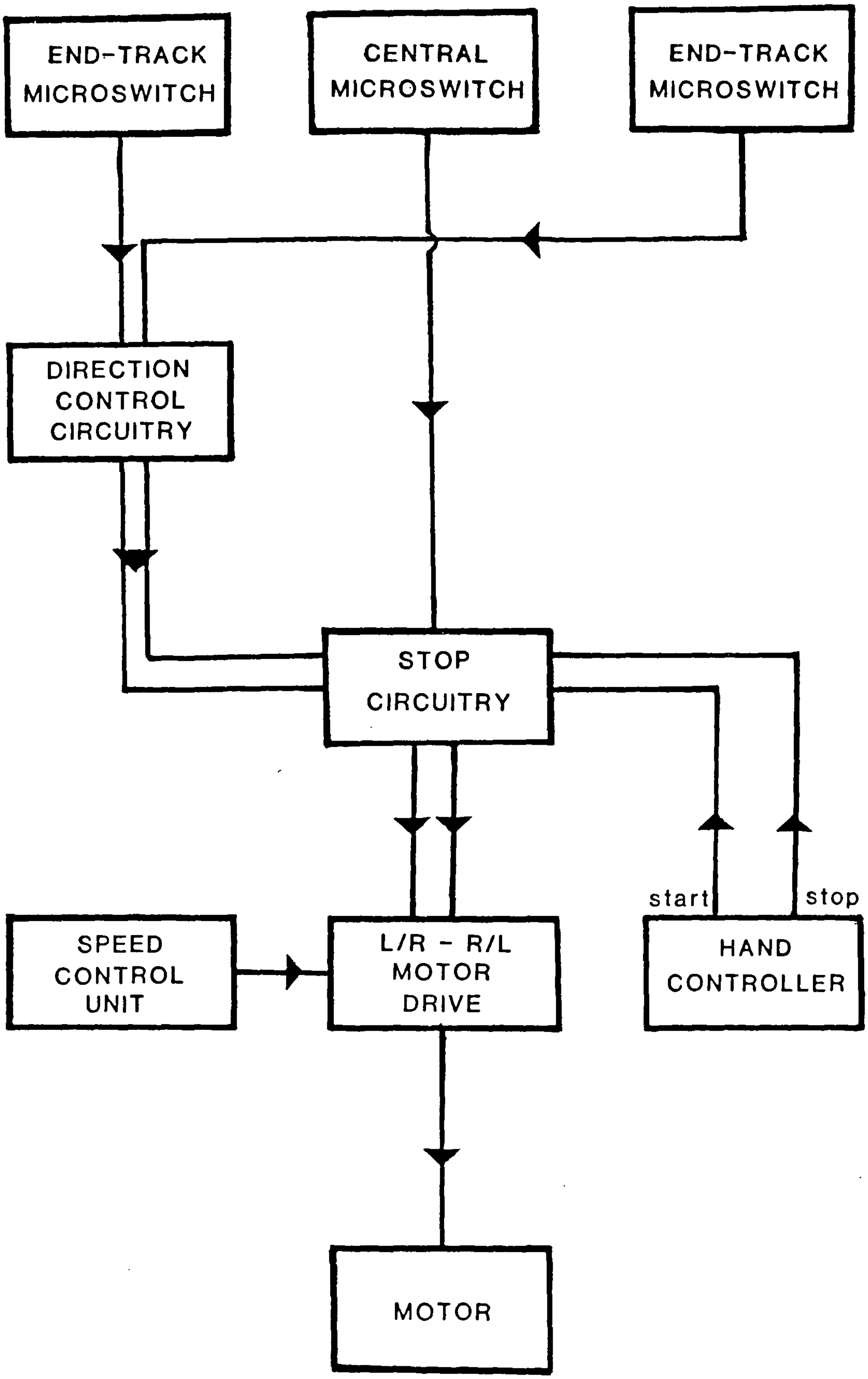


FIGURE 32. Schematic diagram of the electronic system for one track.

control transferred to the other relay, which on being initiated from the hand controller sent the stimulus back in the opposite direction.

If the stimulus was not required to stop in the centre, keeping the control button pressed down kept the stimulus moving. Pressing the stop button on the hand controller at any time cancelled the relay (it was equivalent to the stimulus hitting the central microswitch). There was a control (start) button for each of the tracks so that they could be used independently, and there was a third control button for simultaneous use.

6.2 DISCRIMINATION BETWEEN MOVING AND STATIONARY STIMULI

Training Procedure

Animals were trained to associate moving stimuli with food by allowing them to chase and capture the stimuli. The subjects were six polecats, three males and three females, aged between six and eighteen months at the commencement of training. Initially, each animal was left in the experimental room for one half-hour session to accustom it to the apparatus. The animals were then encouraged to feed from the small dishes attached to the rear of the stimuli. These were situated out of direct view, so that during an experiment a polecat would be unable to see if a particular dish contained food. The food reward used was 1.0ml of "Heinz" strained baby food, "Beef and Oxtail Dinner" per trial. When a subject consistently licked food from the dishes, the stimulus was moved slowly while the animal was actually feeding. The stimulus was moved at $38.0cms^{-1}$ so that the polecat could follow the stimulus while licking up the food reward. The track on which the moving stimulus travelled and the direction of travel was selected at random.

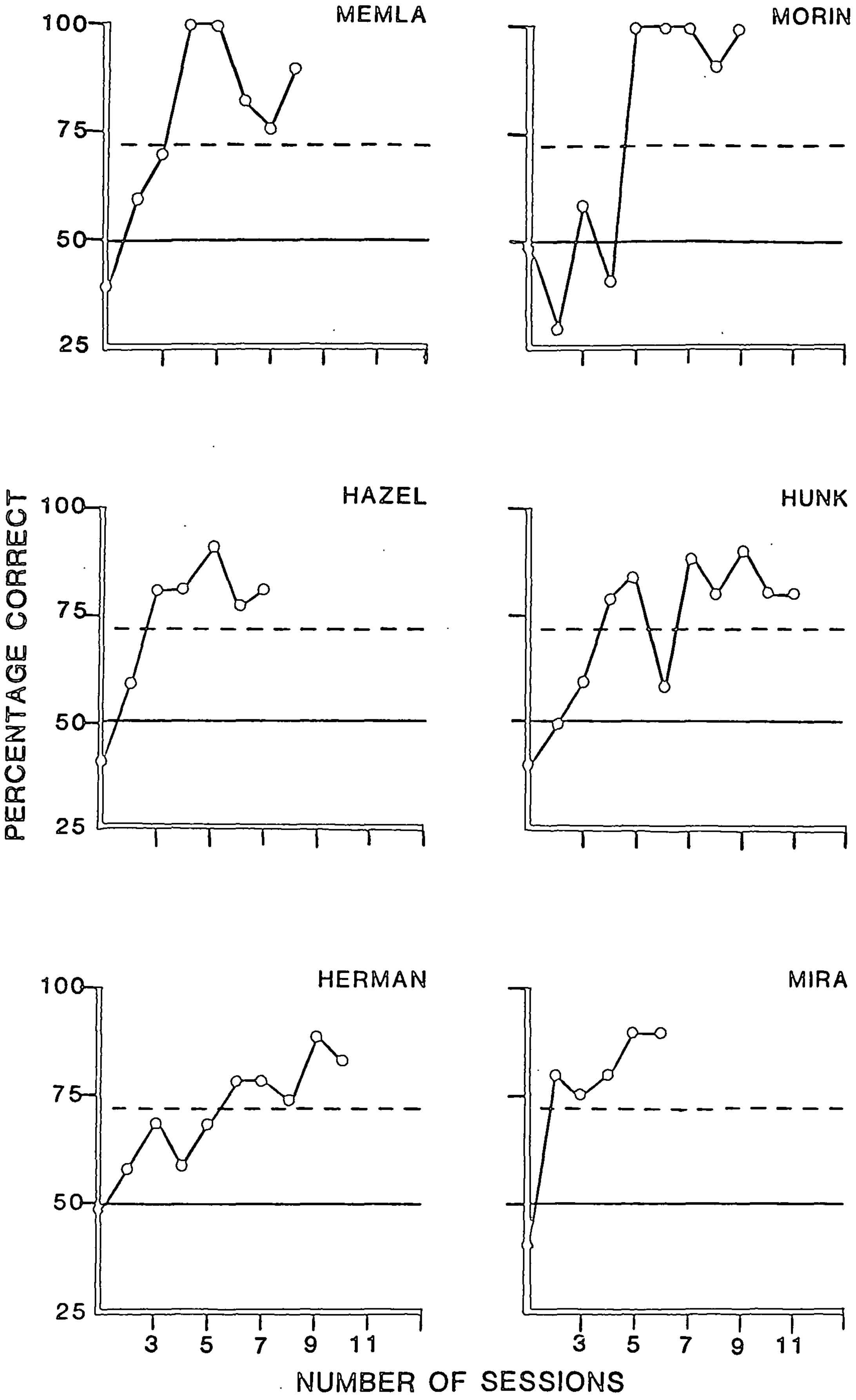
The speed of the stimulus was then gradually increased so that the animal was encouraged to chase it to obtain a food reward. Each polecat was trained to pursue the stimulus rather than wait until it had made its full traverse along the track. When a subject approached the trackway the stimulus was moved; usually the polecat would give chase and as soon as it caught up with the stimulus this was stopped, using the hand control unit, allowing the animal to feed. The subject was released from a carrying box at a point 75cm from the apparatus. The stimulus was moved on the emergence of the head and shoulders of the subject from the box. The animal was trained to return directly to the release-point after feeding from the reward dish on the stimulus. This was achieved by giving an additional small food reward when the polecat entered the carrying box. This established a procedure of release, chase, feed and prompt return to the box.

