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An investigation of the effects of various environmental parameters on the underwater foraging behaviour of the American mink, *Mustela vison* Schreber.

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.....being a thesis presented in candidature
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For my parents, Glyn and Myfeda Davies,

for Zakaria and for Tanya.

ABSTRACT

The aim of this study was to investigate the effects of changes in various environmental parameters on the underwater foraging behaviour of the American mink, *Mustela vison.* The study was conducted in an indoor pool.

The effects of changes in the following parameters were investigated:
(i) Water Depth. This was altered from 0.3 m to 1.65 m.
(ii) Current Flow. Presence of either a deep or a surface current was compared to no current flowing.
(iii) Prey Density. Four prey densities were used, 25%, 50%, 75% and 100%.
(iv) Habitat Complexity. Hides were arranged in a regular, random or clumped pattern. The effects of habitat complexity were investigated in conjunction with prey density.

Results are presented for gross changes in foraging behaviour, i.e. dive rate (number of dives per min), successful dive rate, hide visit dive rate, proportion of dives visiting a hide, proportion of successful dives and proportion of successful hide visits, and for finer changes within each dive, i.e. dive duration, time on bottom, number of hides visited per dive, mean time in hide, proportion of time on bottom spent hide searching, distance travelled underwater, proportion of direct to indirect dives, mean number of turns per dive, directionality of dives and revisiting of hides.

The results showed that as depth increased, animals made fewer dives, but the dives were of longer duration. The extra time on bottom appeared to be used for locating hideswhich could no longer be located aerially before diving. Deep current was found to be not strong enough to seriously affect foraging behaviour. However, the surface disruption caused by the surface current, led to an increased dive rate, possibly in an attempt to locate hides that could no longer be located aerially, although other parameters such as proportion of dives visiting hides, dive duration etc., were generally unaffected by current flow. The conclusion was that mink were well able to continue foraging with current speeds of up to 0.86 m s^{-1}. It was found that as prey density increased, animals, generally, made fewer dives of shorter duration, more of which were successful, although there was considerable individual variation. For habitat complexity, animals, generally, behaved similarly if hides were arranged randomly or in clumps, but when hides were regularly distributed, fewer hide visit dives were performed. However, mean time on bottom tended to be longer, resulting in little difference in foraging efficiency between the three conditions.

A brief review of individual strategies revealed that there were considerable individual differences in foraging strategy. These were not related to sex, thus, some individuals consistently used a strategy of many short duration dives, generally visiting only one hide per dive. Others opted for fewer, longer duration, dives, generally involving more than one hide visit. Further, mean dive duration was not related to body weight.

An investigation into the maximum underwater swimming speed achieved by mink showed that animals could reach speeds of over 1 m s^{-1}. However, comparison with swimming speeds of fish species preyed on by mink, revealed that the fish swam faster. A review of the habits of the fish eaten, however, revealed that most were sedentary, bottom dwellers. The implications from this are that commercially important fish, e.g. salmon and trout, may well be taken mainly as diseased or spent individuals.

The overall conclusion reached was that mink are highly versatile mustelids, and have 'specialised' in the ability to utilize both terrestrial and aquatic habitats.

CONTENTS

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CHAPTER 1

INTRODUCTION

"Look at the *Mustela vison* of North America...."

Charles Darwin,
The Origin of Species

1.1. The study

The aim of this study was to investigate certain aspects of underwater foraging behaviour and foraging efficiency of the American mink, *Mustela vison,* in relation to the environmental parameters of water depth, current flow, prey density and environmental complexity.

Foraging behaviour has been defined by Krebs (1981) as behaviour associated with searching for, subduing, capturing and consuming food. He also states that a distinction is sometimes drawn between 'foraging tactics' and 'foraging strategy'. The 'tactics' of a forager are considered to be the methods by which it attempts to capture food, e.g. sit-and-wait, co-operative chase etc., whereas 'strategy' refers to the idea that foragers aim to achieve a particular goal, e.g. to minimize total daily hunting time, to maximize capture rate or to maximize net rate of energy gain per unit time. Achieving a certain goal may involve the forager in a series of 'decision rules', e.g. where to search, which items to eat etc., and together these would constitute the animal's foraging strategy. Many studies have attempted to investigate some of the decision rules that govern the foraging behaviour of various insects (e.g. Hassell and Southwood, 1978; Hassell, 1980), birds (e.g. Zach, 1979; Houston et al., 1980) and mammals (e.g. Collier et al., 1978; Dunstone and O'Connor, 1979a and b; Barnard and Brown, 1981).

For a mammal, the mink is unusual in that it forages both on land and underwater. When hunting underwater, the mink faces an additional problem, that of oxygen limitation, i.e. the mink can only survive a limited period without breathing, and has to periodically interrupt its underwater foraging to replenish its oxygen supply. This study was, therefore, mainly concerned with investigating its 'foraging strategy', and, in particular, some of the 'decision rules' used when foraging underwater in relation to different environmental parameters.

The study was also concerned with investigating how efficient mink are as underwater predators. Foraging efficiency is the relationship between the number of times an animal initiates a search for food, and the number of times that a search results in success. Krebs (1981) indicates that the most biologically sensible measure of foraging efficiency is the net rate of food intake per unit time. Ideally one should measure the intake of calories per unit time, but this may not be an easy thing to obtain other than on a gross scale of, for example, three food items per minute whose rough calorific value could then be calculated if size and species were known. Since the ability to acquire food as efficiently as possible may be crucial to survival and reproduction, it would be better to have some simple measure of efficiency, such that changes in an animal's foraging strategy could be related to environmental changes. It should then be possible to see how easily the animal could adapt to different conditions.

Mink are generally found in habitats closely associated with water (Mech, 1965), e.g. near rivers, lakes and the sea. They are, therefore, subjected to a wide variety of environmental conditions in terms of water depth, turbidity, current flow, salinity etc. It was not possible to investigate the effect of all these environmental conditions on the underwater foraging behaviour, during this study. However, the effects of water depth and current flow were examined independently, but under the same general experimental regime, such that comparison of results would be possible. Further, the effects of changes in prey density, together with changes in habitat complexity (in terms of spatial distribution of potential prey refuges), were also examined when water depth was the same as that in the current experiment, again allowing comparison across all experiments.

1.2. The study animal: The American mink *Mustela vison* Schreber

1.2.1. Classification

Mink are classified as members of the family Mustelidae within the order Carnivora. This is one of the largest families of the Carnivora and is thought to contain about 67 species in 26 genera divided between five subfamilies (Ewer, 1973). The mink is placed in the largest subfamily, the Mustelinae. The other subfamilies are the Melinae (Badgers), Mellivorinae (Honey Badgers), Mephitinae (Skunks) and Lutrinae (Otters). On the whole the mustelids are a very diverse group and can be found on every continent except Antarctica and mainland Australia.

The subfamily Mustelinae with its 33 species in 10 genera shows the greatest diversity, containing weasels (*Mustela* sp.), stoat (*Mustela erminea*), zorilla (*Ictonyx striatus*), martens (*Martes* sp.), wolverine (*Gulo gulo*) and, of course, mink. Although the Mustelinae are the most diverse subfamily, as a whole the range of variation in size, niche use etc. shown by the Mustelidae is quite remarkable. The family contains members which range in size from the least weasel of North America (*Mustela nivalis rixosa*) which, at body weights of 30-70 g, is the smallest known carnivore, to the sea otter (*Enhydra lutris*) which, with a mean weight of 30 kg, is up to 1000 times heavier (King, 1984).

Broadly speaking mustelids take vertebrate prey of various kinds, but some, such as the badger (*Meles meles*:; Kruuk and Parish, 1981) and skunks (*Mephitis* sp., *Conepatus* sp. and *Spilogale* sp.: Voigt, 1984) have opted for a more omnivorous diet, whilst some members of the Lutrinae specialize in invertebrate prey (e.g. Chanin, 1985). Although principally terrestrial the family includes members which are semi-arboreal (martens), fossorial (badgers), and semi-aquatic (otters and mink) (King, 1984).

Within this framework mink can be described as medium-sized carnivores. They are unusual in that, apart from the members of the subfamily Lutrinae, they are the only mustelids which dive. Darwin (1859), in discussing the "Origin and Transitions of Organic Beings with peculiar Habits and Structure", cites the American mink as a species related to the polecat (*Mustela putorius*) and the otter (*Lutra lutra*), and having habits which are a transitional state between a "land carnivorous animal" such as the polecat, and one with "aquatic habits" such as the otter. Similarly, Chanin (1985) states that "the ancestors of otters were probably weasel-like animals which increased the variety of their diet by taking aquatic prey as well as birds and mammals, much as mink do today." The point is, then, that mink can be thought of as a 'missing link' between the terrestrial and aquatic members of the Mustelidae. However, an interesting point here is that it is now believed that the Lutrinae had already taken up an amphibious mode of life by the Oligocene (some 40 million years ago), but the genus *Mustela* is not thought to have separated from other mustelids until the Miocene (25 million years ago) (Romer, 1974). This implies that the aquatic habit in mink has evolved independently from that in the Lutrinae. However, the fossil history of mustelids is relatively poorly known (Romer, 1974); hence a study of the behaviour of the mink, and comparison with that of the otter may shed some light on their evolutionary relationships.

Mink are thought to have originally evolved in North America and it is believed that during the last glacial phase of the Pleistocene (some 10,000 years ago) there was some migration to Eurasia across the Bering Land Bridge (Birks, 1984). Consequently today mink are divided into two species, although they appear to be very similar both in appearance and behaviour. These are the European mink, (*Mustela lutreola*), which has seven subspecies (Ewer, 1973), and the American mink, (*Mustela vison*) which may have as many as 11 subspecies (Dunstone, 1986).

All the animals used in this study were ranch-bred specimens of the American mink.

1.2.2. Distribution

Before the twentieth century the American mink was confined to the North American continent. There it can still be found from Alaska and Canada, except the North Central region (Hewson, 1972), south through the United States (Ewer, 1973), except in the dry areas of the Southwest (Gerell, 1967a), and into Mexico (Dunstone, 1986). Like many mustelids, the mink is a valuable fur bearer, and in the early 1900's Canada pioneered attempts to farm mink commercially for their pelts (Dunstone, 1986). As demand for mink pelts grew, animals were exported to many European countries in the early 1920's/30's (Thompson, 1962) to establish fur farms. However, many animals managed to escape from their cages, or were deliberately released, and feral populations have now established themselves in much of western Europe. In Russia, a programme of deliberate release of at least 30,000 American mink was begun in the 1930's to establish a source of 'free-range' fur (Thompson, 1967; Birks, 1984), and today feral American mink are certainly found from western Siberia to Altai, Tartaria (Shubin and Shubin, 1975).

Feral mink in Europe are almost certainly hybrids descended from a variety of subspecies. Shackelford (1949, 1950) states that it is the common opinion of mink breeders that three subspecies, the Eastern mink (*M.v. vison* Schreber), the Kenai mink (*M.v. melampeplus* (Elliot)) and the Alaska mink (*M.v. ingens* (Osgood)) were used most extensively in building up stocks. These subspecies derive mainly from the eastern and northern parts of North America. In Britain, it is known that mink from Alaska and Labrador formed the original stock for fur farms (Rice, 1967). Other sub-species were also used, as were mutant colour phase introductions, and Shackelford (1950) points out that the present-day average ranch-bred mink has resulted from a fusion of several subspecies. The smaller European mink *Mustela lutreola* occurs both in the Soviet Union (Novikov, 1962) and farther west, where it now survives only in Finland, eastern Poland, parts of the Balkans and western France (Walker, 1983). There is some evidence that the European mink may fail in competition with the American mink (Westman, 1968), but confirmation is hampered by problems of identification and possible hybridization where the two species occur together (Birks, 1984). It, therefore, cannot be known if the feral American mink populations are particularly successful at exploiting the new habitats available to them simply because of the general habits and biology of the species, or whether there is some element of increased 'vigour' due to the original breeding of several subspecies or to hybridization with the European mink.

The animals used in this study were all obtained from a British mink farm; they are thus descended from cross-bred stock. However, since there is obviously no possibility that hybridization with the European mink could have occurred, it was concluded that information obtained on the behaviour of these animals would be applicable to American mink foraging in the natural environment.

1.2.3. Functional morphology

Mink have the typical body plan of the mustelids, i.e. a long slender body and relatively short legs (Ewer, 1973) (see Plate 1). The skull is long, flattened and wedge-shaped, tapering to the muzzle with a short facial region giving it a pointed appearance. The jaws are short and powerful. Dental formula is I3/3 C1/1 P3/3 M1/2, (Aulerich and Swindler, 1968). The incisors of mink (and mustelids generally) are not specialized, but the canines are elongate. Premolars are small, but the carnassials (grinding teeth) are well-developed (Walker, 1983). Thus, skull and jaws are well adapted to delivering an accurately placed death bite (Ewer, 1973).

The ears are small and rounded. The tail is long and bushy, and can be equal to half the length of head and body (Lever, 1977). There is some sexual dimorphism in size; head-body length of males: 34-54 cm, tail length: 15-21 cm, head-body length of females: 30-45 cm, tail length: 14-20 cm (Birks, 1984). Measures of body weights also show that there is a considerable degree of dimorphism between the sexes, e.g. Corbet and Southern (1987) give values of 1121-1232 g (male) and 619-676 g (female) for wild mink in Britain, but Walker (1983) gives general values of 681-2310 g for males and 790-1089 g for females. Generally, ranch bred males may weigh up to 3 kg but wild mink weigh about half this amount (Lever, 1977). Females typically are about two-thirds the size of males.

Moors (1980) points out that sexual dimorphism in body size is a characteristic feature of mustelids. He calculated the dimorphism for various mustelid species, from his own and published data, based on the ratio of the average weights of adult males and females against the logarithm of the mean weight of adult males. From his figure, it appears that mink in Scotland had a dimorphism of slightly above 1.6, while mink from Montana were

Plate 1: Photograph of a female American mink, showing the typical mustelid features of a long, slender body, and relatively short legs.

roughly 1.9. Both results are above the level of 1.6 defined by Ralls (1977) as denoting extreme dimorphism. Two main theories have been advanced to account for the extreme sexual dimorphism seen in mustelids. These are, firstly, that dimorphism is a strategy for avoiding intraspecific competition by enabling the sexes to exploit different food resources (Brown and Lasiewski, 1972; Moors, 1980). Schoener (1969) predicted that solitary predators which spent much time actively searching for and pursuing prey should be more dimorphic than those which did not show such behaviour. Moors' (1980) ratio of dimorphism in mink would seem to agree with this prediction, and Birks and Dunstone (1985), for example, did find considerable differences in the annual diets of male and female mink in Scotland. However, as Moors (1980) points out, this theory does not explain why males should always be bigger than females. He favours the alternative hypothesis, that the polygynous mating system of mustelids coupled with the lack of parental care by the males, results in a powerful selection for sexual dimorphism. Thus, small females will be favoured because of low overall energy requirements, and their ability to channel larger amounts of available energy into reproduction, while males are large mainly as a result of sexual selection (Erlinge, 1979; Powell, 1979; Moors, 1980). In fact, these two hypotheses are not mutually exclusive, since the evolutionary success of sexual dimorphism is linked to the foraging strategies and to the optimum use by each sex of available resources (Moors, 1980).

From this it can be seen that whatever the causes of the development of sexual dimorphism in mustelids as a whole, and in mink in particular, this size difference between the sexes may have important consequences regarding niche separation in terms of diet, habitat use etc. Further, it is possible that the sexes may have evolved differences in hunting techniques. Throughout this study, the behaviour of individuals of both sexes was studied, with a view to examining, if possible, whether there were any sexual differences in behaviour.

Mink have a very luxurious coat which is highly prized by the Fur Trade. Like the fur of the otter, the mink's pelage is thick and waterproof and is made up of two types of hair: guard hairs and underfur hairs. The long guard hairs have a mean density of $780/cm^2$ in the midback region (Dunstone, 1981). Each of these is surrounded by 9-24 underfur hairs (Birks, 1984). These underfur hairs make up a dense matted layer which, like those of the otter, trap air which serves as insulation against low northern temperatures (Birks, 1984), and as a waterproof layer when the animal is in water (Dunstone, 1981; Mason and Macdonald, 1986). Coat colour can vary, but wild mink tend to be dark brown (Dunstone, 1986) to black (Walker, 1983), and captive breeding has produced a number of colour variants. The ventral surface may be paler and there are often spots of white on chin and chest which allow easy identification of individuals (Thompson, 1971). Since the animals used in this study were obtained from a commerical mink farm, some individuals had coat colours that varied from the wild type. Details are given in Appendix I.

The limbs of mink are short and bear five digits. Each digit carries a claw which is compressed, curved and non-retractile (Walker, 1983). There is a partial web between the toes, but the surface area of the feet is relatively small indicating that, unlike other semi-aquatic mammals, mink lack specialized appendages for swimming (Williams, 1983a). However, small appendages would prevent awkwardness during terrestrial locomotion, and it has been noted that paw surface area is generally reduced in animals that can run at high speed (Williams, 1983a). On land, when travelling at speed, mink move by means of a 'scampering' gait interspersed with a series of bounds. Details of the sequence of limb movements involved in both slow and fast terrestrial locomotion are given by Dunstone (1981). He also gives figures of 48 cm s^{-1} for the mean speed attained by a mink walking and 262 cm s^{-1} as the bounding speed.

Dunstone (1981) does not state what size the mink were, but if it is assumed that the animals were medium-sized males, with head-body length of 45 cm, then mink can travel at speeds of five to six body lengths per second on land. Dunstone (1981) also gives details of the limb movements observed for mink surface-swimming, and swimming fully submerged, and Williams (1983a) describes and presents diagrams for mink surface-swimming. Other authors have also examined the swimming ability of mink in terms of speed of movement and there seems to be a wide variation in published speeds. Dunstone (1981) tested animals in a 2 m x 1 m x 1 m tank of still water and recorded a surface swimming speed of 42 cm s^{-1} . He also studied swimming and diving in a tank of diameter 5 m, depth 1 m, and found that underwater speed when pursuing prey increased to 59 cm s^{-1} (roughly one and a half body lengths per second for an average sized male). However, Poole and Dunstone (1976) recorded a maximum value of 76 cm s^{-1} for underwater pursuit swimming, and Dagg and Windsor (1972) quoted the swimming speed as 83.3 cm s^{-1}, roughly two body lengths per second. Finally, Williams (1983a) observed mink swimming against a current in a water flume, and recorded maximum speeds of 70 cm s^{-1} for surface swimming, roughly one and half to two body lengths per second. The importance of these measurements will be assessed later when the swimming ability of the mink is related to that of many of its fish prey.

Swimming and diving behaviour of otters has been much studied, and data on the Eurasian otter, *Lutra lutra*, can be given for comparison. Otters are more truly amphibious than mink, and Corbett and Southern (1987) quote speeds of 10-12 km h^{-1}

(278-334 cm s^{-1}) for underwater swimming. If mean head and body length for a male otter is approximately 70 cm (Chanin, 1985), then otters are able to achieve underwater speeds of between 4-4.5 body lengths per second.

Terrestrial mustelids are thought to hunt primarily using scent (Walker, 1983), although hearing and vision are well developed. However, scent and hearing will obviously be of little use to the mink when hunting underwater, and the predator would need to rely on visual or tactile cues. Like the otter, the mink's muzzle is surrounded by stiff whiskers, or vibrissae, which may assist in prey location in murky waters. Green (1977) noted that the hunting success of a captive Eurasian otter, whose vibrissae had been cut off, was significantly reduced in murky water as compared with clear water. Similar experiments have not so far been carried out with mink. However, there has been much work done on the visual capabilities of mink both on land and underwater. Psychophysical experiments have been carried out to determine the visual acuity of mink in air and underwater, when illumination at the choice point for the stimulus was 34 mL and discrimination distance was 20 cm (Sinclair et al., 1974). Further studies investigated changes in aerial and underwater visual acuities when animals were tested under conditions of varying stimulus luminence and discrimination distance (Dunstone and Sinclair, 1978a).

The results of those studies showed that visual acuity for static objects declined markedly underwater, from a minimum resolvable angle of 15.1 min in air, to one of 31.4 min underwater. However, when ambient illumination was low, aerial minimum resolvable angle rose to 51.7 min at 0.012 mL, and underwater minimum resolvable angle rose to 95 min at 0.012 mL. This suggests that if mink hunt underwater at higher light levels than in air, they could obtain equivalent acuities in the two media (Dunstone and Sinclair, 1978a). Further, as distance from the stimulus was increased, aerial threshold visual angle rose from 15.4 min at 10 cm, to 19.1 min at 90 cm, whilst underwater vision also deteriorated from a threshold visual angle of 32.7 min at 10 cm, to one of 46.6 min at 90 cm. Results suggested an optimum viewing distance underwater of between 15-60 cm. This correlates with the average detection distance, for mink detecting fish prey underwater, of 35.9 ± 19.9 cm (mean ± S.D.) for static prey and 33.8 ± 26.1 cm for moving prey (Poole and Dunstone, 1976). Sinclair et al. (1974) present comparative visual acuity data for other mammals in air and underwater. It appears from this that the eyes of mink, unlike those of, e.g. the Asian 'clawless' otter (*Amblonyx cineria*) and the California sea lion (*Zalophus californianus*), show little specialized adaptation to underwater vision, (although Dunstone (1976) did show the prescence of an enlarged accomodatory muscle), and these authors suggest that the smallest stationary fish a swimming mink could resolve at 20 cm, would be one with a body depth of approximately 0.2 cm when the fish was viewed at high contrast against a homogenous background. They further suggest that since such ideal viewing conditions would be rare, mink would only be able to detect fish larger than this, unless prey detection is enhanced by the perception of movement.

The ability of mink to detect high-speed directional movement in air and underwater under various conditions of light intensity and discrimination distance was investigated by Clements and Dunstone (1984). The most interesting point to note is that they found broadly equivalent motion perception capability in air and underwater at a detection distance of 10 cm and stimulus radiant intensity of 15 x 10^4 μW sr^{-1}. Results gave a mean stimulus speed of 278 (S.D. ± 33.85) cm s^{-1} in air and 260 (S.D. ± 40.21) cm s^{-1} underwater at threshold. The authors also noted that motion perception capability declined with decreasing stimulus brightness in air and underwater, resulting in an aerial threshold mean of 235 cm s^{-1} at 58 μW sr^{-1}, being approximately equal to that estimated underwater, (227 cm s^{-1}) when a slightly brighter stimulus (900 μW sr^{-1}) was used.

Finally, Clements and Dunstone (1984) found a decrease in motion detection capability as discrimination distance increased; however, these experiments were conducted in air only.

The important point to note from this work is that basically the mink eye seems to have undergone little or no special adaptation to underwater vision (Sinclair et al., 1974; Dunstone, 1976). Nevertheless, poor visual acuity underwater may be partly countered by good motion perception abilities, especially at shorter detection distances, i.e. less than one metre (Dunstone, 1983).

1.2.4. Habitat

In their native North America, mink can be found in a variety of habitats, generally associated with water. They usually frequent freshwater streams, rivers, lakeshores, swamps and marshes (Mech, 1965; Walker, 1983). However, they may also be found near brackish water in estuaries and in coastal habitats, and on offshore islands (Hall, 1929; Hatler, 1976). Occasionally, mink will forage away from water and they may even be found in big cities (Mech, 1965). In general, the preferred habitat is densely vegetated and wooded waterways (Walker, 1983), but, provided cover is good, mink will adapt to other situations (Hall, 1929). A factor which determines mink population density is the availability of den sites (Erlinge, 1972). In North America dens can be found under stones, in tree roots, in unoccupied burrows (e.g. beaver, *Castor canadensis*, muskrat, *Ondatra zibethica*), or self-excavated burrows (Walker, 1983).

Thus, it can be seen that the mink exhibits a high ecological adaptability, being found in at least 12 of the described North American biotic provinces, and having a distribution range which encompasses four of the major climate types (Northcott et al., 1974).

This adaptability may well be the secret for the highly successful acclimatization and dispersal of the mink in Europe and Russia. Many studies have documented the association of mink with watercourses in every country to which they have been introduced (Gudmunsson, 1952; Wildhagen, 1956; Novikov, 1962; Gerell, 1967a; Westman, 1968; Deane and O'Gorman, 1969; Andersen, 1981). In Britain, for example, mink have been found on eutrophic lake and marsh systems, oligotrophic moorland rivers and even a river system running through the city of Exeter (Birks and Linn, 1982). In Scotland, Hewson (1972) reports that mink utilize fast flowing shallow upland rivers and burns, but not streams flowing through heather moorland where cover was scarce, and mink have also been reported in coastal areas and on offshore islands (Birks and Dunstone, 1984; Birks, pers. comm.). In Britain and Europe (e.g. Gerell, 1967a; Erlinge, 1972) as in North America, the availability of den sites will be important in determining population density. Birks and Linn (1982) found that mink in Southern Britain used a wide variety of sites, e.g. tree roots, rabbit burrows, human artifacts (i.e. walls, causeways etc.), and mink would also make dens above ground in scrub, brambles, brushpiles, reed beds etc. In other words, feral mink in Europe seem to be occupying very similar habitats to those occupied in North America. Thus, the high degree of ecological adaptability shown by mink in North America may well have pre-disposed the animal to successful acclimatization in comparable habitats and climate types in Europe. For example, Gerell (1967a) states that there are only small climatic differences between Sweden and the native areas of the mink stocks from which the feral Swedish populations are descended.

1.2.5. Diet

Since this study is concerned with the underwater foraging behaviour of the mink, it is felt that a review of the available information on the specific details of the aquatic components of mink diet, both from North America and Europe, is appropriate. Where available, information on the other components of mink diet will also be briefly discussed.

The diet of the mink has been well studied, both in its native North America and in many countries where it is now feral. Most work has been carried out on the analysis of mink scats (faecal remains), or on gut contents. The advantages of scat analysis is that the diet of individuals (or local populations) can be studied over long periods and information obtained on seasonal variations in diet, sex differences and so on. The disadvantage is that scats contain only those parts of the food intake which cannot be digested (e.g. scales, hair, feathers, bones etc.). Thus, foods consisting mainly of soft parts will be under-represented in the sample. To try to overcome this, different authors have developed different methods of presenting the results of scat analysis, all aiming to produce the best fit between actual prey intake and identifiable items in the scat. In general, either percentage frequency (i.e. the percentage of scats containing aparticular item), or relative frequency (i.e. the number of occurrences of a prey item expressed as a percentage of the total number of occurrences of all items in the sample) are used (Mason and Macdonald, 1986). However, a further complication arises because different species and sizes of prey have different proportions of parts which pass through the gut undigested (Chanin and Linn, 1980). To try and overcome this, workers have attempted to calculate correction factors based on feeding trials with captive animals (e.g. Lockie, 1959, for foxes, *Vulpes vulpes*; Akande, 1972). However, Day (cited in Chanin and Linn, 1980) has pointed out that the correction factors vary not only between different species of prey, but also between different sizes of prey and predator. Hence, most authors continue to use uncorrected percentage frequency or relative frequency, although Wise et al. (1981) have now developed a bulk percentage measure.

Analysis of gut contents would give a better picture of recent diet of the individual, but this method has obvious limitations, particularly if the animal is rare or not easily trapped. Also, large samples may be available for parts of the year only, e.g. Hamilton (1959) was able to obtain mink carcasses from trappers during the open season (autumn and winter), but had to rely on scat analysis to determine spring and summer diet.

A few studies (e.g. Yeager, 1943; Birks and Dunstone, 1984) have looked at prey remains in mink dens. The advantage of this is that accurate identification, often to species level, can be made. However, since small items of prey are probably eaten oncapture (Birks and Dunstone, 1984) and only larger items brought back to dens the information obtained on overall diet of mink will be incomplete. Information from such studies has, therefore, not been included in Table 1.1, but a summary can be given here. Yeager (1943) reviewed the literature and compiled a table of all reports of hoarding at mink dens in North America. The main prey items found were muskrats, but waterfowl, and in one case (Webster, 1889 cited in Yeager, 1943) seven fish, were also found. Similarly, Birks and Dunstone (1984) recovered 96 items from coastal mink dens in Scotland; 62.5% were mammal remains (mostly rabbit, *Oryctolagus cuniculus*), and the remainder were birds. Of these 21 items (21.9%) were seabirds, four (4.2%) were waders, but one pheasant (*Phasianus colchicus*) and one grey partridge (*Perdix perdix*) were also found. The remainder (nine items) comprised crows (*Corvus* sp.) pigeons (*Columba* sp.), and pipits (*Anthus* sp.).

Finally, there have been some observations of wild mink foraging in their natural habitat. This would seem to be the best way of determining accurately the daily and seasonal diet of the animal, if combined with scat analysis and investigation of dens. However, direct observation of these elusive creatures is difficult, e.g. Melquist et al. (1980) radio- tracked

TABLE 1.1 Diet of mink

Locality	Season	Habitat	Method	Sample size	Fish	Mammals	Bird	Reptiles	Amphibians	Crustacea	Invertebrates	Carrion	Unidentified	References
AMERICA New York	Autumn/ Winter	Streams Marshes	Gut(RF)	630	28.78	27.98	2.28	1.20	18.46	12.18	9.10	-	-	Hamilton, 1959 includes * data from Hamilton, 1940
	Spring/ Summer	Tidal flats	Scat	561	21.44	29.09	6.12	2.71	12.49	8.36	19.79	-	-	
New York	Aut/Win	Various	Gut(RF)	70	18.82	54.13	-	-	2.36	16.47	7.06	-	1.18	Hamilton, 1936
Michigan	Winter	-	Gut(%F)	-	11.00	70.00	13.00	2.00	23.00	6.00	-	-	-	Sealander, 1943 cited in Hamilton, 1959
Michigan	Winter	-	Gut(%F)	297	18.35	55.63	5.70	1.59	8.55	7.91	2.27	-	-	Dearborn, 1932 (cited in Hamilton,1959)
	Summer	-	Scat(V%F)	77	2.87	19.64	0.89	0.61	5.75	68.22	2.02	-	-	
Missouri	Winter	Various	Gut(%F)	372	30.90	32.00	5.90	0.30	25.50	19.90	4.00	-	1.90	Korschgen, 1958
North Carolina	-	-	Gut	335	-	-	-	-	-	-	-	-	-	Wilson, 1952
Pennsylvania	Winter	Various	Gut(RF)	105	19.53	41.40	3.13	-	0.78	14.06	17.97	3.13	-	Guilday, 1949
CANADA Alberta	All year	Stream	Scat (%F)	64	6.30	82.8	18.8	-	-	-	15.60	-	-	Gilbert & Nancekivall, 1982
		Lakes		135	32.60	52.5	32.6	-	-	1.50	31.10 <inc. unid>			
RUSSIA Archangel Region	All year	-	Scat (%F)	-	16.40	54.7	5.70	-	37.50	-	-	-	-	Grigor'ev & Egorov, 1969 [Abstract only]
EUROPE Sweden	All year	Trout water	-	-	-	-	-	-	-	-	-	-	-	Erlinge, 1969
Sweden	Summer	Eutrophic lake	Scat (%F)	-	8.00	65-70	-	-	-	60.00	-	-	-	Erlinge, 1972

TABLE 1.1 Diet of mink (cont'd.)

Locality	Season	Habitat	Method	Sample size	Fish	Mammals	Bird	Reptiles	Amphibians	Crustacea	Other Invertebrates	Carrion	Unidentified	References
EUROPE Sweden	All year	Various lakes, streams & islands	Scat	9486	Data are given on nine sites and details of great regional and seasonal are shown. Fish and mammals are most important. Birds, crayfish and water beetles are important locally and seasonally.									Gerell, 1967 & 1968
Britain Scotland	Wint/Spr	Various	Gut (RF)	55	54.32	32.60	13.00	-	-	-	-	-	-	Akande, 1972*
	Sum/Aut	-	Scat	33	39.10	34.80	26.10	-	-	-	-	-	-	
England & Wales	All year	Various	Gut (RF)	204	12.75	32.84	32.84	0.98	1.96	4.9	2.45	-	11.27	Day & Linn, 1972
Scotland	All year	Rivers	Scat (RF)	722	67.00	16.00	7.00	-	1.50	2.0	6.00	-	-	Cuthbert, 1979
		Seashore		78	28.00	15.00	16.00	-	-	33.0	8.00	-	-	
England (Devon)	All year	R Teign	Scat	475	53.90	29.20	10.80	-	2.70	-	2.50	-	0.90	Chanin & Linn, 1980
		R Frome	(RF)	153	34.40	30.60	23.50	0.50	0.50	-	9.30	-	-	
		Slapton Ley		57	52.80	15.30	29.20	-	-	-	1.40	-	1.40	
England (Devon)	All year	Slapton	Scat	513	31.60	29.50	36.90	-	0.50	-	1.20	-	-	Wise et al., 1981
		R. Dart & Webburn	(BF)	448	24.80	57.00	4.80	-	9.60	-	1.80	-	-	
Scotland	All year	Coast	Scat (RF)	2043	29.10	40.90	11.20	-	-	18.7	-	-	-	Dunstone & Birks, 1987

NB. Some studies such as those of Gerell, 1967; 1968 and Jenkins and Harper, 1980 could not be cast into the format for the table and have been omitted.

RF = relative frequency = ie % of total items in sample.

%F = percentage frequency.

BF = Bulk percentage.

V%F = Volumetric percentage frequency.

* indicates data was recalculated from the original source.

26 individual mink for a total of 889 hours, but animals were actually observed foraging for a mere 2.1 hours within that period! Whilst working on coastal mink in Scotland, Ireland (pers. comm.) actually observed mink for five hours out of 1,500 hours spent radio tracking. Similarly, Dunstone and Birks (1987 and pers. comm.), also working in Scotland, report only rare observations of radio-collared animals foraging in rock pools on the shore, and swimming and diving in the sea, despite the fact that prey from these habitats comprise a significant proportion of the diet.

However, despite the limitations of methods employed to obtain information on mink diet, many studies have been carried out. Table 1.1 provides a summary of information obtained from scat analysis and gut content studies. Prey items have been grouped into the following categories:- Mammals, Birds, Reptiles, Amphibians, Fish, Crustacea, other Invertebrates, Carrion and Unidentified. Some authors record the presence of vegetation in guts (Korschgen, 1958; Hamilton, 1959) and scats (Day and Linn, 1972). Others believe vegetation is ingested incidentally (e.g. Wise et al., 1981). Hence, where authors cited it, it has been included under Unidentified in Table 1.1. Some authors presented their results in terms of percentage frequency, others as bulk percentages and finally some presented relative frequency. If possible the raw data was recalculated to give relative frequency of occurrence as (a) this allowed comparison between the largest number of authors and (b) Erlinge (1968), after feeding trials, concluded that frequency of occurrence probably gave a fairly true picture of the relative importance of the different food categories to the predator.

From Table 1.1 it can be seen that mink do indeed have a very varied diet. Many authors noted seasonal variations in diet composition (notably Gerell, 1968; Birks and Dunstone, 1985; Dunstone and Birks, 1987) and diet also varies in relation to locality. The general trend in North America, therefore, is for the diet to consist of a mixture of prey types in varying proportions, depending onwhat is locally available, e.g. crayfish (*Cambarus* sp.) seemed to be an important food both locally and seasonally, and Dearborn (1932) (cited in Hamilton, 1959) gave a volumetric percentage frequency of 68.22% for crayfish in summer scats in Michigan. In other studies, however, crayfish composed less than 20% of the diet.

Table 1.1 also includes results of food studies carried out in countries where mink are now feral, namely Russia, Sweden and Britain. The overall picture obtained from these studies is that in terms of the general categories of prey types involved, mink diet is very similar in general composition to that in North America. Again the actual proportion of the diet made up of, e.g. fish, varied with locality and season, but the ranges were similar to those noted from the North American data, although in Europe fish often seemed to be more important and mammals less so. However, one important point is that generally birds, especially waterfowl, seem to be of greater importance in the diets of American mink in Europe, with amphibians and also crustaceans (notably crayfish, *Astacus astacus*, which are rare in parts of Britain), of lesser importance. Also, since muskrat are not present in Britain and Europe, other mammals are utilized as prey. In some areas of Scotland, for example, rabbits were the most predominant mammal prey (Jenkins and Harper, 1980; Dunstone and Birks, 1987). In other parts of Scotland, mice (e.g. *Apodemus sylvaticus*), voles (*Clethrionomys glareolus*, *Microtus agrestis* and *Arvicola amphibius*) and shrews (*Sorex araneus* and *Neomys fodiens*) made up the bulk of the mammal items (Akande, 1972; Cuthbert, 1979).

The overall picture obtained from these dietary studies is that the mink is a generalized opportunistic carnivore, utilising a large number of animal species as food (Northcott et al., 1974) but with aquatic animals forming a significant component of the diet (Wise et al., 1981). It has been suggested that mink appear to take prey in relation to their local abundance, availability and vulnerability (Hamilton, 1959; Chanin and Linn, 1980) Thus, Chanin and Linn (1980), working in Devon, found that mink took bird prey two to three times more frequently on the River Frome and Slapton Ley (lake) than on the River Teign. They related this to the fact that the bulk of the avian prey in the first two areas, i.e. Ralliformes and Anseriformes, are generally found close to, or in, water, and their poor flying abilities may make them more vulnerable to mink predation than the more 'terrestrial' avian species found on the River Teign, which rely on rapidly detecting ground predators and quick take-off.

Strictly speaking, the aquatic prey items comprise fish, Amphibia, crustaceans, other invertebrates (e.g. water beetles *Dytiscus* sp., Hamilton, 1959) and waterfowl such as ducks, (e.g. *Anas* sp.) coots (*Fulica atra*), moorhens (*Gallinula chloropus*) etc. However, for the purpose of this study only those species that have to be pursued and captured underwater are of interest. This effectively limits the 'interesting' items to Crustacea and fish, since, although waterfowl can form a significant portion of mink diet, it is thought that these are taken in the shallow areas near lake and river banks or on the shore whilst roosting (Wise et al., 1981). Similarly, Amphibia, especially frogs such as *Rana pipiens*, may be important seasonally in North America, but are thought to be taken as torpid individuals from pond bottoms where they overwinter (Hamilton, 1959). Other more aquatic species such as salamanders (*Desmognathus* sp., *Eurycea* sp. and *Ambystoma maculatum*) were much less important in the diet (Hamilton, 1959). In Britain, Amphibia were more important as prey in summer and autumn (Wise et al., 1981), when they are more terrestrial in habit (Smith, 1951). Little information was available as to the identification of 'other invetebrates'. However, Hamilton (1959) showed that water beetles and their larvae, tipulid larvae, Neuroptera larvae and large Plecoptera nymphs were most frequently taken. Mellanby (1968) details the habits of these larvae and, in fact, most are to be found on the bottom of ponds and streams, thus mink would not need to actively pursue such prey. It is only the diving water beetles that might require active pursuit, but even so they may be vulnerable when they surface for air. However, apart from *Dytiscus* sp., these invertebrates are a relatively unimportant component of mink diet and shall not be considered further.

The two final categories are Crustacea and fish. In America, the crustacean element of mink diet is mainly represented by the crayfish for those species living inland. In Britain, crayfish are only locally abundant and hence do not figure prominently in mink diet, but in Sweden, crayfish can be an important item, especially in the warm months (Gerell, 1968). For coastal mink, the shore crab (*Carcinus maenas*) may be seasonally important (Dunstone and Birks, 1987), but again these are probably caught on the shore or in shallow rock pools and do not require underwater pursuit. Thus, as far as underwater foraging behaviour is concerned the animals of greatest importance are fish. Unfortunately, when the diet of mink is elucidated by means of scat analysis, information on the species of fish eaten may be poor. This is because identification to species has to depend on identification of such items as scales, vertebrae and otoliths, and often closely related species, e.g. salmon, *Salmo salar*, and trout, *Salmo trutta*, cannot be separated. However, some information can be gained by comparison with reference collections and a knowledge of the potential prey species available, e.g. by electrofishing (Wise et al., 1981) or rock-pool sampling (Dunstone and Birks, 1987). Watson (1986) provides a key to some marine fish found in the spraints of otters foraging from the coast of Shetland. Wise (1980) outlines a method relating length of vertebra, in faecal material, to fork length of fish, thus allowing the size of fish taken as prey to be estimated.

Table 1.2 gives details of the fish families and, where possible, the species recorded as having been consumed by mink in North America. Table 1.3 provides the same information for European studies. Finally, Table 1.4 gives more detailed information, where available, on the relative importance of the various fish families to the diet of the mink, expressed as a proporton of the total fish consumed.

From these tables it can be seen that cyprinids, salmonids, eel (*Anguilla anguilla*) and burbot (*Lota lota*) are the most important prey classes to the mink, depending on location. Since the aim of this study is to investigate the underwater foraging behaviour of mink, the results obtained for dive duration, speed of underwater swimming etc., may help to explain why certain fish are more commonly predated. A knowledge of the habits, swimming speeds etc. ofthese fish may also shed light on why they are vulnerable to predation by mink, and such information will be discussed in more detail in Chapter 7 where it can be evaluated in the light of the results of this study.

1.3. Diving Physiology

Mink are air-breathing mammals and in order to forage underwater they must voluntarily endure a period of time when respiration is suspended. Dunstone and O'Connor (1979b) showed, using Principal Component Analysis, that 23% of the variation in observed foraging behaviour could be ascribed to oxygen constraints. During the course of this study measurements were made of such parameters as dive duration, time on bottom etc., under varying conditions of water depth, prey density and current flow. It was found that mink were able to change their behaviour in response to changing environmental conditions. An important question is how were mink able to achieve this? To answer this, it is necessary to review the available information on diving physiology. Most work in

TABLE 1.2. Fish families and species recorded in Mink diet from North America

Family	Species	References
Ameiurida	*Ameiurus* sp. (Bullhead)	Hamilton, 1959; Korschgen, 1958
Catostomidae	*Catastomus* sp. (Sucker)	Guilday, 1949; Hamilton, 1959
	C. commersoni (White Sucker)	Gilbert & Nancekivall, 1982
Centrarchidae	*Micropterus dolomieui* (Small mouth bass)	Hamilton, 1959
	Lepomis gibbosus (common pumpkin seed)	
Cyprinidae	*Semotilus* sp. (chub)	Guilday, 1949
	S. atromaculatis (Horned dace)	
	Rhinichthys atratulus (Blacknose dace)	Hamilton, 1959
	Notemigonus crysoleucas (Golden shiner)	
Cyprinodontidae	*Fundulus* sp.? (Killifish)	Hamilton, 1959
	F. heteroclitus (Mummichog)	
Escocidae	*Esox lucius* (Northern pike)	Gilbert & Nancekivall, 1982
	? (pickerel)	Hamilton, 1959
Percidae	*Perca* sp. (perch)	Hamilton, 1959
	Etheostoma nigrum (darter)	
Salmonidae	*Salvelinus fontinalis* (Brook trout)	Hamilton, 1959
	Salmo trutta (Brown Trout)	
Thymallidae	*Thymallus arcticus* (arctic Grayling)	Gilbert & Nancekivall, 1982
Umbridae	*Umbra limi* (mudminnow)	Hamilton, 1959
?	(Brook stickleback)	Gilbert & Nancekivall, 1982

TABLE 1.3. Fish families and species recorded in Mink diet in Europe

Family	Species	References
Anguillidae	*Anguilla anguilla* (eel)	Gerell, 1968; Cuthbert, 1979; Chanin & Linn, 1980; Wise et al., 1981; Birks & Dunstone, 1985; Dunstone & Birks, 1987
Blenniidae	*Lipophrys pholis* (Blenny) *Pholis gunnellus* (Butterfish)	Birks & Dunstone, 1985; Dunstone & Birks, 1987
Cobitidae	*Noemacheilus barbatulus* (stone loach	Cuthbert, 1979; Chanin & Linn, 1980
Cottidae	*Cottus gobio* (Miller's thumb)	Wise et al., 1981
	C. poecilopus (bullhead)	Gerell, 1968 (could not distinguish between these 2 sp.)
	(Sculpins)	Gerell, 1968
	Taurulus bubalis (sea scorpion)	Birks & Dunstone, 1985; Dunstone & Birks, 1987
Cyprinidae	*Rutilus rutilus* (roach)	Gerell, 1968
	Scardinius erythrophtalmus (rudd) *Leuciscus idus* (ide)	Chanin & Linn, 1980; Wise et al., 1981. (can't separate the 2 sp)
	Abramis brama (Bream) *Phoxinus phoxinus* (Minnow) *Tinca tinca* (Tench) *Alburnis alburnis* (Bleak)	Gerell, 1968
Escocidae	*Esox lucius* (Pike)	Gerell, 1968; Erlinge, 1969; Chanin & Linn, 1980; Wise et al., 1981
Flatfish	No further identification	Birks & Dunstone, 1985; Dunstone & Birks, 1987
Gadidae	*Lota lota* (Burbot)	Gerell, 1968; Erlinge, 1969
	Ciliata mustela (5-bearded rockling)	Birks & Dunstone, 1985; Dunstone & Birks, 1987

TABLE 1.3. Fish families and species recorded in Mink diet in Europe (contd.)