A correct response was defined as when the subject chased the moving stimulus, which was then stopped by the operator to allow the animal to feed. An incorrect response occurred when the polecat ignored the moving stimulus and attempted to feed from the non-rewarded stationary one. Unfortunately, as the food reward could not be removed once presented, it was theoretically possible for the animal to obtain a food reward at all times, even when the initial response had been made to the stationary stimulus. In order to train the subject to respond only to a moving stimulus an optimisation learning procedure was used. If an incorrect choice was made, no food reward was given on return to the box and there was a ten second time-delay before the next trial. If after choosing the incorrect stimulus, the animal chased the rewarded stimulus, it was not allowed to catch the stimulus until it had followed it several times up and down the track. In this way, the polecats learned that the optimal strategy was to chase the moving stimulus immediately after release, if they chose the stationary stimulus first they had to work harder to receive a smaller total food reward. There were twenty stimulus presentations or trials in a session. Learning curves for discriminating between the moving and stationary stimuli were compiled, and sessions were continued until the animals had satisfied the criterion for learning, this being established as five consecutive sessions with scores above 72.4% correct (Krechevsky, 1932, see p. 105).

Results

The learning curves for the preliminary discrimination tests involving stationary and moving stimuli are shown in Fig. 33. All six polecats solved the problem quickly, taking a mean of 8.5 ± 1.9 (S.D) sessions to learn that the moving

FIGURE 33. Learning curves for six polecats for the discrimination between stationary and moving stimuli. The 50% chance level is indicated by an unbroken line and the upper 5% chance limit by a dotted line.



stimulus and not the stationary one contained food. There were no significant individual differences in performance.

6.3 DISCRIMINATION OF VELOCITY DIFFERENCES

6.3.1 Slow-moving rewarded stimulus

Training Procedure

Three animals (Hunk, Mira, Morin) were trained to choose a stimulus moving at a constant slow speed ($38cms^{-1}$) and to ignore stimuli moving faster. During training, the discrimination task was between stimuli moving at $38cms^{-1}$ and $100cms^{-1}$. The track on which the rewarded stimulus travelled was varied randomly using a Gellerman series (Gellerman, 1933, see p. 100), as was the direction of travel, left or right.

At the beginning of a trial both stimuli were situated at the centre of their respective trackways. On the release of an animal, both stimuli were moved to the end of the track. The non-rewarded stimulus was usually moved in the opposite direction to the one containing the food reward, but occasionally it was moved in the same direction to facilitate learning of the rule that the slower stimulus contained the food reward.

The polecats tended to run directly to the centre of the trackway and then follow a stimulus rather than intercept a stimulus directly from the release point (95% of the presentations). An animal's choice was recorded as the direction in which the animal turned along the trackway immediately after its release. A correct response was defined as when the polecat chased the slow stimulus and an incorrect response occurred when the fast stimulus was selected. There were twenty trials in each experimental session. Learning experiments were continued until subjects achieved 83.5% or more correct for five consecutive sessions. It was felt that to ensure reliable performance in subsequent experiments, the learning criterion was taken to be above that of the upper 1% chance limit, calculated using the method of Krechevsky (1932).

Threshold Estimation Procedure

The subject was required to choose between two stimuli moving in opposite directions. The slow-moving rewarded stimulus always travelled at $38cms^{-1}$, while the fast stimulus was presented at 48, 73, 84 or $100cms^{-1}$ respectively in different sessions. In all, there were one hundred presentations for each of the speeds tested, with twenty trials during each daily experimental session. One polecat (Hunk) was given an ascending series, then a descending one, another (Morin) was given a descending series followed by an ascending one and the third animal (Mira) was given random presentations.

Fifty control trials were conducted where both stimuli travelled at the same speed ($38cms^{-1}$), although only one carried food. This was to ensure that the animals were responding to speed cues and were not detecting the presence of food on the stimuli.

The frequency of orienting responses shown by the animals was recorded, an orienting response being defined as a hesitant looking back and forth between the stimuli.

6.3.2 Fast-moving rewarded stimulus

Training Procedure

Three different animals (Hazel, Herman and Memla), were trained to discriminate a fast-moving stimulus travelling at $100 cms^{-1}$ from a slower one. The procedure was the same as in the previous experiment (6.3.1), except for the speed of the rewarded stimulus (which was $100 cms^{-1}$). The training trials involved a choice between $100 cms^{-1}$ and $38 cms^{-1}$. Again when the animals scored 83.5% or more correct in five consecutive sessions, the threshold for relative movement detection was estimated.

Threshold Estimation Procedure

The experimental procedure for the determination of the threshold was identical to that for the slow-moving rewarded stimulus, except that the reinforced stimulus always travelled faster than the non-rewarded one. The rewarded stimulus travelled at $100 cms^{-1}$ and the slower stimulus at 38, 48, 73 or $84 cms^{-1}$. There were fifty control trials where both stimuli travelled at the same speed ($100 cms^{-1}$). Any orienting behaviour shown by the animals was recorded.

Results

Learning Curves

The learning curves for the relative movement task are depicted in Fig. 34. The animals took a mean of 7.0 ± 0.9 (S.D.) sessions to reach the learning criterion of 72.4% correct for five consecutive sessions. However, the learning experiments were continued until at least 83.5% correct was achieved for five consecutive sessions. The performance of the animals differed according to the speed of the rewarded stimulus. When this moved slowly, the animals took 8.0 ± 1.0 (S.D.) sessions to reach the 83.5% correct criterion. With a fast-moving stimulus, the criterion was only achieved after a mean of 11.5 ± 3.8 (S.D.) sessions. There appeared to be a tendency for the animals to learn the problem quicker with a slow-moving stimulus but the difference was not significant due to individual variation (Mann-Whitney U Test; "U"=2, p=n.s.).

Velocity Difference Detection Thresholds

The mean percentage correct scores for each animal expressed as a function of the speed of the non-rewarded stimulus are shown in Fig. 35. The threshold was estimated as where the percentage correct function line crossed 75% correct (Schusterman, 1972, see p. 108). When the animals were incapable of discriminating between the two stimuli,

FIGURE 34. Learning curves for six polecats for the discrimination between stimuli moving at different speeds. The 50% chance level is indicated by an unbroken line and the upper 1% chance limit by a dotted line.