Family	Species	References
Gasterosteidae	*Gasterosteus aculeatus* (3-spined stickleback)	Cuthbert, 1979; Chanin & Linn, 1980 Wise et al., 1981; Dunstone & Birks, 1987 Gerell, 1968 did not distinguish between the 2 sp.
	Pygosteus pungitius (10-spined stickleback)	
	Spinachia spinachia (15-spined stickleback)	Birks & Dunstone, 1985; Dunstone & Birks, 1987
Gobiidae	*Gobius* sp.	Birks & Dunstone, 1985; Dunstone & Birks, 1987
Labridae	*Ctenolabrus rupestris* (Jago's goldsinny)	Gerell, 1968
Percidae	*Perca fluviatilis* (perch)	Gerell, 1968; Erlinge, 1969; Cuthbert, 1979; Chanin & Linn, 1980; Wise et al., 1981
Salmonidae	*Salmo trutta* (trout)	Gerell, 1968; Erlinge, 1969; Cuthbert, 1979; Akande, 1972; Birks & Dunstone, 1985; Dunstone & Birks, 1987 (indistinguishable).
	Salmo salar (salmon)	
	Salmo trutta trutta (sea trout)	Chanin & Linn, 1980; Wise et al., 1981 (all 3 sp.)
Thymallidae	*Thymallus thymallus* (Grayling)	Gerell, 1968; Cuthbert, 1979; Akande, 1972; Chanin & Linn, 1980

TABLE 1.4 **Proportion of total fish eaten, made up by different fish families**

Locality	Reference	Season	Method	Total fish as prop. of diet	Ame.	Ang.	Cat.	Cent.	Cob.	Cot.	Cyp.	Cypr.	Esoc.	Gast.	Perc.	Salm.	Thy.	Umb.	BS.	Burbot	Unid.
AMERICA Pennyslvannia	Guilday, 1949	W	Gut	19.53	-	-	4.00	-	-	-	8.0	-	-	-	-	-	-	-	-	-	88.00
New York	Hamilton, 1959	A/W	Gut	28.78	1.86	-	3.26	5.12	-	-	40.93	3.72	1.86	-	3.26	7.44	-	0.47	-	-	33.49
CANADA	Gilbert & Nancekivall, 1982	All	Lakes Scat	32.60	-	-	6.80	-	-	-	-	-	14.50	-	-	-	2.2	-	88.63	-	-
Alberta			Stream	6.30	-	-	-	-	-	-	-	-	50.00	-	-	-	-	-	50.0	-	-
EUROPE	Erlinge, 1969	W		-	-	-	-	-	-	-	3.7	-	25.20	-	3.7	18.5	-	-	-	44.4	-
Sweden		Sp	Scat	-	-	-	-	-	-	-	18.7	-	18.70	-	15.6	3.1	-	-	-	40.6	-
		Su		-	-	-	-	-	-	-	5.5	-	-	-	5.5	-	-	-	-	22.2	-
		A		-	-	-	-	-	-	-	13.3	-	11.10	-	8.9	2.2	-	-	-	44.4	-
Sweden	Gerell, 1968	% occurrence for each species is given for each month (or groups of months) for each of 9 sites, but raw data were not available to combine these percentages to give seasonal figures.																			
BRITAIN Scotland	Akande, 1972	All	Gut/ Scat	45.00	-	-	-	-	-	-	-	-	-	-	-	69.0	10.0	-	-	-	21.00
Scotland	Cuthbert, 1979	All	Scat	67.00	-	34.0	-	-	5.0	-	11.0	-	-	-	2.0	47.0	1.0	-	-	-	1.00
England & Wales	Day & Linn, 1982	All	Gut	12.75	- All remains were of coarse fish (usually cyprinids)																
England	Chanin & Linn, 1980	All	T	53.90	-	16.8	-	-	2.5	-	-	-	-	-	-	34.2	-	-	-	-	0.40
			Scat F	34.40	-	7.7	-	-	1.1	-	6.0	-	1.10	-	-	4.9	1.6	-	-	-	12.00
			S	52.80	-	26.4	-	-	-	-	8.3	-	-	8.3	5.6	1.4	-	-	-	-	2.80
England	Wise et al., 1981	All	R.W.+D Scat	24.80	-	1.9	-	-	-	0.9	-	-	-	-	-	22.0	-	-	-	-	-
			Slapton	31.60	-	11.0	-	-	-	-	13.6	-	1.50	0.4	5.4	<0.3	-	-	-	-	-

NB: For the last 2 studies in England the relative frequency of each prey family is given with regard to diet as a whole, it does not accurately show, as in the other studies, how important each family is to the mink.

NBB: Key to the different fish families in this table is given opposite.

this field has been carried out on marine mammals or diving birds, but there have been a few studies on the physiological responses of mink to immersion in water. The following is a brief review of some of the general principles of physiological responses to diving.

There has long been much interest in how certain vertebrates can survive long periods without breathing while others cannot. For example Bert, in 1870 (reported in Irving, 1939) carried out forcible submergence experiments on a variety of mammals, both 'divers' and purely terrestrial. Irving (1939) further reports data for dive times in a variety of seals and whales ranging from six minutes to two hours, and reports Bert's (1870) information on terminal dive times for terrestrial animals, i.e. dogs *(Canis familiaris)* (4 min 25 s), young cats *(Felis catus)* (2 min 55 s) rabbits *(Oryctolagus cuniculus)* (3 min) and white rat (*Rattus norvegicus* var. *albinus*) (2 min 6 s).

Kooyman (1975) states that there are several adaptations which would directly affect breath holding endurance. These are (a) the oxygen stores of the body, (b) the degree to which the blood oxygen store is limited to obligate aerobic tissue (i.e. restricting blood supply to sensitive tissues, e.g. brain, heart) and (c) the degree of sensitivity to aerobic and anaerobic metabolites. There have been few studies examining the detailed physiological changes that might occur during diving. Andersen (1961) carried out a detailed study using the American alligator, *Alligator mississippiensis*, forcing it to dive for prolonged periods, and Kooyman et al. studied voluntary diving in adult (1980) and juvenile (1983) Weddell seals (*Leptonychotes weddelli*). Such detailed studies, particularly that of Andersen which involved measurements of arterial blood pressure, heart rate, oxygen and carbon dioxide content of arterial blood, lactic acid concentration and pH of arterial blood, variations in the composition of the lung air during diving and rate of oxygen consumption from lungs, are obviously difficult, if not impossible, to carry out on free-diving animals. Thus, many early studies only measured heart rate, and later studies may additionally have measured respiratory frequency and oxygen consumption in a variety of mammals and birds undergoing both forced and voluntary submersions. The most recent studies have also included blood sampling.

Early studies involving forced submersion of diving mammals, e.g. Irving and Orr (1935) (beaver) and Scholander (1940) (various species of seals), observed that heart rate dropped dramatically once animals were immersed in water. This became known as the 'diving bradycardia' and has been repeatedly observed in many studies involving forced submersion, e.g. Harrison and Tomlinson (1960) (common seal, *Phoca vitulina*), Andersen (1961) (American alligator), Andersen (1966) (a review), Elsner et al., (1966) (muskrat and beaver), Gilbert and Gofton (1982a) (American mink), West and Van Viet (1986) (American mink). The development of a 'diving' bradycardia has often been taken as an indication of the occurence of other physiological and metabolic adjustments to diving (see Stephenson et al., 1986) and was interpreted as the principle oxygen conserving response (Kanwisher et al., 1981). Presumably forced submersion of a non-aquatic vertebrate would not be expected to produce a bradycardia, but I could find no observations in the literature. However, Irving (1939) comments that land mammals struggle violently when they are forcibly submerged, whereas he found that muskrats (Irving, 1939) and beavers (Irving and Orr, 1935), exhibited muscular relaxation when submerged, and he assumed that this would assist these animals to conserve their oxygen supply by not wasting energy in struggle. Harrison and Tomlinson (1960) also noted that young adult common seals could be forcibly submerged for periods of up to 15 min before struggling commenced. This implies that bradycardia should develop in those species which are considered to be 'divers' when they are forcibly submerged.

However, reduction in heart rate is not sufficient as a mechanism for prolonging the time vertebrate divers can withstand voluntary or involuntary apnoea. Stephenson et al. (1986) state that it has been repeatedly shown that an "orchestrated set of cardiovascular adjustments" occurs in mammals and birds when submerged in water. They further state that it is generally thought that these adjustments serve to conserve the available oxygen stores (which are principally in the blood haemoglobin, myoglobin, lungs, and (for birds) air sacs (Kooyman, 1975)). The available oxygen is then thought to be directed to those tissues that can least withstand oxygen depletion (i.e. heart, brain) by peripheral vasoconstriction (see Kooyman, 1975). Anaerobic respiration resulting in the accummulation of lactic acid may also occur, and the whole is accompanied by a reduction in cardiac output mainly due to a fall in heart rate (see Stephenson et al., 1986 for further references).

However, work has been done on calculation of oxygen storage capacities (see Kooyman, 1975; Keijer and Butler, 1982). Further, by measuring oxygen uptake between dives, Woakes (1988) states that it is possible to estimate oxygen consumption during a dive. This was done using tufted ducks (*Aythya fuligula*) and Humboldt penguins (*Spheniscus humboldti*) (Woakes, 1988), and it was concluded that during relatively short spontaneous dives, these birds used stored oxygen to allow active tissues to respire aerobically, replacing the oxygen quickly at the surface before commencing the next dive. Further evidence from a number of aquatic birds and mammals was presented by Butler (1988), who also suggested that during the vast majority of natural dives, metabolism is largely, if not completely, aerobic, with the active skeletal muscles, as well as brain and heart, recieving an adequate supply of oxygen. Furthermore, there are several other instances of observations of natural diving behaviour which show that the majority of natural dives are of shorter duration than the maximum demonstrated in restrained animals (Kooyman et al., 1980 (Weddell seals)), or the theoretical maximum before anaerobiosis is necessary (Stephenson et al., 1986 (tufted ducks)). This all leads to the conclusion that anaerobic metabolism may be reserved for emergency situations only (Woakes, 1988).

One question arising from the above information, therefore, is "What is the adaptive significance of the 'classical' diving response, i.e. bradycardia, which is observed in all diving animals when they are involuntarily submerged?". Kanwisher et al. (1981) suggested it is a response to stress, since no bradycardia was seen in voluntarily diving double crested cormorants (*Phalacrocorax auritus*) and Canada geese (*Branta canadensis*), but abrupt bradycardia developed when birds were seized and forcibly submerged. However, prolonged dives, i.e. those of sufficiently long duration to require some degree of anaerobic metabolism in the active muscles, would be expected to be associated with a bradycardia. Such dives might be expected to occur in highly adapted aquatic species. Kooyman and Campell (1972) and Kooyman et al. (1980), working with adult Weddell seals, showed that varying degrees of bradycardia developed depending on how long the animal intended to dive for. Long dives involved a rapid onset of deep bradycardia, and for dives exceeding 20-25 min there was evidence of anaerobic respiration having occurred. Similarly Stephenson et al. (1986) showed that tufted ducks could control the onset and rate of development of bradycardia during diving.

Finally, in those vertebrates which can withstand large periods of apnoea, it might be thought that, as well as circulatory adjustments, and tolerance to some degree of anaerobiosis, there may be some adaptations to increase the available oxygen stores, e.g. proportionately larger lungs. Stahl (1967), carried out an analysis on the scaling of a number of respiratory variables in mammals. Among other things, he showed that there was a clear allometric relationship between body weight and lung capacity in ml (i.e. a log-log relationship), and he was able to calculate a power law formula for a number of variables. Data were obtained from a wide range of species varying in size from mice to elephants, and it is noted that data from detailed studies on individual animals could be compared to the predicted figures at a given weight to demonstrate physiological specialization. Basically, Stahl's results show that larger animals do have proportionately larger lungs, total blood volume etc., but he feels more data are needed from, e.g. cetaceans and other specialised animals, e.g. those living at high altitude. Andersen (1961) states that the three main oxygen stores in a diving animal are lung air, blood and muscles. Kooyman (1975) reviewed some aspects of this and concluded that from the data available, the oxygen carrying capacity of the blood, and perhaps also the blood volume, tended to be greater in diving birds, e.g. Adelie penguin (*Pygoscelis adeliae*), compared to terrestrial birds such as chicken (*Gallus gallus*) and pigeon (*Columba livia*). Regarding the size of lungs of aquatic vertebrates, Irving (1939) notes that for mammals "there is no appearance of an enlargement of thoracic capacity in divers beyond that of active mammals". He examined (but did not measure) lungs from beaver, muskrats, seals and ducks, and concluded that they did not differ in size from the lungs of cats and dogs, nor was the measured air capacity of ducks and chickens different. Kooyman (1975) however, noted that penguins (various species) appear to dive after an inhalation, whereas Weddell seals exhaled to about 50-60% of inhalatory lung volume before diving. Thus, the contribution of the lung-air sac system to the total body oxygen stores of the penguin would be significant. Terrestrial mammals struggling on submergence may also exhale and a valuable oxygen store would be lost.

The muscle myoglobin provides another possible oxygen store. Again, Kooyman (1975) noted that, based on the colour of aquatic bird muscles compared to terrestrial birds, myoglobin is much more concentrated in the former. Nevertheless, this would represent only a very small proportion of the total oxygen store. On the other hand, Andersen (1961) noted that the muscles of the alligator were very pale, suggesting low myoglobin content and hence a low oxygen store.

The conclusion from the above review is that highly adapted aquatic species have evolved a number of adaptations to cope with periods of prolonged apnoea whilst diving. It now remains to review the available physiological data for mink to see how these animals compare.

Dunstone and O'Connor (1979a and b) investigated underwater foraging behaviour in mink searching for live prey. Using Principal Component Analysis they concluded that 23% of the observed variation in behaviour was due to oxygen constraints, whereas 51% of the variance was attributed to factors relating to optimization of foraging. Nevertheless, oxygen constraints are obviously important in the underwater foraging of the mink. From the literature there appears to have been one study on the anatomy of lungs in mink. This was by Lisovschi-Cheleseanu et al. (1960/70) and is in Romanian. The information available in the English abstract states only that the left lung has two lobes, the right four, but there is no information given on lung volume. Furthermore, I have been unable to find any information on oxygen carrying capacity of blood in mink, its volume, or any information on myoglobin as a possible oxygen store. It cannot, therefore, be assumed that mink have, or have not, evolved specializations for enhancing their body oxygen store as a response to their aquatic lifestyle.

There is considerably more information available on the physiological responses made by mink when diving. Gilbert and Gofton (1982a) obtained information on the length of terminal dives of mink, muskrat and beaver caught in leg hold traps. The authors found that as soon as mink were trapped and fell into the water they struggled violently (as did both muskrat and beaver). Heart rate dropped to about half the resting value before capture (i.e. from 227 beats min^{-1} to 119 beats min^{-1}). Brain activity (EEG recording) ceased after an average of 4 min 37 s and heart activity at around 6 min. The loss of the corneal reflex (indicating unconsciousness) occurred before 2 min 30 s. For muskrat and beaver, pronounced bradycardia also occurred immediately animals were immersed. However, for muskrat, unconsciousness occurred at around 3 min 35 s, brain activity ceased at 4 min 03 s and heart at 4 min 21 s (i.e. there was a very short period beetween cessation of struggling and shutdown of physiological functions). These results are particularly interesting since muskrat and mink are similar in size (Walker (1983) states adult muskrat can weigh from 681-1816 g, mink up to 1600 g). For beaver, unconsciousness occurred between 2-5 min, EEG loss at around 9 min and EKG loss (heart rate) at 16 min. Furthermore, post mortems revealed that all mink and nine muskrat died by 'wet' drowning. The remaining muskrat and beaver died by anoxia, i.e. carbon dioxide induced narcosis; in other words, beavers did not attempt to inhale whilst underwater, indicating lower sensitivity to the build-up of carbon dioxide leading to the triggering of an inhalation reflex (as occurs in man, for instance). The conclusion of the authors is that the rapidity with which unconsciousness and brain death occurs in mink, coupled with the predominance of 'wet' drowning all indicate a species which is not physiologically adapted to an underwater environment.

However, Gilbert and Gofton(1982b) measured heart rate values for mink, muskrat and beaver when animals were performing various activities, e.g. resting, swimming and when forced to 'free' dive. For all three species a marked bradycardia developed during diving. For the mink, dives lasted between 5-7 s with only two greater than 17 s. Heart rate dropped from 261 ± 146 (rest) to 163 ± 75 beats min^{-1} (dive). However, the authors note that mink only dived after being disturbed and they suggest that possibly this is a fear bradycardia. This would be consistant with results reported by Kanwisher et al. (1981) for diving birds, and by Smith et al. (1981) who points out that animals which freeze and hide, retreat into nests, burrows or submerge when threatened, exhibit a marked bradycardia, in contrast to the tachycardia inherent in classic "fight or flight" responses. Thus, exhibition of bradycardia by mink during forced diving cannot be taken as an indication of physiological adaptation to diving.

More recently, work has been caried out by Stephenson et al. (1988) using two freely diving female mink. They recorded heart rate and oxygen consumption for the two animals, performing normal foraging dives, in a 1.7 m deep tank, with which the animals were unfamiliar, at the University of Birmingham. Heart rate was also recorded when animals were diving in a shallow pool (0.3 m deep), and deep tank (1.9 m), at the University of Durham, where the animals had been trained. The first point is that there were significant differences in heart rates for similar dives performed at Birmingham and Durham. Briefly, a bradycardia developed during shallow (a few cm) and deep (more than 1 m depth) foraging dives in Birmingham. However, in Durham, bradycardia developed only during dives into enclosed spaces (a series of pipes) in a depth of 0.3 m, when heart rate dropped to very low levels whilst the animals were inside the pipes, but rose once animals emerged. By contrast, non pipe-search dives at 0.3 m and 1.9 m did not result in the development of bradycardia in mink at Durham. The authors suggest that the novel surroundings at Birmingham had an adverse effect on the behaviour and physiology of the mink, and the bradycardia witnessed during diving in Birmingham may be more of a fear response rather than a diving response. However, in Durham, a bradycardia developed only during pipe-search dives. Further, Butler (1988) notes that metabolic data for mink swimming at the surface (from Williams, 1983) at a velocity of 0.7 m s^{-1}, shows oxygen uptake is approximately five times the resting value. When diving underwater for food, Butler (1988) suggests that, based on an underwater swimming speed of approximately 0.5 m s^{-1} (Poole and Dunstone, 1976), mink would use oxygen at a rate of less than four times resting rate. Stephenson et al. (1988) measured average oxygen uptake in a female mink (650 g) during a feeding bout, consisting of a number of dives in quick succession, as 5.2 L kg^{-1} h^{-1}. Butler (1988) estimates that this would be equivalent to swimming at the surface at approximately 0.5 m s^{-1}, and concludes that normal feeding dives are completely aerobic in these animals, although he notes that Stephenson et al. (1988) did show a reduction in heart rate below mean resting levels during voluntary diving behaviour. The implications of these results is that 'psychogenic influences' may be involved in cardiac control, i.e. the mink may be able to 'consciously' initiate the development of bradycardia.

Work on other diving species has shown that this is possible, e.g. Kooyman and Cambell (1972) showed that the speed and intensity of development of bradycardia was related to the dive duration, and Ridway et al. (1975) trained a sea lion (*Zalophus californianus)* to slow its heart rate whether or not it was diving. This does not mean that the development of a bradycardia is solely under volitional control; other nervous mechanisms exist to reflexly control heart rate. West and van Vliet (1986) for example, working with anaesthetized and paralyzed mink, have suggested that the stimulation of receptors in the upper airways coupled with apnoea after exhalation may cause bradycardia to occur as a reflex effect. They also found that rapid onset of bradycardia (presumably accompanied by adjustments in the peripheral circulation), was effective in slowing the reduction of P_{AO_2} (partial arterial pressure of oxygen), i.e. an oxygen conserving response. They also found that stimulation of peripheral arterial chemoreceptors, particularly during lung deflation, had a relatively weak cardioinhibitory influence, which was normally masked by the nasopharyngeal reflex. However, as Butler (1988) points out, the significance of bradycardia in mink during diving is unclear. Other studies, mostly involving diving birds, have further investigated the roles of central and peripheral chemoreceptors on the control and development of bradycardia during diving (see Stephenson et al., 1986; Jones et al., 1988 and references therein). With regard to mink, the conclusion suggested by the above studies is that animals will have some volitional control over the development of bradycardia during diving and this will have important consequences regarding possible dive durations under various conditions.

Iversen (1972) found that the Basal Metabolic Rate for mustelids weighing 1 kg or more was 20% higher than that expected from the mammalian standard curve, and that for smaller mustelids, the elevation was even greater. He suggested that the elongated body shape contributes to this higher resting metabolic rate, since these animals cannot curl into a spherical shape when resting, as rodents can for example. This will obviously have an important effect on how animals can budget their energy supply for various activities. For the mink, it is possible that swimming and diving are energetically very costly. Stephenson et al. (1988) made measurements of gas exchange (i.e. oxygen uptake, VO_2, and carbon dioxide production, VCO_2) but only during dives made at Birmingham University.

Measurements of VO_2 and VCO_2 are useful in estimating the metabolic costs of various activities to mink. Unfortunately, Stephenson et al. were not able to separate VO_2 values for surface activity (i.e. swimming, head dipping etc.) from that during diving per se. They obtained values for VO_2 of 5.21 ± 0.45 ml $O_2\ g^{-1}h^{-1}$ (for 650 g female) and 7.87 ± 0.56 ml $O_2\ g^{-1}h^{-1}$ (for 1000 g female). Williams (1983a and b) measured maximum oxygen uptake for mink surface swimming and running on a treadmill, and found that the VO_2 max. for females (mean weight 969 g) on treadmills was 6.50 ± 0.41 ml O_2 $g^{-1}h^{-1}$ and that VO_2 for females surface swimming at 0.70 m s^{-1} was within 3% of this. For males (mean weight 1236 g) VO_2 max. was lower at 5.90 ± 0.27 ml O_2 $g^{-1}h^{-1}$ and VO_2 for males swimming at 0.70 m s^{-1} was 14% less than this. Williams (1983a) further estimated that there would be a five- to ten- fold reduction in body drag during submerged swimming, presumably resulting in reduced energy expenditure and hence in decreased oxygen consumption. Hence, the values for VO_2 max. obtained by Stephenson et al. (1988) do appear high, and they state that this is probably due to the amount of surface activity.

The main point to arise from the above studies is that diving would seem to be an extremely costly metabolic activity, especially for small mustelids like the mink.

1.4. Optimal Foraging Theory and this Study

Theoretical work by Emlen (1966) and MacArthur and Pianka (1966) which attempted to predict food preferences and foraging behaviour of animals under conditions of varying food availability formed the basis for what is now termed 'Optimal Foraging Theory'. During the succeeding years the literature devoted to attempting to predict the behaviour of animals while they are foraging, or to testing such predictions in the field and laboratory, has grown enormously with a slight tailing off since 1981 (Pyke, 1984). There have been many reviews, e.g. Pyke et al. (1977), Krebs et al. (1983) and Pyke (1984). Furthermore, sections on optimal foraging are now standard features in textbooks of behaviour and behavioural ecology, e.g. Krebs and Davies (1984).

Thus, it might be useful to examine in more detail what is meant by Optimal Foraging Theory, and what predictions it makes and tests concerning foraging behaviour. Finally, the relevance of Optimal Foraging Theory to this study will be assessed.

Originally, proponents of Optimal Foraging Theory attempted to predict the behaviour of animals while they were foraging (Pyke, 1984). It is assumed that foraging behaviour has been shaped by natural selection, so that foraging strategies which maximise individual fitness (i.e. the relative ability of the forager to leave viable offspring (McFarland, 1981)), will exist in Nature (Pierce, 1985). It should thus be possible to"formulate optimal decision rules, particularly concerning foraging efficiency, generating testable, quantitative predictions about foraging behaviour" (Pierce, 1985).

In theory, this sounds simple enough, but in practise the problem is very complex. Optimal Foraging Theory is based on a number of assumptions (see Pyke, 1984). Firstly, the 'fitness' of an individual is considered to be its contribution to the next generation. Biological evolution tends to maximise Darwinian fitness. Thus, organisms possessing heritable characteristics which increase their contributions to survival and reproduction will increase in frequency within a population (Pierce, 1985). Optimal Foraging Theory thus assumes that the 'fitness' of an individual depends on its behaviour while foraging.

Secondly, Optimal Foraging Theory assumes that there should be a heritable component of foraging behaviour. Thus, an animal which forages in a particular manner should be likely to have offspring that tend to forage in the same manner. But, further, the existence of optimal foraging strategies, as such, does not depend on the genetic determination of foraging behaviour, rather it is sufficient that the ability to learn optimal foraging behaviour be heritable (Pulliam, 1975; Pyke, 1984), i.e. optimal foraging theory may apply regardless of whether the foraging behaviour is learned or innate. It, therefore, follows from the above, that the proportion of individuals in a population foraging 'optimally', i.e. so as to enhance their fitness, will tend to increase over time. As foraging behaviour evolves, the average foraging behaviour will increasingly come to be characterised by those characteristics that enhance individual fitness (Pyke, 1984).

It is also assumed that the relationship between forging behaviour and fitness is known. This is generally referred to as the <u>currency</u> of fitness (Schoener, 1971).

Next, it is assumed that the evolution of foraging behaviour is not prevented by constraints such as gene linkage. It is assumed that if such linkages or other effects occur, then ultimately mutations will arise that will circumvent these genetic problems and allow the 'optimal' foraging behaviour to evolve.

The fifth assumption, is that the evolution of foraging behaviour is subject to 'functional' constraints, e.g. the level of information about its environment which is available to a given animal, its ability to store and process this information etc. Further, it is assumed that the level of these 'functional' constraints has been realistically determined.

Finally, it is assumed that foraging behaviour evolves more rapidly than the rate at which the relevant conditions change. This means, basically, that the evolution and adaptation of foraging behaviour should approximately reach completion when individuals are foraging in ways <u>close</u> to those that <u>maximise</u> their expected fitness, i.e. it is hypothesized that animals forage 'optimally' (Pyke, 1984).

From the above brief review it can be seen that the basic assumptions underlying the theory of Optimal Foraging are very large, and many are difficult to test. As a result, there has been much criticism of the use of Optimal Foraging Theory and of many studies which purported to test predictions made from the theory (e.g. Pierce and Ollason, 1987). However, during the course of the development of Optimal Foraging Theory, to simplify matters, workers have tended to develop and test predictions in various categories, namely, diet, patch choice, when to leave patch, movement and central place foraging (Pyke, 1984). Each of these categories has generated a large amount of literature, based either on the mathematics and predictions of the models, or reporting the results of field or laboratory tests of these predictions. Pyke (1984) reviews the development of the various theories in considerable detail, as well as reviewing many of the studies whose results claim to support Optimal Foraging Theory. His conclusion is that Optimal Foraging theory can only be useful when its assumptions, mathematical development and testing are appropriate for the studies to which it is applied.

The aim of the present study was to investigate one aspect of foraging behaviour in the mink, namely, changes in behaviour which occurred when the mink were foraging underwater. This study did not set out to test predictions of Optimal Foraging Theory as such, but the results may at least provide qualitative evidence for, or against, such behaviour. Regarding the five categories into which Optimal Foraging observations are now normally grouped, there was no question of diet choice for the mink, and for all except the density experiment (clumped hide arrangement), there were no food 'patches' provided, so that changes in behaviour regarding patch choice, or time of leaving patches, could also not be examined. This leaves the categories movement and central place foraging. In this study, the mink was certainly operating as a central place forager, in that all food items were brought to the rostrum, but as regards the natural behaviour of the mink, Birks and Dunstone (1984) report that many small prey items will be consumed where caught, and only larger items may be returned to the den, (i.e. to the 'central place'), except when the female has a litter, when most items will be brought back (Dunstone, pers. comm.). On the whole, it is felt that the results of this study can be applied only to the broader predictions of Optimal Foraging Theory, namely an animal should forage optimally to maximize its fitness. To this end, it is felt that foraging 'optimally' can be equated with foraging 'efficiently'. Thus, if a mink makes the most 'efficient' use of its foraging time underwater, this can be considered as providing qualitative support for Optimal Foraging Theory. Various definitions have been proposed for what constitutes foraging efficiency in mink (e.g. Dunstone, 1978) and these will be considered where appropriate.

Finally, it must be noted that as an approach to the study of foraging behaviour, Optimal Foraging Theory may well be useful (Pyke, 1984), but it must be realized that the underlying assumptions are very wide. The environment in which the animals forage is not static, waiting for animals to learn how to 'forage optimally', and the animals themselves are constantly evolving, often in response to other pressures, e.g. disease, predators etc. Therefore, it seems unlikely that any animal can have reached the pinnacle of 'perfect' optimal foraging, but it is possible that that is the direction of their evolution by natural selection.

CHAPTER 2

GENERAL MATERIALS AND METHODS

2.1. Subjects

The subjects used were obtained as six to eight week old unrelated kits from a commercial mink farm. Subjects chosen had either the 'Standard' coat colour (dark brown-black), the 'Dark' colour (black with faint brown sheen) or 'Pastel' (light brown). The exception was a male mink, Boris, who had the so-called 'Pastel-Cross' coat colour (a mottled white and brown form, with a brown cross over the shoulder). All individuals had unique white chin and/or chest markings. All subjects had normally pigmented eyes. See Appendix I for details of experimental use of animals.

2.2. Maintenance

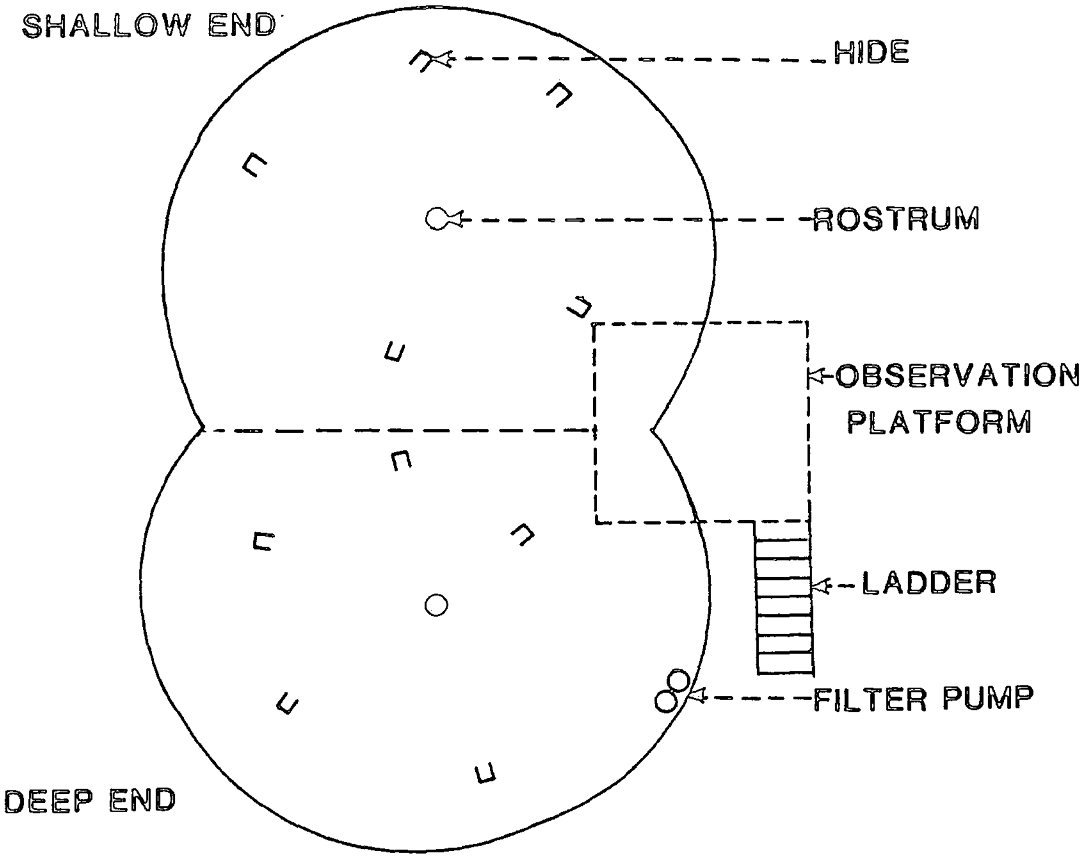
Initially the kits were housed together in one large room, 3 m x 5 m x 3 m, with a sawdust-covered floor. A bedding box was provided together with several items such as bricks, pipes, cardboard tubes etc., as play objects, and to provide an enriched environment. Water was provided *ad libitum.* Kits were fed twice daily, by the experimenter, on a mixture of Spratts ZF6, laboratory rabbit pellets, canned dog food, and a variety of supplementary foods including eels, white fish or liver.

During this period, the experimenter spent several hours a day "playing" with the young mink to accustom them to the experimenter's presence. In this way it was hoped that the animals would not be disturbed by the presence of the experimenter during subsequent trials, but would behave "naturally". At this time the kits were also trained to enter a carrying box as, once adult, they were too intractable to be handled. Since none of the kits had had any previous experience of swimming and diving, preliminary training in the experimental arena was begun as soon as the animals had settled in - about two weeks after arrival (see below).

At 20 weeks of age they were separated and housed within individual wire-mesh cages, 1.0 m x 0.5 m x 0.5 m, with a wooden nest box of 0.3 m x 0.3 m x 0.3 m attached externally. Water was provided *ad libitum*.. Animals were fed once daily between 11.00 and 12.00 hours on a maintenance diet of approximately 100 g of a mixture of Spratts 'ZF6', laboratory rabbit pellets and canned dog food. However, during an experiment animals were usually tested in the morning and fed at the end of the experimental period. Cages were cleaned each morning by high pressure hosing and all excess food from the previous day removed. The animals were kept under a 12 hour light/12 hour dark cycle.

2.3. Experimental Arena

All experiments were carried out in a figure-of-eight shaped pool measuring 6.85 m x 3.55 m (at the narrowest point) (see Fig. 2.1). This was set flush with the concrete floor of a wooden hut measuring 9.10 m by 6.00 m. An observation platform 2.0 m x 0.90 m was suspended from the roof beams 1.75 m above the floor. This extended for 0.80 m over the pool so that both halves could be easily observed. Access to the platform was by means of a fixed open wooden stairway. The hut was equipped with radiators which could be used to maintain a comfortable working temperature of 20^{o}C during the winter. The water in the pool was not heated and temperature fluctuated daily around a mean of 11^{o}C (lowest temperature recorded in winter was 9^{o}C and the highest recorded in summer was 14^{o}C). During all experiments the windows were blacked out and lighting was provided by four fluorescent tubes suspended from the roof beams. A double door system complying with M.A.F.F. regulations for housing mink allowed access to the hut.


SHALLOW END
HIDE
ROSTRUM
OBSERVATION PLATFORM
LADDER
FILTER PUMP
DEEP END

The two halves of the pool had different maximum depths, these being 1.2 m in the 'shallow' end and 1.65 m in the 'deep' end. A filter pump unit was fixed to one side of the 'deep' end, but it could only be used when the pool was filled with water to maximum depth. To maintain water clarity the pool was emptied, cleaned and re-filled approximately every six weeks, and partially emptied and fresh water added once a week during the experimental period. Water clarity was monitored by the experimenter; the water was changed as soon as it began to 'cloud' and sediment began to collect on the pool floor.

The mink were provided with two resting platforms or rostra, one in the centre of each half of the pool. These consisted of a perspex base 0.35 m x 0.30 m which could be weighted with bricks for stability,a plastic tube of diameter 0.15 m screwed onto the base and an adjustable wooden platform 0.45 m x 0.40 mmounted on the tube. This platform could be moved up or down until it was flush with the water surface. The entire rostrum could be easily relocated using a small cup hook screwed onto the top of the plastic tube.

The animals were trained to dive to the pool floor to search for small wooden hides containing a food reward of approximately 5 g of eel flesh. These hides were 0.10 m x 0.10 m x 0.16 m and were fitted with a door flap, held in position by a metal spring, and were weighted by a brick. All hides were painted white on the outside and numbered for easy identification. The inside rear wall was also painted white and a wire staple held the food reward in place when the box was underwater. A cuphook screwed into the top of each hide allowed its easy removal from, or relocation within, the experimental pool. Fish flesh was used instead of live fish prey for all experiments in order to avoid the necessity of allowing for changes in prey behaviour when trying to assess changes in foraging efficiency of the predator. In particular, dead bait afforded a means of controlling for changes in 'pursuit' behaviour as environmental parameters were altered.

The bottom of the pool was divided into a grid of 0.5 m x 0.5 m squares by black tape. This grid system was used as a guide to position the boxes and rostra and to maintain their relative positions once an experiment was underway.

Mink were conveyed from their individual cages to the pool in a carrying box. This was made of wood, except for the top, which was made of a strong, narrow gauge wire mesh. A metal sliding door at one end allowed access for the mink, and a strong wire handle attached to the mesh allowed easy transport ofthebox. The box was 0.5 m x 0.2 m x 0.2 m and gave even the largest male mink sufficient room to turn around. Once in the experimental hut, mink were introduced into the pool as follows. A wooden ramp was placed from the tank edge onto one of the two rostra. The carrying box was placed at the top of the ramp, the metal door opened and the animal would run down the ramp to the rostrum. Once the animal had moved onto the rostrum, ramp and box were removed, thus confining the mink to the rostrum and pool. At the end of the experimental period, ramp and box were replaced and the mink would run up the ramp into the box where it received a food reward of approximately 5 g of eel flesh before being returned to its home cage.

2.4. Observation and Data Recording

Before describing the methods used to record and analyse the data, the following must be noted.

An experimental trial was the period (generally 10 min) for which an animal was observed in the experimental arena.

An experimental session was the period during which several animals would undergo a trial under a given set of experimental conditions.

The behaviour of the mink was recorded using a Sony Rover (model number AV-3420CE) monochrome videorecorder linked to two Hitachi cameras (model number HV625K), which were rigidly mounted over the pool such that each covered one half. For the first experiment, (effect of depth) the cameras were tilted at an angle of 30^{o} to the vertical so that the right hand camera covered the left hand pool side and vice versa. In subsequent experiments the mounting position was altered so that each camera pointed vertically downwards onto the pool below. The images from the cameras were linked through a video camera wiper (mixer Serial number CMW-110CE) and time and date generator (FOR.A VTG 22 video timer) to the videorecorder. A 12" monitor screen showed the picture during the recording and enabled the movement of the animals from one side of the pool to the other to be easily followed. This equipment was situated on the observation platform above the pool. All experimental sessions were monitored by the experimenter and a microphone attached to the videorecorder allowed a simultaneous voice-over commentary to be made on the videotape.

The information on the videotapes was transcribed using an Apple II microcomputer with a real-time clock, and data were stored on floppy disk. Two programmes, written in Applesoft Basic, were used: 'Event' and 'Behpath'. 'Event' allowed the computer to be used as a real-time event recorder. Here, various keys on the keyboard were chosen to represent a particular behaviour, e.g. R = Rest, T = Surface Swim, Y = Dive etc. As the videotape was replayed and the behaviour changed, the appropriate key was pressed. The data were thus stored as a sequence of behaviour codes along with their onset times. The programme also allowed each data set to be uniquely titled for future analysis.

Preliminary analysis of the 'Event' data was achieved using a programme written in Pascal (called 'Key-Anal') on the Durham facility of NUMAC (Northumbrian Universities Multiple Access Computer). This programme calculated the duration of each bout of a particular behaviour, and would print the data as a sequence of behaviours with onset time and duration (Fig. 2.2).

'Key-Anal'could also be used to calculate the summary statistics (i.e. frequency of occurrence, mean duration, standard deviation, range, median, total duration, duration as % of observation time etc.) for each behaviour within a recorded trial, the relative frequency histogram for durations of each behaviour and a list of durations for each bout of behaviour within a trial.