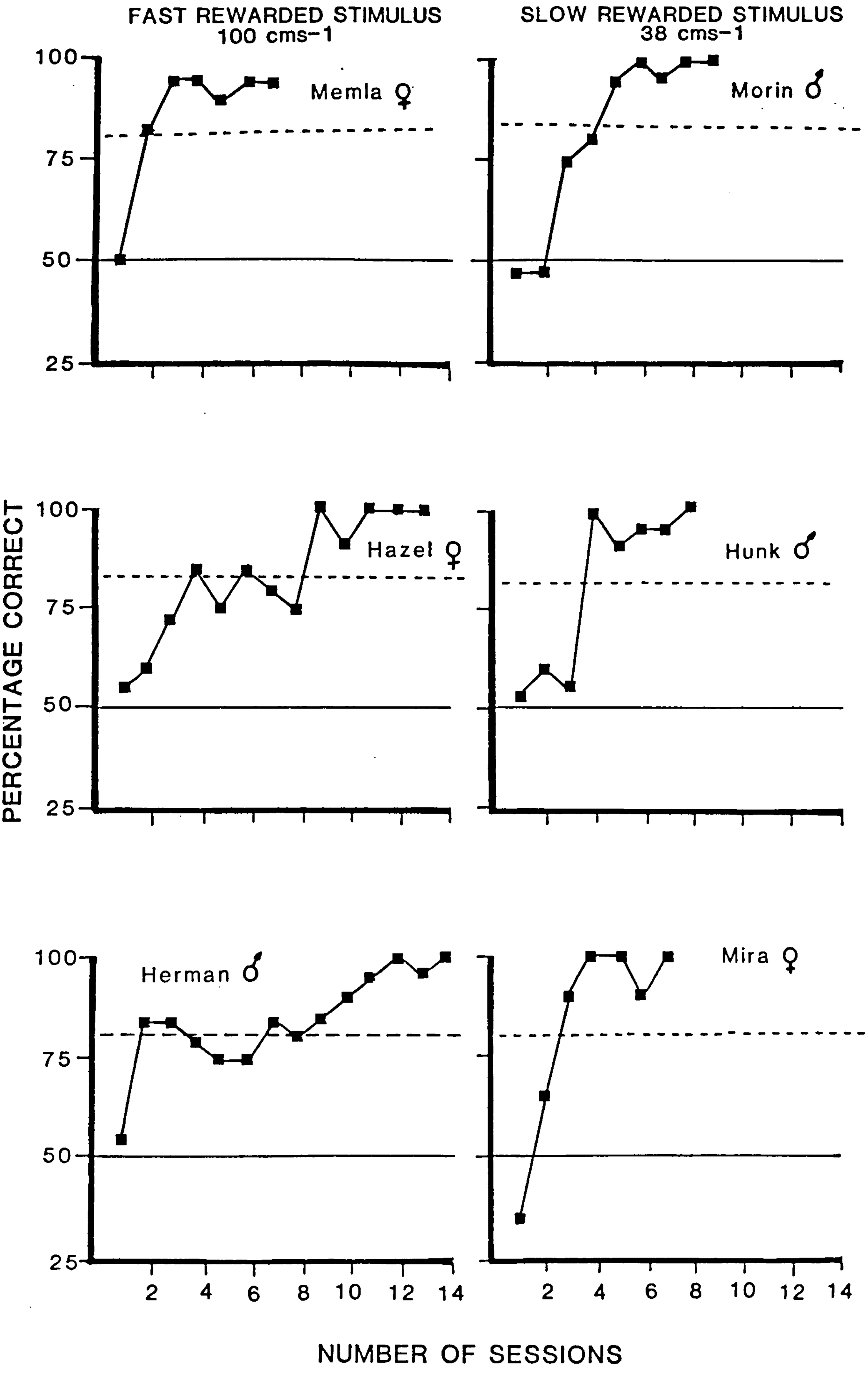
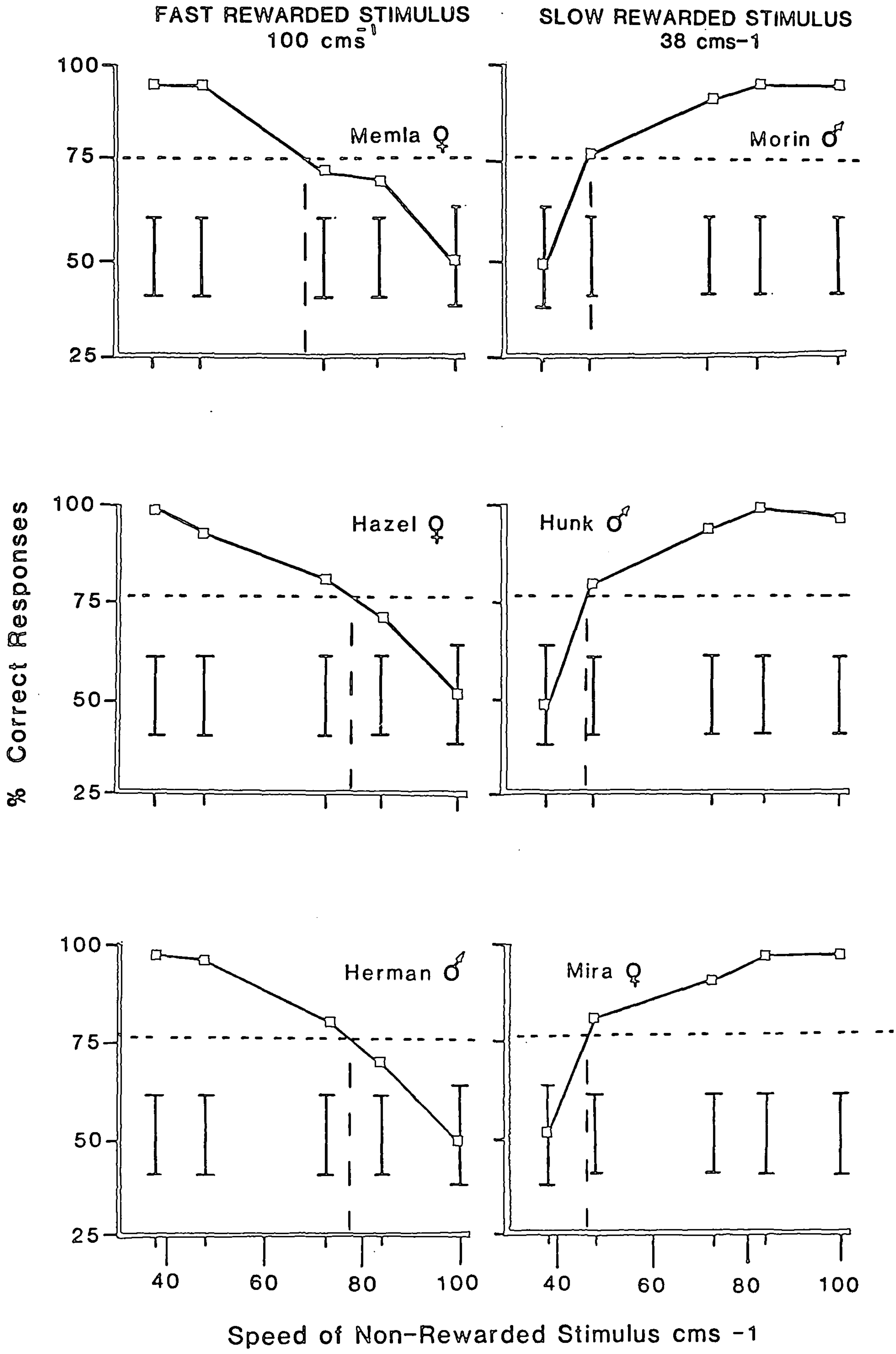


FIGURE 35. Percentage correct responses of six polecats as a function of the speed of the non-rewarded stimulus. The threshold and 5% chance limit bars are indicated.



their response fell to within the chance zone. The 5% chance zone limits are shown in Fig. 35, being calculated using the formula on page 105.

In the experiments involving the use of a slow-moving ($38cms^{-1}$) rewarded stimulus, the polecats could not have discriminated between the two stimuli if the non-rewarded stimulus travelled slower than $48.0cms^{-1}$. The psychophysical functions give a mean threshold speed of $47.0cms^{-1}$ (S.D.±0.8). This is a mean difference in speed of $9.0cms^{-1}$, the animals could therefore detect differences in velocity of 19% (of the fastest speed). However, the subjects could not discriminate between the stimuli moving at $100cms^{-1}$ and $75cms^{-1}$ (S.D.±4.4) respectively. Therefore with a fast rewarded stimulus the discrimination could not take place when the mean difference in speed was $25.0cms^{-1}$ (25%).