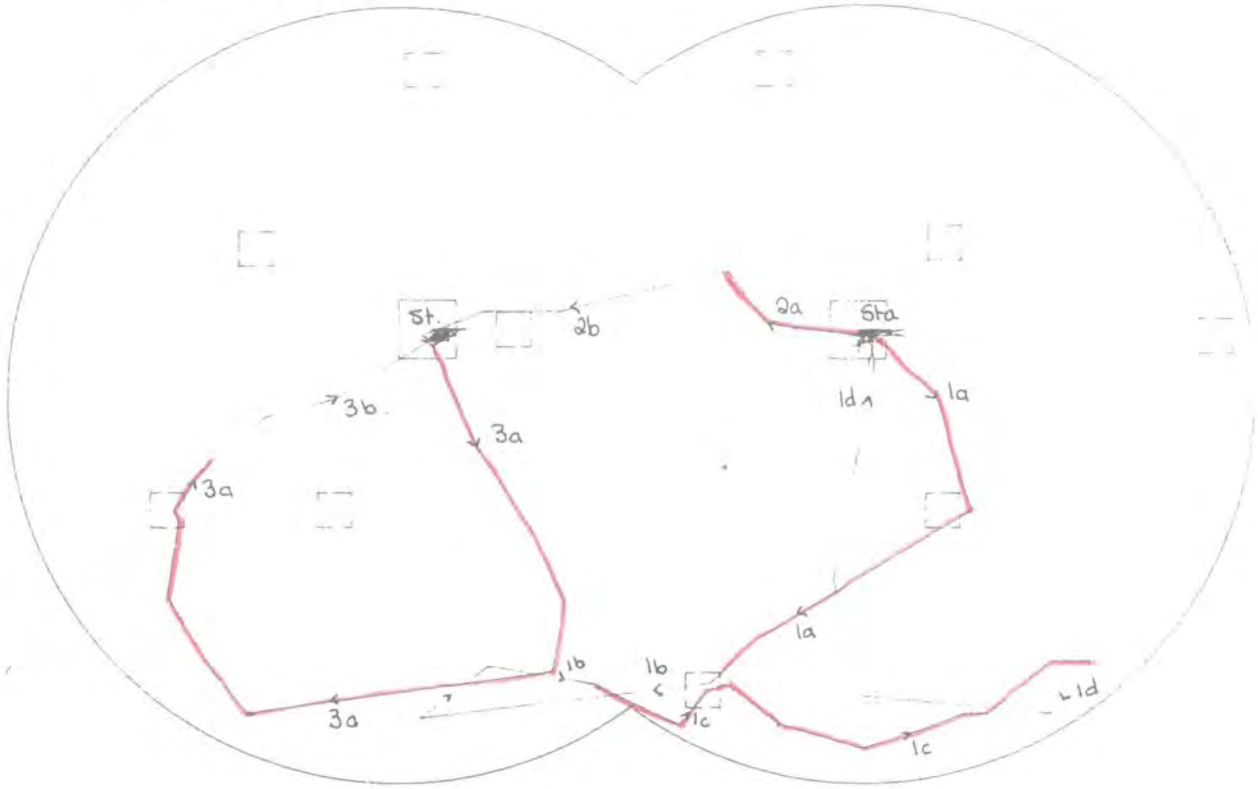
'Behpath' was more complex and was developed as this study progressed. This recorded details of the search path of the animal. For the investigation of the effect of depth on diving activity the system used was as follows. The videotape was replayed through a monitor screen. At the same time the programme 'Behpath' produced a diagrammatic representation of the pool, with hides in position, on the Apple II computer screen. The movements of the mink (as seen on the monitor screen) were copied on the diagrammatic computer image of the pool using a light pen. The computer was programmed by the 'Behpath' programme to record the x,y, co-ordinate position of the light pen on the computer screen at a pre-set interval of 0.5 s. These x,y co-ordinate values and the corresponding real time were stored on floppy disk. The 'Behpath' programme also allowed the experimenter to link a particular behaviour with the position or movement of a mink by using a particular key to represent a certain behaviour. However, for 'Behpath' only three behaviour categories were coded compared to nine using the 'Event' programme. These were Rest, Surface Swimming and Dive. A third programme, written

```
Frequency of ccurrence
--------------------------------------------
Behaviour                  Abs. Freq.
--------------------------------------------
EATING                          1
HIDE SEARCH                    18
FIND FOOD                       6
SWIM UP                        10
PEER                           11
REST                           14
SURFACE SWIM                   18
TANK SEARCH                    23
DIVE                           10
----------------------------------------------------------------------------------------
Data sequence and onset time
Behaviour pattern........                    Onset time       Duration
----------------------------------------------------------------------------------------
REST                                             0.00            0.44
PEER                                             0.44            2.15
DIVE                                             2.59            0.40
TANK SEARCH                                      2.99            1.18
SWIM UP                                          4.18            0.44
REST                                             4.62            3.49
PEER                                             8.10            3.43
SURFACE SWIM                                    11.53           15.67
DIVE                                            27.20            0.52
TANK SEARCH                                     27.72            1.60
SWIM UP                                         29.32            0.37
SURFACE SWIM                                    29.69           19.73
DIVE                                            49.92            0.36
TANK SEARCH                                     49.79            0.33
HIDE SEARCH                                     50.12            1.89
TANK SEARCH                                     52.01            0.37
HIDE SEARCH                                     52.38            1.96
TANK SEARCH                                     54.34            0.34
HIDE SEARCH                                     54.68            1.30
TANK SEARCH                                     55.98            0.40
HIDE SEARCH                                     56.38            1.78
TANK SEARCH                                     58.16            0.95
HIDE SEARCH                                     59.11            1.38
TANK SEARCH                                     60.49            0.62
HIDE SEARCH                                     61.12            1.92
SWIM UP                                         63.03            1.45
FIND FOOD                                       64.48            0.31
SURFACE SWIM                                    64.79            2.00
REST                                            66.78           12.50
PEER                                            79.28            6.43
SURFACE SWIM                                    85.71            4.05
DIVE                                            89.77            0.95
TANK SEARCH                                     90.71            0.42
HIDE SEARCH                                     91.14            2.11
SWIM UP                                         93.25            0.68
FIND FOOD                                       93.93            0.31
SURFACE SWIM                                    94.24            1.14
REST                                            95.38            7.60
----------------------------------------------------------------------------------------
```

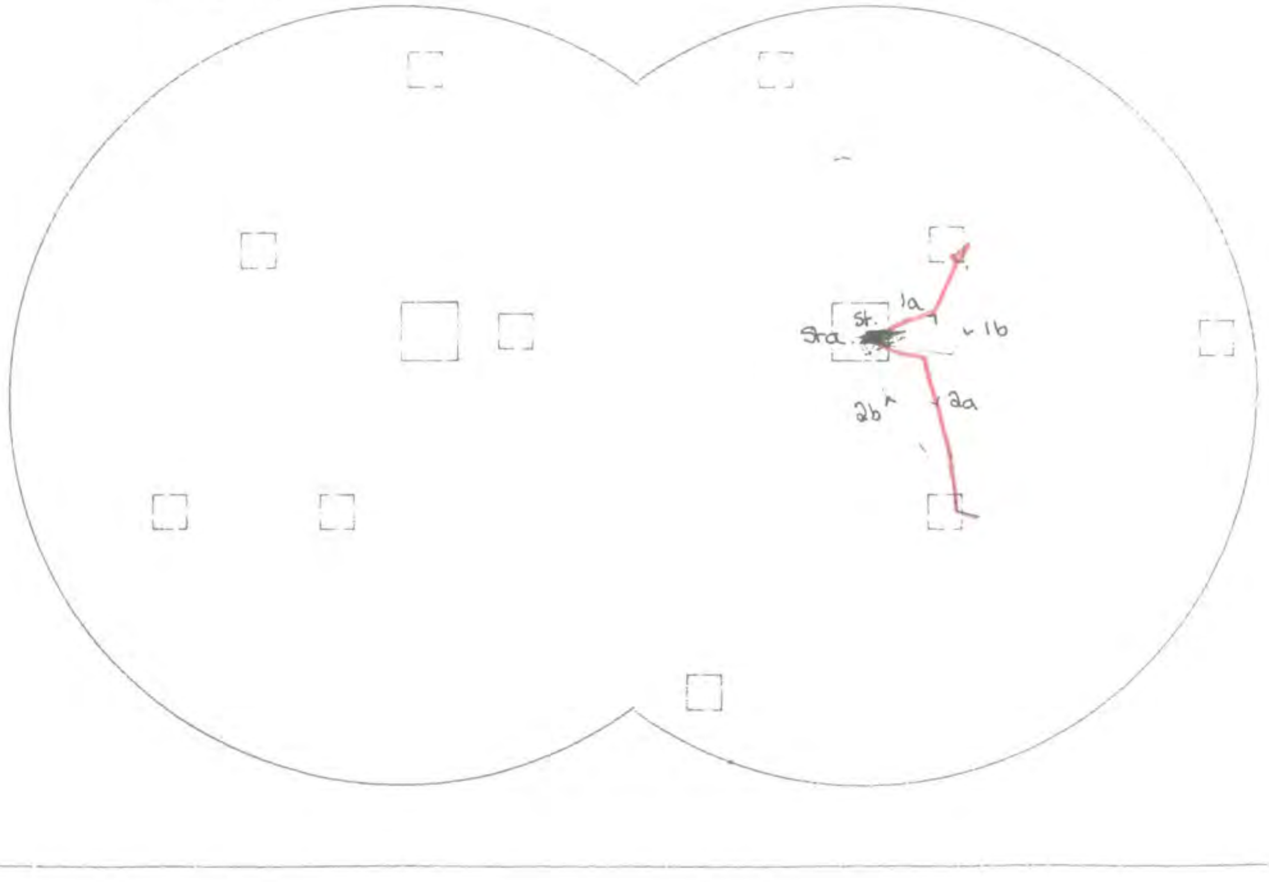
in Applesoft Basic, called 'Listplot', was used to re-display the data, input by the 'Behpath' programme, on the computer screen. This allowed the operator to check that accidental movements of the light pen had not occurred and that the behaviour codes were correct. A point here is that because of the constraint of memory capacity imposed by the Apple II on the size of any single data file, it was not possible to transcribe each 10 min trial of 'Behpath' in its entirety. It was decided instead to subdivide each trial into blocks of approximately 2 min, always terminating with the animal resting. The programme allowed each file to be uniquely titled.

For further analysis, data were transferred to the Durham facility of NUMAC, where it was possible to recombine a given individual's '2 min' subfiles into a complete file for that trial. Preliminary analysis was carried out using two programmes written in Fortran. The first 'Minkplot' produced a hard-copy plot of each '2 min' subfile (see Fig. 2.3.). This programme also allowed each behaviour code used to be represented by a different colour on the output, thus enabling a clearer analysis of searchpath, especially when animals were searching underwater. The second programme entitled 'Dist/Speed' calculated distance travelled, duration and speed (where appropriate) for each behaviour code in the file. The programme calculated distance travelled in units based on the co-ordinate points recorded in the file; a scale factor added to the programme allowed distance to be re-calculated in metres and speed in m s^{-1}.

This light pen system was obviously not ideal because the searchpath of the animal had to be copied from the video image on the monitor, to a facsimile of the pool on the computer screen, hence values for distance travelled etc. could be taken as approximations only. However, since all transcription was done by the experimenter it was felt that whilst the dexa 23.2.82 c2



dexa 23.2.81 c1



absolute values were of low accuracy, trends indicated, i.e. any change in mean values for distance travelled with depth, were probably a true reflection of a change in behaviour.

For subsequent experiments, a new system was provided involving the use of a tracking arm, mounted on a 30 cm monitor screen, and digitiser which was designed and built by the Microprocessor Centre at the University of Durham. Under this system, the video image of the movements of an experimental animal could be accurately followed using a pointer attached to a drawing board arm. 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 co-ordinates of the pointer were therefore registered as voltages. A momentary action switch mounted on the guide stick of the tracking 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 1.3 s (slow), i.e. a reading of the x,y coordinate position of the arm was taken every 1.3 s, and 0.3 s (fast). Slow speed was used when an animal was resting or eating. The fast sampling speed chosen was the maximum available, and was used when the animal was swimming on the surface or underwater, so that the maximum accuracy of distance travelled could be obtained. In all experiments, the operator tracked the position of the anterior portion of the mink's body. As for the light pen system, letter codes were used to distinguish different behaviours so that bout duration, distance travelled etc., could be calculated for each occurence of a particular behaviour.

However, for this digitized data it was decided to use four behaviour categories, namely Rest, Surface Swim, Travel (either down to pool bottom or up to water surface) and Bottom Swimming. Thus, the behaviours now recorded as Travel and Bottom Swim correspond to the behaviour 'Dive' recorded with the light pen system. The extra code for

Travel was introduced because both tracking systems worked on a flat two-dimensional image, but the mink were swimming in a three-dimensional pool. Thus, under the light pen system the movement of the animal from onset to termination of behaviour 'Dive' might be recorded as 3.0 m for example, but this did not take into account the fact that the water depth was, e.g. 0.9 m, and a correction factor had to be applied to all measures of distance travelled underwater (see Appendix II). Under the new digitizing method the introduction of the Travel category meant that more accurate measures of the actual distance travelled on the pool bottom could be made without the complications of correction factors.

As for the light pen system, a modified version of the 'Behpath' programme was used to store the x and y voltage values, and corresponding real-time data on floppy disk. Also a modified version of 'Listplot' could then be used to display data input using 'Behpath' on the computer screen, allowing error checking. As before, data for an individual's trial were stored in '2 min' blocks and transferred to 'superfiles' on NUMAC. Programme 'Plotter', on NUMAC, produced a hard copy plot of the searchpaths in each '2 min' file (see Fig. 2.3), and again different behaviour categories could be represented by different colours on the output. Programme 'Dist' calculated distance travelled etc., for each behaviour in metres, once the appropriate conversion factor had been included. Both programmes were written in Fortran.

Finally, data obtained from both the 'Event' programme and the two 'digitiser' systems, were analyzed further using statistical packages, namely, SPSS on NUMAC, Zoology Dept. Statistical Package on NUMAC, USTAT on the BBC microcomputer at University of Cambridge, Zoology Department, and SPSSX on PHOENIX, University of Cambridge.

These analysis systems allowed small changes in behaviour to be accurately observed, and subtle changes in response to changing environmental conditions could be observed and quantified. The only drawback was that it was an extremely labour intensive system, and a one hour videotape could take anything up to 10-12 h to transcribe onto the Apple microcomputer. However, as mentioned, the amount of information gained was worth this investment of time.

2.5. Behaviour categories recorded

These can be subdivided into two categories.

(a) Out-of-water activities:-

(i) Rest:- this category was used for a variety of behaviours, but all were carried out while the animal was on a rostrum. In transcribing the videotapes using the 'Event' programme, the key coding 'Rest' would be pressed when any of the following behaviours occurred:-'Alert':- this behaviour was usually characterized by the animal standing on hind legs only and scenting the air, or by standing on all four limbs at the edge of the rostrum and scenting the air. Occasionally, animals were disturbed by external noise and would spend at least 1 min in the 'upright-alert' position.

'Scent-marking':- this took place in one of two ways:- (a) anal marking or belly-drag, when hind-legs would be stretched out backwards and the anal scent-gland rubbed back and forth on the rostrum surface, or (b) chin marking, when chin or side of face would be rubbed along the edges of the rostrum surface.

'Auto-grooming':- periods of auto-grooming were generally of a very short duration, approximately 5 s, and involved either licking of a fore-leg or paw, tail grooming, licking of hind quarters, grooming of belly or scratching with hind legs. Occasionally, a grooming bout would last for 1 min or more.

'Exploratory behaviour':- this usually involved sniffing or scratching at the central plastic tube of the rostrum.

'Play':- animals were sometimes seen to chase their tail round and round the rostrum, or to dip their head and forelegs into the water and to scrabble at the water with the forelegs. Play bouts occasionally lasted for over 1 min.

'Quiet':- this was characterized by the animal standing or, very occasionally, sitting on the rostrum.

If any of the above behaviours occurred for a duration of more than 1 min, this was noted separately.

(ii) Eat:- the occurence of this behaviour obviously depended on the animal's success in finding bait. However, in all cases, animals would bring the food reward back to a rostrum to consume it. No animals were ever observed to eat a food reward whilst in the water.

(iii) Peer:- this category was used for two behaviours namely 'Peer' and 'Head dip', which were thought to be used by the mink to help in locating underwater 'prey'. Both behaviours have been briefly defined in Poole and Dunstone (1976), but a fuller description is given below.

'Peer':- animal would crouch down on hind-legs, with fore-legs at edge of rostrum and look into the water. This behaviour usually occurred immediately prior to a dive and sometimes prior to surface swimming.

'Head dip':- animal was crouching at the edge of rostrum with either head only, or head, shoulders and fore-legs immersed in water. Scanning movements of the head would sometimes also occur.

b) In-water activities:-

(iv) Surface swimming:- this was recorded when an animal was swimming on the surface with head out of the water. Generally, this was a directed activity, usually taking the animal towards a rostrum. Occasionally, surface swimming was seen when an animal would leave a rostrum, swim around the pool, 'Dive' to the bottom, and either resurface at a rostrum, or resurface and surface-swim back to the rostrum. Animals were also sometimes seen to exhibit 'Sub-Surface' swimming. Here the swimming actions were the same as above, but the head would be immersed for short periods under water. This behaviour sometimes, but not always, occurred before a surface dive, and it was coded into the 'Event' programme as 'Surface Swimming'. Occasionally, animals would exhibit very prolonged spells of surface swimming, when they would repeatedly circle the pool and often 'Scrabble' at the walls with their fore-legs, and attempt to climb out of the pool. These long bouts were also recorded as surface swimming, and an additional note made by the observer. If a bout of this 'Circling' swimming lasted for longer than 2 min, the animal was deemed to be 'bored' and the session terminated.

(v) Swim down:- This was recorded when an animal swam from either a rostrum or the surface of the water to the bottom of the pool. If diving from a rostrum, the dive was usually preceeded by peering, the animal then launched itself head first into the water using the hind-legs to provide thrust from the rostrum. Individual variation was marked in that some animals would often dive vertically down the rostrum's support column and then begin searching from the column base, whereas others would dive from the rostrum at an angle, sometimes directly to a hide, or sometimes directly to the pool bottom to begin searching.

In dives which followed a bout of 'Surface Swimming' the animal would occasionally dip its head under water before diving. Most of these 'Surface-Swim Dives' occurred near the edge of the pool, when the side of the tank was sometimes, but not always, used to assist the animal to get thrust for the dive. However, some of these 'Surface-Swim Dives' occurred well away from the pool edge, i.e. in midwater. Here the animal would dip its head underwater and use both fore- and hind-legs to propel the body underwater, and then (as far as could be seen) the hind-limbs only were used to swim down to the pool bottom.

Behaviour 'Swim Down' was only recorded if the animal reached the pool bottom. If an animal attempted to dive, but resurfaced before reaching the pool bottom, this was not considered as 'Swim Down', but was recorded as 'Surface Swimming'. Behaviour 'Swim Down' terminated as soon as the fore-quarters of the mink reached the bottom of the pool. 'Swim Down' was usually followed by either 'Bottom Search' or 'Hide Search', although occasionally an animal would swim down to the pool bottom and then up again immediately.

(vi) Bottom search:- this behaviour involved swimming over the bottom of the tank. 'Bottom search' was either directed towards a hide or else involved exploration of the pool floor. Some animals were observed to reach a hide and cling to it whilst giving head movements to search the immediate surroundings. Quite large distances (several metres), could be covered when the animals were bottom searching, and they appeared very agile underwater, often making sharp turns to double back on their path or to get to a new hide.

(vii) Hide Search:- this behaviour was recorded as soon as an animal pushed open the wooden door of a hide. Generally, the head and shoulders would be pushed into a hide, especially by the smaller females who could easily get their fore-legs inside. The larger males could also enter the boxes and reach the back wall where the food reward was situated. Some individuals did show a tendency to simply push the head into a hide, the result being that they occasionally failed to remove a piece of bait. 'Hide Search' occasionally followed the behaviour 'Swim Down' directly, but usually an animal would reach the pool bottom, locate a hide by 'Bottom Searching' and then enter it.

(viii) Find:- This behaviour was used simply as a tag to indicate if a hide search was successful or not. A duration of 0.25 s was usually ascribed to this behaviour by the programme 'Event', (i.e. this was the duration between successive key presses by the observer). This had then to be added to the succeeding behaviour to give the true duration of that behaviour.

For the depth experiment, this tag was inserted as soon as the animal had left a hide after a successful search. Succeeding behaviours were therefore either 'Swim Up' or 'Bottom Search'. However, it was sometimes difficult to see if the hide search had been successful, so in all subsequent experiments, the tag 'Find' was inserted once the animal resurfaced after a successful hide search, and the succeeding behaviour was either 'Surface Swim' or 'Rest'.

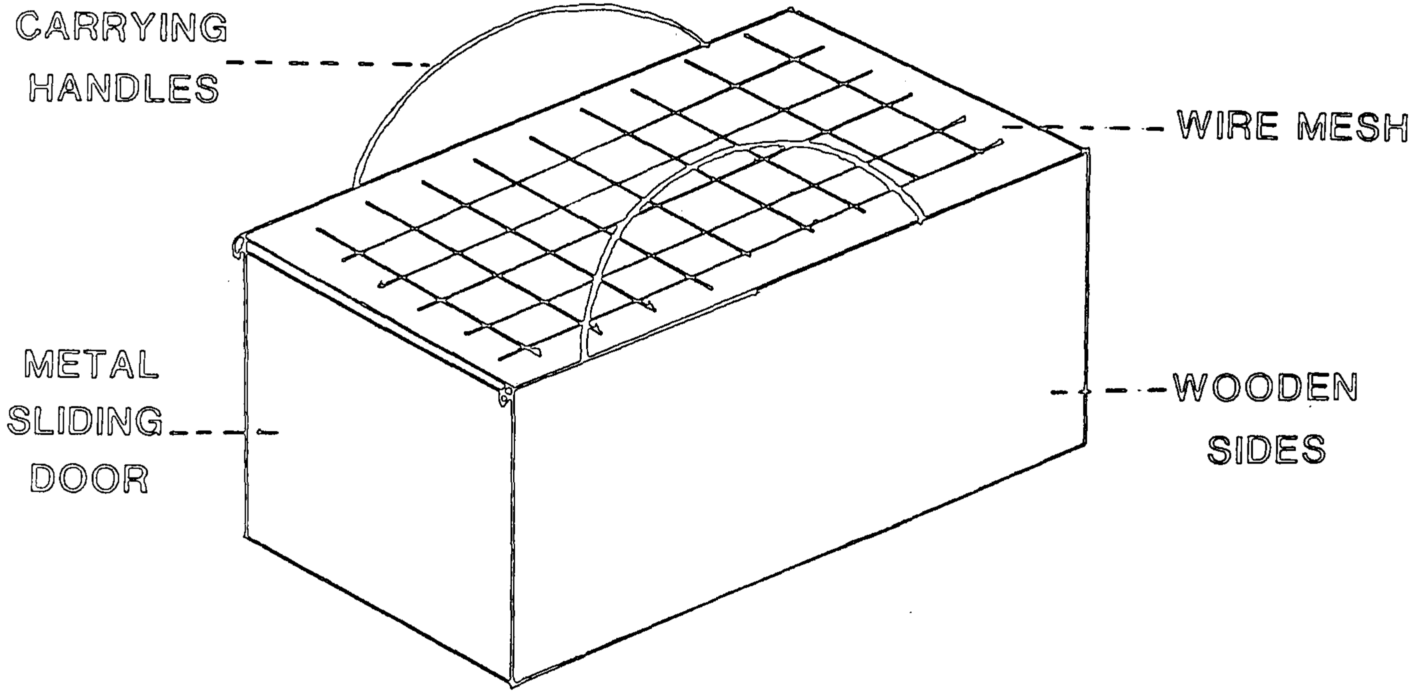
(ix) Swim up:- This behaviour occurred at the termination of all underwater behaviours. It was generally preceeded by either 'Hide Search' or 'Bottom Search'. This behaviour was recorded when an animal left the bottom of the tank and ascended to the surface. However, there was great variation both between, and within, the behaviour of individuals. Sometimes animals would rise passively from the pool bottom to the surface, sometimes they would actively swim up using the hind-legs or, for even greater speeed, the fore-limbs would also be used. The angle of the ascent varied from roughly 90^o to the horizontal (i.e. vertical) to angles of around $10\text{-}15^o$ from horizontal (i.e. a shallow, gradual rise to the surface). These values were estimated during actual observations of the mink foraging and from the recorded videotapes. Sometimes animals would surface close to a rostrum and clamber on, or alternatively they would surface in the middle of the tank, and either swim to the nearest rostrum or, very infrequently, dive again.

(x) Dive:- During analysis of the effects of various parameters on the underwater foraging of the mink, it was felt to be convenient to look at the effect on dive duration in mink. For this purpose, a 'Dive' was considered to begin when an animal began behaviour 'Swim Down' and to terminate when an animal had completed behaviour 'Swim Up'. However, a 'Dive' was only scored if the animal had succesfully reached the bottom of the pool during behaviour 'Swim Down'.

2.6. Preliminary Training

As has been mentioned above (2.1. Subjects) all the mink used in experiments had been purchased as six to eight week old kits from alocal mink farm. It was therefore necessary to accustom these kits not only to the experimental tank and hides, but also to water, and to encourage them to gain proficiency in swimming and diving. The animals were also trained to enter a carrying box 16 cm long x 10 cm x 10 cm (Fig. 2.4) as, once adult, they were too intractable to be handled.

The four animals used in Experiment I were born in April/May 1980, some five months before this study began. These animals were reared together in the laboratory for a period of 16 weeks. During this time the animals were familiarized with the carrying box, the experimental pool and with water up to a depth of 0.60 m (shallow end). By October


CARRYING HANDLES
WIRE MESH
METAL SLIDING DOOR
WOODEN SIDES

1980 these animals were proficient at swimming but not necessarily at diving. At this point a more rigorous training programme was implemented. Since these animals were effectively mature by this stage, and liable to be aggressive towards one another, all further training was carried out individually in the experimental pool.

Initially, the animals were familarized with the hides, which were placed outside the pool. Hide doors were wedged open and all hides contained a food reward. Over a period of up to five days (depending on the individual), the doors were gradually closed until the animals were readily opening the doors to gain access to the food reward. Each animal was allowed to explore the hides during at least two sessions each day for a minimum period of 15 min. After this, access was allowed to the pool itself via the wooden ramp. The water level had been fixed at 0.20 m in the shallow end, and a resting place was provided in each side. This water depth was just sufficient to ensure that the mink had to swim when not resting. During this period, pieces of eel about 2-3 cm long were loosely attached by string to the end of a 2.5 m long pole. These were used to encourage the animals to chase on the water surface and then to dive and chase on the pool bottom. If an animal dived successfully it was allowed to remove the bait. Occasionally, a 12 cm long toy 'shark' was used instead of eel bait. When under water, the bait was pulled close to a hide to encourage searching behaviour. These training periods lasted 15 - 30 min and animals could enter and leave the pool freely. Baited hides were still placed outside the pool.

Once animals were consistently opening and searching the hides placed outside the pool, all such hides were removed, except for one placed to one side of the top of the ramp. Two others were placed at intervals down the ramp and one box was placed on each of the two resting places, i.e. within the pool, but out of the water. After a few days the animals readily ran down the ramp into the pool without encouragement. Now, once access had been gained to the pool, the ramp was removed. This procedure was continued for ten days until the animals were surface swimming and opening any hides on the rostra, and any held at the water surface. Gradually, those hides held at the water surface were lowered so that they were half covered with water, completely covered, and finally submerged and standing on the bottom of the pool. After ten weeks of training the animals were regularly swimming and diving to the bottom in both shallow and deep ends of the pool and searching hides. The water level was then gradually raised over a further period of eight weeks until the animals were consistently opening boxes and retrieving the reward in depths of up to 0.60 m (shallow) and 1.05 m (deep). At this point the training period for these animals was deemed to be complete.

During the course of the study further young mink were purchased from the same mink farm. In May 1981, five males and four females were obtained and in May 1982 a further three males and one female were purchased. See Appendix I for details of experimental use and coat colour.

A similar training regime was followed for each group and is outlined below. Initially, the young kits were housed together in a large room (see 2.2. Maintenance). For the first two weeks kits were not moved from this room and the experimenter spent an average of four to six hours each day feeding and playing with them. After this initial period, the kits were taken daily to the experimental pool. The 'deep' end of the pool was filled with water to a depth of 0.10 m and the 'shallow' end left completely dry for the young animals to play in. Thus, in this case, animals did not have the free run of the hut, but were confined to the pool. It was noticed from the outset that some of the mink were more inquisitive, regarding water, than others and readily plunged in to swim in the few centimetres available. Once the first kits had begun swimming the others followed. A variety of objects such as a ball, polystyrene squares, bricks and pipes were provided as play objects and, in the case of the pipes, retreats. Eight hides were placed around the sides of the pool in the 'shallow' end.

Initially, as above, the doors of the hides were wedged open and all were baited with eel. Bait was immediately replaced once an animal had sucessfully investigated a hide and care was taken to ensure that all the young mink were able to search hides, as there was a tendency for the more inquisitive animals to 'get in first'.

After a few days, most of the animals were readily entering the hides and retrieving the food reward. The doors of the hides were now held only partially open so that the animals had to push them open to gain access to the food reward. After a week all the mink were successfully investigating the hides and the doors were now completely closed. During this period the water level in the 'deep' end was simultaneously being raised by 2-3 cm per day until it reached a depth of 0.40 m. A further six hides were arranged around the edge of the water and four more were placed further in so that animals were accustomed to getting wet when retrieving food from closed hides. All hides were now removed from the dry 'shallow' end and distributed in the 'deep' end in such a way that some were completely submerged, some partially and some just at the water's edge. As the animals became adept at opening the hides in the shallower parts they were gradually moved until all hides were submerged. Simultaneously, the water level was raised as before until the 'shallow' end was under 0.03 m. The rostra and pipes were now provided as resting places and the water level was raised by 2-3 cm per day to a depth of 0.20 m ('shallow') and 0.65 m ('deep'). Hides were now distributed throughout the pool, and all were totally submerged. The water depth was such that all animals now had to swim between resting places. This training scheme had taken nearly 12 weeks to complete.

It had been hoped that by following a gradual training process all animals would have become proficient at the task of diving, locating hides and searching them for a food reward. However, in each year only 75% of the animals became proficient. From the 1981 group, the 'Standard' colour male Corin was reluctant even to swim. The 'Pastel' male, Elron, could swim competently, but was reluctant to open hides underwater. Furthermore, two females, Greta (Pastel) and Helva (Standard) proved to be extremely difficult to trap in the carrying box and showed some reluctance to dive, although both would search hides once underwater. As a result, none of these four animals were used in subsequent experiments. From the 1982 group, the male Mervin (Standard), was reluctant to swim. The remaining three animals were trained successfully, but again the female, Ladie (Standard), was extremely difficult to trap in the carrying box and was not used in subsequent experiments.

By the end of this training period in both years, the young mink had reached sub-adult age and were now transferred to individual cages in the main Animal House (see 2.2. Maintenance). The water depth was now raised over a period of five days to a level of 0.60 m ('shallow') and 1.05 m ('deep'). Those animals that were to be used in subsequent experiments were brought in for a 15-30 min daily observation period to ensure proficiency in diving and hide location at this new depth.

At this point the training period was deemed complete and experimental work could now begin.

CHAPTER 3

THE EFFECT OF DEPTH ON THE UNDERWATER FORAGING BEHAVIOUR OF THE MINK

3.1. Introduction

The aim of this experiment was to investigate the effect of different water depths, from a minimum of 0.30 m to a maximum of 1.65 m, on the underwater foraging behaviour of the mink. In particular, it was hoped that any effect depth might have on foraging strategy would be identified. Since the mink is an air-breathing mammal, foraging underwater produces an additional constraint, namely that of oxygen deficiency. It might be expected that changes in water depth would affect the duration of dives and that this in turn might have a major effect on foraging efficiency. It was hoped that this experiment would give some insight into the sort of 'decision rules' that mink might use when foraging under conditions of varying water depth.

3.2. Materials and methods

3.2.1. Subjects

Four animals were used in this experiment, three females (Dexa, Inka, Titan) and one male (Raja).

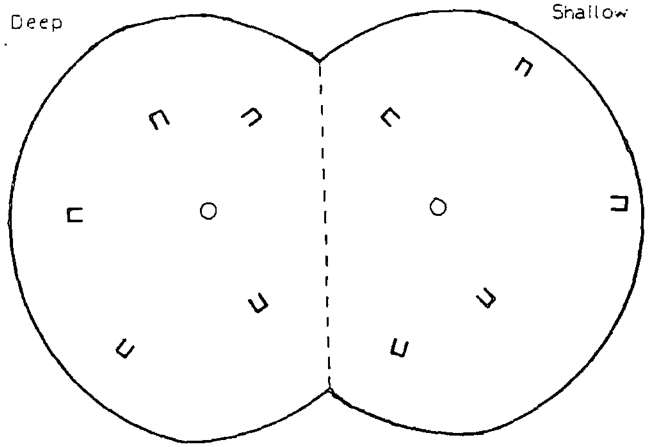
3.2.2. Maintenance

The four animals used in this experiment were approximately five months old by October 1980, i.e. they were effectively mature. The animals were housed in individual cages, and a strict training regime was carried out to ensure proficiency in swimming, diving and hide searching, (see General Materials and Methods: 2.6. Preliminary Training.)

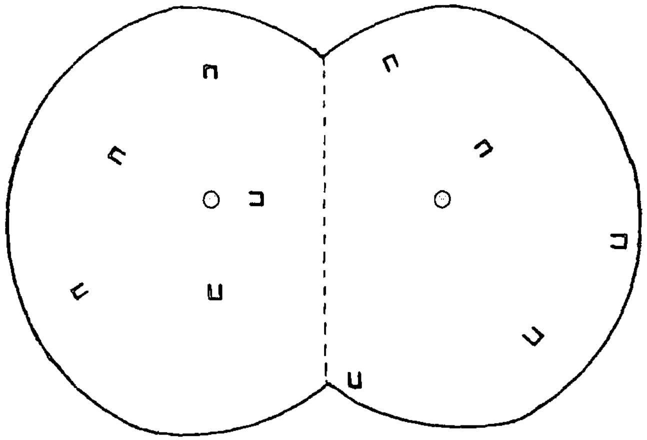
By the end of February 1981 the animals were proficient at diving and searching hides, and successfully retrieving food rewards in water up to 1.05 m deep. All animals were tested between 10.00 and 14.00 hours and were fed 75 g of a mixture of Spratts ZF6, rabbit pellets and canned dog food on their return to their 'home' cage. The amount of food given was approximately 25% less than the normal amount given as the maintenance diet when animals were not participating in an experiment. The remainder of the diet was made up by food rewards obtained during the experimental period. If any animal was particularly unsuccessful at obtaining food rewards during the experimental trial, then a suitable amount of eel was added to the diet for that day. On average, animals would receive about 50 g of eel per day. Excess food was removed at 0900 hours each day by high pressure hosing.

3.2.3. Experimental procedure

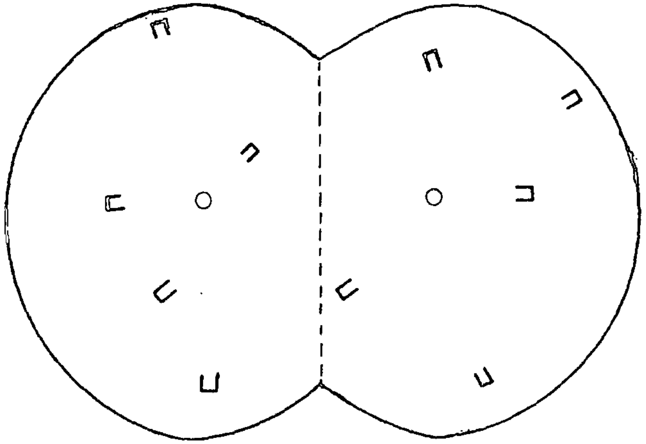
The experiment was carried out in the grid-marked pool (see General Materials and Methods: 2.3. Experimental Arena). Pieces of eel flesh (approximately 5 g in weight), were used as bait concealed inside wooden hides. Ten hides were distributed evenly in the two halves of the pool, but during any trial only five of the ten contained bait, i.e. prey density was 50%. Two resting platforms, or rostra, were also provided, one in the centre of each half of the pool. The hides were arranged according to one of four 'distribution patterns', with only one hide in any one grid square, so that, as far as possible, there were the same number of hides at 0.5 m, 1.0 m, 1.5 m and 2.0 m distance from each of the rostra (Fig. 3.1). The hide distribution pattern was altered for each session, as shown in Table 3.1. The order of change was determined by the observer to give the greatest variation in hide positions. A random number table was used at the beginning of each session to select which five of the ten hides should be baited. The baited hides were fixed for each trial of an individual animal within that session.



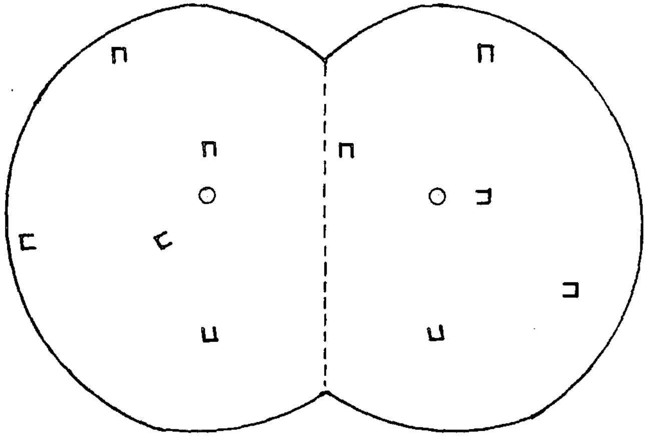
BEHPATH I



BEHPATH III



BEHPATH II



BEHPATH IV

Table 3.1: Sequence of hide distribution patterns used in depth experiment.

Date	Session Number	Hide Pattern	Water Level
23.2.81	1	1	I
23.2.81	2	2	I
23.2.81	3	3	I
24.2.81	4	3	II
24.2.81	5	4	II
24.2.81	6	1	II
2.3.81	7	2	III
4.3.81	9	1	III
7.3.81	10	4	III
9.3.81	11	2	III
11.3.81	12	1	IV
12.3.81	13	2	IV
14.3.81	14	3	IV
15.3.81	15	4	IV
16.3.81	16	1	IV
23.3.81	17	2	IV
24.3.81	18	1	IV
25.3.81	19	2	IV
26.3.81	20	3	IV
26.3.81	21	1	IV
28.3.81	22	3	III
29.3.81	23	4	III
30.3.81	24	4	III
31.3.81	25	2	III
1.4.81	26	3	II
2.4.81	27	4	II
3.4.81	28	1	I
4.4.81	29	2	I
5.4.81	30	4	III
5.4.81	31	3	III
6.4.81	32	1	I
7.4.81	33	3	IV
28.4.81	34	3	II
29.4.81	35	2	II
30.4.81	36	1	IV
2.5.81	37	1	IV
4.5.81	38	3	IV
5.5.81	39	2	IV
6.5.81	40	4	IV
7.5.81	41	3	I
8.5.81	42	2	I
11.5.81	43	1	III
12.5.81	44	4	III
13.5.81	45	2	III
14.5.81	46	1	III

N.B. Key to Water Levels given in Table 3.2

However, if the random table indicated, for instance, that all hides in the 'shallow' end and none in the 'deep' end should be baited, alternative hides were chosen by the observer, such that there were always three baited hides in one end of the pool and two baited in the other. Detailed notes of which hides were baited for each session were kept by the observer, and appropriate modifications were made if a similarly positioned hide was consistently to be baited from the random number table. This was carried out to avoid the mink developing a position tendency. Also, if the 3:2 hide baiting ratio indicated, e.g. three shallow : two deep, for more than three sessions, modifications were made. It was hoped that this would result in a highly variable environment as far as location of 'prey' items was concerned, and that this would avoid any possibility of the mink being able to learn where rewarded hides were situated. Finally, during any individual's trial, baited hides from which food had been removed were not replenished during that trial, but they were refilled prior to the next individual's trial.

Access to the pool was provided by the removable wooden ramp and the position of entry to the pool, deep or shallow end, right or left sides etc., was varied for each individual and for each trial. It was hoped that, by altering the entry point for each trial, this would inhibit learning of position of baited hides in relation to the entry point.

Experiments were carried out at four different water levels which corresponded to actual water depths as given in Table 3.2. The experiment was carried out in three parts - the water levels were raised, sequentially, from level I to IV (Ascending Series), the depth was then held at level IV before being lowered, in order, to level I (Descending Series) and finally the water levels were altered as follows:- III, I, IV, II, IV, I, III, (Random Series). The aim of these three series was to try and eliminate any possibility that changes

Table 3.2: Water levels and corresponding real water depths.

Level	Depth in shallow end in m	Depth at centre of deep end in m
I	0.30	0.75
II	0.60	1.05
III	1.00	1.45
IV	1.20	1.65

Table 3.3: Number of dives recorded for each animal at each of the four water levels.

		Animal								
		Dexa		Inka		Raja		Titan		
Water Level	Presentation Series	No. dives	Total	No. dives	Total	No. dives	Total	No. dives	Total	TOTAL
I	Asc	36		37		39		36		
	Desc	35	111	31	118	31	115	27	110	454
	Rand	40		50		45		47		
II	Asc	32		39		32		43		
	Desc	45	100	29	101	35	96	43	127	424
	Rand	23		33		29		41		
III	Asc	49		37		41		50		
	Desc	36	131	33	129	43	110	47	174	544
	Rand	46		59		26		77		
IV	Asc	34		16		15		45		
	Desc	40	116	44	95	41	63	48	129	403
	Rand	42		35		7		36		

Grand total 1825

in foraging performance at a given water depth, were due to learning, practise or any training effect in the experimental situation.

The experiment thus began with the Ascending Series and the water depth at level I. Each animal was given several trials until a minimum of 25 dives had been recorded at that level before altering the water depth. Generally, each animal was given only one trial per day. Each trial was timed to last until 20 dives were completed, or for 10 min, whichever was soonest. As a result, the maximum number of dives recorded for each animal at a given level varies considerably (Table 3.3). With regard to the minimum figure, at the greatest depth, i.e. level IV, one animal, the male Raja, appeared to be much less competent in the Random Series, and his trials were discontinued. Also, at the maximum level in the Ascending Series, animals were able to escape from the pool and total dive number (Table 3.3) and mean dive number per trial (Table 3.4) were much lower than those recorded in the Descending Series, after a barricade had been erected around the pool to prevent escapes. However, although in trials with a low dive rate, such factors as interval between successive dives will be affected, factors within a dive such as time on bottom, number of hides visited etc., should be influenced mainly by the water depth, and hence data for dives occurring in these trials were included in the analysis. The criterion of "at least 25 dives per animal per water Level" resulted in dives not being equally distributed between the two water depths in each level, and hence the number of dives recorded for each water depth will be even more variable (Table 3.5).

Data were obtained on a total of 1825 dives over the various water depths for the four animals. Of these, 122 dives involved a movement of the animal between the shallow and deep ends of the pool. These dives were excluded from subsequent analysis, which was based on data from 1703 dives (Table 3.5).

Table 3.4: Mean number of dives per trial (+ S.E.) recorded for each animal at each of the four water levels. (n)= number of trials for each animal under a given condition.

Water Level	Presentation Series	Animal			
		Inka	Dexa	Raja	Titan
I	Asc	18.5 ± 0.5(2)	11.3± 3.9(3)	18.5 ± 0.5(2)	18.0 ± 3.0(2)
	Desc	15.5 ± 0.5(2)	17.5 ± 1.5(2)	15.5 ± 0.5(2)	27.0 (1)
	Rand	25.0 ± 5.0(2)	20.0 ± 4.0(2)	22.5 ± 0.5(2)	23.5 ± 0.5(2)
II	Asc	19.0 ± 1.0(2)	10.7 ± 3.4(3)	16.0 ± 1.0(2)	19.5 + 1.5(2)
	Desc	14.5 ± 0.5(2)	22.5 ± 1.5(2)	17.0 ± 1.0(2)	21.5 ± 4.5(2)
	Rand	16.5 ± 0.5(2)	11.5 ± 4.0(2)	14.5 ±2.5(2)	20.5 ± 0.5(2)
III	Asc	7.0 ± 0.9(5)	7.8 ± 1.3(6)	11.3 ± 1.3(4)	11.8 ± 2.7(4)
	Desc	10.7 ± 2.2(3)	12.0 ± 1.0(3)	14.0 ±1.2(3)	20.5 ± 1.5(2)
	Rand	11.4 ± 2.8(5)	8.6 ± 1.0(5)	13.5 ± 3.5(2)	18.8 ± 2.2(4)
IV	Asc	5.3 ± 1.8(3)	6.6 ± 1.4(5)	3.5 ± 0.9(4)	14.7 ± 0.9(3)
	Desc	11.0 ± 1.8(4)	10.0 ± 1.5(4)	9.8 ± 2.1(4)	12.0 ± 1.1(4)
	Rand	7.0 ± 1.3(5)	6.8 ± 1.4(6)	3.5 ± 1.5(2)	11.7 ± 3.4(3)

Table 3.5: Number of dives recorded for each animal at each water depth.

			Number of dives recorded for each animal								
Water Level	Water Depth in m.	Presentation Series	Dexa	Total	Inka	Total	Raja	Total	Titan	Total	TOTAL
		Asc	24		26		19		21		
I	0.30	Desc	18	60	15	60	18	67	14	63	250
		Rand	18		19		30		28		
		Asc	15		27		20		23		
II	0.60	Desc	21	51	13	61	11	60	17	65	237
		Rand	15		21		29		25		
		Asc	12		10		20		13		
I	0.75	Desc	16	48	16	56	12	46	8	38	188
		Rand	20		30		14		17		
		Asc	26		27		32		30		
III	1.00	Desc	13	52	23	78	10	55	20	75	260
		Rand	13		28		13		25		
		Asc	13		6		12		14		
II	1.05	Desc	20	40	12	26	21	33	23	52	151
		Rand	7		8		0		15		
		Asc	19		8		12		21		
IV	1.20	Desc	24	63	26	55	28	46	25	66	230
		Rand	20		21		6		20		
		Asc	21		3		7		12		
III	1.45	Desc	19	69	7	38	29	47	25	86	240
		Rand	29		28		11		49		
		Asc	13		8		3		22		
IV	1.65	Desc	14	49	11	30	9	13	19	55	147
		Rand	22		11		1		14		

Grand Total = 1703

3.3. Results

Before carrying out any detailed analysis on the effect of depth on parameters such as diving rate, success, number of hides visited per dive etc., it was first necessary to see if there were any significant differences between the behaviour of individual animals at the same water depth. However, since each animal was tested at any given water depth three times in all, (Ascending, Descending and Random) it was also necessary to investigate whether an individual's behaviour at a given depth was consistent at each presentation of that depth.

3.3.1. Analysis of variance

Both the above points were tested using Analysis of Variance tests on dive duration, distance travelled and speed, controlling for Animal, Depth and Series. The results of these Anova tests are given in Tables 3.6-3.8 but a brief summary can be outlined as follows. (Results were only given as significant if $p<0.01$).

	Significant Main effects	Significant two-way Interactions
a) Dive duration		
(i) Unsuccessful dives	Animal, Depth	Animal x Depth
(ii) Successful dives	Depth	-
(iii) Dives which did not visit a hide	Animal, Depth	Animal x Depth Animal x Series
b) Distance travelled		
(i) Unsuccessful dives	Animal, Depth	Animal x Series
(ii) Successful dives	Depth	-
(iii) Dives which did not visit a hide	Animal, Depth, Series	Animal x Depth Depth x Series
c) Speed		
(i) Unsuccessful dives	Animal, Depth, Series	-
(ii) Successful dives	Depth	-
(iii) Dives which did not visit a hide	Animal, Depth, Series	Animal x Depth Animal x Series

Table 3.6: Analysis of variance of dive duration by Animal, Depth and Series Presentation.

(i) Unsuccessful hide visit dives

Source of Variation	Sum of Squares	df	Mean Square	F	Signif. of F
Main Effects	1119.582	12	93.298	25.645	0.0001
Animal	74.825	3	24.942	6.856	0.0001
Depth	1003.346	7	143.335	39.399	0.001
Series	10.618	2	5.309	1.459	0.233
2-way interactions	226.917	41	5.535	1.521	0.022
Animal x Depth	165.018	21	7.858	2.160	0.002
Animal x Series	38.816	6	6.469	1.778	0.101
Depth x Series	34.315	14	2.451	0.674	0.801
3-way interactions	166.892	37	4.511	1.240	0.160
Animal x Depth x Series	166.892	37	4.511	1.240	0.160
Explained	1513.392	90	16.815	4.622	0.00
Residual	2073.664	570	3.638		
Total	3587.056	660	5.435		

730 cases analysed
69 cases (9.5%) were missing (i.e. dives travelling between deep and shallow sides of the pool, and cases where data were lost).