The mean percentage correct responses of the animals were plotted as a function of the difference in velocity between the stimuli for the five speed choices presented (Fig. 36). The percentage correct scores of the animals in both experiments were similar when the choice was between very different speeds, but as the speeds of the two stimuli converged, the animals trained to the fast stimulus made incorrect responses more frequently than subjects trained to the slow stimulus ($\chi^2=4.1$, d.f.=1, $p=0.05$)

The log frequency of correct responses for each subject were plotted against the log of the percentage difference in stimulus speed to give Fig. 37. The two slopes were significantly different ('t'=6.3, d.f.=11, $p<0.01$). The

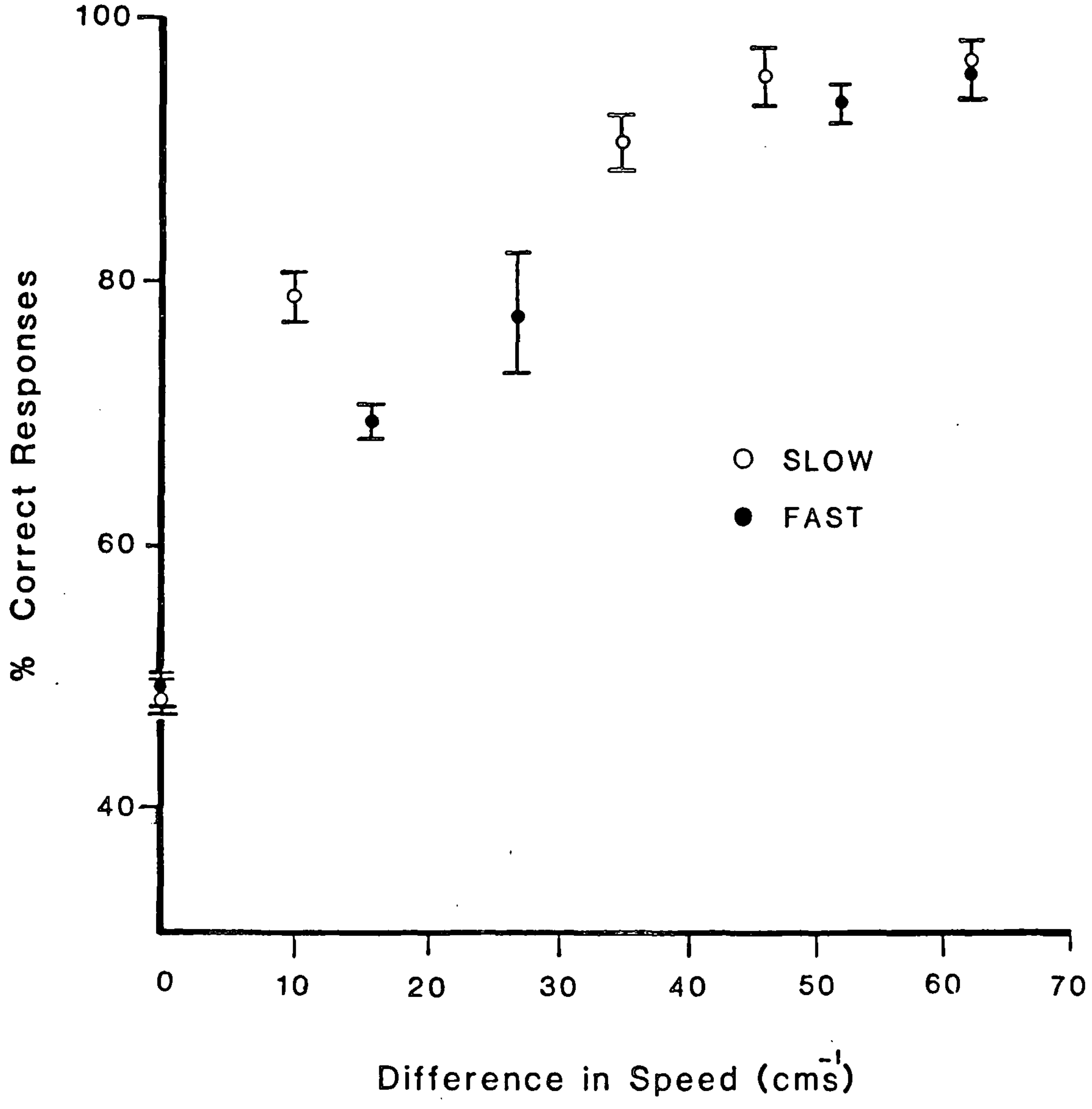
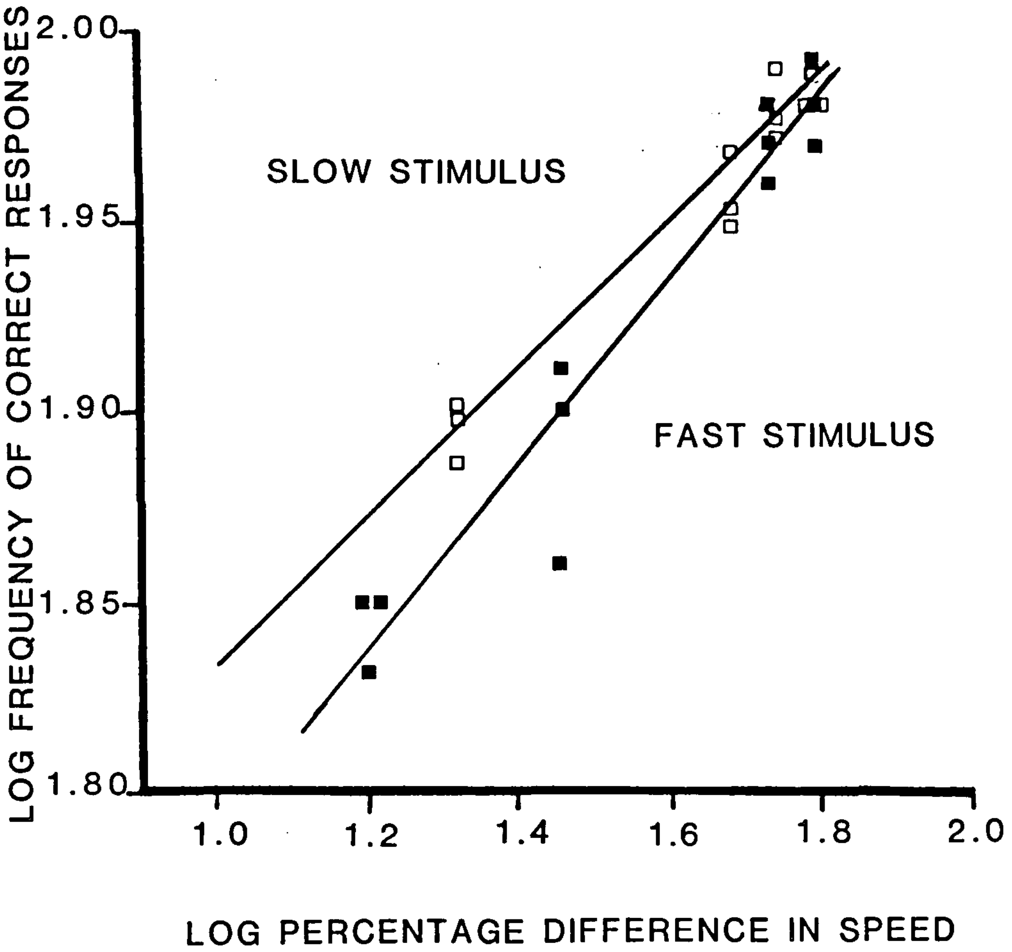


FIGURE 36. Mean percentage correct scores as a function of the difference in velocity between the stimuli. Standard error bars are indicated.

FIGURE 37. Log frequency of correct responses as a function of the log percentage difference in stimulus speed.



polecats had less difficulty discriminating between the two stimuli if the slow rather than the fast stimulus was rewarded. The results for the control experiment, where the choice was between stimuli moving at the same speed, gave a percentage score within five percent of the chance level (50%) in all cases (see Fig. 36). This suggests that the animals were not using alternative cues such as the sight or smell of food in the reward dishes.

Orienting Responses

The percentage orienting responses shown by each individual are shown in Fig. 38. There was an increase in orienting responses as the speeds of the two stimuli converged. As in the directional movement perception experiments (Ch. 5), orienting responses occurred most frequently when the discrimination task was difficult. However, when discrimination was impossible, i.e. when there was no difference in stimulus speed, there was a decline in frequency of occurrence of these head movements. The frequency of orienting responses differed according to the speed of the rewarded stimulus. There was a significantly higher frequency of orienting behaviour when the slow stimulus was rewarded than when the fast one was rewarded (χ^2=31.0, d.f.=1, $p < 0.01$)