(ii) Successful dive

Source of Variation	Sum of Squares	df	Mean Square	F	Signif. of F
Main Effects	279.819	12	23.318	7.031	0.0001
Animal	22.168	3	7.389	2.228	0.086
Depth	253.550	7	36.221	10.922	0.0001
Series	11.686	2	5.843	1.762	0.174
2-way interactions	140.546	41	3.428	1.034	0.424
Animal x Depth	74.596	21	3.552	1.071	0.381
Animal x Series	27.541	6	4.590	1.384	0.222
Depth x Series	50.370	14	3.598	1.085	0.373
3-way interactions	86.201	33	2.612	0.788	0.791
Animal x Depth x Series	86.201	33	2.612	0.788	0.791
Explained	506.567	86	5.890	1.776	0.00
Residual	722.975	218	3.316		
Total	1229.542	304	4.455		

322 cases analysed
17 cases (5.3%) were missing (i.e. dives travelling between deep and shallow sides of the pool, and cases where data were lost).

Table 3.6: (Cont'd.)
Anova of dive duration by Animal, Depth and Series Presentation.

(iii) No hides visited during dive

Source of Variation	Sum of Squares	df	Mean Square	F	Signif. of F
Main Effects	997.674	12	83.139	21.158	0.0001
Animal	462.593	3	154.198	39.242	0.0001
Depth	517.494	7	73.928	18.814	0.0001
Series	15.010	2	7.505	1.910	0.149
2-way interactions	445.383	41	10.863	2.765	0.0001
Animal x Depth	301.872	21	14.375	3.658	0.0001
Animal x Series	75.279	6	12.546	3.193	0.004
Depth x Series	100.197	14	7.157	1.821	0.033
3-way interactions	164.463	39	4.217	1.073	0.355
Animal x Depth x Series	164.463	39	4.217	1.073	0.355
Explained	1607.520	92	17.473	4.447	0.00
Residual	2239.779	570	3.929		
Total	3847.299	662	5.812		

773 cases analysed
110 cases (14.2%) were missing (i.e. dives travelling between deep and shallow sides of the pool, and cases where data were lost).

TABLE 3.7: Analysis of variance of distance travelled by Animal, Depth and Series Presentation.

(i) Unsuccessful hide visit dives

Source of Variation	Sum of Squares	df	Mean Square	F	Signif. of F
Main Effects	251.642	12	20.970	21.729	0.0001
Animal	21.289	3	7.096	7.353	0.0001
Depth	227.448	7	32.493	33.668	0.0001
Series	1.805	2	0.902	0.935	0.393
2-way interactions	53.863	41	1.314	1.361	0.070
Animal x Depth	30.395	21	1.447	1.500	0.071
Animal x Series	13.428	6	2.238	2.319	0.032
Depth x Series	9.451	14	0.675	0.699	0.776
3-way interactions	42.358	37	1.145	1.186	0.212
Animal x Depth x Series	42.358	37	1.145	1.186	0.212
Explained	347.862	90	3.865	4.005	0.0
Residual	570.708	581	0.965		
Total	908.570	671	1.354		

730 cases analysed
58 cases (7.9%) were missing (i.e. dives travelling between deep and shallow sides of the pool, and cases where data were lost).

(ii) Successful dives

Source of Variation	Sum of Squares	df	Mean Square	F	Signif. of F
Main Effects	95.749	12	7.979	8.723	0.0001
Animal	8.202	3	2.734	2.989	0.032
Depth	88.997	7	12.714	13.899	0.0001
Series	1.142	2	0.571	0.624	0.537
2-way interactions	39.958	41	0.975	1.065	0.375
Animal x Depth	22.111	21	1.053	1.151	0.298
Animal x Series	8.521	6	1.420	1.553	0.162
Depth x Series	12.196	14	0.871	0.952	0.504
3-way interactions	23.461	33	0.711	0.777	0.804
Animal x Depth x Series	23.461	33	0.711	0.777	0.804
Explained	159.168	86	1.851	2.023	0.000
Residual	199.412	218	0.915		
Total	358.580	304	1.180		

322 cases analysed
17 cases (5.3%) were missing (i.e. dives travelling between deep and shallow sides of the pool, and cases where data were lost).

TABLE 3.7: (Cont'd.)
Anova of distance travelled by Animal, Depth and Series Presentation.

(iii) <u>No hides visited during dive</u>

Source of Variation	Sum of Squares	df	Mean Square	F	Signif. of F
Main Effects	124.394	12	10.366	14.852	0.0001
Animal	74.213	3	24.738	35.444	0.0001
Depth	38.265	7	5.466	7.832	0.0001
Series	9.306	2	4.653	6.666	0.001
2-way interactions	86.291	41	2.105	3.016	0.0001
Animal x Depth	55.852	21	2.660	3.811	0.0001
Animal x Series	5.129	6	0.855	1.225	0.292
Depth x Series	22.705	14	1.622	2.324	0.004
3-way interactions	46.878	40	1.172	1.679	0.006
Animal x Depth x Series	46.878	40	1.172	1.679	0.006
Explained	257.564	93	2.770	3.968	0.0
Residual	439.706	630	0.698		
Total	697.270	723	0.964		

773 cases analysed
49 cases (6.3%) were missing (i.e. dives travelling between deep and shallow sides of the pool, and cases where data were lost).

TABLE 3.8: Analysis of variance of speed by Animal, Depth and Series Presentation.

(i) Unsuccessful hide visit dives

Source of Variation	Sum of Squares	df	Mean Square	F	Signif. of F
Main Effects	1.568	12	0.232	2.847	0.001
Animal	0.372	3	0.124	2.701	0.045
Depth	0.820	7	0.117	2.552	0.014
Series	0.329	2	0.164	3.580	0.028
2-way interactions	2.484	41	0.061	1.320	0.092
Animal x Depth	0.919	21	0.044	0.953	0.521
Animal x Series	0.306	6	0.051	1.110	0.355
Depth x Series	0.974	14	0.070	1.515	0.100
3-way interactions	2.061	37	0.056	1.213	0.185
Animal x Depth x Series	2.061	37	0.056	1.213	0.185
Explained	6.113	90	0.068	1.805	0.005
Residual	26.164	570	0.046		
Total	32.277	660	0.049		

730 cases analysed

69 cases (9.5%) were missing (i.e. dives travelling between deep and shallow sides of the pool, and cases where data were lost).

(ii) Successful dives

Source of Variation	Sum of Squares	df	Mean Square	F	Signif. of F
Main Effects	0.443	12	0.037	2.932	0.001
Animal	0.044	3	0.015	1.170	0.322
Depth	0.384	7	0.055	4.357	0.0001
Series	0.022	2	0.011	0.886	0.414
2-way interactions	0.462	41	0.011	0.893	0.658
Animal x Depth	0.242	21	0.012	0.915	0.572
Animal x Series	0.088	6	0.015	1.167	0.325
Depth x Series	0.140	14	0.010	0.791	0.679
3-way interactions	0.330	33	0.010	0.793	0.784
Animal x Depth x Series	0.330	33	0.711	0.010	0.784
Explained	1.235	86	0.014	1.139	0.225
Residual	2.748	218	0.013		
Total	3.983	304	0.013		

322 cases analysed

17 cases (5.3%) were missing (i.e. dives travelling between deep and shallow sides of the pool, and cases where data were lost).

TABLE 3.8: (Cont'd.)
Anova of speed by Animal, Depth and Series Presentation.

(iii) No hides visited during dive

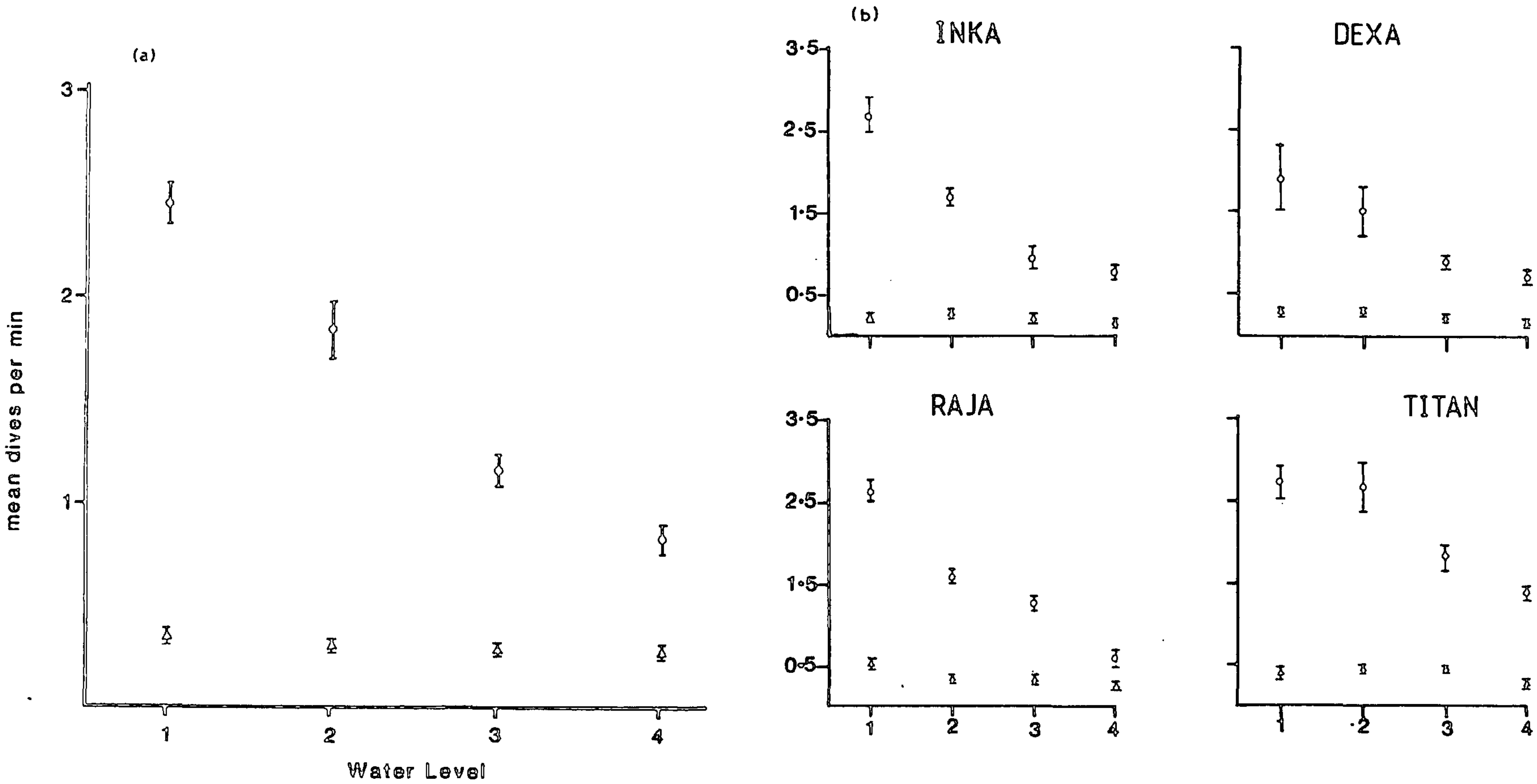
Source of Variation	Sum of Squares	df	Mean Square	F	Signif. of F
Main Effects	53.718	12	4.476	30.817	0.0001
Animal	10.732	3	3.577	24.628	0.0001
Depth	42.593	7	6.085	41.889	0.0001
Series	3.710	2	1.855	12.769	0.0001
2-way interactions	11.152	41	0.272	1.873	0.001
Animal x Depth	5.176	21	0.245	1.697	0.027
Animal x Series	1.983	6	0.331	2.276	0.035
Depth x Series	3.098	14	0.221	1.523	0.098
3-way interactions	7.006	39	0.180	1.237	0.158
Animal x Depth x Series	7.006	39	0.180	1.237	0.158
Explained	71.876	92	0.781	5.378	0.0
Residual	82.797	570	0.145		
Total	154.673	662	0.234		

From these results it can be seen that series presentation order of the depths has a significant effect on the behaviour of animals (i.e. significant two-way interactions), when either unsuccessful dives, or dives when no hides are visited, are considered. The results also show that Depth is the most important factor influencing the behaviour of individuals, regardless of whether a dive was successful or not, and the significant two-way interactions show that individuals may be behaving differently at a given depth.

These results show that data could be grouped for the same depth from different presentation series for each individual. It was also decided to group the data for all subjects at a particular depth to see if general trends in behaviour could be established. However, because of the indications that there was considerable individual variation in behaviour at a given depth, the results for individual animals are, whenever possible, included for comparison.

3.3.2 Dive rate

Values were calculated from the total number of dives per trial (regardless of whether they were in the deep or shallow sides of the arena) divided by the total duration (in min) of the trial. A mean value of dive rate ± S.E. could then be calculated for each individual and for all animals for each water level. It was not possible to calculate a dive rate for each of the eight water depths since the exact amount of time spent in each half of the pool during a trial could not be obtained from the data. Fig. 3.2 shows the mean dive rate for the combined data (Fig. 3.2a), and the individual results (Fig. 3.2b), at each of the four water levels. Linear regression analysis was carried out using all data, to see if there was a correlation between the two variables, and if so, to examine the rate of change of the dependent variable by examining the slope of the regression line.


(a)
mean dives per min
3
2
1
1
2
3
4
Water Level
(b)
INKA
DEXA
RAJA
TITAN
3·5
2·5
1·5
0·5
3·5
2·5
1·5
0·5
1
2
3
4
1
·2
3
4

The graph of the combined results shows that there was a marked linear decline in diving rate ($r = -0.72$, $df = 138$, $p<0.001$) as water level increased. Further, the slope of -0.54 indicates that the diving rate drops by roughly half the number of dives per minute for each change in water level. A similar trend can be seen for the individual results where all four animals show a clear negative correlation between diving rate and increasing water level (Inka: $r = -0.83$, $df = 34$, $p<0.001$, Dexa: $r = -0.64$, $df = 41$, $p<0.001$, Raja: $r = -0.90$, $df = 29$, $p<0.001$, Titan: $r = -0.77$, $df = 28$, $p<0.001$).

A point to be made here concerns the fact that diving rate is being correlated with water levels, not absolute depth. These were numbered I - IV for convenience, but in fact the difference in real water depth (as measured in the shallow end) is not identical for each of the four levels, but rises from 0.30 m (level I) to 0.60 m, 1.00 m and finally to 1.20 m (level IV) (see Table 3.2). However, since the correlation between diving rate and the four water levels is very strong, it is unlikely that there would not be a significant difference if the real water depth at each of the four levels showed an equal change between levels, e.g. rising from 0.30 m to 0.60 m, 0.90 m and 1.20 m.

3.3.3. Hide visit dive rate

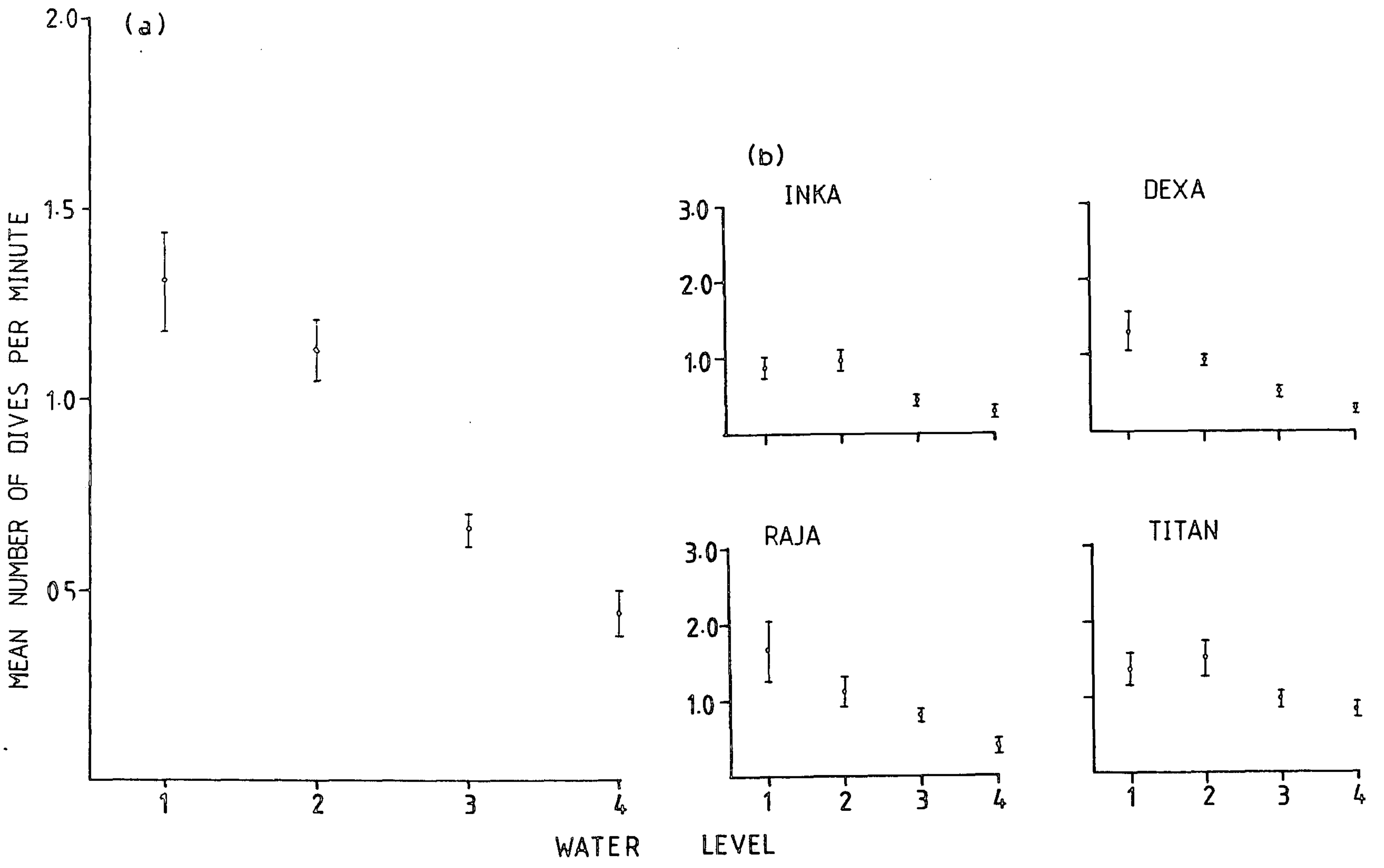
The number of successful dives in a trial is a useful measure of the foraging efficiency of animals under different conditions. However, in many cases mink failed to search any hides during a dive. Obviously, these dives have no opportunity of being scored as successful. The rate of dives visiting hides was therefore calculated for each trial of each animal, and a mean value ± S.E. could then be obtained. Trials in which all dives failed to visit hides were excluded from the analysis, since in these cases animals had been distracted.

Fig. 3.3a shows the overall results, and linear regression analysis shows that hide visit dive rate declines sharply with increasing water level, ($r = -0.65$, df = 138, $p<0.01$). However, the slope of the line is less steep than that for diving rate, and mean hide visit dive rate declines by only roughly one third, for each rise in water level. Individual results (Fig. 3.3b) show a similar pattern with significant negative linear correlations for each individual. Thus, Inka ($r = -0.72$, df = 34, $p<0.001$), Dexa ($r = -0.78$, df = 41, $p<0.001$), Raja ($r = -0.71$, df = 29, $p<0.001$) and Titan ($r = -0.61$, df = 28, $p<0.001$). For Dexa, hide visit dive rate declines with water level at a similar rate to that for the overall results. For Raja, the decline is a little steeper, but for the remaining females, it is somewhat shallower. However, since overall dive rate also declines with water level, these results are not surprising.

3.3.4. Successful dive rate

Here, the total number of successful dives in a trial was divided by the total duration of that trial in min. As above, the successful dive rates for each trial of each animal at a particular depth were summed and divided by the total number of trials at that depth to obtain the mean successful dive rate ± S.E.

The results are shown in Fig. 3.2, from which several points can be noted. Firstly, the actual values for mean successful dive rate are very low, all being less than 0.5 dives per min (i.e. less than one successful dive in every two min). Secondly, from the results of linear regression analysis using all the data, there appears to be a strong negative correlation between successful dive rate and water depth for the overall results ($r = -0.41$, df = 138, $p<0.001$). However, the very low value of the slope shows that as water level increases from level I to level II for example, successful dive rate will decrease by 0.06


(a)
2.0
1.5
1.0
0.5
MEAN NUMBER OF DIVES PER MINUTE
1
2
3
4
(b)
INKA
3.0
2.0
1.0
DEXA
RAJA
3.0
2.0
1.0
TITAN
1
2
3
4
1
2
3
4
WATER LEVEL

dives per min (or roughly one dive per 20 min) from the rate at level I. This suggests that successful dive rate does not alter substantially with increasing water level.

When the individual results are examined, it is found that there are three significant negative linear correlations, for Inka ($r = -0.43$, $df = 34$, $p<0.01$), for Dexa ($r = -0.59$, $df = 41$, $p<0.001$) and for Raja ($r = -0.53$, $df = 29$, $p<0.01$). For Titan, it appears that there was no linear relationship between the two variables. In each case where there is a significant linear correlation, the slope of the regression line is again very small (ranging from 0.05 to 0.07, depending on the individual). Thus, the rate of change of successful dive rate with water level is very small.

Two further points of interest emerge from Figs. 3.2 and 3.3. Firstly, there is a marked decline in dives which visited hides (and which, therefore, could potentially be successful) as water level increased, and although successful dive rate did decline with water level, the rate of change was very much smaller. Secondly, comparison of the slopes for combined results of dive rate (-0.54) and hide visit dive rate (-0.31), suggests that dive rate declined more rapidly with water level. This implies that the proportion of total dives visiting a hide changed with depth. In fact, it appears that a smaller proportion of the total dives involved hide visits at the lower levels than is the case for water levels III and IV, i.e. at shallow depths more dives involved searching the pool without entering a hide.

For all subsequent analyses it was possible to calculate results for each of the eight depths, since the variables to beinvestigated were not 'rates' which depend on the amount of time spent in each half of the pool.

3.3.5. Proportion of dives visiting a hide to total dive number

Data were calculated for each trial of each animal for each depth from :-

$$p^{v} = \frac{n^{vt}}{n^{t}}$$

where p^{v} = proportion of dives involving a hide visit.

n^{vt} = number of dives visiting a hide in trial t.

n^{t} = total number of dives in trial t.

From this it can be seen that the maximum value for p^{v} must be 1.0 (i.e. all dives during a trial involved at least one hide visit) and the minimum value must be 0.0 (i.e. none of the dives in trial t visited a hide).

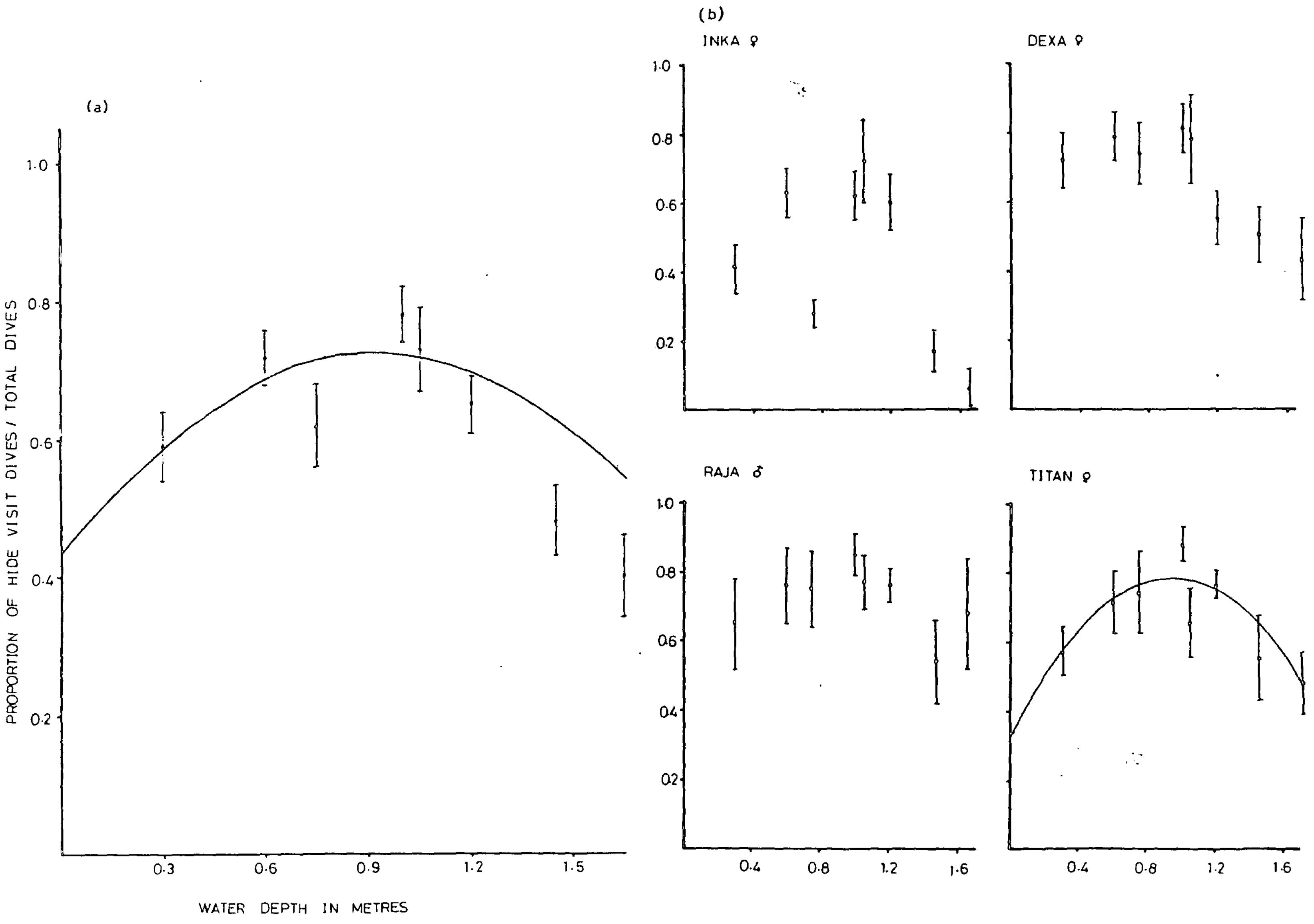
The mean proportion of dives involving a hide visit, for All Animals and individuals at a given depth could then be calculated from :-

$$\bar{p}^{v} = \frac{\Sigma p^{v}}{N}$$

where $\bar{p}^{v}$ = mean value of proportions of hides visited.

N = total number of trials at the given depth.

Fig. 3.4a presents the results for All Animals at each depth. A linear regression analysis was carried out using all the data, to investigate whether there was any correlation between the two variables. Arcsine transformations were not carried out, since all of the proportion values were above 0.1 and below 0.9. The results for the combined data for All Animals indicate that there is no linear correlation between the two variables ($r = -0.07$, df = 239, p=ns), although it appears that for depths up to 1.00 m, the proportion of dives visiting hides does increase, and then decreases with further increase in depth. When individual results are considered (Fig. 3.4b) the picture is similar, but for female Dexa, there is a significant negative linear correlation between proportion of dives visiting


(a)
PROPORTION OF HIDE VISIT DIVES / TOTAL DIVES
1.0
0.8
0.6
0.4
0.2
0.3
0.6
0.9
1.2
1.5
WATER DEPTH IN METRES
(b)
INKA ♀
DEXA ♀
RAJA ♂
TITAN ♀
1.0
0.8
0.6
0.4
0.2
0.4
0.8
1.2
1.6

hides and depth ($r = -0.24$, $df = 73$, $p<0.05$). For the remaining animals, there is no significant linear correlation between the two variables, although in each case it can be seen from the graphs that there may be a curvilinear relationship between the two variables.

In order to investigate this further, curvilinear analysis was carried out on all the data for All Animals, and for individuals. It was decided to use the additional parameters of $(\text{depth})^2$ and $(\text{depth})^3$, since squaring has the effect of expanding the higher values of the independent variable, possibly resulting in a linear relationship becoming apparent. In each case, the method used was forced entry of the new variables into the regression equation.

Significant results were obtained for All Animals, and Titan. The equations representing the lines of best fit are given in Fig. 3.4. These results show that there is a quadratic relationship between the proportion of dives visiting a hide and water depth, for All Animals and Titan, and it appears that the proportion of dives visiting a hide increases with depth, until a depth of around 1.00 m is reached. Thereafter, as depth increases, the proportion of dives visiting a hide declines.

3.3.6. Proportion of successful dives

In this analysis, only those dives in which at least one hide was visited were included, since dives in which no hides were visited could not be expected to be successful.

Data were calculated for each trial of each animal at a given depth from:-

$$p^{st} = \frac{n^{st}}{n^{t}}$$

where p^{st} = proportion of successful dives for trial t.

n^{st} = number of successful dives in trial t.

n^{t} = total number of dives which involved a hide visit in trial t.

A mean value for all animals at a given depth could then be calculated from:-

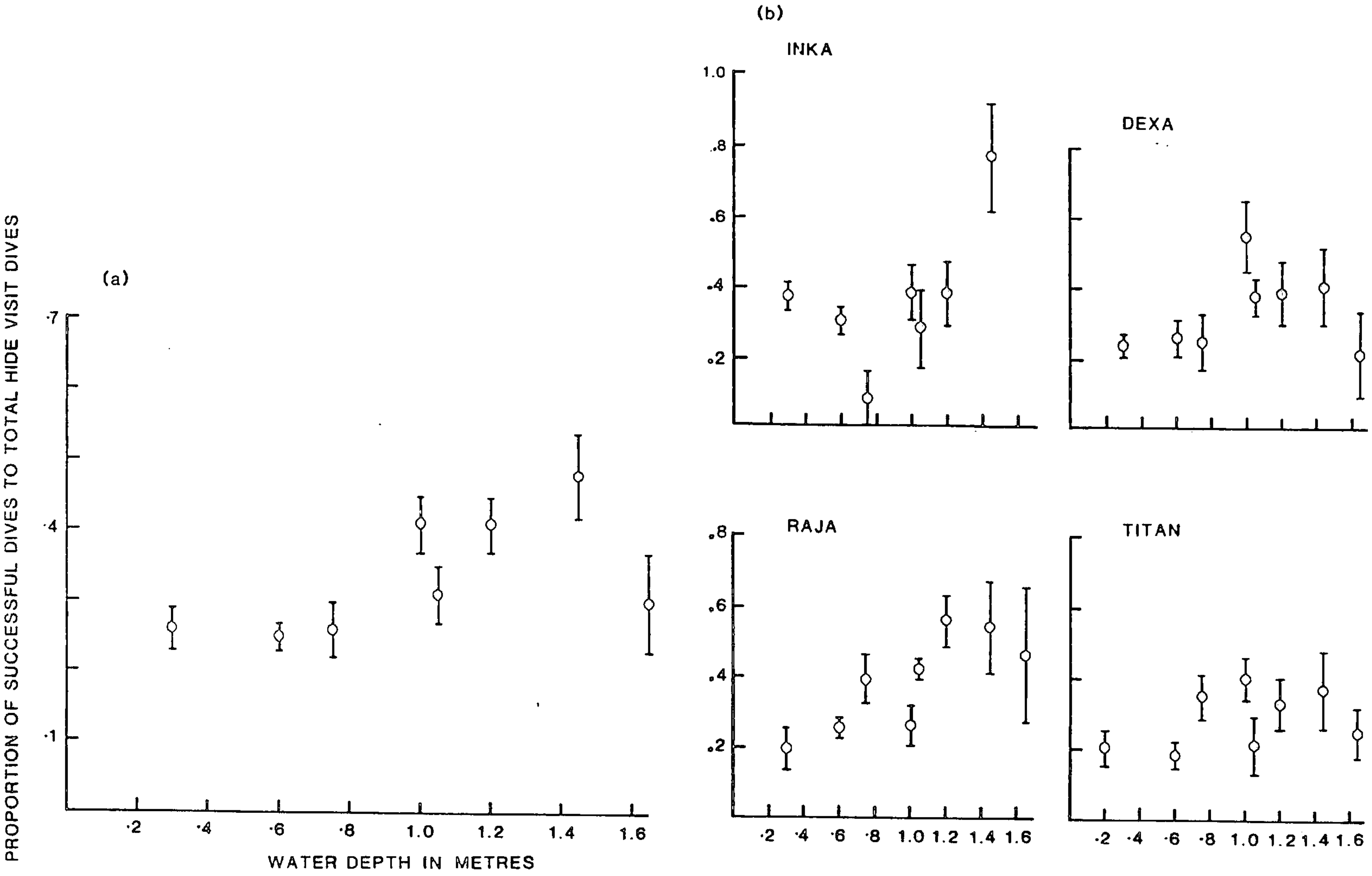
$$\bar{p}^{st} = \frac{\Sigma\, p^{st}}{N}$$

where $\bar{p}^{st}$ = mean value for proportion of successful dives.

N = number of trials at the given depth.

The values of p^{st} were plotted for both the combined data (Fig. 3.5a) and individual results (Fig. 3.5b). Linear regression analysis was carried out using all data. Significant linear correlations were obtained for All Animals ($r = 0.18$, $df = 239$, $p<0.01$), Inka ($r = 0.29$, $df = 52$, $p<0.05$) and Raja ($r = 0.40$, $df = 50$, $p<0.01$). In each case, the proportion of successful dives increases with depth. It was also noted from the data that many instances (43 trials out of 241) involved dives which visited hides, but none of these visits were successful. These trials were spread between all individuals and over all depths, and would obviously contribute to the very low values of mean proportion of successful dives to total hide visit dives illustrated in Fig. 3.5a and b.

Finally, from Fig. 3.5 it can be seen that there is possibly a curvilinear relationship between the two variables in some cases. As outlined in section 3.3.5 above, a curvilinear analysis using Depth, $(\text{Depth})^2$ and $(\text{Depth})^3$ was carried out for all animals and individuals, using the forced entry method. However, the only significant correlations were linear relationships for All Animals, Inka and Raja. The slopes of the linear regression lines are similar for Inka and Raja, and show that for each metre increase in depth, the proportion of successful dives would rise by 25%. For the two remaining females, the graphs of the mean data indicate a trend for proportion of successful dives to


(a)
PROPORTION OF SUCCESSFUL DIVES TO TOTAL HIDE VISIT DIVES
·7
·4
·1
·2
·4
·6
·8
1.0
1.2
1.4
1.6
WATER DEPTH IN METRES
(b)
INKA
1.0
.8
.6
.4
.2
DEXA
RAJA
.8
.6
.4
.2
TITAN
·2
·4
·6
·8
1.0
1.2
1.4
1.6

increase with depth, but linear regression using all data showed that there was no significant linear relationships between the two variables.

A final complicating factor in the analysis of changes in success as depth increases is the fact that dives scored as 'hide visit' dives often involved visits to more than one hide. However, only one of these hide visits (the last) would actually be successful as, once an animal located a food reward, it would terminate the dive and resurface to eat or cache its prey. Hence, the following parameters were also examined.

3.3.7. Proportion of successful hide visits

This was calculated from the following:-

$$p^{sht} = \frac{n^{sht}}{n^{ht}}$$

where p^{sht} = proportion of successful hide visits for trial t.

n^{sht} = number of successful hide visits in trial t.

n^{ht} = total number of hide visits in trial t.

As for the previous calculations a mean value (± S.E.) for all animals at a given depth could be obtained from:-

$$\bar{p}^{sh} = \frac{\Sigma p^{sht}}{N^{h}}$$

where $\bar{p}^{sh}$ = mean value for proportion of successful hide visits.

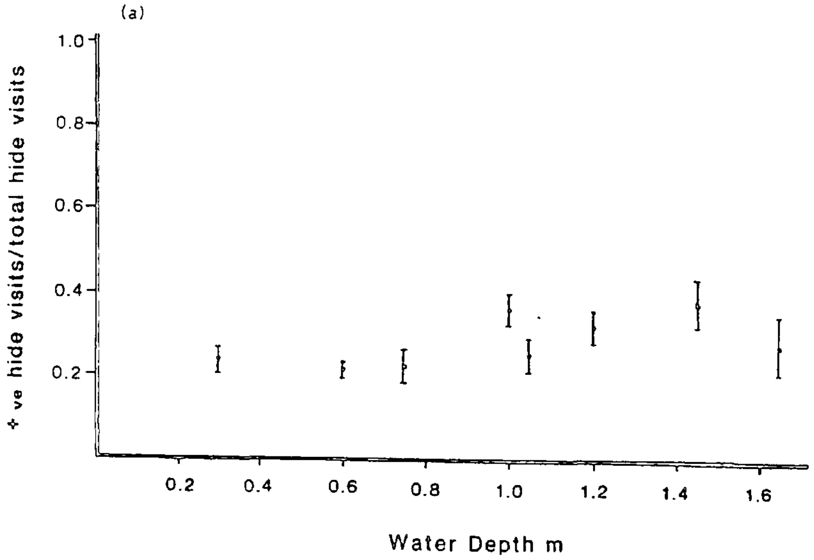
N^{h} = number of trials in which hides were visited.

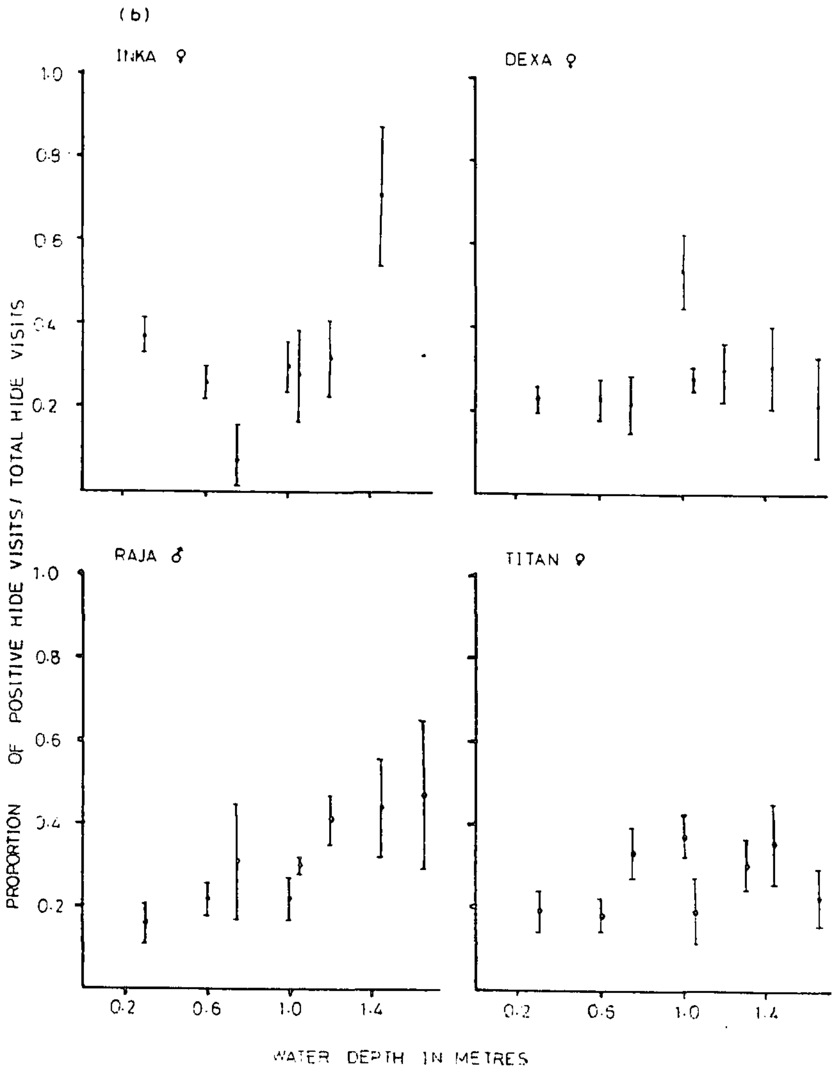
All trials in which no hide visits occurred, were excluded from the analysis. In some trials, all hide visits were unsuccessful, (i.e. proportion value was 0.0), but these were included in the analysis since animals had not been distracted, buthad searched a number of hides and, therefore, were potentially capable of locating a food reward. The results are presented in Figs. 3.6a and b.

The results for All Animals (Fig. 3.6a) show that there is a significant positive linear correlation between the two variables ($r = 0.15$, $df = 239$, $p<0.05$). However, the slope of the regression line is very small (0.10), showing that for each metre increase in depth, the proportion of successful hide visits to total hide visits would increase by 10%.

When the individual results (Fig. 3.6b) are considered, the variation between animals can be seen. The male, Raja, shows a very clear linear relationship ($r = 0.43$, $df = 50$, $p<0.01$), with an increase in proportion of successful hide visits with depth at a rate of 25% per metre rise in depth. However, for the three females the results all show that there is no significant linear correlation. Further, curvilinear analysis showed that there were no significant correlations between the two variables when Depth, $(\text{Depth})^2$ and $(\text{Depth})^3$ were used. The large standard errors give some indication of the considerable variability both between animals (see Fig. 3.6a) and between trials for an individual at a given depth (Fig. 3.6b).

The overall picture given by the analyses carried out so far is that although the diving rate drops rapidly with increasing depth, the degree of success in obtaining a food reward declines at a very much slower rate (see Fig. 3.2a). This suggested that the ratio of successful dives to total dives visiting a hide rose with depth, which was, generally, found to be true. However, the proportion of dives visiting a hide to total dives, for All Animals, followed a more curved relationship with a peak at depth of 1.0 m.


(a)
+ ve hide visits/total hide visits
1.0
0.8
0.6
0.4
0.2
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
Water Depth m


(b)
INKA ♀
DEXA ♀
RAJA ♂
TITAN ♀
PROPORTION OF POSITIVE HIDE VISITS/ TOTAL HIDE VISITS
1.0
0.8
0.6
0.4
0.2
1.0
0.8
0.6
0.4
0.2
0.2
0.6
1.0
1.4
0.2
0.6
1.0
1.4
WATER DEPTH IN METRES

3.3.8. Dive duration

Results of Analysis of Variance tests on the successful and unsuccessful dive durations shown by animals, at each Depth and Series Presentation Order are shown in Table 3.6. Animal, Depth and Success parameters were important in explaining the variation in dive duration. Significant two-way interactions between Depth and Animal, and Success and Animal were obtained. Thus, in calculating mean dive duration for animals at the different depths, successful and unsuccessful hide visit dives were treated separately and dives in which no hides were visited were excluded from the analysis.

Mean durations of unsuccessful dives were calculated, both for individuals and for All Animals, at the eight depths from the following:-

$$\bar{d}^u = \frac{\Sigma d^u}{n^u}$$

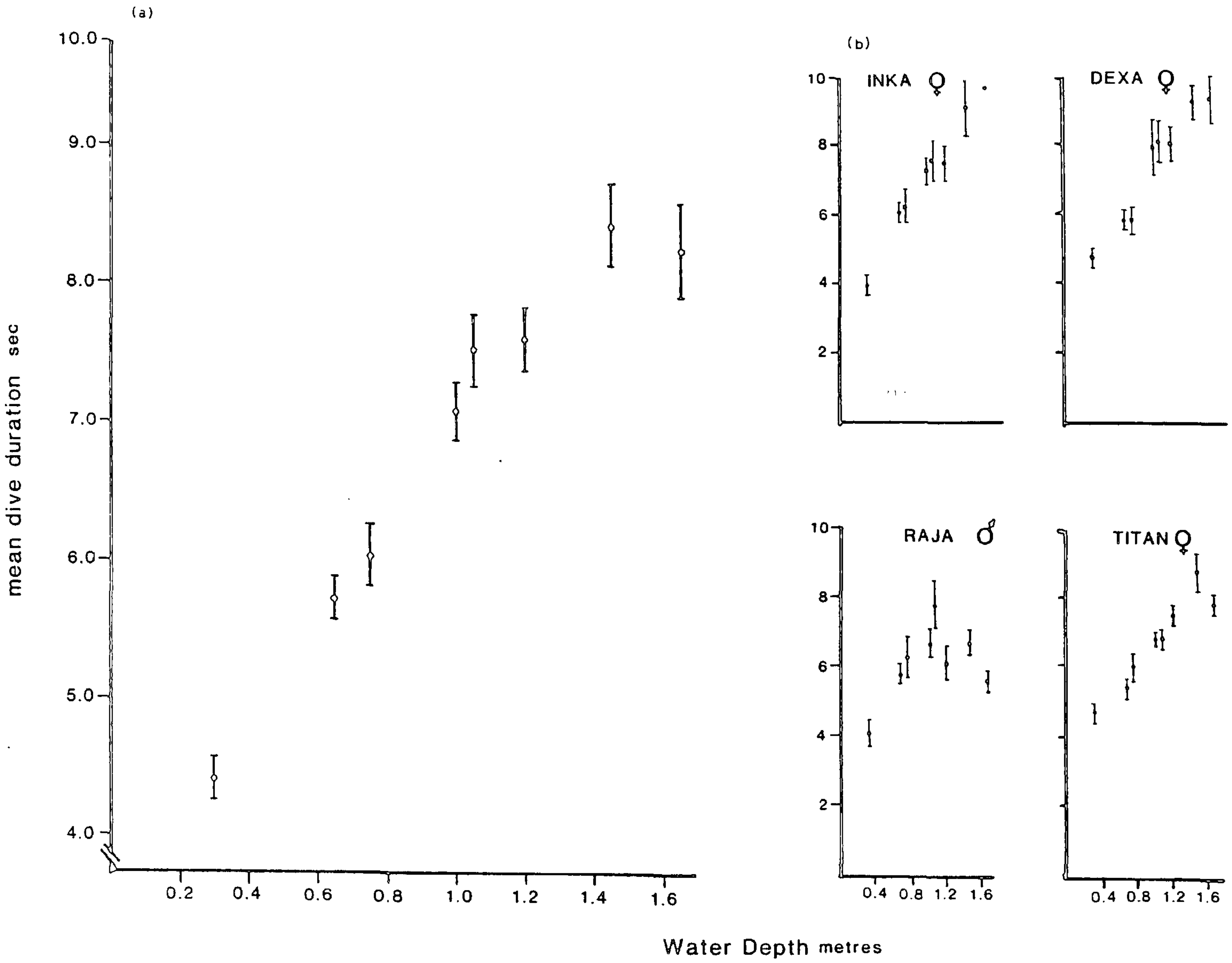
where $\bar{d}^u$ = mean unsuccessful dive duration.