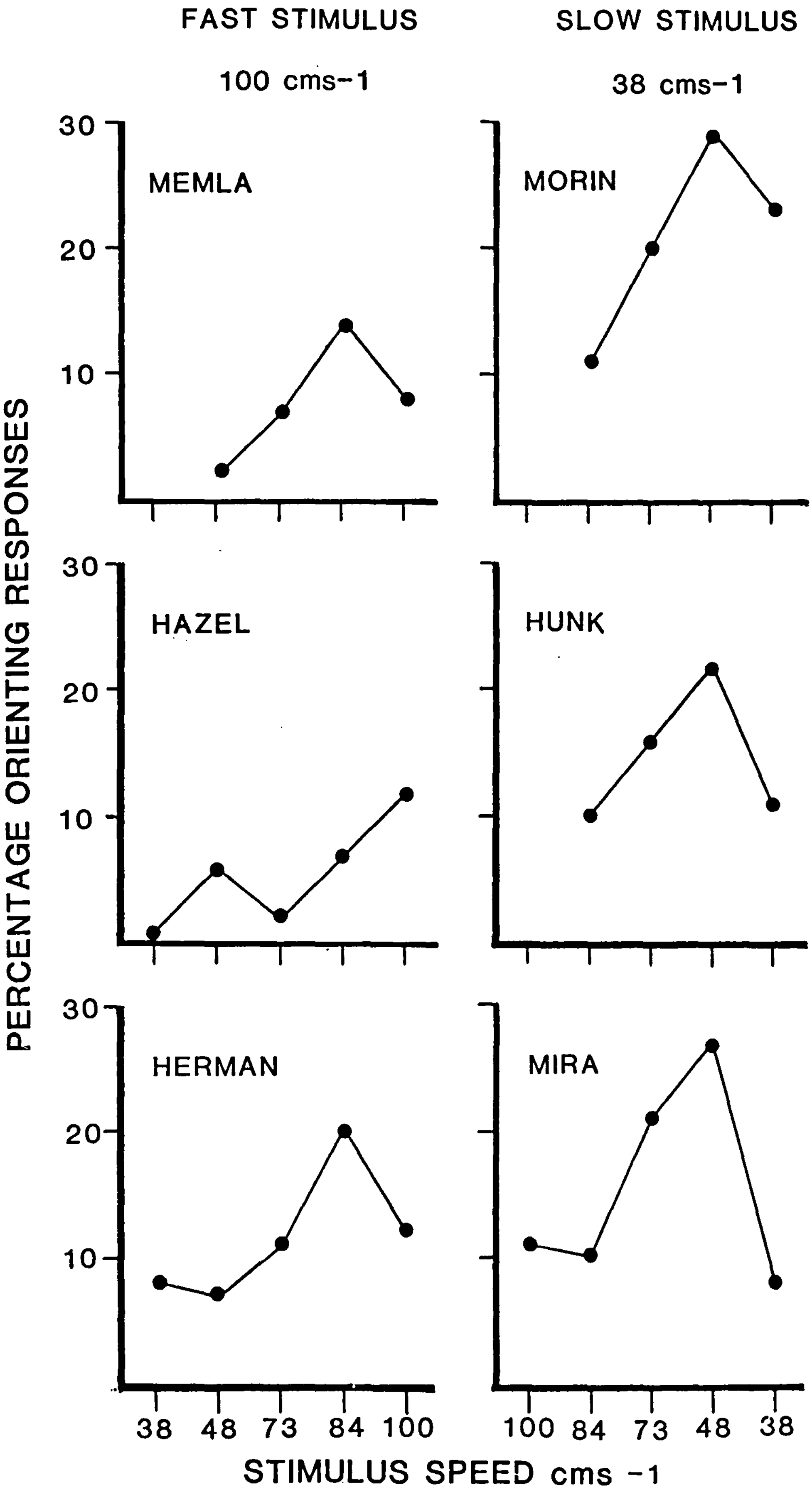


FIGURE 38. Percentage frequency of orienting responses as a function of the speed of the non-rewarded stimulus for six polecats.

6.4 DISCUSSION

These experiments show that the polecat has the ability to discriminate between two moving objects which differ in speed and direction. Rather than being indicative of an ability to detect differences in velocity, the results could suggest that the polecat can accurately measure the velocity of moving objects. For example, the polecats may have been responding precisely to stimuli moving at $38cms^{-1}$ and ignoring stimuli moving at other speeds, i.e. were discriminating the absolute rather than the relative velocities of the stimuli. Such an ability is unlikely, though there is scope for further investigation in future studies.

It is possible that the animals detected which stimulus contained food using olfactory cues, but if this was the case it would have been unlikely that a decline in discrimination ability occurred as the speeds of the stimuli converged. Further evidence against this is provided from the control experiments where both stimuli travelled at equal speed. Also, both dishes would have been heavily tainted with the smell of food, so olfactory cues would have been unreliable.

The dishes were out of sight when the animals were required to make the discrimination, but it is possible that a polecat pursuing a stimulus may have been able to see (and smell) that the dish contained food. This however, would only have served to confirm to the animal that it had made a correct choice.

Supplementary evidence that the animals were making decisions based on the relative speeds of the stimuli is provided from the occurrence of orienting responses, since these were observed more frequently during difficult discriminations (i.e. when speeds were similar). Although the frequency of orienting responses was greatest when the problem was difficult, it is perhaps anomalous that more orienting responses occurred when the rewarded stimulus was slow than when it was fast. Perhaps this behaviour was a means by which the higher correct scores were achieved with a slow rewarded stimulus. The traverse of a fast stimulus may have attracted attention, with the polecat watching it briefly before giving its attention to the rewarded stimulus.

The sensory basis underlying the discrimination was not examined. Although the use of olfactory cues can be eliminated, both visual and auditory information were available to the animals. Vision was probably the most important modality, but the sound of the stimuli moving along the track was an additional cue. Although sound was kept to a minimum as far as was mechanically possible, it was still available and varied according to the speed of the stimulus. It is likely that the combined sound from both tracks could have made auditory cues less reliable than vision. There is scope in future experiments to investigate the sensory basis of relative movement detection.

It would be extremely useful for a predator to be able to discriminate velocity differences, any means by which subtle differences in individual prey movement can be perceived must surely be of advantage to a predator. There is ample field evidence that large predators such as the spotted hyaena, *Crocuta crocuta*, (Kruuk, 1972) selectively predate sick or otherwise slower-moving ungulates. Observations by Mech (1970) have shown that wolves (*Canis lupus*) kill significantly more young and old animals relative to the proportion occurring in the natural populations. The reasons for this are diverse, factors other than speed such as oddity of movement (e.g. abnormalities caused by injuries) or spatial oddity attract predators (Curio, 1976). However, it is accepted that slower-moving animals are more vulnerable to predation.

There are two possible explanations for the selection of prey according to speed of movement. It could be an inevitable consequence of the mechanics of the hunt; slower animals are caught in a shorter time. Alternatively, predators may actively select a victim before the attack. Schaller (1972) observed that cheetahs (*Acinonyx jubatus*) captured young Thomson's gazelles (*Gazella thomsonii*) after a shorter chase than adults, a direct consequence of the slower running speed and lower stamina of fawns. There is also indirect evidence from field studies that selection of prey before the hunt can occur, e.g. in the spotted hyaena (Kruuk, 1972). The present study provides direct evidence for an ability to select objects according to relative speed in the polecat.

Although field studies have provided evidence for non-random prey selection, comparatively little experimental work has been done on the phenomenon. Such observed prey selection would require a predator to be able to estimate accurately velocity differences between moving objects. Application of this type of discriminatory ability to predatory behaviour has not been investigated fully, although several workers have investigated discrimination of velocity differences in human subjects. Most findings suggest that humans can detect differences in velocity of between 4 and 10% (Brandalise and Gottsdanker, 1959; Brown, 1961; McKee, 1981), compared to 20% in the polecat. However, these experiments are not directly comparable to the present study as the stimuli used were different, e.g. rotating disks and gratings and it is also easier to work with human subjects as they can communicate what they perceive. More recently, Thompson (1984) using gratings, found his subjects to have a much poorer ability, comparable to the results in this study.

The asymmetry in results according to the speed of the rewarded stimulus is likely to have a behavioural, rather than a perceptual explanation. It is unlikely that the polecats found it harder to discriminate between the stimuli when the rewarded stimulus moved quicker, rather the animals tended to select the slower-moving stimulus. Predators need to minimise the energetic costs of capturing prey, as the goal of a predator is the maximisation of the net rate of calorific intake during a foraging period (Charnov, 1976). One way to do this is to only chase slower-moving prey. The observed selection of slower-moving stimuli by the polecat may have an innate basis; it was both harder to train the animals and their performance was poorer when they were required to choose a fast stimulus. However, this cannot be verified, for although the polecats were naive of live prey, they had indulged in play with siblings in which they could have learned that slower objects are easier to catch than faster ones.

Although the precise underlying sensory basis of the discrimination was not investigated, the experiments demonstrated that the polecat has the ability to discriminate between objects moving at different velocities. This ability to discriminate slower objects from faster ones is experimental evidence for predators having the ability to select prey according to their speed of movement.

CHAPTER SEVEN GENERAL DISCUSSION

This study has shown that weasels and polecats are sensory generalists, with vision, audition and olfaction all contributing to the location of potential prey. Neither species appears to specialize in the use of a particular distance sense to locate prey.

It could be argued that the experimental conditions used to investigate the distance senses were artificial and not of any relevance to the animals' natural predatory behaviour. However, because precise field observations are not feasible for either of these species, a compromise had to be made. On the negative side are the artificial conditions in a small indoor arena, on the positive side is the collection of data to allow the accurate quantification of search-paths, which would not be possible under natural conditions.