Σd^u = sum of all dive durations for unsuccesful dives.

n^u = total number of unsuccessful dives at the given depth.

Mean successful dive durations were calculated in a similar way.

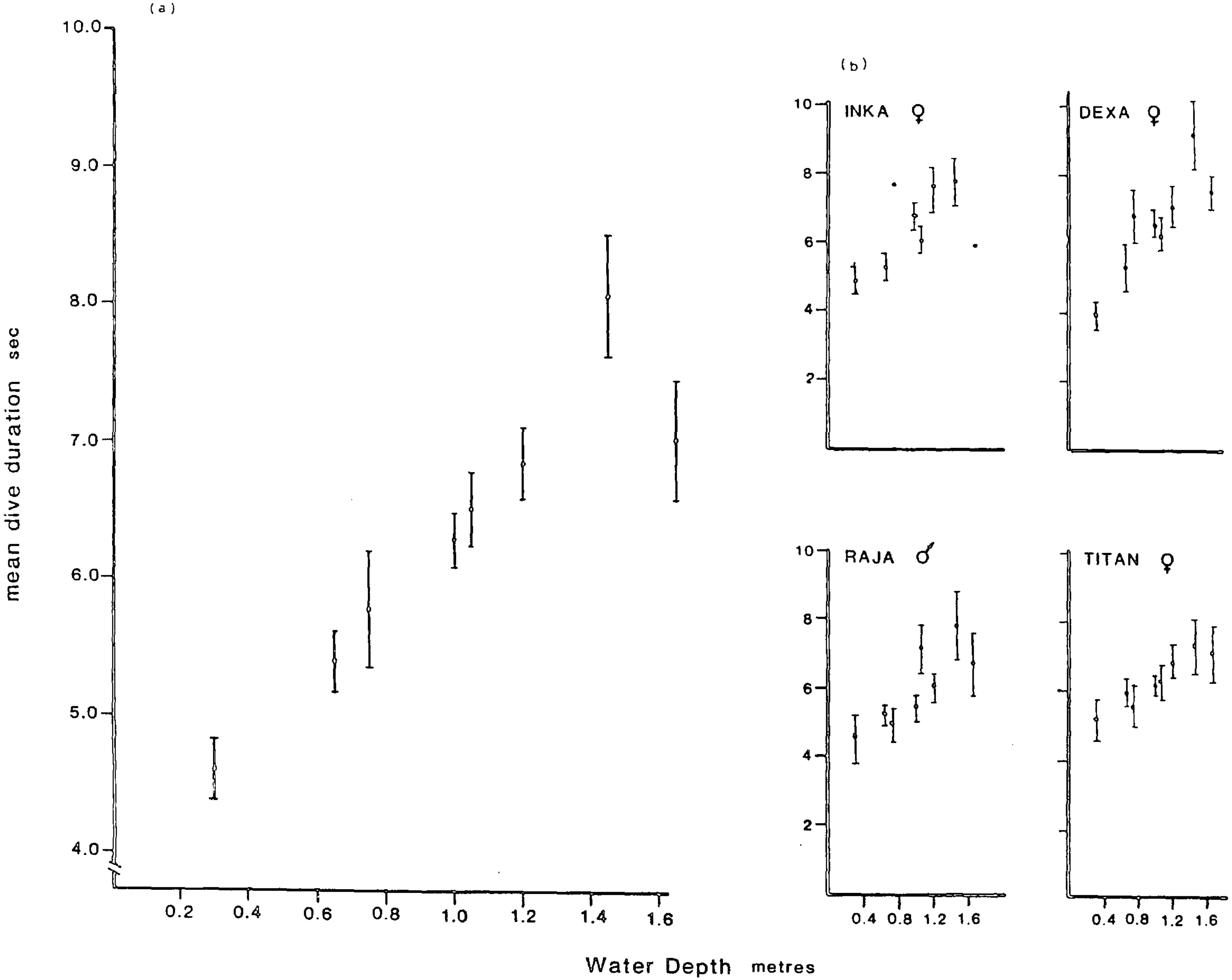
Fig. 3.7 presents the data for mean duration of unsuccessful dives. Linear regression analysis using all the data for All Animals shows that there is a linear correlation between the variables ($r = 0.52$, $df = 659$, $p<0.001$) with dive duration increasing with depth. The slope of the line indicates that for each metre increase in water depth, dive duration increases by roughly 3 s. When individual results are considered, it can be seen that, in each case, there is a positive linear correlation between dive duration and water depth, (Inka: $r = 0.55$, $df = 115$, $p<0.001$. Dexa: $r = 0.59$, $df = 173$, $p<0.001$. Raja: $r = 0.34$, $df = 155$, $p<0.001$. Titan: $r = 0.59$, $df = 212$, $p<0.001$), although for Inka and Dexa,


(a)
(b)
mean dive duration sec
Water Depth metres
10.0
9.0
8.0
7.0
6.0
5.0
4.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
INKA ♀
DEXA ♀
RAJA ♂
TITAN ♀
10
8
6
4
2
0.4
0.8
1.2
1.6

dive duration increases at a greater rate (roughly 4 s per metre rise in water depth) than for Titan and Raja.

Fig 3.8 presents the data for mean successful dive duration plotted against depth. Again, linear regression analysis for all data for All Animals shows that mean successful dive duration increases linearly with depth ($r = 0.43$, $df = 303$, $p<0.001$), although, in this case, successful dive duration increases by only roughly 2 s for each metre rise in water depth. For individual data, again, in each case, there is a significant positive linear correlation between successful dive duration and depth (Inka: $r = 0.51$, $df = 56$, $p<0.001$. Dexa: $r = 0.50$, $df = 79$, $p<0.01$. Raja: $r = 0.41$, $df = 77$, $p<0.001$. Titan: $r = 0.34$, $df = 85$, $p<0.01$). Further, as for data for overall results, the slopes of the significant regression lines show that successful dive duration, generally, increases at a slower rate with depth, than that for unsuccessful dives.

There are a few points to note from the above graphs. Firstly, although both successful and unsuccessful dive durations show an increase with depth, there does seem to be a marked drop in the mean dive duration at the maximum tested depth of 1.65 m, and this is true for both combined data, and, generally, for individual results. It would be interesting to see what results would be obtained at greater depths, up to 2.0 m, for example. Secondly, the mean values for successful dives are generally slightly smaller than those for unsuccessful dives at the same depth, although Standard Error bars indicate that there is overlap between the two plots. To investigate this a paired t-test was carried out on the mean combined data for All Animals, where the values for unsuccessful dive durations (Fig. 3.7a), at each of the eight depths, were compared to the corresponding eight values for successful durations (Fig. 3.8a). The result was significant at the 5% level ($t = 3.44$, $df = 7$, $p<0.05$), and showed that mean successful dive durations were shorter than mean


(a)
10.0
9.0
8.0
7.0
6.0
5.0
4.0
mean dive duration sec
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
Water Depth metres
(b)
INKA ♀
DEXA ♀
RAJA ♂
TITAN ♀
10
8
6
4
2
0.4 0.8 1.2 1.6

unsuccessful dive durations. Further, the data for the two regression lines for all the combined data for All Animals were compared to see if they were statistically significant using:-

$$t = \frac{slope_a - slope_b}{\sqrt{S.E._a^2 + S.E._b^2}} \qquad \text{where } df = df_a + df_b$$

where t = t-test statistic.

$slope_a$ = slope of regression line a.

$S.E._a$ = standard error of slope of regression line a.

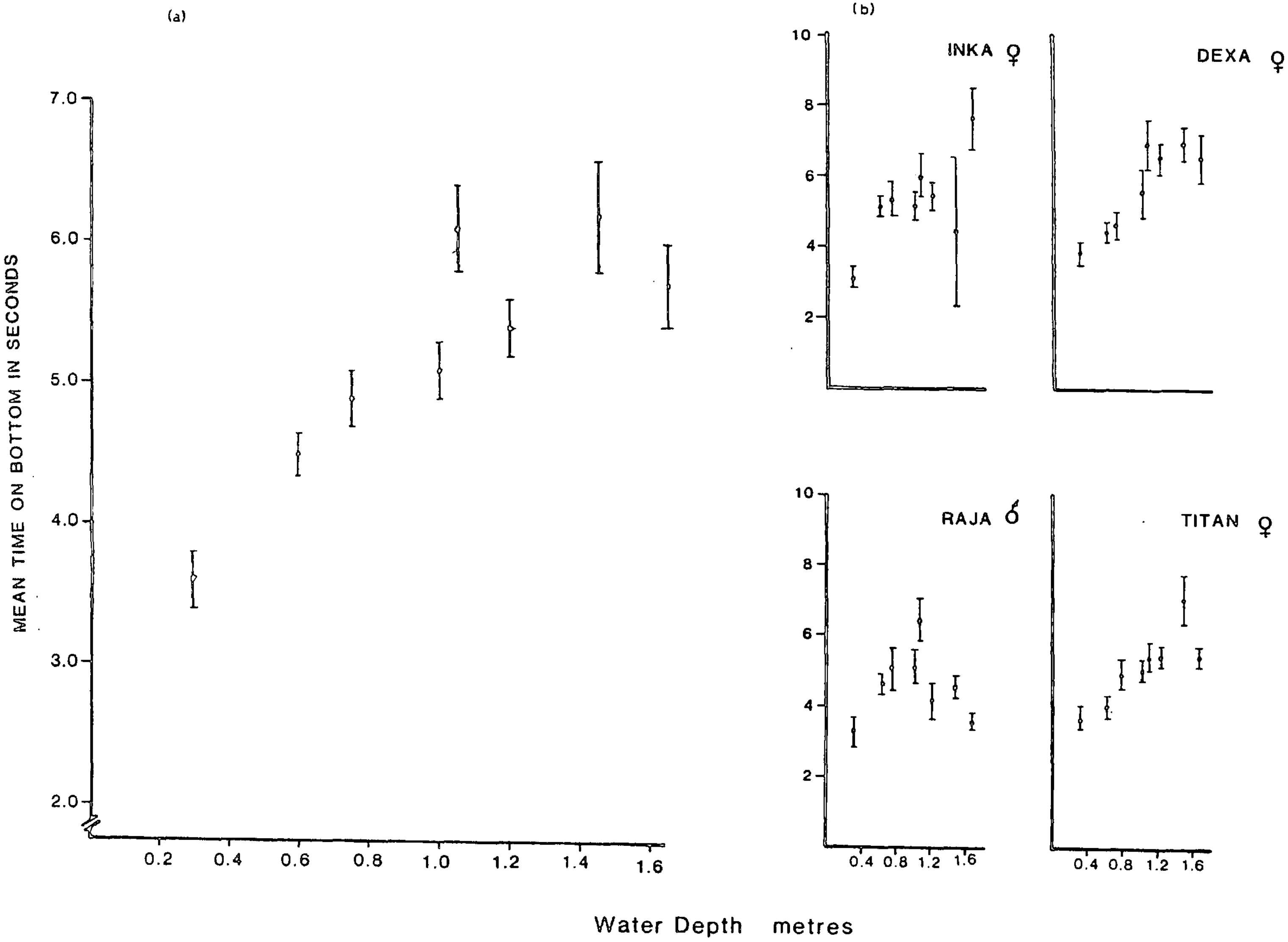
df_a = number of degrees of freedom for regression line a.

Substituting the data for the regression lines for unsuccessful and successful dive durations, the result showed that $t = 2.29$, $df = 962$, $p<0.001$. Thus, there was a highly significant difference between the two regression lines.

In Figs. 3.7 and 3.8 the values for mean dive duration give the total time spent underwater, i.e. from the moment the animal goes below the water surface, until it returns to the water surface, after a period travelling on the bottom of the pool. As depth increases it would be reasonable to suppose that travel time to and from the water surface and the pool bottom also increases, and this would itself lead to an increase in dive duration with increasing depth. Therefore, a more appropriate measure of the time available for mink to search for prey would be mean time on bottom.

3.3.9. Time on bottom

Mean time on bottom was calculated from the keyboard-entered data. Data for unsuccessful dives only were analysed, and data for dives in which no hides were visited were excluded. For each dive the time spent bottom-searching plus the time spent hide-


(a)
MEAN TIME ON BOTTOM IN SECONDS
7.0
6.0
5.0
4.0
3.0
2.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
(b)
INKA ♀
DEXA ♀
RAJA ♂
TITAN ♀
10
8
6
4
2
0.4
0.8
1.2
1.6
Water Depth metres

searching was summed to give the time spent on bottom during that dive. Thus, data for duration of behaviours 'dive', 'swim-up', and 'find food' (which was merely a tag used to indicate success of a dive, and was only keyed in once animals had begun to swim up), were not included.

The mean values for time on bottom during unsuccessful dives could be calculated both for individuals, and for All Animals at each of the eight depths from the following:

$$d^{tbu} = \frac{\Sigma d^{tbu}}{n^{u}}$$

where d^{tbu} = mean duration on bottom forunsuccessful dives at the given depth.

Σd^{tbu} = sum of all values for time on bottom for unsuccessful dives at the given depth.

n^{u} = total number of unsuccessful dives at the given depth.

Fig. 3.9a presents the data for mean time on bottom for all unsuccessful dives which visited at least one hide. Linear regression analysis using all data, revealed significant positive linear correlations between the variables, for All Animals ($r = 0.37$, $df = 627$, $p<0.001$), Inka ($r = 0.40$, $df = 115$, $p<0.001$), Dexa ($r = 0.34$, $df = 144$, $p<0.001$) and Titan ($r = 0.41$, $df = 186$, $p<0.001$). The slopes of the significant regression lines indicated that for each one metre increase in water depth, time on bottom increased by between roughly 2-3 s, depending on the individual. However, for the male Raja there was no significant linear relationship between the two variables, but curvilinear analysis of all the data showed that a quadratic curve gave the best fit. The equation is given in the Figure legend. Here, unsuccessful time on bottom increased with depth up to around 1.00 m, and declined thereafter.

For successful dives, animals will terminate the dive once a food item is obtained, and it would be expected that this would have the most important effect on mean time on bottom regardless of depth. Thus, data for successful time on bottom with depth were not analysed.

From the above analyses it would appear that the increased dive duration with depth is a 'real' phenomenon involving a greater amount of time spent on the bottom, and is not an artifact due to increased travel times to and from the surface. The next point to investigate is whether the animals are also altering their foraging patterns at greater depths to obtain the best use of their increased foraging time.

3.3.10. Number of hides visited per dive

One method by which mink could maintain a relatively steady success rate in spite of a sharply decreased dive rate as depth increases, would be to visit a greater number of hides in each dive. However, there is a complicating factor, in that, if an animal searches a hide and finds food, it terminates the dive, but if that hide had not contained food it is possible that the animal may have continued its search and located other hides. Thus, it may give a better idea of whether mink are potentially capable of increasing the number of hides visited per dive as depth increases if unsuccessful hide visit dives only are considered.

The mean number of hides visited per dive was calculated for unsuccessful dives, both for individuals and All Animals, at the eight depths from the formula below. Standard Errors could also be obtained:-

$$\bar{n}^{hv} = \frac{\Sigma\, hv_1 + hv_2 + \ldots\ldots hv_n}{n^{hv}}$$

where $\bar{n}^{hv}$ = mean number of hides visited per dive at given depth.

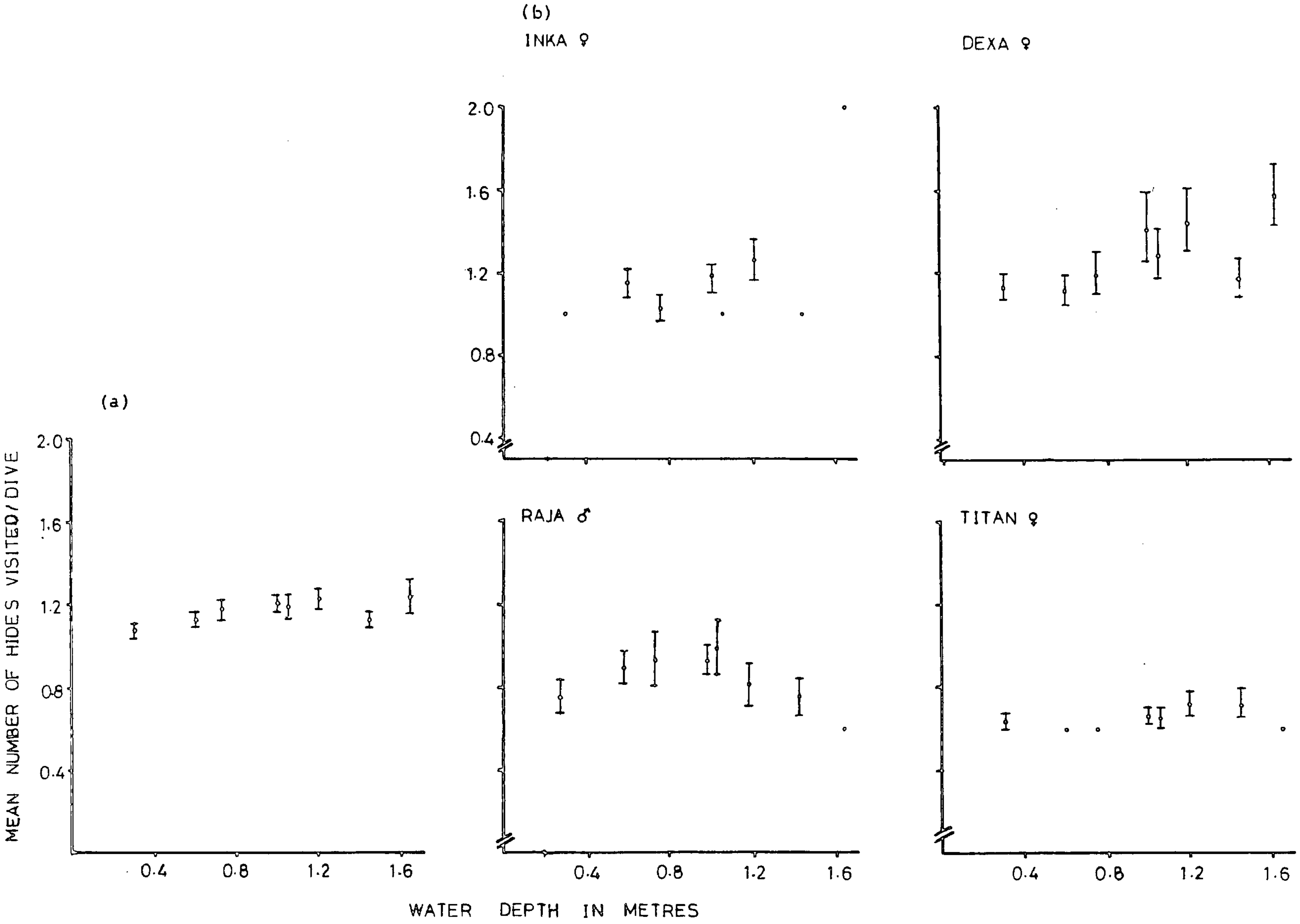
hv_n = number of hides visited during one unsuccessful dive at a given depth.

n^{hv} = total number of unsuccessful dives which visited a hide at that depth.

Fig. 3.10a illustrates the data for mean number of hides visited per unsuccessful dive for All Animals. The results of linear regression analysis, using all data, show that there is a significant positive linear correlation between the two variables for All Animals ($r = 0.10$, $df = 670$, $p<0.05$). However, the slope of the line indicates that for each one metre rise in water depth, the number of hides visited per dive increases by only 0.1 visits. The actual mean values at different depths vary only from 1.08 visits per dive to 1.24 visits per dive indicating that, for the most part, unsuccessful hide visit dives involve a visit to just one hide.

For the individual results (Fig. 3.10b), linear regression analysis for all data, shows that there is a significant linear correlation between the variables only for female Dexa ($r = 0.19$, $df = 179$, $p<0.01$), and the slope shows that number of hide visits will increase by roughly 0.2 for each one metre rise in depth. For the other individuals it again seems that there is no change in mean number of hides visited per dive with depth.

The most important point to emerge from this analysis is that the majority of unsuccessful dives involve a visit to just one hide.


(a)
(b)
INKA ♀
DEXA ♀
RAJA ♂
TITAN ♀
MEAN NUMBER OF HIDES VISITED/DIVE
2.0
1.6
1.2
0.8
0.4
0.4
0.8
1.2
1.6
WATER DEPTH IN METRES

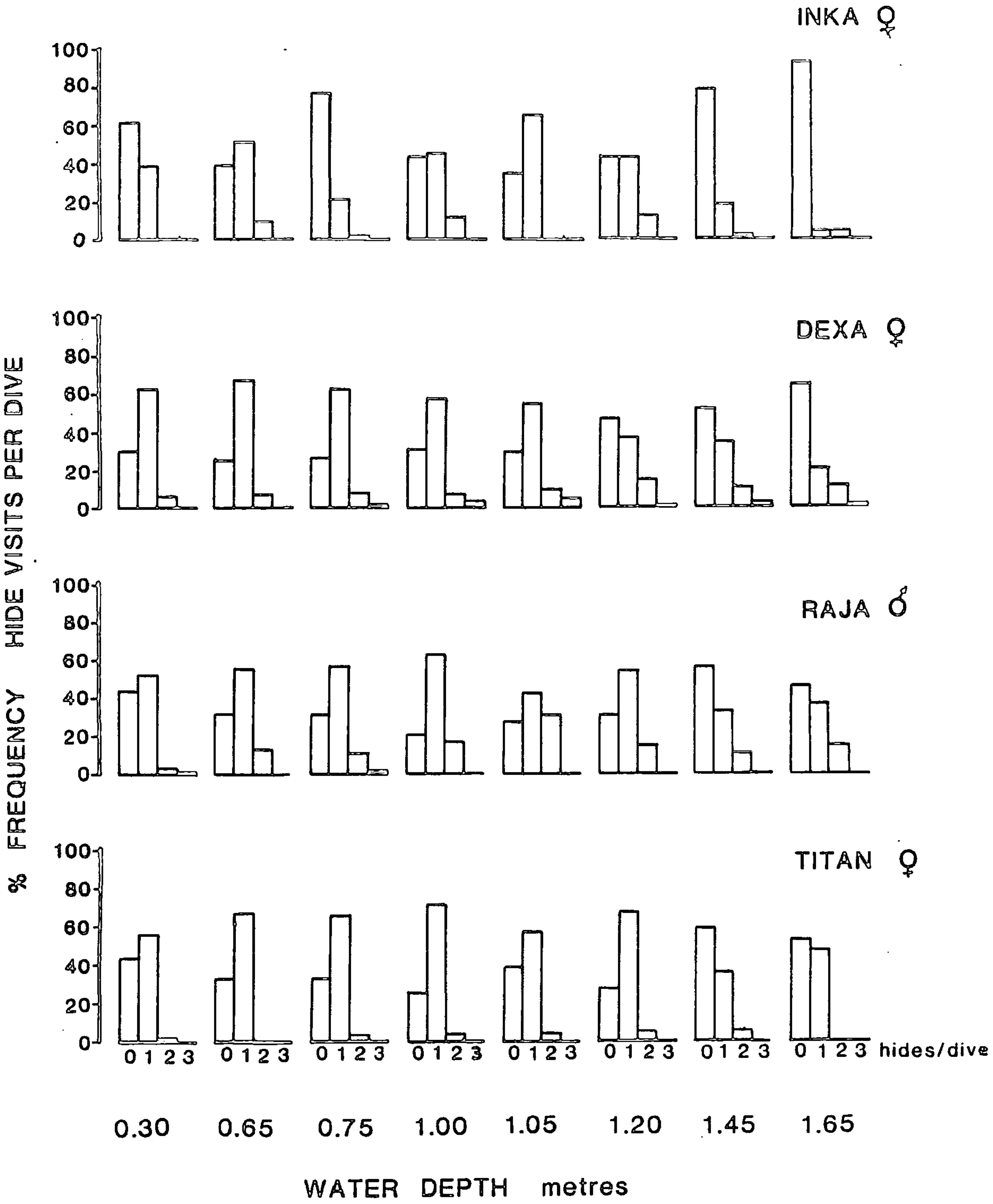
3.3.11. Frequency of hide visits within a dive

The inter-animal variability in mean number of hides visited per dive with depth is illustrated in Fig. 3.11 which shows the percentage frequency of dives visiting 0,1,2 and 3 hides per dive at the various depths for each animal. Data for successful, unsuccessful and non-hide visit dives have been combined. Several points emerge, firstly, in no dive were more than three hides visited. Secondly, despite great variation, both between animals and for the same animal at different depths, it can be seen that at least 25% of dives at all depths do not involve a visit to any hide. Thirdly, the majority of those dives involving hide visits, involve one hide only. The variation between animals can be easily seen, e.g. the female Dexa has a small percentage of dives in which three hides were visited at all depths greater than 0.75 m, whereas none of the other animals have any dives in which three hides were visited at depths greater than 0.75 m.

3.3.12. Mean time in hide

Although dive rate decreases sharply with depth, successful dive rate decreases much more slowly, from which it might have been expected that mink might alter their foraging strategy with depth and visit more hides per dive, i.e. increasing the opportunity of encountering prey. In view of the observed increase in time on bottom with depth, this would seem to be a logical assumption. However, the above analysis shows that whilst there is an indication that some animals may visit more hides per dive with depth, generally most dives involve a visit to one hide only. It is possible, therefore, that mink may be altering the efficiency of their hide-searching behaviour by searching individual hides more thoroughly as depth increases.

Data for unsuccessful hide visits only were analysed. For dives involving multiple hide visits, each occurrence of hide searching was treated as a separate event, i.e. if a dive


INKA ♀
DEXA ♀
RAJA ♂
TITAN ♀
% FREQUENCY HIDE VISITS PER DIVE
100
80
60
40
20
0
0 1 2 3
hides/dive
0.30
0.65
0.75
1.00
1.05
1.20
1.45
1.65
WATER DEPTH metres

involved two hide visits, the first unsuccessful, the second successful then the data relating to each visit were analysed under the appropriate category, thus, the data for the unsuccessful visit were not excluded from the analysis, even though overall the dive would have been scored as successful.

Mean time in hide for unsuccessful visits could be calculated for each individual at a given depth from:-

$$\bar{d}^{hs} = \frac{\Sigma\ d_1{}^{hs} + d_2{}^{hs} + ... d_n{}^{hs}}{n^{hs}}$$

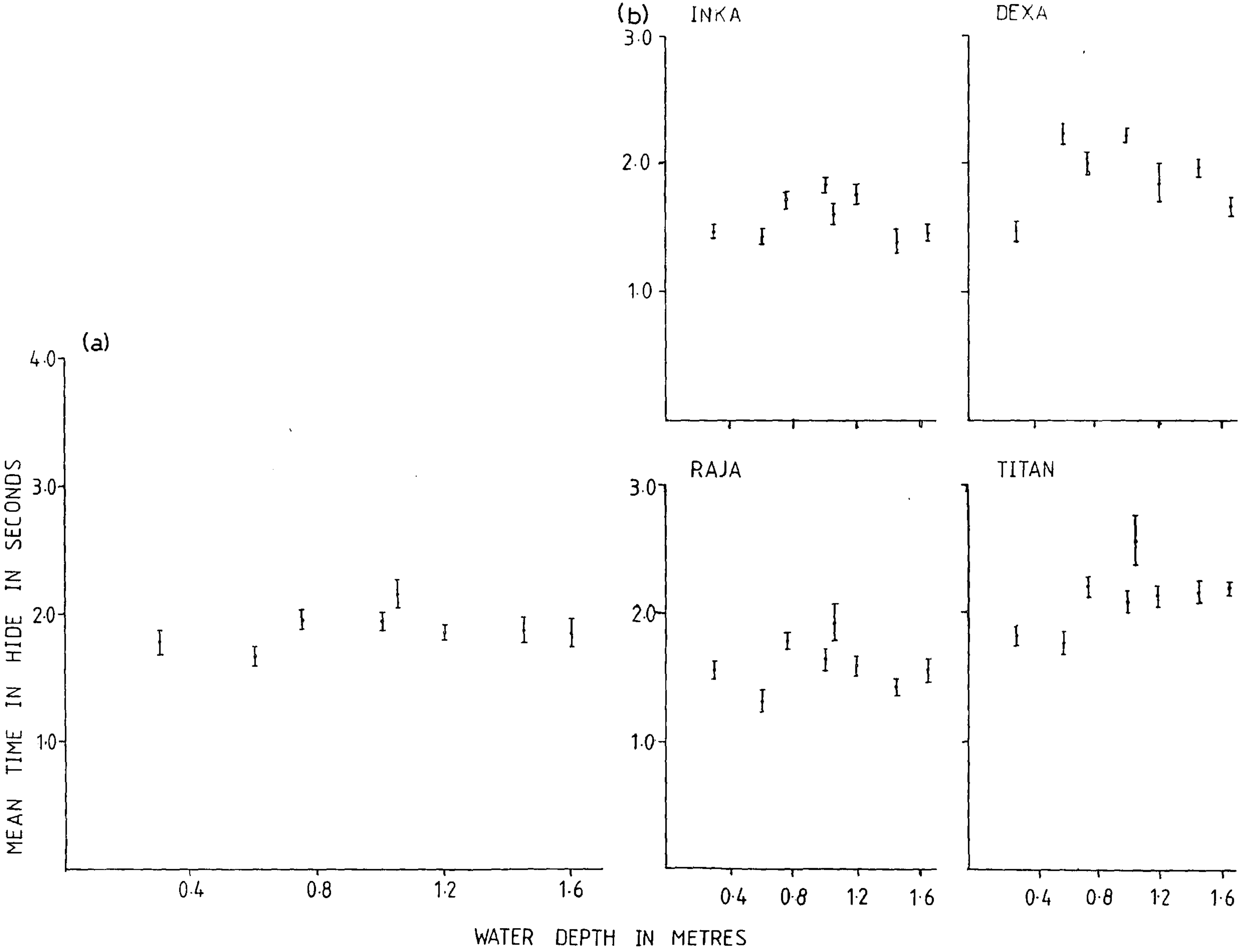
where $\bar{d}^{hs}$ = mean duration in seconds of unsuccessful hide searching for the individual at the given depth.

$d_n{}^{hs}$ = duration of each occurrence of behaviour, 'unsuccessful hide search', for the individual at the given depth.

n^{hs} = number of occurrences of behaviour, 'unsuccessful hide search', for the individual at the given depth.

The overall mean value for time in hide with depth (± S.E.) for All Animals could be calculated from the above by summing durations of each occurrence of behaviour hide search for all animals, divided by the total number of occurrences of behaviour hide search at the given depth.

Fig. 3.12a illustrates the results for mean time in hide for unsuccessful visits for All Animals. Linear regression analysis, using all data, shows that there is no significant linear relationship between the two variables. Thus, the slope of the line is not significantly different from the horizontal, and it appears that mean time in hide remains around the same value (approximately 2 s) for all depths. There is considerable individual variation, which can be seen from the results in Fig. 3.12b. From this, linear regression



(a)
4.0
3.0
2.0
1.0
MEAN TIME IN HIDE IN SECONDS
0·4
0·8
1·2
1·6
(b)
INKA
DEXA
RAJA
TITAN
3.0
2·0
1·0
WATER DEPTH IN METRES

analysis shows that there is a significant correlation between the variables only for female Dexa (r = -0.13, df = 249, p<0.05), where time in hide decreases by approximately 0.3 s per one metre rise in water depth. For the remaining individuals, there appears to be no change in mean unsuccessful time in hide with depth. In fact, generally, the values for mean time in hide are all between 1-2 s, with most around 1.5s, regardless of depth. Curvilinear analysis of all data for All Animals and individuals, showed that there were no significant results.

Thus, although time spent on bottom for unsuccessful dives increases with depth, animals, generally, do not seem to be showing any clear pattern of using this 'extra' time either to visit more hides per dive, or to search each hide visited for a longer period. Although female Dexa does appear to visit more hides per dive as depth increases, and to search each hide for a shorter duration. Since the durations involved are very small, e.g. mean time on bottom for an unsuccessful dive at depth 1.05 m is only 5.84 s, and mean time for an unsuccessful hide visit at that depth is 2.15 s, it is possible that changes are biologically, but not statistically, significant.

3.3.13. Proportion of time on bottom spent hide searching

The durations involved in activities such as 'hide searching' and 'time on bottom' are very small, a few seconds only. Since individual behaviour is so variable, it is possible that significant changes in these behaviours with depth are masked by this variability. It appears from Fig. 3.12 that the mean time to search an unbaited hide is roughly 1-2 s, regardless of depth. From Fig. 3.9, however, mean time on bottom for unsuccessful dives increases with depth, but from the overall results of the mean number of hides visited per dive with depth, it appeared (Fig. 3.10) that most unsuccessful dives visited only one hide. However, individual variation in all of these parameters was very great.

Thus, calculation of mean time on bottom spent hide searching with depth, may reveal significant changes in behaviour that would not otherwise be apparent.

The proportion of time on bottom spent hide searching was calculated for all unsuccessful hide visit dives, for each of the eight depths from:-

$$p^{tbh} = \frac{d_{hs1} + d_{hs2} + \ldots d_{hsn}}{d_{tb}}$$

where p^{tbh} = proportion of time on bottom spent hide searching.

d_{hsn} = duration of each bout of hide searching in a given dive.

d_{tb} = total duration of time on bottom for that dive.

From these data, a mean value of proportion of time on bottom spent hide searching (± S.E.) could be calculated for individuals and All Animals at the eight depths from:-

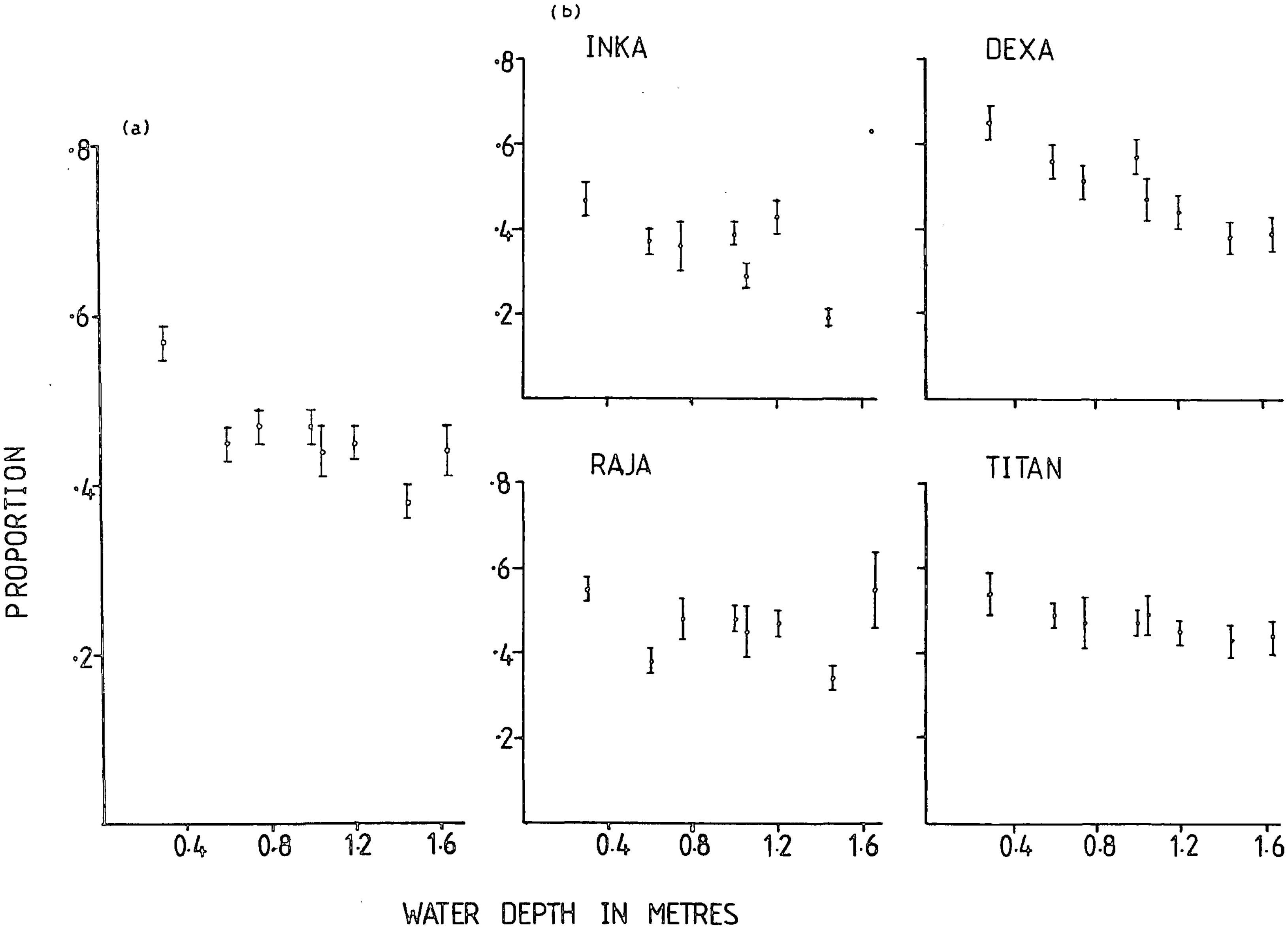
$$\bar{p}^{tbh} = \frac{\Sigma\, p^{tbh}}{N}$$

where $\bar{p}^{tbh}$ = mean proportion of time on bottom spent hide searching at a given depth.

$\Sigma\, p^{tbh}$ = sum of proportion of time on bottom spent hide searching for dives at a given depth.

N = number of dives at that depth.

Fig. 3.13 illustrates the data for All Animals and individuals for unsuccessful dives. Linear regression analysis of all data for All Animals shows that there is a significant negative correlation between the proportion of time on bottom spent hide searching and depth, ($r = -0.19$, $df = 660$, $p<0.001$), although as indicated by the very small value for slope, for each one metre change in water depth, the proportion of time on bottom spent hide searching falls by roughly 10%.


(a)
(b)
INKA
DEXA
RAJA
TITAN
PROPORTION
·8
·6
·4
·2
0·4
0·8
1·2
1·6
WATER DEPTH IN METRES

As with many of the results given previously there is great individual variation. When data for individuals are examined, it can be seen that there is a significant negative correlation for two of the females: Dexa ($r = -0.37$, $df = 176$, $p<0.001$), and Titan ($r = -0.15$, $df = 212$, $p<0.05$). For Titan, the decline in proportion of time on bottom spent hide searching with depth is approximately the same as that shown by the data for All Animals, but for Dexa, the decline is twice as great. For the two remaining animals linear regression analysis, and curvilinear analysis, indicated no significant correlation between the variables.

Thus, it appears that, generally, the proportion of time on bottom spent hide searching decreases with depth. This is perhaps not surprising in view of the fact that mean number of hides visited per dive and mean time in hide did not appear to alter with depth, although mean time on bottom increased markedly as depth increased. The question is, therefore, what are the animals doing with the extra time on bottom, as depth increases, if they are not visiting more hides per dive or searching individual hides for a longer time?

3.3.14. Distance travelled underwater

The method of calculation of distance travelled underwater in each dive, is outlined in Appendix II. The main point to note here is that the figures obtained are very approximate and must be interpreted with caution. From the figures for distance travelled in each dive, it was possible to calculate a mean value for each depth, for individuals and for All Animals from:-

$$\bar{d}_{tm} = \frac{\Sigma d_{tm}}{N}$$

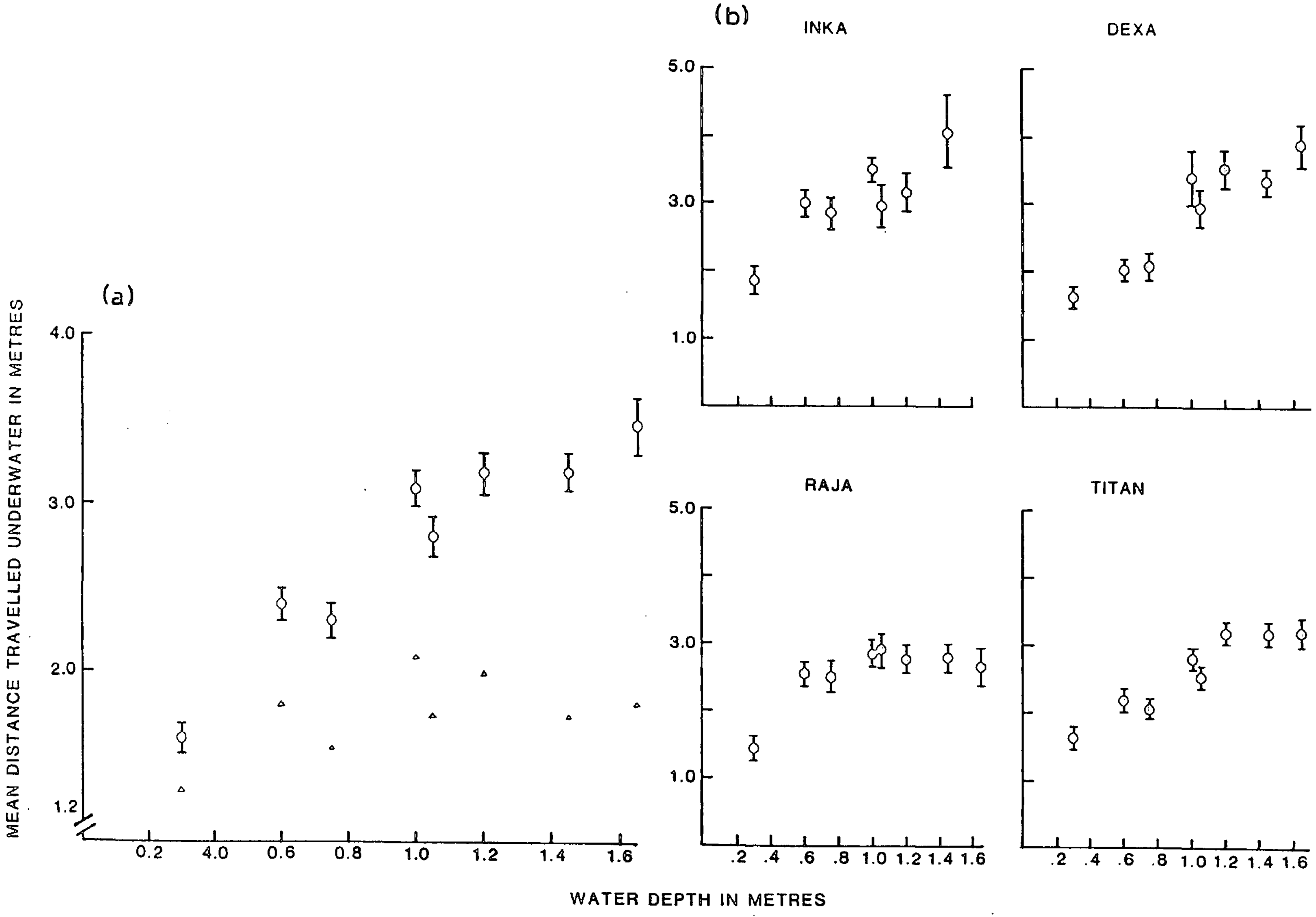
where $\bar{d}_{tm}$ = mean distance travelled at a given depth.

Σd_{tm} = sum of all values of distance travelled at that depth.

N = number of dives at given depth.

Data were analysed for unsuccessful dives only. Fig. 3.14 presents the data for mean distance travelled with depth for All Animals and for individuals. Data for All Animals shows that there is a significant linear correlation between the two variables ($r = 0.47$, df = 670, $p<0.001$), and distance travelled increases with depth. The same relationship holds for each individual: Inka ($r = 0.40$, df = 116, $p<0.01$), Dexa ($r = 0.56$, df = 179, $p<0.001$), Raja ($r = 0.39$, df = 157, $p<0.01$) and Titan ($r = 0.52$, df = 212, $p<0.001$). The slopes of the significant regression lines show that, for the male Raja, distance travelled per dive increases by approximately 1.2 m for each 1 m rise in water depth. For Titan, the increase is roughly 1.3 m, for Inka, 1.4 m and for Dexa, 1.8 m.

However, there is a problem with the interpretation of these results. Ideally, a study should have been done on distance travelled along the pool bottom, and not total distance travelled in each dive, to eliminate the fact that distance travelled might appear to increase with depth simply because the travel distance to the pool floor increased. It was possible to eliminate the distance travelled as an animal swam from pool bottom back to the surface at the end of a dive, but at the beginning of a dive the distance travelled through the water was estimated by calculation of a 'depth correction factor', (see Appendix II), which allowed for the fact that the computer recorded the distance travelled from a two-dimensional screen image, whereas the animals were hunting in a three-dimensional environment, and hence the 'real' distance travelled would be greater than the 'recorded' distance travelled by some factor which was related to the water depth. However, addition of a 'depth correction factor' means that it is possible that some of the observed


(a)
(b)
INKA
DEXA
RAJA
TITAN
MEAN DISTANCE TRAVELLED UNDERWATER IN METRES
4.0
3.0
2.0
1.2
5.0
3.0
1.0
0.2
4.0
0.6
0.8
1.0
1.2
1.4
1.6
.2
.4
.6
.8
1.0
1.2
1.4
1.6
WATER DEPTH IN METRES

increase in distance travelled with depth is an artifact, and can be related to the actual change in water depth itself. In an attempt to overcome this, using the data for unsuccessful dives only for All Animals, the actual depth of water was subtracted from the mean value of distance travelled, and these data are also presented in Fig. 3.14a. Again, this is not entirely satisfactory, since the depth correction factor was not simply a case of adding on the water depth. Linear regression analysis of these data shows that there was no significant relationship between mean distance travelled and depth.

Thus, it appears that as depth increases and time on bottom increases, some of this extra time may be used for searching the pool bottom. In those cases where animals do not seem to be travelling greater distances on the pool bottom as depth increases, the extra time may accrue because animals are swimming more slowly. Since speed and distance are not independent variables, and my calculations of distance travelled are not reliable, no attempt was made to investigate speed of movement at various depths.

3.3.15. Direct/Indirect dives

If an animal was able to easily locate a hide, it would be expected that it would swim straight to that hide, i.e. the animal would perform a 'direct' dive. Thus, dives which involved no turns were classed as 'direct', and those involving one or more turns were classed as 'indirect'. A 'turn' was defined as 'a deviation from the original path having an angular displacement of at least 30^{o}, sustained for a minimum of 0.5 m'.

Data were obtained from the plots produced from the Behpath data (see General Materials and Methods: Fig. 2.2). Where an animal visited more than one hide during a dive, the number of turns was scored only for the section of the dive leading to the first hide visit, and for this analysis only those dives which involved a hide visit were included, despite the fact that in many cases animals approached hides during dives but did not enter them. Data for successful and unsuccessful dives were combined since this analysis dealt only with location of the hide, and retrieval of a food reward from a particular hide during a dive would not be expected to influence hide location during that dive.

For each animal at a given depth, proportion of direct dives was obtained from:-

$$p^{Dn} = \frac{\Sigma\, n^{D}{}_{1} + n^{D}{}_{2} + \ldots\ldots d^{D}{}_{n}}{\Sigma\, n^{1} + n^{2} + \ldots\ldots n^{n}}$$

where p^{Dn} = proportion of direct dives for animal n at given depth.

$n^{D}{}_{n}$ = number of direct dives in trial n at a given depth.

n^{n} = total number of hide visit dives in trial n at the given depth.

An overall mean value for all animals at each depth could then be obtained from:-

$$\bar{p}^{D} = \frac{\Sigma\, p^{D1} + p^{D2} + \ldots\ldots p^{Dn}}{N}$$

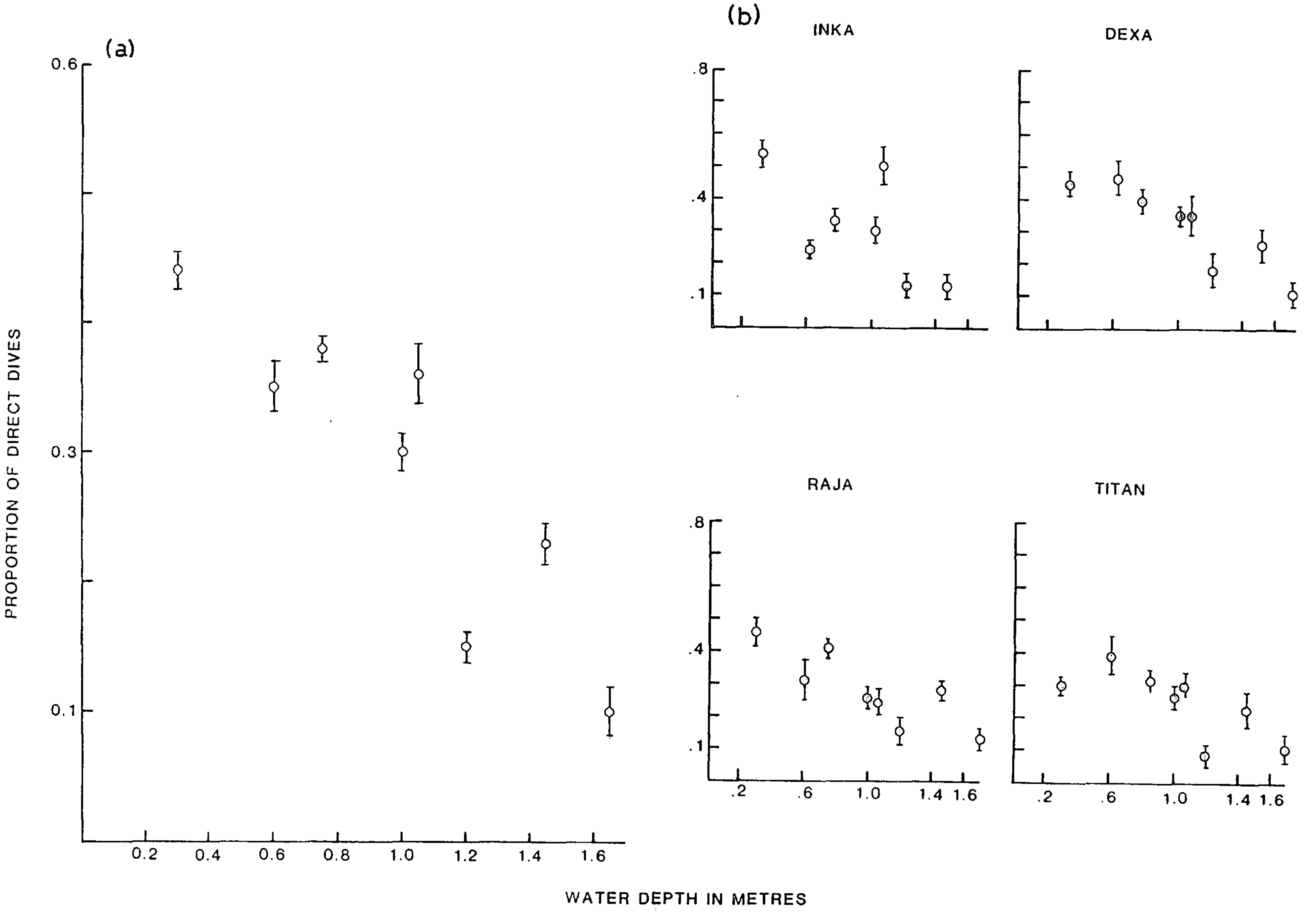
where $\bar{p}^{D}$ = mean proportion of direct dives at given depth.

p^{Dn} = proportion of direct dives for animal n at given depth.

N = number of animals.

By calculating mean proportion of direct dives in this way it was also possible to calculate the Standard Error.

The proportion of direct dives (Fig. 3.15) does show a significant decrease as depth increases ($r = -0.89$, df = 138, $p<0.001$), and the slope indicates that the proportion of direct dives drops by roughly a quarter of its value at 0.3 m depth, for each rise of 1 m in water depth. There is considerable variation between animals, and this can be seen when the individual results are studied. In all cases there is a significant negative correlation



(a)
(b)
PROPORTION OF DIRECT DIVES
0.6
0.3
0.1
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
WATER DEPTH IN METRES
INKA
DEXA
RAJA
TITAN
.8
.4
.1
.2
.6
1.0
1.4
1.6

between the variables, Inka ($r = -0.77$, $df = 34$, $p<0.001$), Dexa ($r = -0.90$, $df = 41$, $p<0.001$), Titan ($r = -0.74$, $df = 29$, $p<0.001$) and Raja ($r = -0.81$, $df = 29$, $p<0.001$). Generally, the slopes of the regression lines show that for individuals the proportion of direct dives also decreases by 20-25% for each metre rise in depth. However, for Inka, the decline is much steeper, being roughly 30% per 1 m of water depth.

One final point to note is that even at the shallow depths where proportion of direct dives is greatest, the results show that, generally, less than 50% of all hide visit dives are direct.

3.3.16. Mean number of Turns per dive

Another measure of the ease with which hides are located may be gained from an analysis of the mean number of turns per dive made during indirect dives. These data were obtained for each animal at a given depth from:-

$$td^n = \frac{\Sigma\, tt}{\Sigma\, n}$$

where td^n = mean number of turns per dive for animal n at a given depth.

tt = total number of turns recorded during indirect hide visit dives at given depth for animal n.

n = total number of indirect hide visit dives at the given depth for animal n.

Standard Error bars could also be calculated from these data. An overall value for mean number of turns per dive at a given depth could then be calculated, in a similar way, from:-

$$\overline{TD} = \frac{\Sigma\, tt^1 + tt^2 + \ldots tt^n}{\Sigma\, n^1 + n^2 + \ldots n^n}$$

where $\overline{TD}$ = mean value of number of turns per dive for all animals at a given depth.

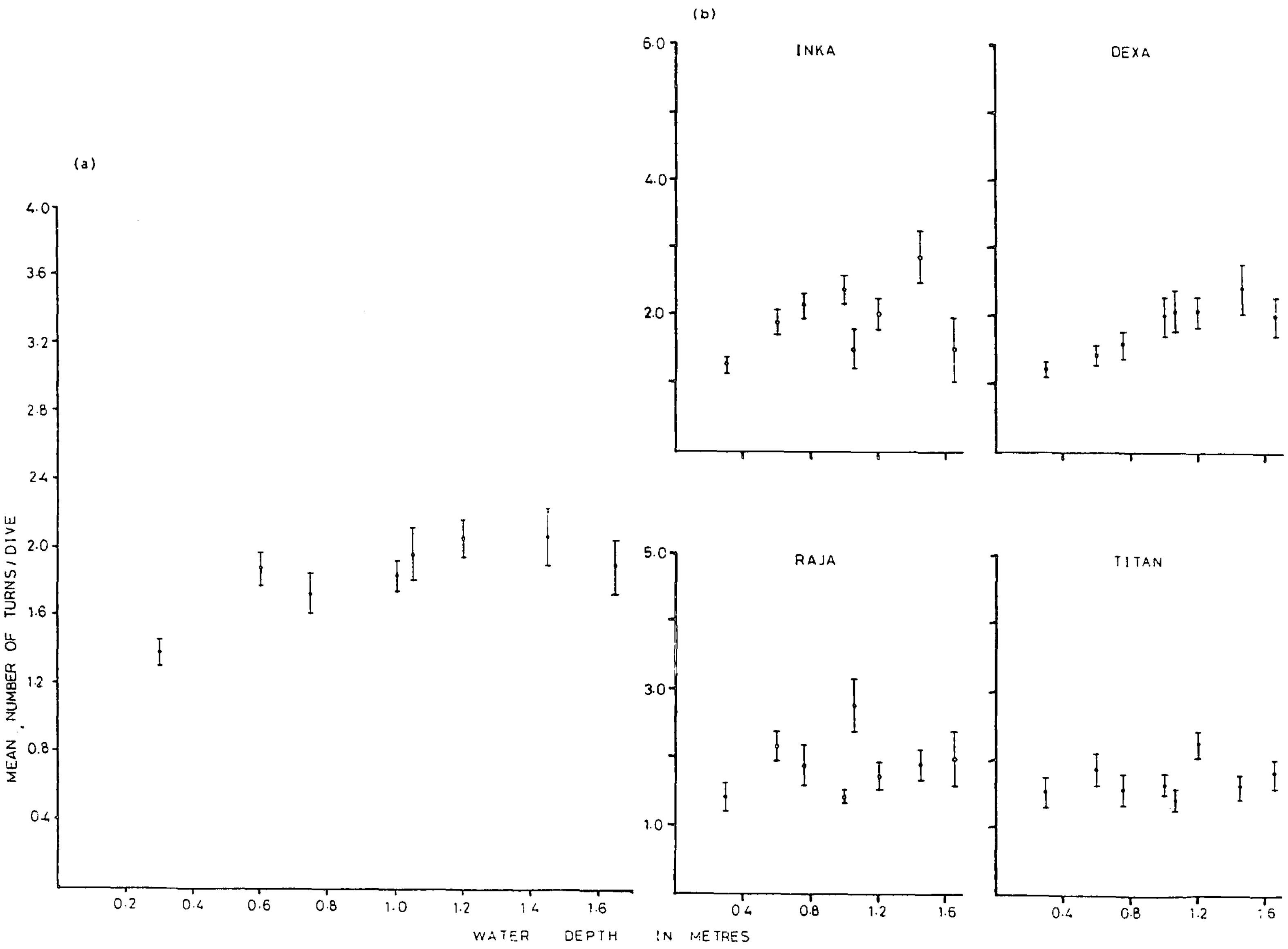
tt^n = total number of turns recorded for animal n at the given depth.

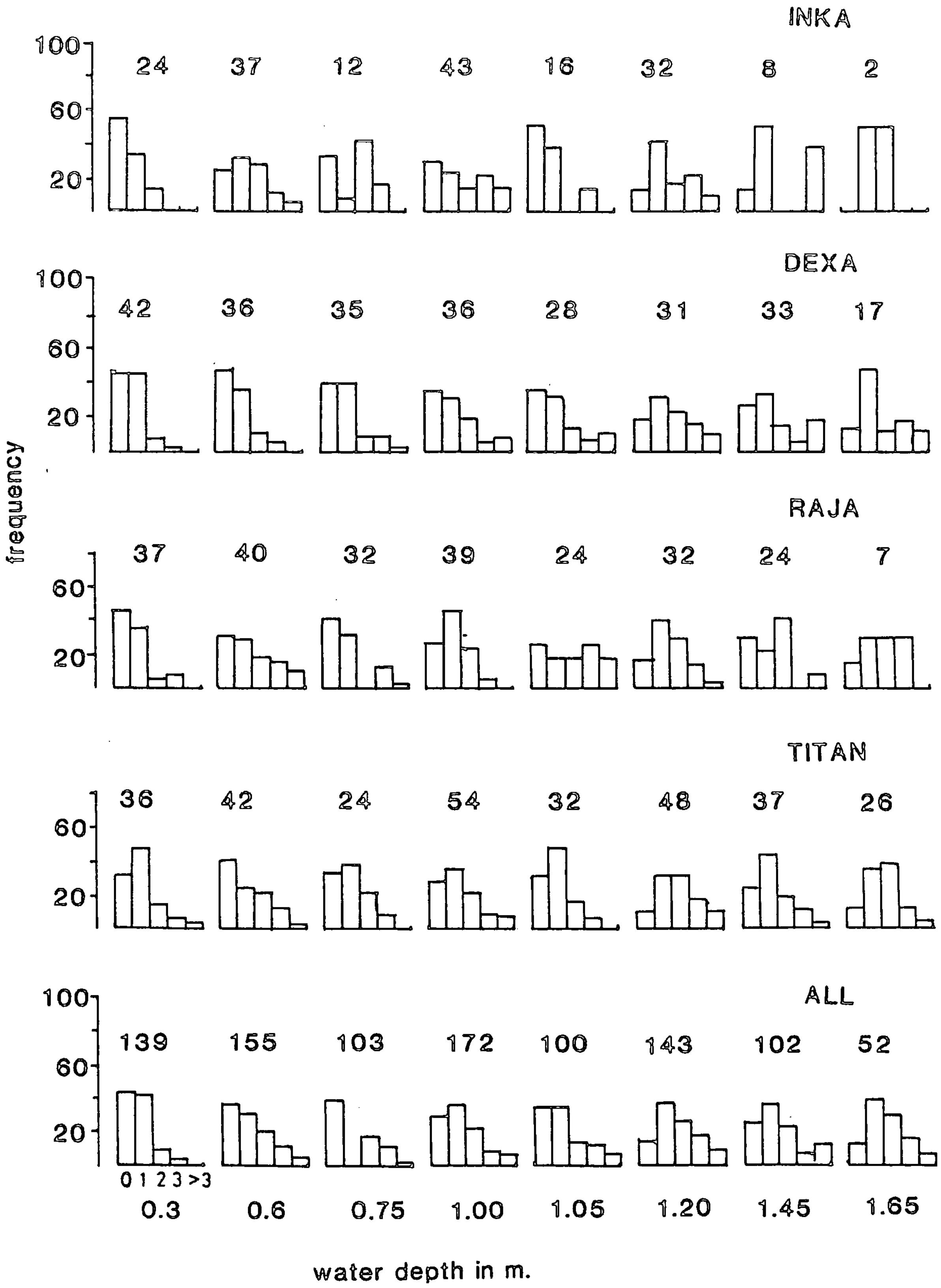
n^n = number of hide visit dives recorded for animal n at given depth.

Fig. 3.16 illustrates the data for mean number of turns per dive for All Animals and individuals. Linear regression analysis of all data for All Animals, (Fig. 3.16a) indicates that the number of turns per dive increases by roughly 0.4 turns for each 1 m rise in depth, ($r = 0.75$, df = 671, $p<0.001$). When the results of linear regression analysis on the data for individuals are examined, it can be seen that there is a significant correlation between the two variables in only one case, Dexa, where $r = 0.88$, df = 166, $p<0.001$, and here mean number of turns per dive increases by roughly 0.8 turns for each 1 m rise in water depth. From Fig. 3.16b it can be seen that for the remaining animals, mean number of turns per dive does not appear to vary with depth, and the mean is, generally, around 1.5 turns per dive, although there is some variability in the behaviour of a given individual at a particular depth.

This can perhaps be better illustrated in the form of a histogram of the percentage frequency of hide visit dives having no turns (i.e. direct dives) and those having 1, 2, 3 or >3 turns per dive. Fig. 3.17 presents these data for each animal at each depth, and for All Animals.

The histograms presented in Fig. 3.17 show that as depth increases, the % frequency of dives having two or more turns, generally, seems to increase, with a corresponding decline in the % frequency of direct dives. The great variability between individuals can be most easily seen if the % frequency of dives having more than three turns is examined,


(a)
(b)
MEAN NUMBER OF TURNS/DIVE
4.0
3.6
3.2
2.8
2.4
2.0
1.6
1.2
0.8
0.4
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
WATER DEPTH IN METRES
INKA
DEXA
RAJA
TITAN
6.0
4.0
2.0
5.0
3.0
1.0
0.4
0.8
1.2
1.6


INKA
100
60
20
24
37
12
43
16
32
8
2
DEXA
100
60
20
42
36
35
36
28
31
33
17
frequency
RAJA
60
20
37
40
32
39
24
32
24
7
TITAN
60
20
36
42
24
54
32
48
37
26
ALL
100
60
20
139
155
103
172
100
143
102
52
0 1 2 3 >3
0.3
0.6
0.75
1.00
1.05
1.20
1.45
1.65
water depth in m.

e.g. at the maximum depth of 1.65 m, 10% of Dexa's dives involved more than three turns, roughly 2% of Titan's dives involved more than three turns, none of Raja's dives involved more than three turns, and for Inka the maximum number of turns was two. The maximum number of turns recorded in a single dive was seven, for Dexa at depth 1.00 m.

Thus it is possible that the increased amount of time on bottom with depth reflects the fact that animals are less able to locate hides from 'out-of-water' as depth increases. Thus, the extra time available has to be used for hide location, rather than 'hide searching'. Although distance travelled underwater showed an increase with depth, it was not a very clear relationship, and it seems possible that instead of travelling farther underwater as depth increases, animals may well be travelling a similar distance but making more turns during the dive, and thus presumably swimming more slowly overall.

3.3.17. Revisiting of hides

The final parameter to be investigated was concerned with the underwater foraging strategy. In this experiment there were ten hides distributed equally between the two halves of the pool. Of these, only five were baited at the beginning of each trial, i.e. prey density was 50%. Food rewards were distributed in a random fashion and were not replenished during a trial. Thus, the greatest degree of success should be achieved if mink followed a foraging strategy whereby they did not revisit hides that had already been investigated. The question arises as to whether mink altered their foraging strategy with depth. This could be investigated by scoring the number of 'new' hides visited during a trial, as well as the number of 'revisits'. However, this would lead to certain biases, e.g. the first hide visited would always be new, and once ten hides had been visited, the probability that the next hide visit would be a revisit would be greater than 50%. Further, since the effect of depth was to be investigated this meant that the hide visits in each half of the pool must be considered separately. Initially, therefore, it was decided to examine the third hide visit in each half of the pool, since then there would be a 50:50 chance of that visit being to a 'new' or an 'old' hide. In order to obtain more data it was then decided to examine the second to fourth hide visit inclusive, in each half of the pool, for each trial. Visits were scored as being to 'new' hides or 'revisits' and the results, for individuals and for All Animals combined, are given in Table 3.9. The null hypothesis is that there is an equal chance, if animals are foraging randomly, of these visits being to either new or old hides. A Chi-Square analysis was carried out and the results are also given in Table 3.9.

From these results it can be seen that there is considerable variation in individual behaviour. In a few cases the data were insufficient for a Chi-square analysis to be carried out. Nevertheless, the first point is that, generally, the male Raja, seems to be foraging randomly, except at depth 1.45 m where he does seem to be actively searching new hides, and not revisiting. For the females, at the lower depths, (up to 0.75 m), they all appear to be foraging randomly. At the higher water depths however, individual differences become apparent. Inka appears to forage randomly regardless of depth. For the remaining two females, results were significant at depths 1.00 m and 1.20 m, and in all cases the strategy was one of searching new hides. When the data for individuals are combined, significant results are obtained for all but two depths, and in all cases the data suggest that animals do not revisit.

3.4. Discussion

Previous studies (e.g. Poole and Dunstone, 1976; Dunstone, 1978) have investigated the underwater predatory behaviour of the mink using live fish in small tanks with water at fixed depths of either 0.45, 1.00 or 1.5 m depending on the experiment, but as far as is

Table 3.9: Number of new hide visits and revisits for 2nd to 4th hide visit in each half of the pool, in each trial.

Water Depth		INKA	DEXA	RAJA	TITAN	ALL
	N	9 (6)	16 (11.5)	9 (6.5)	9 (7)	43 (31)
0.30	R	3 (6)	7 (11.5)	4 (6.5)	5 (7)	19 (31)
	χ^2	3.00	3.52	1.92	1.14	9.29
		p=ns	p=ns	p=ns	p=ns	$p<0.01$
	N	9 (9)	15 (10.5)	9 (9)	11 (9)	44 (39)
0.60	R	9 (9)	6 (10.5)	12 (10.5)	7 (9)	34 (39)
	χ^2	0.00	3.86	0.43	0.89	1.28
		p=ns	p=ns	p=ns	p=ns	p=ns
	N	4 (-)	15 (10)	10 (6)	8 (13)	37 (26)
0.75	R	3 (-)	5 (10)	2 (6)	5 (13)	15 (26)
	χ^2	-	5.00	5.33	3.85	9.31
			p=ns	p=ns	p=ns	$p<0.01$
	N	18 (15)	22 (13.5)	10 (9.5)	24 (15)	74 (53)
1.00	R	12 (15)	5 (13.5)	9 (9.5)	6 (15)	32 (53)
	χ^2	1.20	10.70	0.05	10.80	16.64
		p=ns	$p<0.01$	p=ns	$p<0.01$	$p<0.01$
	N	7 (11)	8 (8.5)	9 (6)	11 (7.5)	30 (25)
1.05	R	4 (11)	9 (8.5)	3 (6)	4 (7.5)	20 (25)
	χ^2	2.91	0.06	3.00	3.27	2.00
		p=ns	p=ns	p=ns	p=ns	p=ns
	N	11 (12.5)	20 (13.5)	15 (11)	22 (14.5)	68 (51.5)
1.20	R	14 (12.5)	7 (13.5)	7 (11)	7 (14.5)	35 (51.5)
	χ^2	0.36	6.26	2.91	7.76	10.57
		p=ns	$p<0.05$	p=ns	$p<0.05$	$p<0.01$
	N	4 (-)	21 (13)	12 (6.5)	16 (10.5)	53 (32.5)
1.45	R	1 (-)	5 (13)	1 (6.5)	5 (10.5)	12 (32.5)
	χ^2	-	9.85	9.31	5.76	25.86
			$p<0.01$	$p<0.01$	p=ns	$p<0.01$
	N	1 (-)	12 (7.5)	4 (-)	11 (8)	28 (18.5)
1.65	R	1 (-)	3 (7.5)	0 (-)	5 (8)	9 (18.5)
	χ^2	-	5.40	-	2.25	9.76
			p=ns		p=ns	$p<0.01$

N = number of new hides visited.
R = number of revisited hides.
(n) = expected number for Chi-square test.
df = 2

known this is the first study to investigate the specific effect of various water depths on the underwater foraging behaviour of the mink.

Before discussing the results obtained it is first necessary to discuss the reasons behind aspects of the experimental regime, e.g. prey type, trial length etc. As explained previously (2.3) the prey used was 5 g pieces of eel hidden inside wooden 'hides'. The use of 'non-living' prey items meant that any changes noted in the foraging behaviour of the mink could be related to changes in the foraging environment, and were not a response to changes in the behaviour of the prey. Poole and Dunstone (1976) found that the hunting behaviour of mink was highly organised in respect of prey behaviour, whilst that of the prey species used (goldfish, *Carassius auratus*) was more unpredictable. They tested three different prey species and concluded that their vulnerability to predation may be linked with previous experience of predators. Finally, the authors found that mink were aided by the fact that they tended to locate prey from out of water, and that an important stimulus for eliciting diving behaviour in the mink was movement of the fish.

The point thus arises that in this study mink were expected to dive to a stationary target, a hide, and search it for a food reward, i.e. the targets did not move so an important stimulus for eliciting diving behaviour was not present. But, Poole and Dunstone (1976) also noted that mink would spontaneously retrieve inanimate objects and dead fish from the tank, and in fact it was found to be relatively easy to train young mink to perform the required task. Thus, it was possible to investigate the diving behaviour of the mink under changing environmental conditions without complications of changes in the prey behaviour. Finally, mink have been observed to use 'hide searching' on land, in the wild (Birks and Dunstone, 1985) when they enter confined spaces, e.g. rabbit burrows, where prey are likely to be hiding. Previous experiments by Dunstone (1978) and Dunstone and

O'Connor (1979a) have also examined the underwater behaviour of mink with live prey when 'hides' or 'refuges' have been provided, and mink were observed to readily enter confined spaces underwater in the search for prey.

For this experiment, ten hides were distributed throughout the pool (see 3.2.3.). For recording data on the behaviour of the mink, it was decided to test each animal once daily for a period of 10 min beginning when the animal had been released in the pool, or until 20 dives had been completed, whichever was soonest. The reasons for choosing a time limit of 10 min were twofold. During training it was noted that mink would often make the first dive within seconds of being released in the pool. Subsequent dives would follow rapidly for a few minutes and then animals would rest and eat any 'prey' items. After 30 min in the pool animals generally either gave up foraging and rested, or else tried to escape from the pool. Thus, training sessions lasted for a maximum of 30 min. Experimental sessions were shorter, mainly due to constraints on the number of videotapes available for recording data, and the length of time required to transcribe the recorded data onto the Apple microcomputer. A session length of 10 min was selected, as most animals performed at least 10 dives during that period. It was further decided that for each presentation of each water level, an overall minimum number of 25 dives would be recorded for each animal, as this would yield a fairly large sample size. (However, this did mean that the number of dives recorded for each depth would be unequal, see Table 3.5). Thus, a second constraint was added to the timing of trials, namely, if an animal performed at least 20 dives its trial was terminated even if the 10 min limit had not been reached. This ensured that all animals received at least two trials under any given set of conditions. This was to ensure that any changes in behaviour observed under these conditions were consistent, i.e. they represented a 'real' change in behaviour and were not the result of the animal being hungry, excited etc. For example, external noises did affect the animals, and on several occasions, particularly with the female Inka, trials were terminated because low-flying aircraft or other loud external noises had caused her to adopt the 'alert' posture for several minutes. Stephenson et al. (1988) for example, note that heart rate was reduced in response to loud noises when mink at Durham University were engaged in non-aquatic, exploratory or hunting activity, and suggest that this may be a fear bradycardia. In any event, this illustrates that animals could be easily disturbed and diving behaviour disrupted. Nevertheless, the four animals did, for the most part, complete the required number of dives (see Table 3.3.) and data were collected on a total of 1825 dives for the four animals over eight water depths.

Dunstone (1978) showed that mink foraging for live fish would concentrate their search effort into the area of a successful capture or attempted capture. There was thus a possibility of mink learning the prey distribution and altering their behaviour accordingly. In the present experiment the aim was to investigate changes in the mink's behaviour in relation to water depth, and hence the prey density was kept constant. However, unlike Dunstone's (1978) experiments, the prey involved here was static (eel pieces in hides), although in his case the position of refuges did remain fixed. There was thus an even greater chance here that mink could learn the distribution of prey. In an attempt to counter this, both the position of hides, and which hides were baited, were varied for each trial of an individual, and the position of entry of the individual to the pool was varied with each trial.

The results obtained during this study will now be briefly summarized and their relevance to the mink's foraging abilities in the wild, and to theoretical predictions of foraging behaviour, will be discussed. It has been suggested that mink belong to a class of foragers termed 'hunters', i.e. they have to actively search for and then pursue prey.

Their predatory behaviour would therefore be considered to be limited by the predator's speed, stamina and the element of surprise, but mink hunting underwater would be further constrained by the fixed limit to the time they can spend underwater, either searching for, or pursuing, prey (Dunstone, 1978). Data from recent physiological studies, both on mink and diving birds will be examined and its relevance to the observed changes in underwater foraging behaviour assessed.

The results of the investigation into the effect of depth on the foraging behaviour of the mink can be divided into two categories. Firstly, gross changes of behaviour in relation to depth were examined by analysis of mean dive rate, mean hide visit dive rate and mean successful dive rate, under any given condition. Secondly, more subtle changes in behaviour could be investigated by examining what mink did during each dive, i.e. what were the changes in total dive duration, number of hides searched per dive, distance travelled and so on, at a given depth. An important point to note here is that Analysis of Variance tests were used to examine the interactions between variations in dive duration, distance travelled and speed, in relation to Depth, Animal and Series Order (Tables 3.6-3.8) under differing conditions of foraging success (i.e. successful dives, unsuccessful dives and non hide visit dives).

The results indicated that, generally, Animal and Depth factors significantly affected the dive duration and distance travelled, but the order in which depths were presented was unimportant. Data for All Animals were lumped, despite the indications that variation in individual behaviour had an important effect. It is possible that these variations were the result of differences between the sexes, since mink are highly dimorphic in size. However, since the animals used were three females and one male, it was not possible to analyse on the basis of sex. Instead, data for All Animals were combined to see if general trends could be established. Data for individuals were therefore included only for comparison.

With regard to gross changes in behaviour, it was found that dive rate declined sharply with increasing water level (Fig. 3.2). At the deeper water levels, animals were performing fewer dives per min and hence there was the possibility that their success rate per min would also decline. In fact, although there was a significant negative linear correlation between successful dive rate and water depth (Fig. 3.2) for All Animals, the slope (-0.06) shows that the decline in success rate is very slight, a decrease of roughly one dive per 20 min as water level increases from level I to level IV. Among the individual results, only that for Titan did not show a significant linear correlation between successful dive rate and depth (Fig. 3.2b). The actual values for successful dive rate were very low, less than 0.5 dives per min, even though ten hides were provided, of which five were baited. However, low capture efficiency has been demonstrated in other studies, e.g. Dunstone (1978) investigated the fishing strategy of mink when either 1,5,10 and 15 fish were available, with four hides for the fish. He found that in only five out of 515 visits did the predator manage to capture fish within one of the refuges, despite the fact that fish tended to 'hide' from the predator and the mink thus benefitted from the element of surprise. However, mink did not necessarily visit hides within each dive. Many dives (42% of the total over all depths) involved searching of the pool floor only, and since all prey items were located within hides, there was no possibility of these being successful.

There was a sharp decline in the rate of hide visiting dives with water level as depth increased for All Animals, (Fig. 3.3). The slope of the regression line was -0.31, compared to a slope of -0.54 for dive rate, indicating that hide visit dive rate did not fall in step with dive rate. This implies that there is a change in the proportion of dives visiting a hide with depth. Thus, at the greater depths a larger proportion of dives visit hides. This might be expected to affect the degree of foraging success which animals could achieve, and indeed the result for successful dive rate does indicate this, since, despite a fall in both overall dive rate and hide visit dive rate, successful dive rate declines only slowly with depth. Results for each individual also showed significant negative linear correlations for mean rate of hide visiting with depth (Fig. 3.3b).

Because of the way data were collected, diving rates could only be related to water levels, and not to the true water depths, (see 3.3.4). All subsequent analyses did not involve consideration of the time spent in each half of the pool, so data could be related to actual water depth.

From the above discussion, it would be expected that the proportion of dives visiting hides would be significantly correlated with depth, results (Fig. 3.4a) show a significant negative linear relationship only for the female Dexa, but a possible curvilinear relationship could be seen in other cases. Significant results using curvilinear analysis, were obtained for All Animals and Titan. In both cases it appears that, at the lower depths (from 0.3 m to 1.0 m),the proportion of dives visiting hides increases, but after depth of 1.0 m it decreases again, i.e. the best fit is a quadratic curve.

A final indication of gross changes in behaviour was obtained from an analysis of the proportion of successful to total dives. A difference in the proportion of successful dives was expected at the various depths, since overall dive rate declined steeply with depth, but successful dive rate declined very slightly. The results for the combined data (Fig. 3.5a), showed that there was a significant positive linear correlation between the proportion of successful dives and depth. Individual results showed two significant positive linear correlations, for the female Inka and the male Raja. In both cases proportion of successful dives increased by roughly 25% for each metre increase in water depth. This was roughly twice the rate observed for the combined results. However, many trials (17.8%) were completely unsuccessful, and these would obviously contribute to the low mean values. Prey density was 50% and food items were randomly distributed in hides throughout the pool, and the large number of trials which were unsuccessful is surprising. More detailed analysis of the foraging strategies employed by mink at various depths may lead to an understanding of this phenomenon.

It is, thus, apparent that there are gross changes in foraging behaviour occurring with increasing depth. Animals are making fewer dives overall as depth increases, the proportion of these dives which visit hides, generally, increases (until depth 1.0 m) and then declines. However, the proportion of successful dives, generally, increases with depth. The next step is to investigate the more subtle changes in behaviour of animals within a dive to see how this could be achieved.

Most of the subsequent analyses were carried out to investigate how depth affected the underwater foraging behaviour of the mink, and specifically how foraging success and efficiency were affected. Data for dives which did not involve hide visits were therefore excluded, since these dives could not possibly have been successful. Furthermore, Analysis of Variance tests (see 3.3.1) had shown that foraging success had a significant effect on such factors as dive duration, so data for successful and unsuccessful hide visit dives were, for the most part, analysed separately.

Linear regression analysis of unsuccessful dive duration showed that there was a very strong positive correlation between duration and depth for All Animals and individuals. For successful dives a similar result was obtained, namely a strong positive linear correlation with depth. Since successful dives will be terminated once a food reward is obtained, it is of interest that there are positive correlations between successful dive duration and depth. This implies that the correlation may be due to the fact that as depth increases, so the travel time to reach the bottom of the pool will also increase. Thus, the significant correlations between both successful and unsuccessful dive durations may be artifacts, and be simply a function of the changes in water depth.

It was also noted that mean successful dive durations were significantly shorter than the equivalent mean unsuccessful duration at any given depth, (see 3.3.8). This is not unexpected, since successful dives are terminated once a food item is obtained, whereas unsuccessful dives would be expected to be prolonged to maximize encounter rate with prey. In this study, however, mink have the additional constraint that they are air-breathing mammals hunting underwater. Thus, it is expected that there must be some balance between extending dive duration to maximize encounter rate and the physiological limitations of oxygen demand (Dunstone, 1978). This point will be considered in more detail in the General Discussion, where results from all experiments will be considered. Furthermore, mean successful dive durations tended to be only about 0.5 to 1.5 s shorter than mean unsuccessful durations. This is possibly due to the small number of hides (ten) and prey items (five), such that even for successful dives, animals may have been nearing their dive duration limit, before encountering prey. Hence, it would not be expected that animals would be able to increase their dive duration with increasing depth. Nevertheless, this is the case, and implies that at the lower depths, animals are making shorter dives than would be expected. It is possible that this is related to physiological constraints and will also be discussed more fully below, but, generally, from the results so far examined it would appear that at low depths animals adopt the strategy of many, short dives, but at greater depths they make fewer dives of longer duration. This implies that at the greater depths, animals are able to forage for a longer period in each dive. Thus, they are potentially able to search more of the pool floor or search more hides and this might explain why the successful dive rate decreased more slowly with depth, despite the fact that hide visit dive rate declined markedly. The question arises as to whether the dives at greater depths do allow the animals more time for underwater foraging, or whether the observed increases in mean dive duration are merely a reflection of the increased amount of time required to dive to greater depths.

To answer this, data for time on bottom during unsucessful dives were analysed, to reveal that there was a positive linear relationship between time on bottom and depth for unsuccessful dives for All Animals. The relationship also holds for the three females, but for the male Raja, the line of best fit was a quadratic curve, with a peak approximately at depth 1.0 m. Thus, it appears that for unsuccessful dives for females there is a real increase in the amount of time available underwater for foraging as depth increases. For the male, this is true up to depths of 1.0 m, but thereafter foraging time available declines.

The main point to emerge is that, generally, at greater depths mink are capable of extending the time spent foraging underwater. The next question is whether the mink are using this 'extra' time to employ different foraging strategies to make the most efficient use of the available foraging time. Thus, there may be subtle changes in behaviour as depth increases, e.g. animals may search more hides per dive, or they may search each hide for a longer period to ensure that a prey item is not overlooked etc. The results of analyses on such items will be discussed below. Dunstone (1978) defined efficiency for mink hunting underwater as either, the number of successful searches to total number of searches, or, as the number of pursuits to total number of searches.

Dunstone's experiment was different from the present study in that mink were hunting live fish. Prey items had to be located either from out of water, or underwater (search phase of dive), and then pursued and captured (pursuit phase of dive). In this study, mink had to locate stationary hides, again either whilst out of water or when underwater during a dive, (search phase). They then had to open a hide and investigate it to see if there was a prey item. Strictly speaking this must also be included as 'search phase'. There is thus no true 'pursuit' phase during successful hide visit dives, unless the very short time required for animals to remove the bait from the back wall of the hide is considered as such. However, it was not possible to actually measure how long this behaviour took, so effectively dives during this experiment consisted of a search phase only. Dunstone's definitions can, however, be modified to give a measure of efficiency that is applicable to this study. Thus:-

$$E = \frac{\text{number of successful dives}}{\text{total number of dives}}$$

This would give an indication of gross changes in searching efficiency with depth. The results (Fig. 3.5) actually showed that, for All Animals, there was a linear increase in the proportion of successful dives with depth. Individual results showed that the same was true for one female and for the male, (Fig. 3.5b).

However, many hide visit dives actually involve visits to more than one hide. In the case of a successful dive visiting, say, three hides, only the last visit would actually be successful. The dive would be scored as successful, but the actual amount of searching behaviour carried out before this success was achieved, is not made apparent. It would seem therefore, that a better idea of searching efficiency under different conditions could be obtained by examining the ratio of the number of successful hide searches (S+), to total hide searches (St).

However, unlike Dunstone (1978) who calculated the S+/St ratio using all the data for the two animals tested under the same conditions, in this study, Analysis of Variance on data for dive duration (Table 3.5) had revealed that an individual might be behaving differently in separate trials under the same conditions. Thus, it was decided to calculate a value for efficiency (the S+/St ratio) for each trial of an individual at any depth, and to then obtain a mean value ± Standard Error to get some idea of variation in behaviour both for a given individual and between animals. The results (Fig. 3.6a) for All Animals show that there is a significant positive linear relationship between the proportion of successful hide visits to total number of hide visits as depth increases, although the mean values varied only between 22% (at 0.65 m) to 39% (at 1.45 m). There is much individual variation (Fig. 3.6b), and one interesting result is that amongst individuals it is only the male Raja whose results show a significant positive linear correlation between this measure of efficiency and depth, whereas for the females it appears that there are no significant linear changes in efficiency with depth. Further, results of curvilinear analysis using $(\text{depth})^2$ and $(\text{depth})^3$ showed no significant correlations between the two variables.

This is a very interesting result, since dive rate (Fig. 3.2) was shown to decline with water level. Also, the proportion of dives visiting a hide did not vary in a linear fashion with depth, (except for female Dexa, where there was a significant negtive correlation), i.e. at depth 1.65 m roughly 40% of dives visited hides, (Fig. 3.4), but at this depth the mean dive rate was only 1 per min, compared to over 2 per min at the shallowest depth (Fig. 3.2), where a mean of just under 60% of dives visited hides. Thus, at the greater depths, it would seem that there would be fewer opportunities (per min) for success, i.e. fewer dives overall and no real increase in the proportion visiting hides. Despite this, the ratio of S+/St remains similar across depths, and indicates that mink are probably altering their foraging strategy in some way, such that overall their foraging efficiency does not deteriorate. Kruuk et al. (1985), found that for otters hunting off the coast of Shetland, the percentage of dives which were successful, actually increased as depth varied from 1-10 m. They related this increase to the fact that otters spent longer on the bottom as depth increased. But, they also found that success varied with dive duration, irrespective of depth. Their conclusion was that for dives of duration greater than 25 s, otters were altering their fishing strategy in some way.

One way in which mink could potentially increase their foraging success, is to use the extra time on bottom for searching more hides. The results, for All Animals, (Fig. 3.10a) do indicate that the number of hides visited per unsuccessful dive did increase with depth. Individual results (Fig. 3.10b) showed no change in number of hides visited per dive with depth, except for female Dexa, where there was a significant positive linear correlation. There is considerable individual variation, but the general conclusion is that, in the majority of cases, dives involved a visit to one hide only, at all depths.

It can be seen from Fig. 3.11, that at all depths, at least 25% of dives did not visit hides, no dive involved visits to more than three hides, and most dives which did visit hides visited just one.

Thus, the question remains as to what mink are using the extra time on bottom for, at the greater depths, and how are they managing to maintain their efficiency ratio at around 30%, when the proportion of dives visiting a hide, generally, decreases after depth 1.0 m, and the mean number of dives per min also declines with depth. Since the measure of efficiency is a ratio, this implies that the proportion of hide visit dives which are successful is constant over depth, but in fact for All Animals, Inka and Raja there were significant positive linear correlations (Fig. 3.5). However, prey density was constant throughout the experiment, and bait was distributed at random. If all dives involve random visits to hides, it might be expected that at the greater depths, (more than 1.05 m), overall fewer hides will be visited, and it might be expected that, by chance, fewer hide searches would be successful. Since this does not seem to be the case, (Fig. 3.6), the conclusion is that mink are adopting a different hide searching strategy at the greater depths. An analysis of data on revisiting of hides (Table 3.9) showed that there were considerable individual differences. For the three females, it appears that at depths below 0.75 m, foraging is random, i.e. there was an equal chance that animals would search a new hide or revisit a previously investigated hide. At the greater depths, the results for Inka, showed that foraging continued to be random, but for the other two females, there was a shift towards a strategy of searching new hides. For the male Raja, the only significant result was obtained at depth 1.45 m, and again this indicated a non-revisit strategy. When the combined data were studied, results were significant for all but two depths (0.60 m and 1.05 m) and in all cases, results pointed towards a non-revisit strategy. Thus, at the greater depths, it seems that animals may be more selective about which hides to visit, and may avoid revisiting hides. This strategy would enable them to make the best use of the limited number of foraging opportunities (i.e. dives) at the greater depths.