The method of presenting the prey was artificial but ethical considerations necessitated direct contact between the predator and prey being avoided. All subjects were naive of live prey and thus learned to associate the containers with potential prey.

Artificial presentation of prey has been used in other studies of predatory behaviour (e.g. Polsky, 1978). It is a useful method for studying predatory behaviour as it allows the manipulation of variables in a way which is not possible under natural conditions. It also eliminates the variability in prey behaviour with its subsequent effect on the behaviour of the predator. Presentation of prey behind screens does not appear to have deleterious effects on a predator's ability to locate prey (Polsky, 1978).

It is possible that the predators were not sufficiently rewarded for finding the mouse as they were not allowed to kill it. This is unlikely since finding the mouse was probably rewarding in itself, and in addition, the subjects received a verbal signal from the experimenter which was associated with a food reward given on return to the carrying box.

Predatory behaviour is a loose chain of responses including searching for relevant stimuli, hunting potential prey, capturing, killing and feeding (Baenninger, 1978). Any of these components of predatory behaviour may occur independently. The present experiments were only concerned with the stimuli used in finding prey, which could be, but not necessarily need be, different from the stimuli controlling prey capture and killing. As killing behaviour is under different motivational control from feeding behaviour (Krames *et al*., 1973; Adamec, 1976; Hastings and Cherry, 1980), it is possible that searching behaviour is independent from killing. Therefore different phases of the predatory sequence may be under different sensory control. Lindquist and Bachmann (1982) showed how the importance of the senses changed during the predatory sequence of the tiger salamander (*Ambystoma tigrinum*). The importance of the senses may also change according to environmental conditions (Wells, 1978). It is quite possible that the relative importance of audition and olfaction may have changed if the present experiments had been repeated without illumination.

The experimental design remained consistent with only the prey stimuli being manipulated. The design of sense hierachy experiments by other workers has been weakened by confounding variables, by making alterations to environmental conditions (e.g. illumination), the prey and the sensory capabilities of the predator (e.g. by inducing anosmia, Wells, 1978).

In the present experiments it could have been possible to keep the design consistent by manipulating the predators' sensory capabilities e.g. by blinding, using ear plugs and inducing anosmia. However, this would have been unsatisfactory for ethical reasons. Moreover, reducing or eliminating the sensory capability of a predator is not satisfactory as the effect on the animal's performance may give rise to spurious results. For example, blinding a predator may result in a long latency to prey capture, but this may be due to the animal moving slower than normal.

The present experiments manipulated the amount and type of sensory input available to a predator and approximated to various conditions that may confront a hunting weasel e.g. audition + olfaction (AO) could represent prey out of sight in thick cover, and vision + olfaction (VO), an immobile mouse.

It appears that stimuli were satisfactorily occluded during the "no senses" experiments, as mean search-time was significantly longer than all other conditions (except audition only). This suggests that attempts to occlude sensory information, in particular olfaction, were successful, i.e. the lids were airtight. There is some evidence that the weasels could detect the presence of the mouse when near the container, as on occasions the time spent near the mouse container was longer than that spent investigating an empty container. The mean time spent with prey in the "no senses" treatment was longer than the mean time spent investigating an empty container. Also, although the incidence of orientation to the mouse was low in "no senses" experiments (Table 14), the fact that it occurred at all suggests that the mouse could be detected at a distance, although during these trials this distance was short (Fig. 8). It was noted though, that orienting behaviour also occurred in relation to empty containers.

Learning and performance during visual discrimination tasks depends on such factors as illumination and distance from the stimulus (Kennedy, 1936), but an important factor is the size of the stimulus used. The small transient nature of the stimulus used in the threshold determinations for fast movement detection (Ch. 5) probably represented a difficult discrimination problem. A higher threshold may have been obtained if a larger stimulus had been used. It is possible that if the subject turned its head momentarily during a trial, it may have missed seeing the stimulus altogether. The procedure used therefore may have given an underestimate of the animals′ movement detection ability due to inattention. Other workers have reported difficulty in training animals to discriminate abstract stimuli during movement discrimination tasks (Hodos et al., 1975; Berkley et al., 1978). In contrast, the polecats learned the velocity difference task extremely quickly. This was probably because the stimulus was large and had a long distance of travel. Also, the food reward was directly associated with the stimulus, which must have aided the learning of the task. In addition, the stimuli moved slower in the velocity difference task. The maximum speed available was only 100cms^{-1} compared to the speed range of 100-400cms^{-1} used in the high-speed movement detection threshold experiments.

Experimental procedures dependent on behavioural responses of animals may have an important bearing on any conclusion reached about an animal's sensory biology. The slightly lower high-speed movement detection threshold of the weasel compared to the polecat, for example, may have been due to lack of attention by the weasels. Weasels are active excitable animals, and therefore, could be prone to inattentiveness, but lack of attention could also have occurred as a result of apparatus design. Pressing the switch was difficult for the weasels, therefore it probably rendered the whole task more difficult. A psychophysical procedure may measure an animal's motivation for a particular type of task, as well as its sensory capability.

The results for the experiments on the importance of the distance senses can be related to the nature of the predators' activity rhythms and foraging behaviour. It might be expected that these predators do not specialize in the use of vision as they often hunt at night when vision will be of limited value. Even when hunting in daylight, conditions will not always favour vision, for example their small size often precludes the use of vision when hunting in dense cover. Also many of the prey species taken are small and spend a significant proportion of their time concealed in vegetation or in underground burrows. Weasels and polecats therefore are in complete contrast to the large predators known to rely on vision when hunting, such as the coyote (Wells and Lehner, 1978) and African hunting dog (Estes and Goddard, 1967). These large predators are diurnal and feed on conspicuous large prey such as ungulates living in open habitats.

It is therefore surprising that the present experiments demonstrated that neither air-borne olfactory cues nor auditory cues have a greater importance than vision. The increased opportunity for the use of vision which is afforded by day-time activity (in weasels in particular) appears to have increased its importance from what it would otherwise be. The limited number of observations on wild polecats (e.g. Herrenschmidt, 1982) suggest that they are mainly crepuscular. Hence there may be some opportunity for the use of vision as the polecat eye is well adapted for dim light conditions (Baumeister, 1975; Pontenagel and Schmidt, 1980). Vision is probably the most efficient way of locating a distant prey animal (Maiorana, 1981), therefore it must be advantageous for a predator to develop its use, providing conditions are suitable.

The low importance of auditory cues may have been due to the artificial method of stimulus presentation. A live mouse moving under dry leaves for example, might have provided a more "interesting" stimulus. Auditory stimuli may be easy to localise, but are not always available as animals do not continually produce sound. This unreliable availability may be the reason for audition's low position in the hierachy, but it is more likely that weasels and polecats may not be able to localise sound as accurately as other predators with large moveable ears such as canids. In some hunting situations though, auditory cues may be the only ones available, for example in the predation of bird's nests containing nestlings (Dunn, 1977).

Auditory cues assume a greater importance when they are combined with other cues. There is evidence from studies of a wide variety of vertebrates that prey is detected more rapidly when several senses can be used compared to when only single-sense cues are available. Some sensory combinations are more effective than others, for example the use of olfactory cues by amphibians is enhanced if visual cues are also available (e.g. Sternthal, 1974). Auditory and olfactory (air-scent) cues together appear to be valuable to weasels for finding prey.

Weasels spend a large part of their foraging effort in prey burrows (Pounds, 1981) and when underground sound and scent stimuli will be available. The polecat does not appear to use auditory + olfactory (air-scent) stimuli combined to the same effect as the weasel. This may be because the polecat does not hunt in prey burrows to the same extent, certainly it is too large to enter burrows of small rodents. This type of prey may be caught above ground and in such a situation, vision could be used. Erlinge et al. (1974b) found that stoats catch voles by digging at their burrow entrances, causing them to leave their refuges and subsequently they are caught in the open. Polecats may catch small rodents in a similar fashion.

Polecats probably hunt rabbits underground, although it is not known what proportion of such prey are taken in burrows compared to above-ground. When locating prey underground, the polecat may rely on substrate-scent rather than auditory and olfactory (air-scent) cues. Although there was no significant difference between the two species in the time taken to find prey using a scent trail, the polecat appeared to determine directional information from a scent trail more efficiently than the weasel (see p. 87).

Comparative data on the use of substrate-borne olfactory stimuli is lacking. It is perhaps surprising that this capability has not been investigated as the present study and that of Herman (1973) have shown it is potentially more important than air-borne olfactory cues. Previous authors have, however, noted the low importance of air-borne olfactory cues. For example, olfactory localisation of prey occurs at shorter distances than when visual or auditory stimuli can be used by the red fox (Osterholm, 1964). It is probable that olfactory location is a later step in the predatory sequence, after the fox has been alerted to the presence of prey by other senses. Langley (1983a) noted that Onychomys leucogaster responded to auditory stimuli from a distance, but when in close proximity to prey responded to olfactory cues.