Of course, foraging success at the greater depths could also be increased, if dives involved visits to more than one hide, and there was no revisiting between dives. The results for mean number of hides visited per dive (Fig. 3.10) however, suggest that, generally, the majority of dives, even at maximum depth, visit only one hide. It is possible that at the greater depths, animals may search each hide more thoroughly, and time in hide would increase with depth. This might also account for the increase in time on bottom with depth. However, the results for unsuccessful dives, (Fig. 3.12) show that there was no significant correlation between the two variables for All Animals, thus indicating that, in fact, there was little change in time in hide with depth. Individual animal data gave a similar picture, except for Dexa, where there was a significant negative linear correlation.

Thus, it does not seem that the additional time available for foraging at the greater depths is used to investigate each hide visited more thoroughly and at the lower depths, e.g. 0.3 m, in 19 out of 138 hide visit dives, animals searched a hide that was known to be baited and failed to retrieve the food, and at the maximum depth of 1.65 m it was found that 15 out of total of 56 hide visit dives failed to retrieve food from baited hides. This certainly does not lead to the assumption that hides are being searched more thoroughly at greater depths.

Thus, it seems possible that the relatively consistent success rate achieved by the mink over all depths may in part be due to a tendency to search more hides per dive as depth increases, and to a switch from random searching, to a strategy of not revisiting hides that have already been searched. Thus, although dive rate declines with depth, if an animal obtained five prey items per trial at shallow depths, (where dive rate was roughly two per min, Fig. 3.2), and only two prey items per trial at maximum depth, (where dive rate was less than one per min), the efficiency ratio would be the same. It is possible that the very low level of prey density has an effect on foraging efficiency, although it would be expected that efficiency would only be affected if all the bait was removed during a trial. In actual fact there were six trials, out of a total of 142, in the entire experiment, where animals obtained all five prey items, and in each case trials were terminated once all bait was removed. However, if the same experiment was repeated with 40 hides for example, 50% of which were baited, then changes in such behaviours as mean number of hides visited per dive, mean time in hide etc., may become more apparent with depth. Finally, on this theme, the proportion of time on bottom spent hide searching was analysed for unsuccessful dives, since it was felt that as the differences in time on bottom were actually small (a few seconds) and the number of hides visited per dive did not show a significant change with depth, changes in foraging behaviour may be being masked by the great variation in individual results.

The result for All Animals (Fig. 3.13a) shows that there was a significant negative linear correlation between the proportion of time on bottom spent hide searching and depth. The individual results (Fig. 3.13b), show that for two of the females, there is a significant negative correlation with depth. The conclusion therefore is that mink are not using the extra time available on the pool bottom as depth increases to search either more hides per dive, or to search each hide more thoroughly. The question therefore is what is this extra time available being used for?

Poole and Dunstone (1976) observed that mink generally located live prey from out of water before diving in pursuit. However, Dunstone (1978) notes that mink often had difficulty in aerially locating fish which were more than 0.5 m from the rostrum, probably because of reflection of light at the water surface. He found that mink would immerse the head ('head dipping') and scan the tank underwater, enabling them to detect fish at greater distances. In this study, mink generally performed 'peering' (see 2.5) movements, which can be considered as equivalent to aerial location, or 'head-dipping' (Poole and Dunstone, 1976; Dunstone, 1978) movements, before every dive from the rostrum. Unfortunately, when data were transcribed using 'Event', the 'peering' and 'head dip' categories were lumped together as 'peering' and it was not possible to see if the amount of 'head-dipping' increased as depth increased. However, from Dunstone's (1978) observations, it would be expected that as depth increases beyond 0.5 m, then surface reflection would become a problem. Furthermore, the 'prey' items in this study were static, and since, in general, moving targets are more readily detected by the mammalian eye than stationary ones (Walls, 1942; Dunstone and Clements, 1979), then this could pose a further problem for mink as depth increases. Further, since the position of hides was varied with each session, individuals would not be able to learn their position from one trial to the next. If this idea is correct it is possible that the extra foraging time on bottom at greater depths is actually being used to locate hides. This can be investigated by examining the distance travelled underwater, the number of dives in which the mink swims direct to a hide, and the mean number of turns performed from when an animal reaches the pool bottom, until it searches the first hide.

Further, Croxhall (pers. comm.) suggested that mink foraging at the maximum depth, may search a hide, and they may then 'locate' another hide but not search it, particularly if this hide was more than 0.5 m distant. Thus, it would be expected that the next hide visit dive would be shorter, because the animals had an approximate idea of where a hide was located, and could dive more directly to it. Alternatively, the next hide visit dive may be longer, since if the animal was able to direct the dive more efficiently towards a hide (which had been located underwater during the previous dive), if this was not baited, the animal might 'decide' that it had sufficient reserves to move on and locate and search a second hide. Data for the maximum depth of 1.65 m were examined, and it was found that for the females, there were a total of 21 dives involving an unsuccessful hide search, which were followed by another hide search dive. Of these, 17 were of shorter duration than the previous hide visit dive, and all visited one hide which was not the same as the hide visited in the previous dive. The remaining four dives were all of longer duration, three involved a visit to two new hides, and one a single visit to a new hide. Thus, there is a possibility, that mink are locating hides whilst underwater and directing their subsequent foraging efforts more specifically.

To see if water depth does affect the ability of mink to detect prey aerially, the results for mean distance travelled underwater were examined. The results, for All Animals, for distance travelled underwater, (Fig. 3.14) showed a strong positive linear correlation with depth. Individual results (Fig. 3.14b) also showed that distance travelled underwater increased with depth. However, as described in 3.3.14, data for distance travelled on the pool bottom could not be separated from distance travelled throughout the dive, hence some of the increase seen above would be a function of the increase in depth, and the results must therefore be interpreted with caution. Thus, analysis of the proportion of direct dives visiting hides with depth might indicate whether mink were able to locate hides out of water at the maximum depth. The results for all animals (Fig. 3.15a) showed that the proportion of direct dives was significantly negatively correlated with depth. Individual results (Fig. 3.15b) also showed negative correlations. However, even at the shallowest depth, less than 50% of all hide visit dives were direct, thus, in the remaining dives, animals would appear to be actually locating hides whilst searching underwater.

This could be investigated by examining the data for mean number of turns per dive with depth, where the prediction would be that the mean number of turns per dive would increase with depth. Dunstone and Sinclair (1978b) studied the orienting behaviour of mink during aerial and underwater visual discrimination tasks. They defined an orienting response as "a fixating response made by the animal as it approached the stimulus display". They noted that typically the animal would slow down and fixate the stimulus display by means of head movements before making a choice. Underwater they found that the peak number of orienting responses occurred 20 - 30 cm from the target. Poole and Dunstone (1976) noted that the optimum range for detection of fish prey underwater was 35 cm. For this experiment, a turn was therefore defined as a deviation from the original path having an angular displacement of at least 30^o sustained for at least 0.5 m. By choosing 0.5 m it was felt that there would be no possibility of confusing actual deviations in trajectory with lateral scanning movements of the head. Also, in this study the nearest hide was 0.5 m from the base of the rostrum, and others were as far as 2.5 m. Thus, the number of turns recorded per dive could be related to the difficulty mink had in locating a hide. Data for all hide visit dives were analysed. Results for All Animals (Fig. 3.16a) showed that there was a positive linear correlation between number of turns per dive and depth. For individuals (Fig. 3.16b), only the data for female Dexa showed a significant linear correlation, and number of turns per dive increased with depth. Individual variation could be seen most clearly when a histogram of % frequency of dives having 0,1,2, etc. turns/dive was plotted (Fig. 3.17). Thus, the general pattern was, that the % frequency of direct dives decreases and % frequency of dives involving 2 or more turns increases with depth.

The overall conclusion from this study on the effect of depth, is that, at shallow depths animals appear to adopt the strategy of many, short duration dives, generally, visiting one or no hides per dive, which have been located from out of the water. As depth increases, the mink switch to a strategy of fewer, longer duration dives which, generally, visit one, or more than one hide per dive. However, hides are now difficult to locate from out of the water, and extra time is spent locating hides underwater. Animals were frequently seen to dive vertically from the rostrum, push off from the base and zig-zag across the pool floor until a hide was located. The net result was a steady success rate over all depths, although in real terms mink generally obtained less food at the maximum depths, for a greater effort.

CHAPTER 4

EFFECT OF CURRENT FLOW ON THE UNDERWATER FORAGING BEHAVIOUR OF THE MINK

4.1. Introduction

In their natural state, mink live in a wide variety of habitats, but the main feature is their proximity to water. This may be freshwater rivers and lakes (Mech, 1965), seawater (Dunstone and Birks, 1987) and estuaries. The important feature of some of these habitats is that the water is not static, hence, when hunting for prey, mink may have to contend with an appreciable current flow. This experiment attempted to investigate how the underwater foraging behaviour of the mink was affected by water movement.

The aim of this experiment was to study the effect of a current flow on the underwater foraging behaviour of the mink. The water depth was kept at a constant level and the effect of two types of current tested. One was a 'deep' flowing current, arranged to flow in either a clockwise or anticlockwise direction. The second was a 'surface' current, again arranged to flow in either a clockwise or anticlockwise direction.

4.2. Materials and Methods

4.2.1. Subjects

Eight animals were used in this experiment, five females (Dexa, Flash, Inka, Karla and Titan) and three males (Amber, Boris and Jaspa).

4.2.2. Maintenance

Three of the animals (Dexa, Inka and Titan) were fully grown adult females, aged 18 months, at the start of this experiment. They had been used previously (see Appendix I), and were familiar with the arena and the general experimental set-up. The remaining five animals had been obtained at eight weeks of age from a mink farm. These animals underwent a 12 week training period, (see General Materials and Methods: 2.6. Preliminary Training). At this point, the young animals, now aged 5 months, were moved to individual cages in the Animal House, where the adult females were already resident. The three adults were then given a period of re-familiarization before the experiments began.

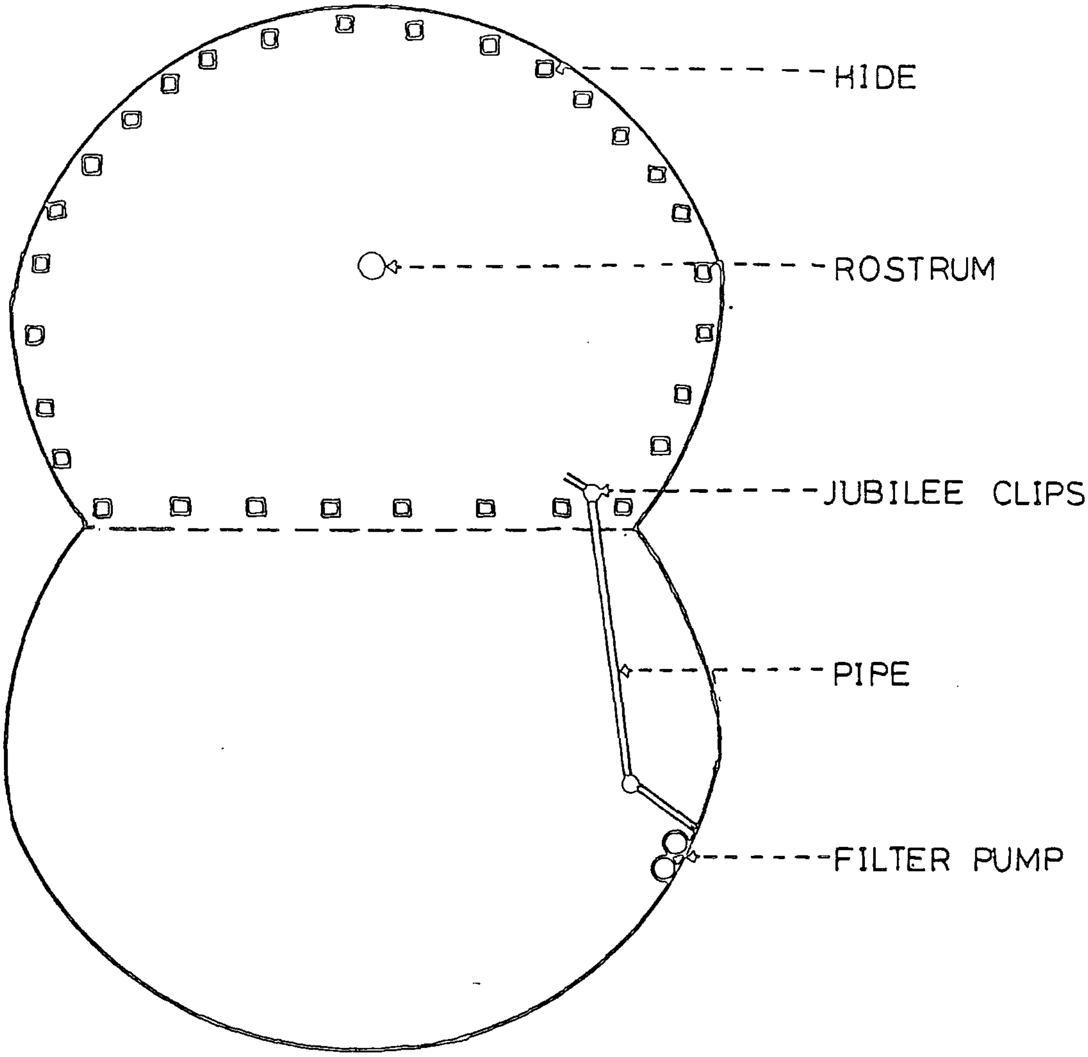
4.2.3. Experimental Arena

The experiment was carried out in the grid-marked pool (see General Materials and Methods: 2.3. Experimental Arena). However, for this experiment a partition constructed of heavy duty plastic was erected across the narrow 'waist' of the figure-of-eight shaped pool to confine the mink to one side. The water level in the experimental section was fixed at 0.60 m, which was equivalent to the shallow water depth of level II in the previous experiment.

A water current was produced using a pump unit situated outside the 'deep' end of the pool. This pump unit was driven by a 0.75 h.p. motor. Water from the pool was drawn in through an intake pipe, and pumped out of an exhaust pipe, to which sections of plastic tubing were attached (Fig. 4.1), in such a way that the direction of the current could be varied. A hole cut in the partition allowed the tubing to pass into the 'shallow' side of the pool.

4.2.4. Experimental Procedure

In this experiment 30 hides were distributed evenly on the tank floor around the edge of the pool (Fig. 4.1). Ten of these were baited with 5 g pieces of eel giving a prey density


HIDE
ROSTRUM
JUBILEE CLIPS
PIPE
FILTER PUMP

of 33.3%. The hides were arranged so that they were approximately equidistant from neighbouring hides. A single resting platform (or rostrum) was provided, and was positioned near the centre of the semi-circular pool. As before, access to the pool was provided by a removable wooden ramp and the position of entry of the mink to the rostrum was varied for each individual and for each trial.

Four different current types were used - two 'deep' currents, i.e. the pipe was so arranged that the pumped water emerged at a height of approximately 0.20 m from the floor of the pool, and two 'surface' currents, i.e. the end of the piping was twisted so that the water stream was directed vertically to the water surface. For the deep currents, the end of the pipe was anchored with a lead weight to prevent movement and disruption of the current flow. The four current types used were therefore as follows:-

C1: - deep current in clockwise direction
C2: - deep current in anticlockwise direction
SC1: - surface current in clockwise direction
SC2: - surface current in anticlockwise direction

The velocity of the currents produced under these various conditions was measured using a Current Flow Meter, lent by the Geography Department. For the deep currents, measurements were made at the mouth of the exhaust pipe, and approximately 1/3rd and 2/3rds of the distance around the outside of the pool. These are represented by A, B and C respectively in Fig. 4.2. For the surface current, a reading was taken where the current emerged to the surface (Fig. 4.2 A'), but it was found that readings varied greatly, probably because efficient working of the flow meter depended on it being completely submerged. Thus, readings for surface currents were taken only as current emerged to the water surface, and the values obtained were noted as being very much lower than those for deep currents (Table 4.1).

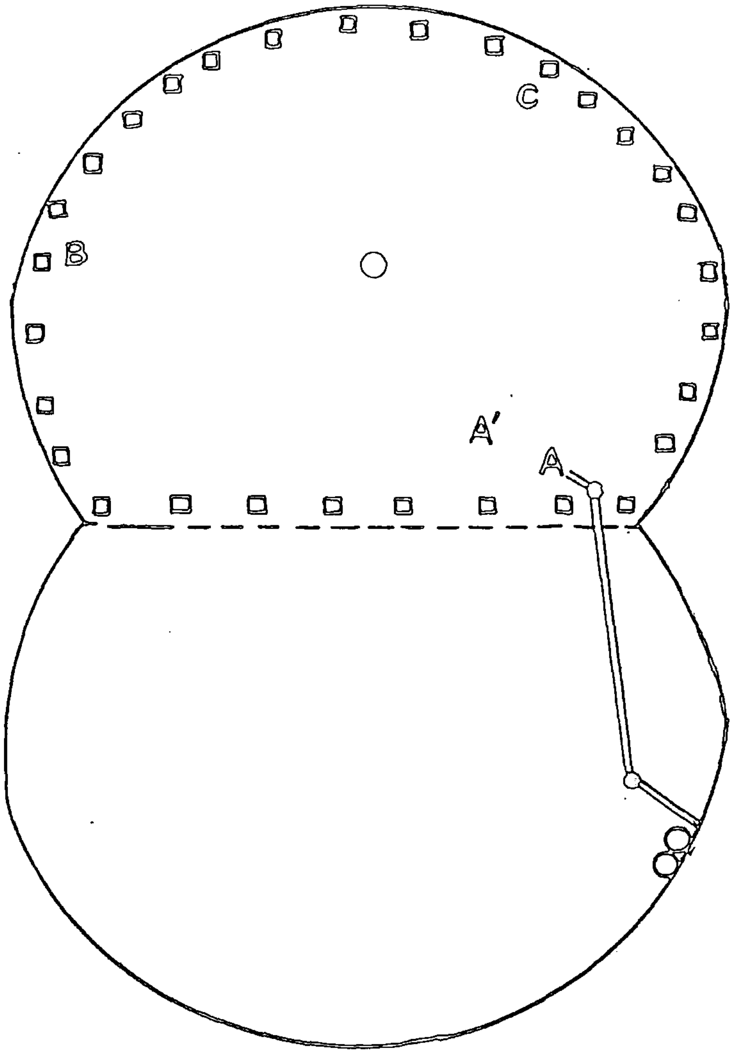

C
B
A'
A

TABLE 4.1 Measurement of current velocities in m s^{-1}

Current	A	B	C	A^1
C1	0.86	0.38	0.07	-
C2	0.84	0.27	0.07	-
SC1	-	-	-	0.63
SC2	-	-	-	0.60

Table 4.2: Sequence of current types used in experiment

	Date	Current type	Description
Phase 1	27/10/81 to 11/11/81	Control	No current flowing
	25/11/81	C1	Deep current clockwise
	2/12/81	C2	Deep current anticlockwise
Phase 2	3/12/81	SC2	Surface current anticlockwise
	6/12/81	C1	Deep - clockwise
	7/12/81	C2	Deep - anticlockwise
	8/12/81	SC1	Surface - clockwise
	9/12/81	SC2	Surface - anticlockwise
	13/12/81	Control	No current
	14/12/81	SC1	Surface - clockwise
	15/12/81	C1	Deep - clockwise
	17/12/81	SC2	Surface -anticlockwise
	18/12/81	C2	Deep - anticlockwise
	18/12/81	SC2	Surface anticlockwise
	19/12/81	C1	Deep - clockwise
	19/12/81	SC2	Surface - anticlockwise
	19/12/81	C2	Deep - anticlockwise
	19/12/81	SC1	Surface - clockwise

The direction of flow of current from the pipe mouth, at either A or A', was determined as follows. For deep currents a metal cylinder was used. This was lowered to the pool bottom close to the flow outlet at A. Once the current was switched on, the water flow pushed the cylinder around the bottom of the pool, enabling the direction of flow to be mapped (Fig. 4.2). For surface currents a buoyant 'cotton reel' was released at A' and the direction of movement was noted (Fig. 4.2). All measurements of current velocities and direction of flow were conducted whilst the 30 hides were in position.

The experiment consisted of two phases. For each phase, animals received one trial per day which lasted for 10 min or until they had completed 15 dives, whichever was sooner. The dive limit was changed from that of 20 dives used in the previous experiment, because it had been found that at the depth used in this experiment, most animals completed 15 dives or more, during a 10 min trial. Thus, by lowering the trial dive limit, animals would have to complete a number of trials under any given condition, to achieve the overall minimum of 35 dives. (This limit was greater than that in the depth experiment simply to ensure that animals would have to undergo more than two trials under any experimental condition.) Thus, if changes in behaviour were consistent between trials under the same conditions, it would then be reasonable to suppose that these conditions might be affecting the behaviour. Otherwise, if animals underwent only one or two trials under a particular set of conditions it might not have been possible to state whether changes in behaviour were the result of chance or were a response to the experimental conditions.

All trials were conducted in the afternoon and animals were fed at the end of the experimental period. The arena was prepared as described above and each day the position of the 10 baited hides were varied using random number tables. During any individuals's trial, baited hides which were emptied were not refilled, but all emptied hides were replenished prior to testing the next individual. All data were recorded on videotape and transcribed using the Apple II microcomputer system as described in General Materials and Methods: 2.4. Observation and Data Recording.

In the Control phase, the outlet pipe was present in the tank but no current was produced. Animals were tested for one trial per day until all individuals had achieved at least 35 dives under these conditions.

The Experimental phase began with current type C1 (i.e. deep current anticlockwise). The current type was varied daily in the sequence given in Table 4.2. It was hoped that this, together with the changes in which hides were baited would provide as variable as possible an environment for the mink to search for 'prey', particularly since all currents, of neccesity, began at the same point. Detailed records were kept for each individual, and animals were tested until they had completed a minimum of 35 dives for each of the four current conditions. One control session was interpersed among the various current conditions.

Data were recorded for a total of 1211 dives for all animals under Control and Experimental conditions.

4.3. Results

The aim of this experiment was to see what effect a current flow had on the underwater foraging behaviour of the mink. It might be expected that, like changes in water depth, the main effect of a current would be on the energetic requirements for foraging. Thus, it would seem reasonable to suppose that foraging would be more costly, in terms of energy used, if animals were hunting in areas where a deep current was flowing, compared to disruption of the water surface only. However, in view of the fact that mink generally tend to locate potential prey visually from out of the water, disruption of the water surface might also be expected to have a great effect on their foraging efficiency. To examine these problems, it was necessary to investigate various aspects of the underwater foraging behaviour of mink, particularly measures of foraging efficiency, and details of precisely what animals did during each dive. Thus, similar parameters to those examined in the investigation of the effect of depth on foraging behaviour, will be examined here.

Before carrying out any detailed analyses on the effect of current flow however, it was first necessary to see if individuals behaved consistently under the same conditions, and then to examine the effect of current flow. However, since in this experiment the subjects were five females and three males, it was also thought that it might be possible to determine whether there were sex differences in behaviour under the different current conditions. Finally, since each of the two current types, deep and surface, had two directional alternatives, (clockwise and anticlockwise) it was also necessary to see if the behaviour of the animals differed between C1 and C2 and between SC1 and SC2.

4.3.1. Analysis of Variance

The effect of current flow on dive duration, time on bottom, total time in hide, total distance travelled underwater and speed of travel underwater were investigated by means of Analysis of Variance tests. In the previous experiment it had been shown that foraging success was an important factor influencing diving behaviour. This was examined in the first Anova test performed where the independent variables were Animal, Current Type and Foraging Success. The results are given in Tables 4.3-4.7 but a summary can be outlined as follows:-

	Sig. Main Effects.	Sig. Two-way Interactions.	Sig. Three-way Interactions.
a) Dive duration	A, S	A x C ; A x S	-
b) Time on bottom	A, S	A x C ; A x S	-
c) Total time in hide	A	-	-
d) Distance travelled underwater	A, S	A x C ; A x S	-
e) Speed underwater	A,C,S,	-	-

Where A = Animal, C = Current Type and S = Foraging Success.

From these results it can be seen that foraging success does have an important influence on changes in the various parameters of behaviour studied, not only as a Main Effect, but more importantly when interacting with changes due to individual differences in behaviour. Furthermore, in all cases animal is a Main Effect which shows that individuals are behaving differently under the same current type conditions. However, the most interesting results are the remaining significant two-way interactions, where it can be seen that current type and animal were important in explaining changes in three of the parameters studied.

Since foraging success was obviously important in producing behavioural changes a second series of Analysis of Variance tests were carried out. Here, the effect of animal and current type were investigated for dives which visited hides and which were either successful or unsuccessful. Dives which did not visit hides were not included in the analysis as it was not possible to be sure whether animals were using these dives to explore the pool bottom, and to obtain information on possible sites for food rewards, or whether animals were playing, e.g. many of these dives were directed towards investigating the current outflow pipe. The results are given in Tables 4.8 to 4.12 and the main points are summarized below:-

TABLE 4.3: Anova of dive duration by Animal, Current Type and Foraging Success

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	4641.003	13	357.000	48.848	0.0001
Animal	647.752	7	92.536	12.662	0.0001
Current	29.99	4	7.498	1.026	0.393
Success	3229.301	2	1614.650	220.931	0.0001
2-Way Interactions	1425.170	50	28.503	3.900	0.0001
Animal Current	493.813	28	17.636	2.413	0.0001
Animal Success	852.518	14	60.894	8.332	0.0001
Current Success	72.632	8	9.079	1.242	0.271
3-Way Interactions	458.854	50	9.177	1.256	0.112
Animal Current Success	458.984	50	9.177	1.256	0.112
Explained	6525.027	13	57.744	7.901	0.0001
Residual	8017.307	1097	7.308		
Total	14542.334	1210	12.018		

1211 Cases were processed.
0 Cases (0.0%) were missing.

TABLE 4.4: Anova of time on bottom by Animal, Current Type and Foraging Success

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	4178.211	13	321.401	45.470	0.0001
Animal	651.054	7	93.008	13.158	0.0001
Current	15.345	4	3.836	0.543	0.704
Success	2952.776	2	1476.388	208.870	0.0001
2-Way Interactions	1422.827	50	28.457	4.026	0.0001
Animal Current	479.900	28	17.139	2.425	0.0001
Animal Success	843.462	14	60.247	8.523	0.0001
Current Success	72.933	8	9.117	1.290	0.245
3-way Interactions	456.910	50	9.138	1.293	0.086
Animal Current Success	456.910	50	9.138	1.293	0.086
Explained	6057.947	113	53.610	7.584	0.0001
Residual	7754.112	1097	7.068		
Total	13812.059	1210	11.415		

1211 Cases were processed.
0 Cases (0.0%) were missing.

TABLE 4.5: Anova of total time in hide by Animal, Current Type and Foraging Success

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	404.713	13	31.132	10.101	0.0001
Animal	382.638	7	54.663	17.737	0.000
Current	17.539	4	4.385	1.423	0.225
Success	1.972	2	0.986	0.320	0.726
Explained	404.713	13	31.132	10.101	0.0001
Residual	1852.231	601	3.082		
Total	2256.944	614	3.676		

1211 Cases were processed.
600 Cases (49.5%) were missing. (Non hide visit dives.)

TABLE 4.6: Anova of distance travelled underwater by Animal, Current Type and Foraging Success

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	361.511	13	27.809	15.515	0.0001
Animal	163.610	7	23.373	13.041	0.0001
Current	13.102	4	3.276	1.828	0.121
Success	178.767	2	89.383	49.870	0.0001
2-Way Interactions	253.394	50	5.068	2.828	0.0001
Animal Current	150.391	28	5.371	2.997	0.0001
Animal Success	83.682	14	5.977	3.335	0.0001
Current Success	21.557	8	2.695	1.503	0.152
3-Way Interactions	76.783	47	1.634	0.911	0.643
Animal Current Success	76.783	47	1.634	0.911	0.643
Explained	691.687	110	6.288	3.508	0.0001
Residual	1566.494	874	1.792		
Total	2258.182	984	2.295		

1211 Cases were processed.
226 Cases (18.7%) were missing. (Data lost during transcription of videotapes.)

TABLE 4.7: Anova of speed of underwater travel by Animal, Current Type and Foraging Success

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	5.002	13	0.385	13.569	0.0001
Animal	2.024	7	0.289	10.197	0.0001
Current	0.613	4	0.153	5.404	0.0001
Success	1.062	2	0.531	18.730	0.0001
2-Way Interactions	1.885	50	0.038	1.330	0.066
Animal Current	1.088	28	0.039	1.370	0.096
Animal Success	0.674	14	0.048	1.697	0.051
Current Success	0.073	8	0.009	0.324	0.957
3-Way Interactions	1.444	47	0.031	1.083	0.328
Animal Current Success	1.444	47	0.031	1.083	0.328
Explained	8.331	110	0.076	2.671	0.0001
Residual	24.783	874	0.028		
Total	33.114	984	0.034		

1211 Cases were processed.
226 Cases (18.7%) were missing. (Data lost during transcription of videotapes.)

TABLE 4.8: Anova of dive duration by Animal and Current Type.

(i) Successful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	429.030	11	39.003	3.398	0.001
Animal	375.027	7	53.575	4.668	0.001
Current	49.802	4	12.450	1.085	0.365
2-Way Interactions	337.046	25	13.482	1.175	0.266
Animal Current	337.046	25	13.482	1.175	0.266
Explained	766.076	36	21.280	1.854	0.004
Residual	2329.789	203	11.477		
Total	3095.866	239	12.953		

240 Cases were processed.
0 Cases (0.0%) were missing.

(ii) Unsuccessful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	967.626	11	87.966	9.656	0.0001
Animal	925.555	7	132.222	14.514	0.0001
Current	27.471	4	6.868	0.754	0.556
2-Way Interactions	353.541	28	12.626	1.386	0.096
Animal Current	353.541	28	12.626	1.386	0.096
Explained	1321.167	39	33.876	3.719	0.0001
Residual	3015.456	331	9.110		
Total	4336.623	370	11.721		

371 Cases were processed.
0 Cases (0.0%) were missing.

TABLE 4.9: Anova of time on bottom by Animal and Current Type.

(i) Successful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	490.037	11	44.549	3.901	0.0001
Animal	400.952	7	57.279	5.016	0.0001
Current	73.487	4	18.372	1.609	0.173
2-Way Interactions	327.107	25	13.084	1.146	0.295
Animal Current	327.107	25	13.084	1.146	0.295
Explained	817.144	36	22.698	1.988	0.003
Residual	2318.119	203	11.419		
Total	3135.263	239	13.118		

240 Cases were processed.
0 Cases (0.0%) were missing.

(ii) Unsuccessful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	913.750	11	83.068	9.129	0.0001
Animal	889.849	7	127.121	13.971	0.0001
Current	13.902	4	3.475	0.382	0.822
2-Way Interactions	343.526	28	12.269	1.348	0.116
Animal Current	343.526	28	12.269	1.348	0.116
Explained	1257.276	39	32.238	3.543	0.0001
Residual	3011.850	331	9.099		
Total	4269.126	370	11.538		

371 Cases were processed.
0 Cases (0.0%) were missing.

TABLE 4.10: Anova of total time in hide by Animal and Current Type.

(i) Successful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	131.590	11	11.963	3.661	0.0001
Animal	106.058	7	15.151	4.636	0.0001
Current	19.625	4	4.906	1.501	0.203
2-Way Interactions	61.336	25	2.453	0.751	0.799
Animal Current	61.336	25	2.453	0.751	0.799
Explained	192.926	36	5.359	1.640	0.018
Residual	663.383	203	3.268		
Total	856.310	239	3.583		

240 Cases were processed.
0 Cases (0.0%) were missing.

(ii) Unsuccessful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	296.171	11	26.925	8.770	0.0001
Animal	287.270	7	41.039	13.367	0.0001
Current	11.104	4	2.776	0.904	0.462
2-Way Interactions	73.874	28	2.638	0.859	0.675
Animal Current	73.874	28	2.638	0.859	0.675
Explained	370.045	39	9.488	3.090	0.0001
Residual	1016.242	331	3.070		
Total	1386.287	370	3.747		

371 Cases were processed.
0 Cases (0.0%) were missing.

TABLE 4.11: Anova of distance travelled underwater by Animal and Current Type

(i) Successful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	42.695	11	3.881	2.122	0.022
Animal	29.595	7	4.228	2.311	0.029
Current	14.606	4	3.652	1.996	0.098
2-Way Interactions	32.455	24	1.352	0.739	0.805
Animal Current	32.455	24	1.352	0.739	0.805
Explained	75.150	35	2.147	1.174	0.252
Residual	278.036	152	1.829		
Total	353.186	187	1.889		

240 Cases were processed.
52 Cases (21.7%) were missing. (Data lost during transcription of videotapes.)

(ii) Unsuccessful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	103.486	11	9.408	5.354	0.0001
Animal	87.371	7	12.482	7.103	0.0001
Current	12.652	4	3.163	1.800	0.129
2-Way Interactions	79.778	27	2.955	1.681	0.022
Animal Current	79.778	27	2.955	1.681	0.022
Explained	183.264	38	4.823	2.744	0.0001
Residual	463.933	264	1.757		
Total	647.197	302	2.143		

371 Cases were processed.
68 Cases (18.3%) were missing. (Data lost during transcription of videotapes.)

TABLE 4.12: Anova of speed of underwater travel by Animal and Current Type

(i) Successful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	0.414	11	0.038	2.426	0.008
Animal	0.245	7	0.035	2.250	0.033
Current	0.166	4	0.041	2.668	0.034
2-Way Interactions	0.491	24	0.020	1.318	0.161
Animal Current	0.491	24	0.020	1.318	0.161
Explained	0.905	35	0.026	1.666	0.019
Residual	2.359	152	0.016		
Total	3.265	187	0.017		

240 Cases were processed.
52 Cases (21.7%) were missing. (Data lost during transcription of videotapes.)

(ii) Unsuccessful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	1.240	11	0.113	6.947	0.0001
Animal	1.055	7	0.151	9.282	0.0001
Current	0.137	4	0.034	2.114	0.079
2-Way Interactions	0.620	27	0.023	1.416	0.089
Animal Current	0.620	27	0.023	1.416	0.089
Explained	1.861	38	0.049	3.017	0.0001
Residual	4.285	264	0.016		
Total	6.146	302	0.020		

371 Cases were processed.
68 Cases (18.3%) were missing. (Data lost during transcription of videotapes.)

	Significant Main Effects	Sig. Two-way Interactions
(a) Dive duration		
(i) Successful	A	-
(ii) Unsuccessful	A	-
(b) Time on bottom		
(i) Successful	A	-
(ii) Unsuccessful	A	-
(c) Total time in hide		
(i) Successful	A	-
(ii) Unsuccessful	A	-
(d) Distance travelled underwater		
(i) Successful	A	-
(ii) Unsuccessful	A	-
(e) Speed underwater		
(i) Successful	A, C	-
(ii) Unsuccessful	A	-

Where A = Animal, C = Current Type.

The results show, generally, that regardless of the success of a dive the most important factor explaining variation in behaviour was animal, with individuals behaving differently from one another under the same current condition, and between current conditions.

In this experiment three male and five female animals were used. It was thus possible to carry out a further series of Anova tests to see if the variation due to animal was in fact a reflection of differences in behaviour between the sexes. The results are given in Tables 4.13 to 4.17. From these, it appears that, generally, sex of an animal does not have a significant effect on changes in behaviour, at the 0.1% level of significance, although in several cases, particularly for successful dives, sex was the only significant Main Effect, at the 1% level of significance. In only one case, speed of travel underwater for successful dives, was current type a significant Main Effect, although only at the 0.5% level of significance.

TABLE 4.13: Anova of dive duration by Sex and Current Type

(i) Successful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	161.183	5	32.237	2.591	0.027
Sex	107.180	1	107.180	8.614	0.004
Current	38.575	4	9.644	0.775	0.542
2-Way Interactions	72.833	4	18.208	1.463	0.214
Sex Current	72.833	4	18.208	1.463	0.214
Explained	234.017	9	26.002	2.090	0.031
Residual	2861.849	230	12.443		
Total	3095.866	239	12.953		

240 Cases were processed.
0 Cases (0.0%) were missing.

(ii) Unsuccessful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	61.219	5	12.244	1.057	0.384
Sex	19.148	1	19.148	1.652	0.199
Current	50.430	4	12.607	1.088	0.362
2-Way Interactions	91.844	4	22.961	1.981	0.097
Sex Current	91.844	4	22.961	1.981	0.097
Explained	153.063	9	17.007	1.468	0.158
Residual	4183.560	361	11.589		
Total	4336.623	370	11.721		

371 Cases were processed.
0 Cases (0.0%) were missing.

TABLE 4.14: Anova of time on bottom by Sex and Current Type

(i) Successful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	222.936	5	44.587	3.596	0.004
Sex	133.851	1	133.851	10.796	0.001
Current	52.226	4	13.056	1.053	0.381
2-Way Interactions	60.790	4	15.198	1.226	0.301
Sex Current	60.790	4	15.198	1.226	0.301
Explained	283.727	9	31.525	2.543	0.008
Residual	2851.537	230	12.398		
Total	3135.263	239	13.118		

240 Cases were processed.
0 Cases (0.0%) were missing.

(ii) Unsuccessful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	50.210	5	10.042	0.877	0.496
Sex	26.309	1	26.309	2.298	0.130
Current	32.284	4	8.071	0.705	0.589
2-Way Interactions	85.943	4	21.486	1.877	0.114
Sex Current	85.943	4	21.486	1.877	0.114
Explained	136.153	9	15.128	1.321	0.224
Residual	4132.974	361	11.449		
Total	4269.126	370	11.538		

371 Cases were processed.
0 Cases (0.0%) were missing.

TABLE 4.15: Anova of total time in hide by Sex and Current Type.

(i) Successful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	68.041	5	13.608	4.099	0.001
Sex	42.509	1	42.509	12.804	0.0001
Current	14.696	4	3.674	1.107	0.354
2-Way Interactions	24.677	4	6.169	1.858	0.119
Sex Current	24.677	4	6.169	1.858	0.119
Explained	92.718	9	10.302	3.103	0.002
Residual	763.592	230	3.320		
Total	856.310	239	3.583		

240 Cases were processed.
0 Cases (0.0%) were missing.

(ii) Unsuccessful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	50.940	5	10.188	2.782	0.018
Sex	42.040	1	42.040	11.481	0.001
Current	6.599	4	1.650	0.451	0.772
2-Way Interactions	13.482	4	3.370	0.920	0.452
Sex Current	13.482	4	3.370	0.920	0.452
Explained	64.422	9	7.158	1.955	0.044
Residual	1321.865	361	3.662		
Total	1386.287	370	3.747		

371 Cases were processed.
0 (0.0%) were missing.

TABLE 4.16: Anova of distance travelled underwater by Sex and Current Type.

(i) Successful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	23.247	5	4.649	2.552	0.029
Sex	10.147	1	10.147	5.569	0.019
Current	12.238	4	3.059	1.679	0.157
2-Way Interactions	5.619	4	1.405	0.771	0.545
Sex Current	5.619	4	1.405	0.771	0.545
Explained	28.86	9	3.207	1.760	0.079
Residual	324.320	178	1.822		
Total	353.186	187	1.889		

240 Cases were processed.
52 Cases (21.7%) were missing. (Data lost during transcription of videotapes.)

(ii) Unsuccessful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	21.745	5	4.349	2.051	0.072
Sex	5.629	1	5.629	2.655	0.104
Current	17.413	4	4.353	2.053	0.087
2-Way Interactions	4.281	4	1.070	0.505	0.732
Sex Current	4.281	4	1.070	0.505	0.732
Explained	26.025	9	2.892	1.364	0.204
Residual	621.172	293	2.120		
Total	647.192	302	2.143		

371 Cases were processed.
68 Cases (18.3%) were missing. (Data lost during transcription of videotapes.)

TABLE 4.17: Anova of speed of underwater travel by Sex and Current Type

(i) Successful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	0.208	5	0.042	2.481	0.034
Sex	0.038	1	0.038	2.269	0.134
Current	0.164	4	0.041	2.445	0.048
2-Way Interactions	0.077	4	0.019	1.153	0.333
Sex Current	0.077	4	0.019	1.153	0.333
Explained	0.285	9	0.032	1.891	0.056
Residual	2.980	178	0.017		
Total	3.265	187	0.017		

240 Cases were processed.
52 Cases (21.7%) were missing. (Data lost during transcription of videotapes.)

(ii) Unsuccessful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	0.232	5	0.046	2.342	0.042
Sex	0.046	1	0.046	2.323	0.129
Current	0.184	4	0.046	2.322	0.057
2-Way Interactions	0.118	4	0.029	1.491	0.205
Sex Current	0.118	4	0.029	1.491	0.205
Explained	0.350	9	0.039	1.964	0.043
Residual	5.796	293	0.020		
Total	6.146	302	0.020		

371 Cases were processed.
68 Cases (18.3%) were missing. (Data lost during transcription of videotapes.)

The conclusions from the above results are that the behaviour of individuals during a dive is very variable, and is mainly affected by foraging success. As a result, it is difficult to isolate changes in behaviour which can be related to the effect of current flow. Thus, it was decided to investigate changes in underwater foraging behaviour in more detail. For some results, it appeared that there may have been differences in the behaviour of the sexes. However, it was decided that since mink show such extreme sexual dimorphism, especially with regard to size, and that there was no overlap in body weights between the sexes, in the animals used, it was possible that the differences observed were the result of size differences and not a reflection of sexual differences in behaviour. Thus, the data were not presented for each sex, but simply as the combined results for all animals, with data for individuals presented for comparison, in the hope that any consistent changes in behaviour would become apparent.

Finally, each of the two types of current flow, i.e. deep and surface, had two directional alternatives, anticlockwise and clockwise. Since individual behaviour was so variable, it was also necessary to see if there were significant differences in behaviour when C1 was compared with C2, and SC1 with SC2. Further, since foraging success is an important factor, data for successful and unsuccessful dives were analysed separately. To investigate this, a series of Oneway Analysis of Variance tests were carried out, with Current Type being the only independent variable. The dependent variable list used was the same as that for the above Anova tests, i.e. dive duration, time on bottom, distance travelled underwater and speed of travel underwater, and these variables were tested against the five current types, i.e. no current, deep clockwise, deep anticlockwise, surface clockwise and surface anticlockwise. The results for the between group tests are expressed as an F ratio, and Table 4.18 gives the associated probability values. It can be seen that there were no significant values. To investigate in more detail any changes in

TABLE 4.18: Summary of Results of Oneway Anova (giving values of probability of F) and results of the matrix comparison produced by Scheffe's Procedure, for individuals only.