Such studies suggest that auditory cues are more satisfactory than air-borne olfactory cues for finding prey, but there was no evidence for this in the present study. However, supplementary evidence for the relatively low importance of air-borne olfactory cues comes from the apparent inability of the polecats to detect the presence of food on the stimuli used in the relative movement discrimination experiments (Ch.6).

Interestingly weasels and polecats appear to detect olfactory stimuli at close range, i.e. when their nose is almost in contact with the stimulus. Novikov (1956) reported "that the polecat is noted for its poor sense of smell". Korytin (1977) showed that mustelids soon habituated to olfactory stimuli and possessed a poor olfactory acuity. In addition, he generalised that the sophistication of the olfactory sense is inversely correlated to an animal's own scent. Carnivores such as viverrids and mustelids with large scent glands and a conspicuous body odour showed poorer responses to olfactory stimuli than other carnivores, e.g. canids. However, other authors have shown that the olfactory sense is very important to these predators. Viverrids and mustelids have a well-developed olfactory discrimination capability, being able to distinguish between the scent of different individuals (Gorman, 1976; Kruuk *et al*., 1984). In scent discrimination tests though, the olfactory stimulus is concentrated and the animal is able to sniff the scent at close-range. It is possible that they do not have this ability when the stimulus is at a distance.

Although ground-scent and air-scent are both influenced by weather conditions, the former is probably longer lasting. Determination of the direction in which a prey animal has moved appears to be difficult, although presumably a scent gradient occurs along the trail. Once detected, a fresh scent trail is the clearest indication of the whereabouts of prey. However, finding a scent trail is probably difficult as the stimuli are only available over a restricted spatial area. Substrate scent may be particularly useful for relocating a prey animal that has already been encountered. An additional disadvantage of using scent trails is that prey animals use strategies to prevent predators from following their scent. For example, Murie (1935) observed a hare generating a convoluted path when followed by a weasel. Scent trails are likely to be of limited use in bird predation, particularly of nests, although an exception may be ground-nesting birds.

As a weasel or polecat moves around its home-range, it preys on whatever it happens to encounter. It is probably because they are opportunistic predators and may encounter prey under a variety of conditions, that all of the distance senses are equally important. The time of day or microhabitat may determine which of the senses can be used. For example, prey may be encountered in the open during the day, enabling vision to be used, or alternatively they may hunt underground. In many hunting situations, a polecat or weasel is probably alerted to the presence of prey at a distance, by encountering a scent trail. Following such stimuli will be particularly important in prey burrow systems. When near the prey, all the senses may contribute to the fine details of localisation and the capture of prey.

Information is available on an additional mustelid species, the skunk Mephitis mephitis, allowing some tentative conclusions on the interrelationships between ecology and sensory biology to be discussed. Langley (1979) believes auditory cues are more important to skunks than are visual cues. However, the design of Langley's experiments was not ideal as olfactory and tactile cues were always available. Langley (1979) therefore demonstrated that auditory + olfactory cues were preferred to visual + olfactory cues, he did not investigate the use of these senses on their own. The present experiments suggest that auditory + olfactory cues may be more important to weasels than visual + olfactory cues in combination (see p. 88), although this difference was not as marked as in the skunk where attack latency was significantly reduced when auditory cues were present.

Langley's conclusions need to be treated with caution as crickets were captured by the skunks when neither visual nor auditory cues were available. The presence of olfactory cues may have been particularly important since Slobodchikoff (1978) has shown that skunks recognise prey by odour.

The greater importance of olfaction and audition to skunks compared to weasels could be due to differences in ecology. Skunks are nocturnal (Langley, 1979) and are less specialized predators feeding mainly on insects and carrion (Ewer, 1973). There is not however, a sufficient difference between the lifestyle of polecats and weasels to support a significant difference in sensory biology. It is possible that the most important factor is the nature of the circadian rhythm. In addition, vision may achieve a greater importance in animals that are active predators.

Phylogenetic relationships rather than ecology may be important. The sensory ecology of an ancestral species may dictate the relative importance of the senses as possessed by modern-day species. Feldman and Phillips (1984) showed that related species do not always show different sensory adaptations if they occupy different niches; changes in the visual system may not occur if an animal's way of life changes. For example, the fossorial rodent, Geomys bursarius, possesses a retina characteristic of a diurnal species with good visual acuity. Polecats and weasels may show similarities in sensory biology because they are closely related species derived from a common ancestor. Therefore it is recommended that further experiments are conducted on other mustelid species in order to resolve the relationship, if any, between ecology and the use an animal makes of its senses.

Actual detection of prey by weasels appears to occur at very close range. The criterion for detection was overt orientation, therefore the mouse may have been detected at greater distances than was recorded. The farthest mean detection distance was only 60cm, recorded during the three senses control treatment (VAO). Detection of prey at close range is confirmed by the observations of Pounds (1981) on wild weasels, where prey was detected from distances estimated to be less than two metres. The discrimination distances used in the directional movement detection experiments (Ch. 5), correspond to the mean detection distances observed. The mean detection distance during the vision only treatment was 48cm, and it was noted that there was a slight decline in movement detection ability at a viewing distance of 50cm. Weasels may not be able to detect, or alternatively may have no interest in visual stimuli (without additional information available to other senses) at distances greater than 50cm.

Some of the larger mustelids such as fishers, _Martes pennanti_ and martens, _Martes americana_, show different searching strategies according to the type of prey taken (Powell, 1978, 1982; Spencer and Zielinski, 1983). Pounds (1981) also noted that a variety of hunting strategies were adopted by individual weasels. There was a trend in the present experiments for female weasels to search more systematically than males (i.e. container-directed search), which could be a reflection of differences in behaviour under natural conditions. Female weasels spend more time hunting in vole burrow-systems, therefore they may systematically investigate possible locations for prey, while males catch more prey in the open during random encounters (Pounds, 1981). Significant male-female differences in behaviour in the present experiments could mainly be attributed to this difference in searching behaviour, although an additional factor was variation in speed of movement which was proportional to the difference in size between the sexes. However, conclusions about searching behaviour can only be tentative, owing to the small number of subjects used and the small size of the arena.

There was no evidence for area-restricted searching around the location of the prey animal, which is not entirely unexpected, as this is normally a characteristic of predators whose prey exhibits a clumped distribution (Smith, 1974b). On the few occasions when area-restricted type searching occurred, it was in relation to substrate scent cues and was not a modification of searching behaviour as a result of learning.

Models of optimal search-paths have been developed, where the most efficient strategy is to minimise revisiting sites (Pyke et al., 1977; Krebs and Davies, 1978). This is also the optimal strategy for spatial memory radial-maze experiments and other win-shift tasks (Olton et al., 1981). Optimal search-path models suggest that directional search-paths are more efficient than random search. In the wild, weasels improve their chances of encountering prey by hunting in suitable habitats and when hunting they tend to maintain a constant direction although their movements tend to be irregular (Pounds, 1981).

Weasels may not show strong win-shift strategies because they are active predators. Wilkie et al. (1981) suggested that predators are less likely to show win-shift strategies than granivorous animals, because their food supplies are less likely to be depleted after their visit to a site. Recent experiments on rats have shown that win-shift strategies occur when a food supply is depleted by the visit of the "predator" and win-stay strategies are characteristic of non-depleted food supplies (Herrman _et al._, 1982; Haig _et al._, 1983). The opportunistic nature of the foraging behaviour of the weasel was probably exerting its effect in the present experiments as the weasels showed neither a strong win-shift nor a win-stay strategy when searching for the mouse.

Insectivorous predators such as tits spend some of their foraging effort returning to sites in order to sample prey availability (Krebs _et al._, 1978). Pounds (1981) suggested a similar explanation for the long excursion movements made by weasels which were conducted to maintain familiarity with the home-range and to assess the status of hunting areas. In addition, such movements probably also involve the animal scent-marking its range (Erlinge _et al._, 1982).

While there are theoretical models of searching behaviour, relatively few quantitative studies of searchpaths have been conducted. In those cases where speed of movement of "predators" have been estimated, it has not always been with a great deal of accuracy (e.g. Murdie and Hassell, 1973). Smith (1974a) recorded the movements of thrushes by relating their positions to a grid of marker pegs and estimates of the birds′ positions were spoken into a tape recorder. MacDonald (1980) used a similar method when observing foxes hunting for earthworms. Such field observations pose problems for the estimation of the distance travelled by an animal, when the exact path cannot be recorded.

The relatively accurate method of recording movement-paths used in the present study gave quantifiable measures of behaviour such as speed of movement and number of pauses made. Although there were no gross changes in searching behaviour as the diversity and type of sensory information available was manipulated, changes in search-time could be related to minor changes in the behaviour of the animals. Some of the variables measured were inter-correlated, but provided additional information which aided the assessment of the relative importance of the senses.

A discussion of the relevance of movement detection needs to take into account its relationship with other sensory cues, and also the ability of the predator to detect movement. Visual movement cues were not available in the single sense treatments, during which mean search-times were long. Indeed, an alternative explanation of the search-time results could be that it was the absence of movement cues that was important, rather than the diversity of sensory information available. However, it is difficult to distinguish between the two factors. The additional information provided by movement cues when three sensory modalities were available did not appear to be important as there was no significant effect on search-time for the weasels. The polecats in fact, had significantly shorter search-times in VAOd trials than in the control. This may imply that under such conditions movement cues are not needed or are irrelevant. Occasionally though, when a moving mouse was present, the approach to the mouse was slow and cautious (pers. obs.), thereby increasing search-time.

It may be that polecats are not so dependent on visual movement cues in order to detect prey, Eibl-Eibesfeldt (1956) noted that experienced animals attack stationary rats. Polecats take a wider variety of prey than weasels and may take non-moving prey more often, for example carrion features more frequently in the diet (Danilov and Rusakov, 1969). Although prey movement does not appear to be essential to polecats for finding prey, it is important in eliciting chasing reactions (Eibl-Eibesfeldt, 1956; Apfelbach and Wester, 1977). The fact that polecats do not always use movement cues need not imply that they cannot detect them, as this animal's ability to detect movement, at close range at least, is equivalent to that of the weasel.

While substrate scent cues are probably the most useful cues for determining the location of potential prey, movement cues are most important at close range. They are probably most relevant when weasels or polecats are in close proximity to prey, immediately prior to a capture attempt. In such a situation a predator needs to be able to to detect fast movement and also to determine its direction. The movement detection thresholds obtained in the present study (polecat mean, $292cms^{-1}$, weasel mean, $267cms^{-1}$) correspond to the running speeds of small rodents (Dagg, 1977), but they were lower than the maximal speeds of movement of rodents quoted by Garland (1983). Therefore they could represent a "giving-up" speed, rather than a true measure of the maximum speed that is physiologically perceptible. Polecats and weasels are not morphologically adapted for sustained fast pursuit of prey and therefore probably do not pursue fast-moving animals. Such a situation is indicative that the prey has already detected the predator, which would be another factor in deterring pursuit (Smythe, 1970). However, the maximal speeds quoted by Garland (1983) may not have much relevance to the normal speeds of movement of prey experienced by these predators. Behavioural estimates of visual abilities are often different from those estimated physiologically (Schneider, 1968a, b; Bell, 1982). Boulet (1955) showed that the perch, Perca fluviatilis, ignores moving objects which are physiologically perceptible if they are moving too fast for an immediate capture. Therefore a neurophysiological study of movement perception in the polecat or weasel may result in a different estimate of movement detection ability than that estimated by behavioural testing.

The high-speed movement detection thresholds of the polecat and weasel correspond to that of the American mink (Dunstone and Clements, 1979; Clements and Dunstone, 1984), therefore three closely related species of mustelid have all been found to have an equivalent ability to detect fast-moving stimuli. These animals are all active predators, therefore suggestions for further study include the use of more strictly nocturnal, less predacious members of the Mustelidae, such as the badger or skunk in both movement discrimination tasks. The movement detection thresholds are considerably higher than the preferences shown by ferrets for "prey" models moving at 25-45cms^{-1} in the experiments of Apfelbach and Wester (1977). This optimal range of model speed which elicited hunting or chasing reactions is low considering that these predators are capable of moving at much faster speeds. It does approximate though to the mean speed of movement shown by polecats in the present study. If olfactory and auditory stimuli had also been available the ferrets may have chased models moving at faster speeds. The fact that senses other than vision contribute to the location of prey needs to be stressed. Conditions which caused a reduction in visual movement perception capability in the present experiments, such as a long viewing distance or narrow screen width, may have been limiting because vision was the only sense that could be used.

Apfelbach and Wester's (1977) ferrets were not trained to respond to the models but had to rely on "innate" behaviour patterns. Mammals are not suitable subjects for behavioural studies of sensory capabilities which rely on innate behaviour, as they modify their behaviour by learning much more readily than lower vertebrates. Amphibians are particularly valuable subjects for such studies as they do not undergo short-term changes in motivation (Ewert, 1974) and because of this, the stimulus control of their predatory behaviour has been extensively analysed (e.g. Ingle and McKinley, 1978; Ewert et al., 1979; Luthardt and Roth, 1979a). The psychophysical procedures used in the present study probably give a better estimate of a mammal's sensory abilities.

The mustelid species so far tested, have high-speed movement detection thresholds of approximately $20^o s^{-1}$ over the retina. This is lower than the threshold for man of $50^o s^{-1}$ reported by Pollock (1953) and Caelli et al. (1978), but it must be noted that angular thresholds are dependent on stimulus conditions such as size of stimulus and discrimination distance. The value of $20^{o}s^{-1}$ corresponds to the angular speed reported by Kaufman et al. (1971) to represent the fusion threshold of human subjects. The high-speed thresholds of polecats and weasels are higher than that of a rat whose threshold has been estimated, using the same apparatus and an identical procedure to the present study, as $200cms^{-1}$ by Knowles (1983). However, this threshold was only determined in one subject and may not be representative. The ability of the polecat and weasel to detect fast movement appears to be intermediate between a nocturnal prey species and a diurnal species with well-developed visual abilities.

The weasel was shown to possess a fairly consistent movement detection ability over a range of distances at which visual detection of prey appears to occur (i.e 10-50cm). It would be interesting to conduct experiments at further viewing distances to confirm my hypothesis that at greater discrimination distances movement perception ability will be reduced. The thresholds were also fairly consistent at the stimulus radiant intensities used, suggesting that the weasel eye is well-adapted for dim-light conditions. There was only a slight decline in ability to detect the moving stimulus when it had a low contrast against the background illumination. The greatest decreases in threshold however occurred under conditions of narrow screen width, when the distance of traverse, and thereby the time the stimulus was visible was limiting.

As well as being able to discriminate the direction of fast-moving objects, it would be advantageous if a predator could detect differences in speed of moving stimuli, as prey animals do not always occur in isolation. The present study has demonstrated that polecats can discriminate the speed of an object relative to another moving stimulus. It is likely that polecats use this ability to select slower-moving prey in the wild, as in some circumstances polecats may encounter prey in a group, e.g. when hunting rabbits. Although there is no direct evidence for the selection of slower-moving prey by the polecat, the American mink (Poole and Dunstone, 1976) and the European otter (Erlinge, 1968) have been shown to be more successful at catching slower-moving prey during predatory encounters. Therefore the polecat is likely to do the same.

The ability to discriminate the relative speed of prey is more obviously of advantage to the larger social carnivores which predate group-living ungulates, but it is also likely to be important to predators such as the polecat which do not chase prey over long distances. Polecats may assess prey by more subtle cues than predators which run down prey. It would therefore be interesting to obtain comparative data on dogs or other predators which may not assess prey before deciding to attack.

The relative importance of the distance senses to the polecat and weasel fits neither the pattern shown by strictly diurnal species nor that by nocturnal mammals. The nature of their activity rhythm affords them a greater opportunity for the use of vision than more strictly nocturnal predators. The opportunistic nature of their foraging behaviour probably exerts the most important effect, with all the distance senses being approximately equivalent for the location of prey. The ability of these predators to detect fast-moving stimuli is also intermediate between diurnal and nocturnal species.

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APPENDIX NOTES ON STATISTICS

The following conventions were used in the figures and tables:

***	$p < 0.001$
**	$p < 0.01$
*	$p < 0.05$

Use was made of the Statistical Package for the Social Sciences (SPSS) (see Statistical package for the social sciences 2nd Edition, 1975. New York: McGraw-Hill).

Where Anova revealed a significant difference between treatments for a dependent variable, a planned comparison procedure was used between the base-line VAO condition and the other treatments. A comparison was made with this control as it was not known at the time of testing whether the "no senses" condition was an adequate control. 'T' tests were used although this procedure does have limitations. All levels of significance were indicated on the histograms in chapter four, although some results significant at the 0.05 level may have occurred by chance. These results were included as many of the variables measured showed the same trend across the experimental treatments and therefore give support to the main conclusions of the experiment.