			Amber	Boris	Jaspa	Dexa	Flash	Inka	Karla	Titan
Dive Duration	+ve	Prob. of F	0.71	0.52	0.38	0.23	-	0.84	0.66	0.21
		Scheffe	ns	ns	ns	ns	-	ns	ns	ns
	-ve	Prob. of F	0.63	0.01	0.07	0.56	0.62	0.39	0.54	0.17
		Scheffe	ns	ns	ns	ns	ns	ns	ns	ns
Time on Bottom	+ve	Prob. of F	0.74	0.48	0.29	0.59	-	0.59	0.51	0.15
		Scheffe	ns	ns	ns	ns	-	ns	ns	ns
	-ve	Prob. of F	0.75	0.01	0.05	0.70	0.64	0.42	0.72	0.25
		Scheffe	ns	ns	ns	ns	ns	ns	ns	ns
Time in Hide	+ve	Prob. of F	0.57	0.51	0.54	0.26	-	0.90	0.07	0.34
		Scheffe	ns	ns	ns	ns	-	ns	ns	ns
	-ve	Prob. of F	0.66	0.07	0.35	0.77	0.76	0.80	0.77	0.19
		Scheffe	ns	ns	ns	ns	ns	ns	ns	ns
Distance	+ve	Prob. of F	0.80	0.38	0.17	0.58	-	0.39	0.37	0.15
		Scheffe	ns	ns	ns	ns	-	ns	ns	ns
	-ve	Prob. of F	0.01	0.01	0.05	0.52	0.96	0.52	0.61	0.59
		Scheffe	ns	ns	ns	ns	ns	ns	ns	ns
Speed	+ve	Prob. of F	0.61	0.91	0.32	0.29	-	0.14	0.80	0.18
		Scheffe	ns	ns	ns	ns	-	ns	ns	ns
	-ve	Prob. of F	0.08	0.08	0.05	0.69	0.32	0.37	0.25	0.89
		Scheffe	ns	ns	ns	ns	ns	ns	ns	ns

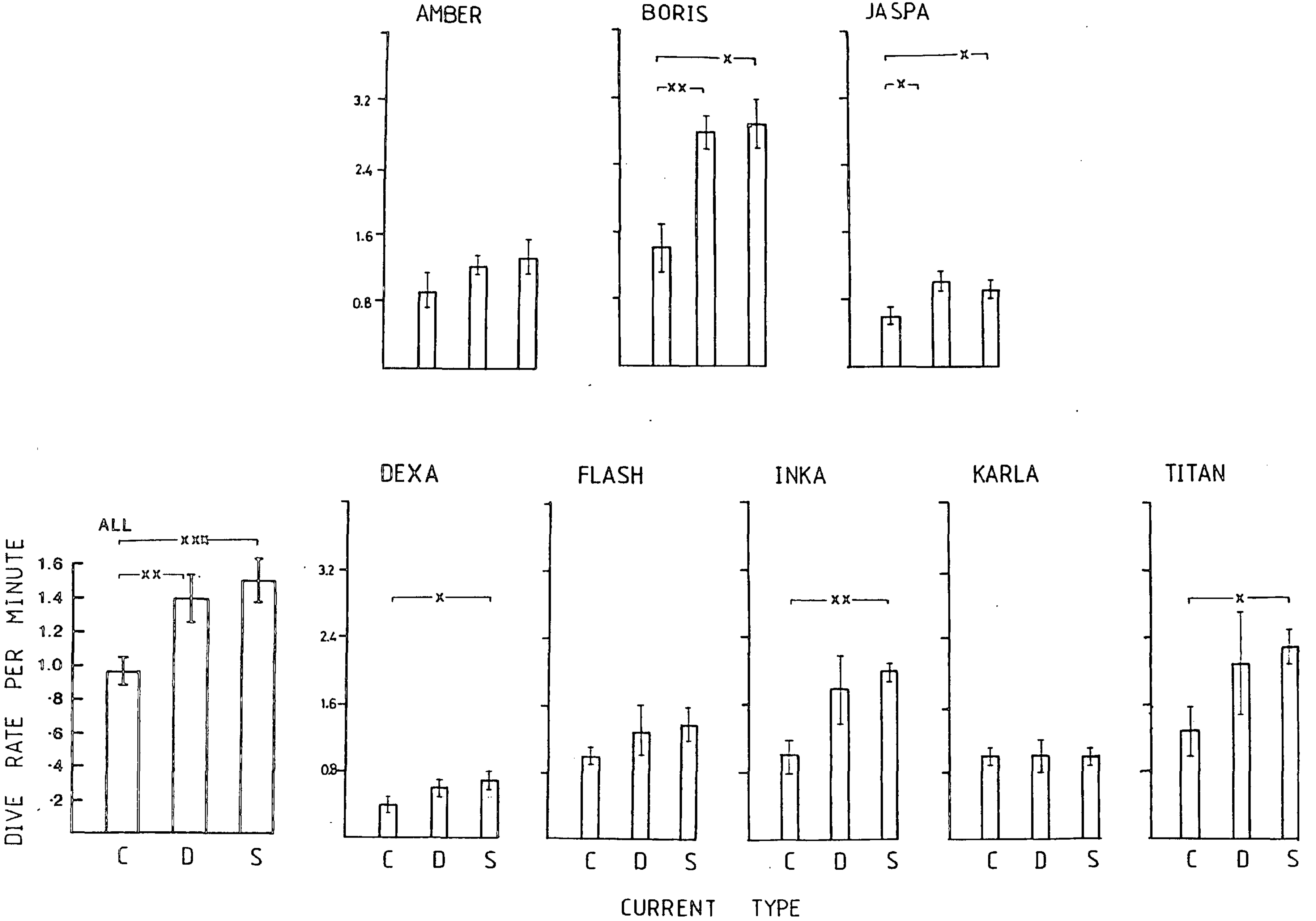
In each case df=4
From the table it can be seen that there were no significant matrix interactions and probability values for F (between group comparison) were also not significant.

behaviour between deep and surface current directions, the Multiple Range Test "Scheffe's Procedure" analysis was carried out, at a significance level of 1% (i.e. $\alpha = 0.01$). A significance level of 1% rather than 5% was chosen since this procedure would involve tests on a five by five matrix, and at a significance level of 0.05, it is probable that one in twenty significant results would be due to chance. By selecting 0.01 as the significance level, only one in a hundred significant results could be due to chance. The results are summarized in Table 4.18, from which it can be seen that analysis of the matrix showed that for no pairs of current direction variables, were the mean values signficantly different. This implies that behaviour for the two directional alternatives for deep and surface currents could be combined for detailed analysis, and the two conditions compared to the control, i.e. no current.

4.3.2. Dive Rate

Mean values for dive rate were calculated for each animal, and for all animals combined, for each of the current conditions. The results are given in Fig. 4.3. A series of t-tests were carried out to investigate whetherthere were any significant differences in behaviour between the control and each of the current conditions, and between current types. Significant results are shown on Fig. 4.3.

The first point to note is that when the control condition is compared to deep current, significant results were obtained only for All Animals (t= -2.75, df = 84, $p<0.01$), for Boris (t= -3.56, df = 7, $p<0.01$) and Jaspa (t= -2.84, df = 11, $p<0.05$). In all three cases mean dive rate per minute is greater when deep current is flowing (Fig. 4.3). For the remaining individual results, generally, the mean values for dive rate appear to be greater when deep current is flowing compared to control, but the S.E. bars show that there is often considerable overlap between the two, and hence none of the results were

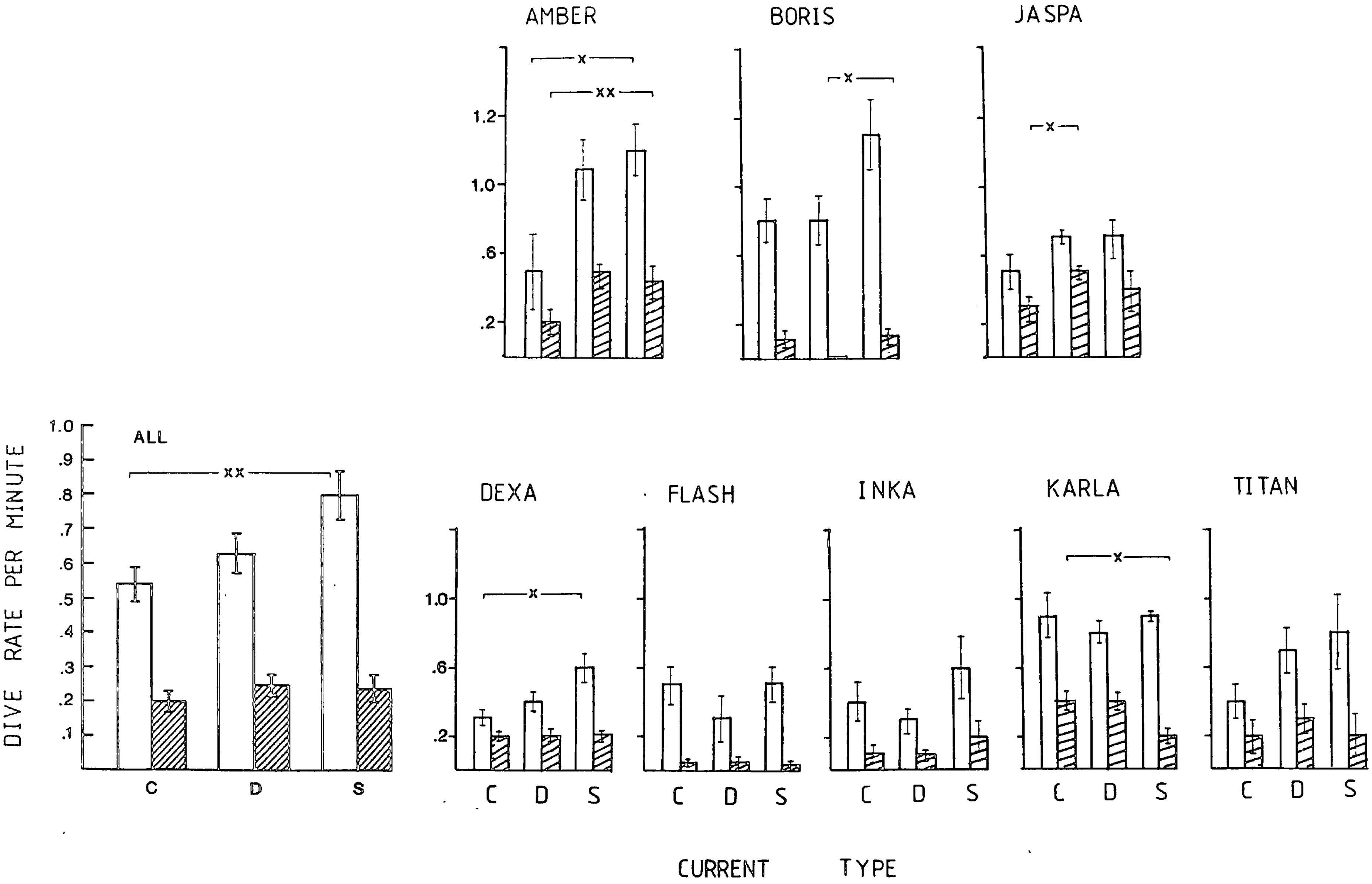

AMBER
BORIS
JASPA
DEXA
FLASH
INKA
KARLA
TITAN
ALL
3.2
2.4
1.6
0.8
1.6
1.4
1.2
1.0
·8
·6
·4
·2
x
xx
xxx
DIVE RATE PER MINUTE
C
D
S
CURRENT TYPE

significant. When the mean dive rates per minute for control and surface current are compared, it can be seen that there are many more significant results: All Animals (t= -2.33, df = 77, $p<0.001$), Boris (t= -3.27, df = 7, $p<0.05$), Jaspa (t= -2.42, df = 12, $p<0.05$), Dexa (t= -2.75, df = 8, $p<0.05$), Inka (t= -3.78, df = 8, $p<0.01$) and Titan (t= -3.11, df = 7, $p<0.05$). In all cases mean dive rate per minute is greater when surface current was flowing. There were no significant differences between mean dive rate per minute when deep current was flowing, compared to surface current.

From these results it appears that the presence of a current, either deep or surface, caused the animals to perform more dives per minute.

4.3.3. Hide visit Dive Rate

If current flow has an energetic constraint on the behaviour of mink, it might be expected that the number of dives visiting hides would vary depending on whether a current was flowing or not. A mean value for hide visit dive rate was calculated for each trial of each animal. Trials in which all dives failed to visit hides were excluded from the analysis, since animals had, in all cases, been distracted. The results are illustrated in Fig. 4.4. A series of t-tests were carried out and the significant results are also shown in Fig. 4.4, from which it can be seen that in only a few cases are the results significant. When control and deep conditions were compared, there are no significant results. When control and surface current conditions are compared, significant results are obtained for All Animals (t= -3.23, df = 74, $p<0.01$), Amber (t= -2.92, df = 6, $p<0.05$) and Dexa (t= -2.65, df = 8, $p<0.05$). In all cases hide visit dive rate is greater when surface current is flowing. Finally, when deep and surface current conditions are compared, no significant results are obtained.


AMBER
BORIS
JASPA
x
xx
x
x
1.2
1.0
.6
.2
ALL
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
DIVE RATE PER MINUTE
xx
C
D
S
DEXA
FLASH
INKA
KARLA
TITAN
x
x
1.0
.6
.2
C
D
S
C
D
S
C
D
S
C
D
S
C
D
S
CURRENT TYPE

4.3.4. Successful Dive Rate

Successful dive rate per minute can be used to give some measure of the foraging efficiency of the mink hunting under different conditions. Trials in which no hides were visited were excluded from the analysis. The results are shown in Fig. 4.4, and significant t-test results are indicated.

When control and deep current data are compared, a significant difference is obtained for Jaspa (t= -2.23, df = 11, $p<0.05$), with a greater number of successful dives when the deep current was flowing. For comparisons between control and surface current there are signficant differences for Amber (t= -3.75, df = 6, $p<0.01$) and Karla (t= 3.16, df = 5, $p<0.05$). For Amber, the mean number of successful dives per minute is greater when surface current is flowing, but the reverse is true for Karla. Finally, there is a signifcant difference between deep and surface current conditions for Boris (t= -2.89, df = 6, $p<0.05$). However, Boris had no successful dives when the deep current was flowing and a mean value of only 0.13 dives per minute when surface current was flowing, thus, this result may be an artifact.

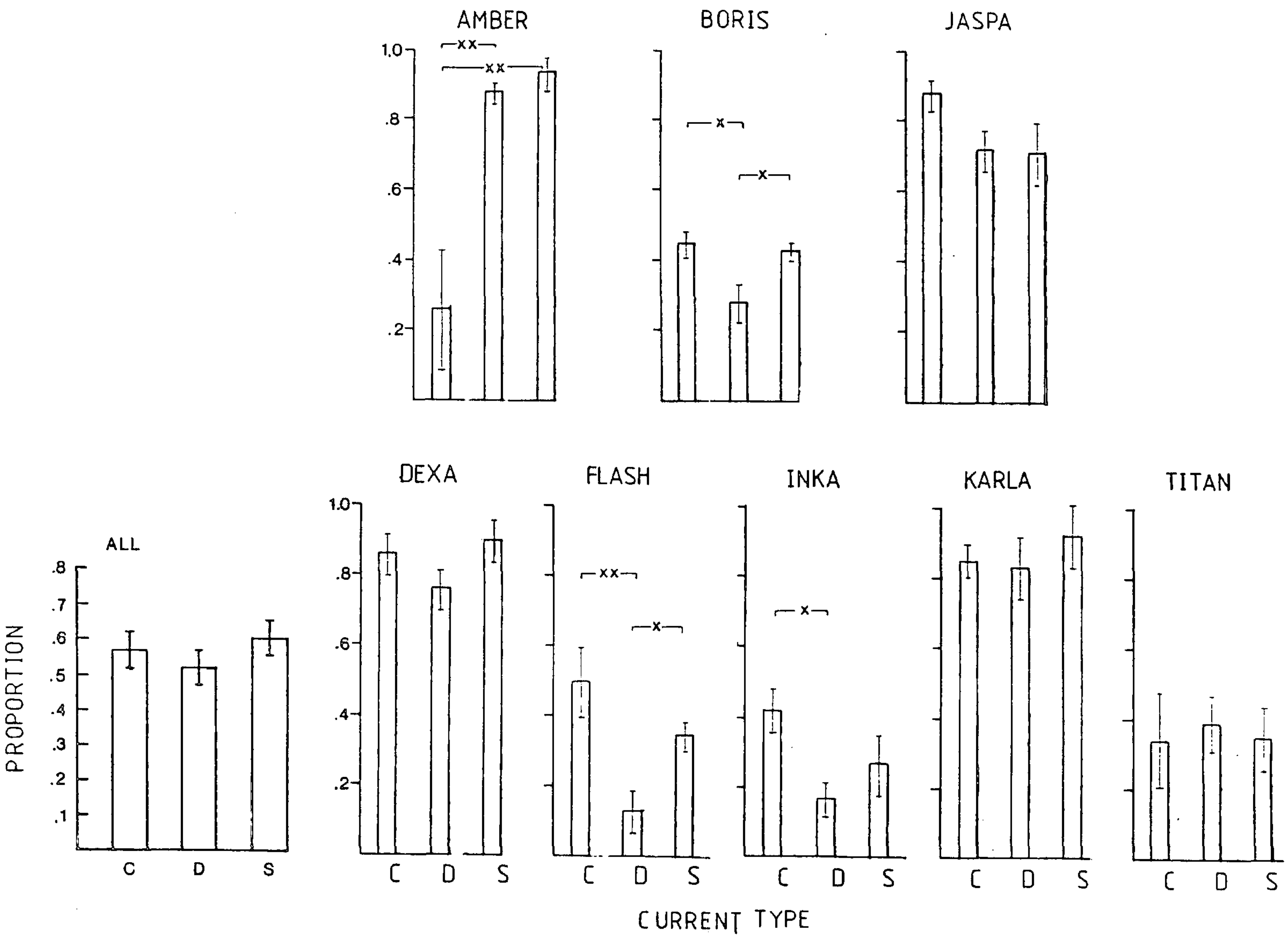
The final point to note from Fig. 4.4. is that values for mean successful dive rate per minute are very low, less than 0.5, i.e. less than one successful dive in every two minutes, and most (19 out of 27 results) have values of 0.25 or less (i.e. one successful dive every four minutes). Of the eight results that show a mean successful dive rate per minute greater than 0.25, four occur when a deep current is flowing, two when a surface current is flowing and two in the control.

4.3.5. Proportion of dives visiting a hide

The task facing the foraging mink was to search hides to obtain a food reward. It has been noted that in many cases, animals would dive to the pool bottom but would not search any hides. If current flow has an effect on the energetics of foraging, then it might be expected that animals would concentrate their foraging efforts on searching hides when current was operating. Thus, the proportion of dives visiting a hide should yield information on whether animals are indeed concentrating their foraging efforts to the most rewarding sites, i.e. the hides.

Data were calculated for each trial of each animal under each current condition from the formulae given in Section 3.3.5. Fig. 4.5 illustrates the mean proportion of hide visit dives ± S.E. for individuals and all animals, and presents the results of t-test analysis for all combinations of current type.

Statistical analysis revealed that there were a number of significant results. When data for control and deep current were compared, significant results were obtained for Amber ($t= -3.96$, $df = 9$, $p<0.01$), Boris ($t= 2.43$, $df = 7$, $p<0.05$), Flash ($t= 3.29$, $df = 9$, $p<0.01$) and Inka ($t= 3.09$, $df = 10$, $p<0.05$), and for each animal, except Amber, the proportion of dives visiting a hide was less when deep current was flowing. When data for control and surface current were compared, only data for Amber ($t= -3.84$, $df = 8$, $p<0.01$) were significant, and here proportion of dives visiting a hide was greater when surface current was flowing. Finally, when surface and deep currents were compared, significant differences were obtained for Boris ($t= -2.48$, $df = 6$, $p<0.05$) and Flash ($t= -3.10$, $df = 9$, $p<0.05$), and in both cases more dives visited hides when surface current was operating.


AMBER
BORIS
JASPA
1.0
.8
.6
.4
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xx
xx
x
x
ALL
.8
.7
.6
.5
.4
.3
.2
.1
PROPORTION
C
D
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DEXA
FLASH
INKA
KARLA
TITAN
xx
x
x
CURRENT TYPE

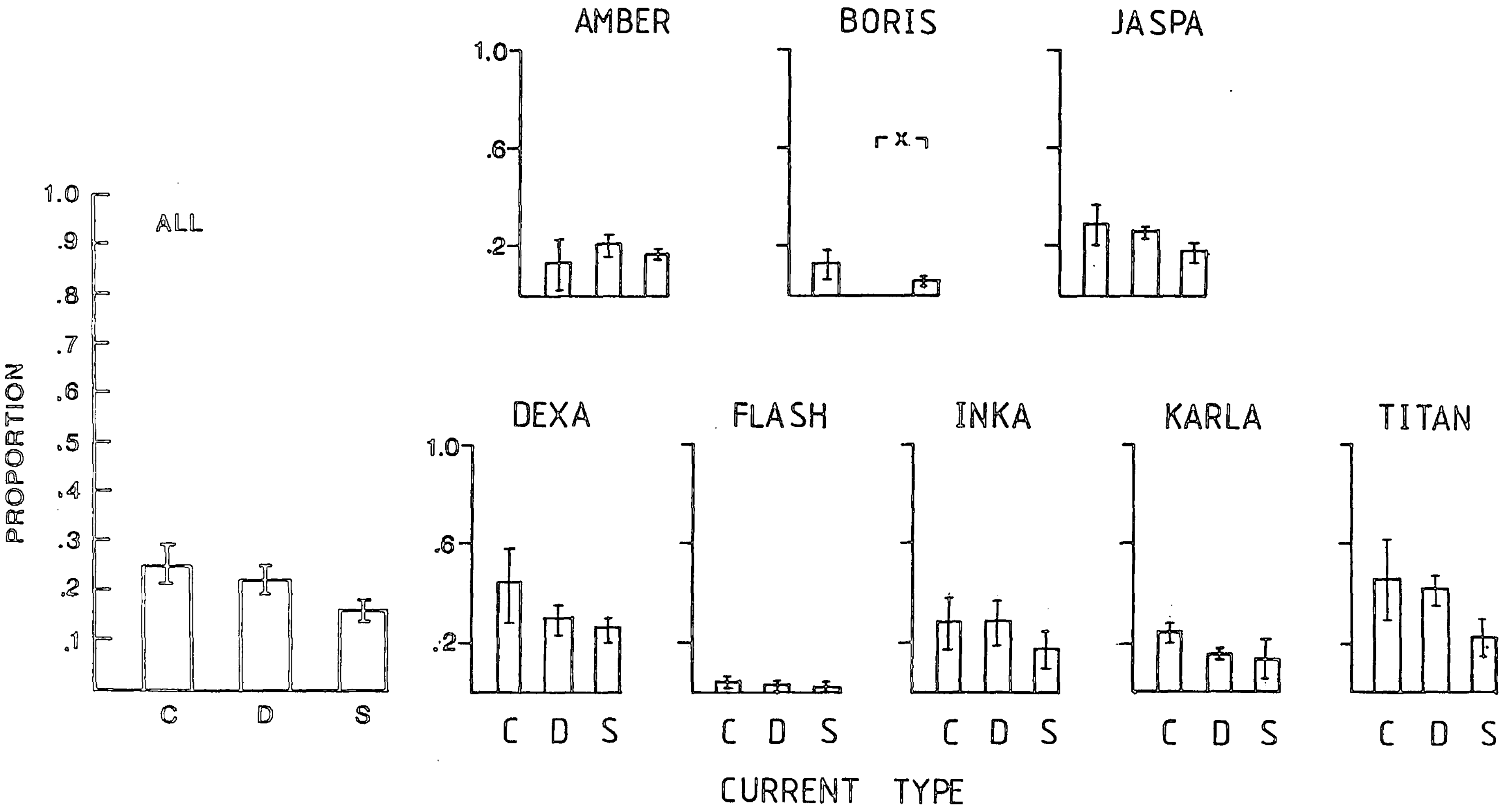
It can be seen from Fig. 4.5 that there is considerable variation between animals, but generally (in 15 out of 27 cases) more than 50% of dives involved hide visits regardless of whether a current was flowing or not. It is particularly interesting however, to note that where there is a significant difference (except for Amber) the proportion of dives visiting a hide is less when a current is operating than in the control. This is particularly interesting in view of the results for overall dive rate, when number of dives per minute appears to be greater in the experimental situations compared to control.

4.3.6. Proportion of successful dives to total hide visit dives

In the experiment on the effect of depth on the underwater foraging behaviour of mink, this variable was examined with a view to providing information on the efficiency of the foraging strategies employed by the animals. In this experiment, the positions of hides were constant and the success of a dive would depend to a great extent on the number of hides visited, and the likelihood of visiting one containing a food reward. Further, where more than one hide was visited, only the last visit could actually be successful. Thus, a clearer picture of changes in foraging efficiency might be obtained if changes in the proportion of successful hide visits and not dives were examined.

4.3.7. Proportion of successful hide visits to total number of hide visits

This was calculated using the formula given in Section 3.3.7. All trials in which hides were not visited were excluded from the analysis. Fig. 4.6 illustrates these data and signficant t-test results, from which it can be seen that there is only one statistically significantly result. This was for Boris comparing deep and surface current conditions, where $t=-3.00$, $df = 6$, $p<0.05$, and this may be suspect since Boris did not perform a single successful hide visit when the deep current was operating. From the Figure it can be seen that, generally, the proportion of successful hide visits to total hide visits is



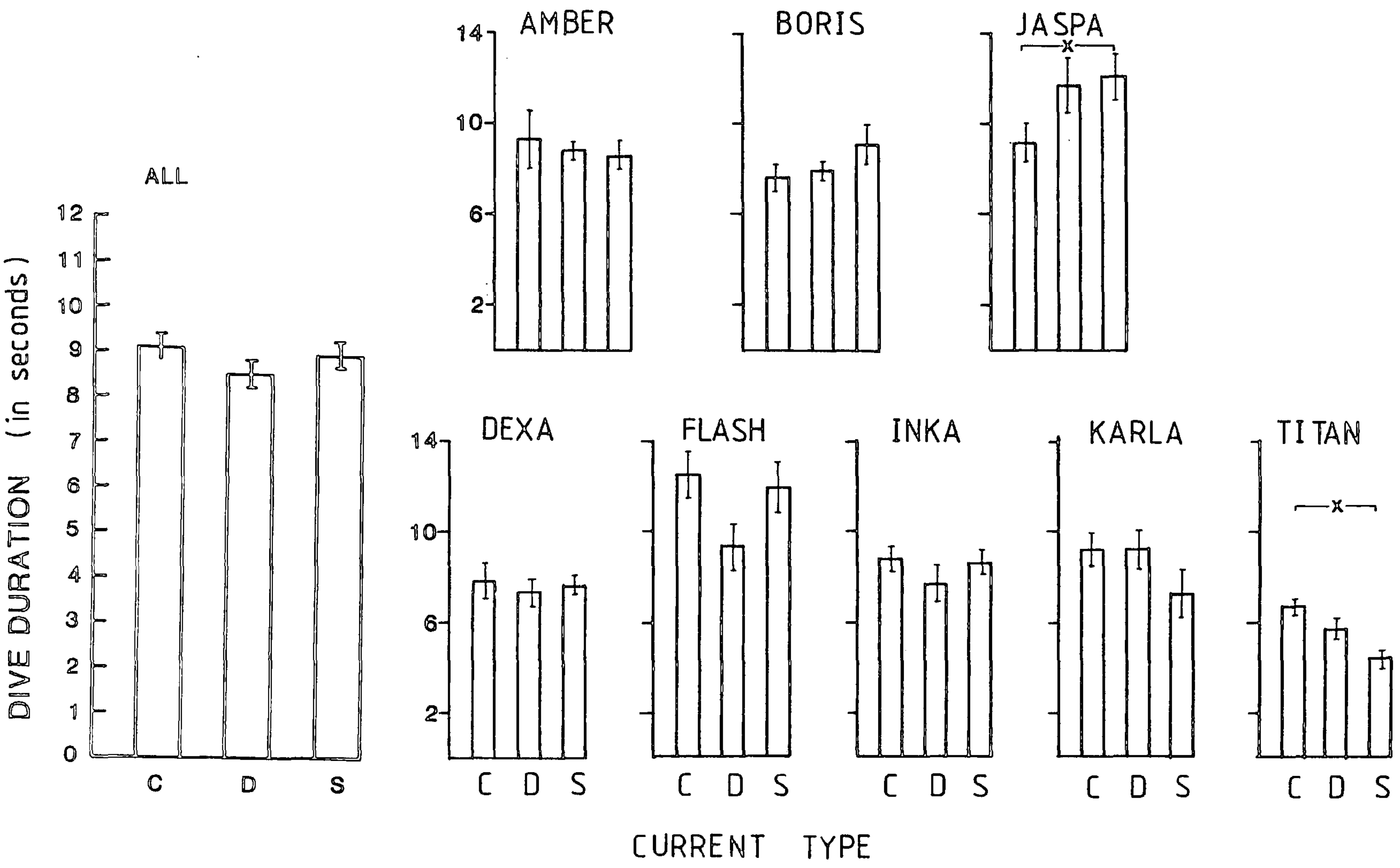
AMBER
BORIS
JASPA
1.0
.6
.2
⌐ X ¬
ALL
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
PROPORTION
C
D
S
DEXA
FLASH
INKA
KARLA
TITAN
1.0
.6
.2
C D S
C D S
C D S
C D S
C D S
CURRENT TYPE

consistent between the three current conditions. However, there are great individual variations in the actual proportions of successful hide visits. If the animals visited every hide once during a trial, the expected proportion for successful hide visits to total hide visits would be 0.33 since 33% of the hides were baited. But, in some cases as many as 40% or more of hide visits were successful. This implies that either the animals located baited hides by chance, or else their foraging strategy produced a greater degree of success than might have been expected by chance. Thus, it is necessary to examine the foraging strategies employed in greater detail.

4.3.8. Dive Duration

If current flow imposes an energetic cost to the foraging behaviour of mink, it might be expected that dive duration could change when different current conditions are operating. The results of the Analysis of Variance tests (Tables 4.3-4.7) indicated that foraging success was an important factor influencing dive duration. Since successful dives are terminated as soon as a food item is obtained, subsequent analyses will consider unsuccessful dives only. Of these, dives in which no hides were visited will also be excluded from the analysis, since it cannot be known whether animals are using such dives to investigate the environment, or whether their feeding motivation is low.

Mean unsuccessful dive duration ± S.E. was calculated, and the results are illustrated in Fig. 4.7. A series of t-test analyses were carried out to investigate the mean dive duration under different conditions of current flow. The results show that there are no cases where there is a significant difference in mean unsuccessful dive duration, when the control is compared to deep current, or when deep and surface currents are compared. Significant results were obtained in only two cases, when control and surface current


ALL
DIVE DURATION (in seconds)
0
1
2
3
4
5
6
7
8
9
10
11
12
C
D
S
AMBER
BORIS
JASPA
x
14
10
6
2
DEXA
FLASH
INKA
KARLA
TITAN
x
14
10
6
2
C D S
C D S
C D S
C D S
C D S
CURRENT TYPE

were compared: Jaspa, t= -2.24, df = 25, p<0.05, (duration was greater for surface current), and Titan, t= 2.28, df = 17, p<0.05, (duration was greater in the control).

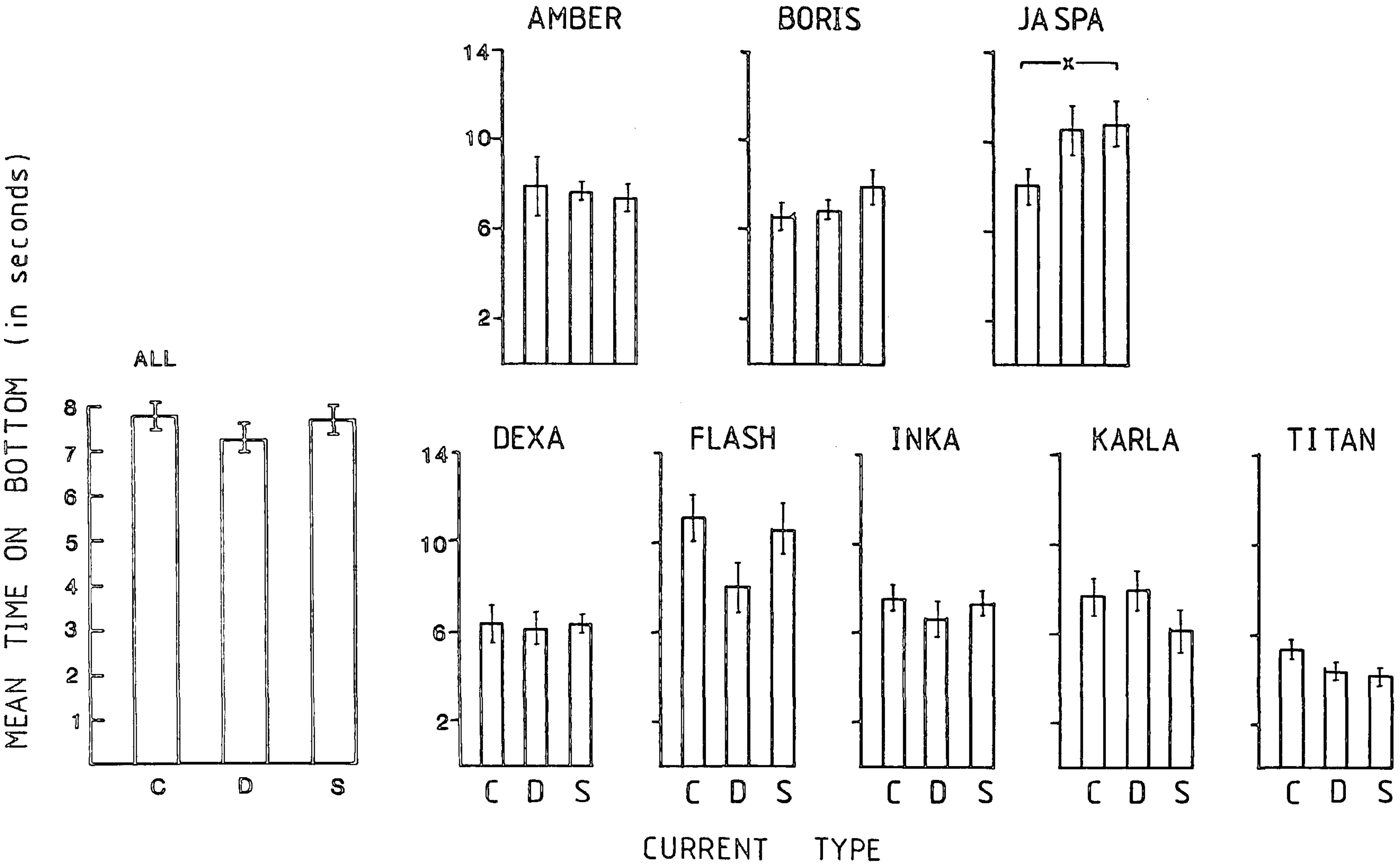
Finally, it should be noted that, whilst most of the t-test results were not statistically significant, it can be seen from Fig. 4.7 that for All Animals, individual females and male Amber, mean dive duration is greater in the control condition, although S.E. bars indicate there is considerable overlap. When the two experimental conditions are compared it can be seen that in some cases mean duration is greater when a deep current is flowing and for some animals when surface current flows. Thus, there seems to be no consistent trend of change in mean dive duration with current condition.

One further point is that there is considerable variation in the actual mean values of dive duration for individuals. Thus, the male Jaspa and female Flash often dive for periods greater than 10 s, whereas for other animals the maximum mean durations were less than 10 s.

4.3.9. Time on Bottom

Mean time on bottom (± S.E.) during unsuccesful dives was calculated, and the results are illustrated in Fig. 4.8. In only one case was the result of t-test analysis significant. Thus, for Jaspa (comparison of control and surface), t= -2.14, df = 25, p<0.05. Here, mean time on bottom was roughly 2.5 s greater when surface current was operating.

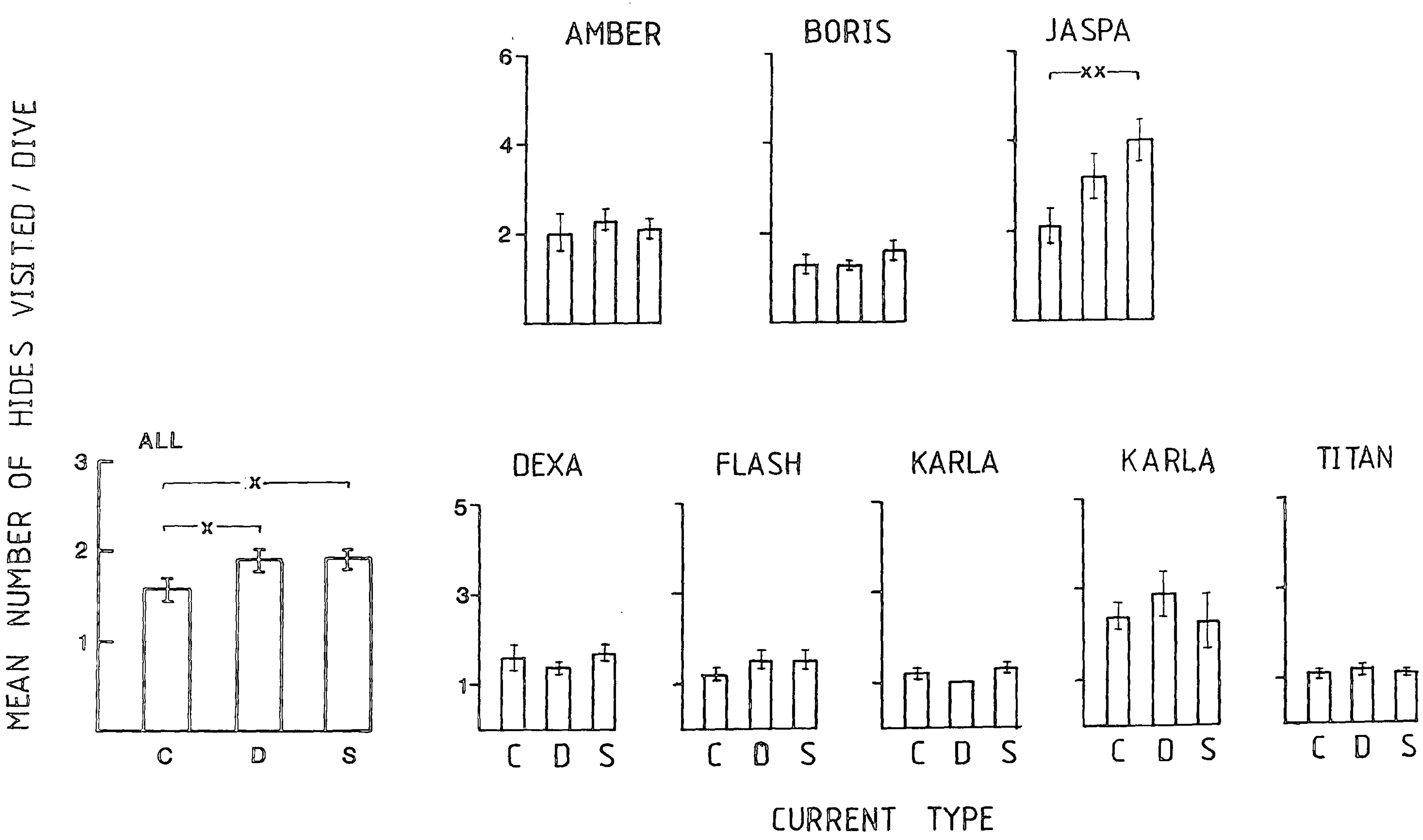
From Fig. 4.8, it can be seen that, generally, for All Animals, individual females and male Amber, mean time on bottom is greater in the control, although S.E. bars indicate considerable overlap with the results for experimental conditions. This is similar to the results observed for mean dive duration. For the remaining male results, mean time on


MEAN TIME ON BOTTOM (in seconds)
ALL
8
7
6
5
4
3
2
1
C
D
S
AMBER
BORIS
JASPA
x
14
10
6
2
DEXA
FLASH
INKA
KARLA
TITAN
14
10
6
2
C D S
C D S
C D S
C D S
C D S
CURRENT TYPE

bottom appears greater when surface current is flowing, although unlike the results for dive duration none are significantly different from either control or deep conditions. Further, when the two experimental conditions are compared, it can be seen that, as for mean dive duration, in some cases mean time on bottom is greater when deep current flows and in others vice versa. As was noted for dive duration, male Jaspa and female Flash often spend considerably longer on the bottom (with mean values >10 s) than the other animals (whose mean values are all <8 s).

4.3.10. Mean number of hides visited per dive

The foraging efficiency of the mink will depend on the number of hides searched for prey items. If a current has an energetic effect on the behaviour of the mink they might be expected to visit a different number of hides per dive in the experimental compared to the control condition. The optimal strategy would be to visit as many hides per dive as possible, thus, the question is, whether the current reduces or increases the number visited. To investigate this, the mean number of hides visited per unsuccessful dive under the control and experimental conditions was calculated as outlined in 3.3.10. The results are given in Fig. 4.9, and it can be seen that there are three significant results. For control compared to deep, All Animals: t= -2.21, df = 221, $p<0.05$. For control compared to surface, All Animals: t= -2.25, df = 254, $p<0.05$; Jaspa: t= -3.25, df = 25, $p<0.01$. In each case, the mean number of hides visited per dive was greater when a current was flowing. It can also be noted that Jaspa, whilst searching more hides per dive under the experimental conditions than the other males, seems to search a similar number per dive as the other males, in the control. However, since Jaspa was also the only male to have a significant difference in mean dive durations between surface current and control conditions, the greater number of hides visited per dive is not really surprising. A more interesting result is that of female Karla, who searches roughly twice as many hides per

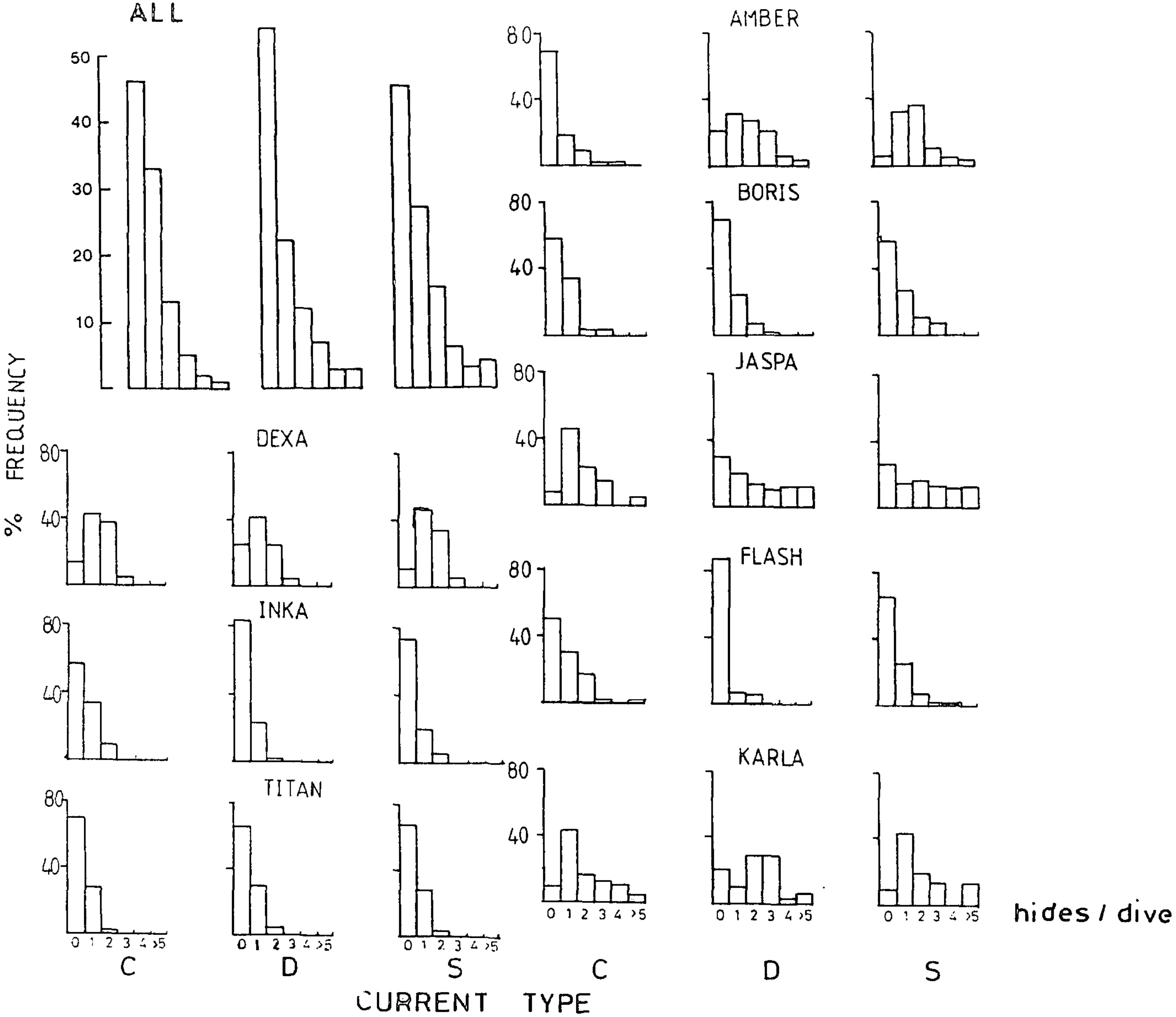

MEAN NUMBER OF HIDES VISITED / DIVE
AMBER
BORIS
JASPA
xx
6
4
2
ALL
3
2
1
x
x
C
D
S
DEXA
FLASH
KARLA
KARLA
TITAN
5
3
1
C D S
C D S
C D S
C D S
C D S
CURRENT TYPE

dive than any other female (for all conditions), yet her mean dive durations were of the same order as those for the other females. This does at least suggest that mink are capable of altering the rate of hide visits.

The final point to note is that in 16 out of the 27 results, the mean number of hides visited per dive was 1.5 or more. This can be compared to the results obtained in the depth experiment where the maximum mean value, at water depth 0.60 m, was 1.26 hides per dive, for the male Raja. The mean value for All Animals at this depth was only 1.13 hides visited per dive. It was also noted that many dives involved three or more visits to hides, with the maximum being nine for male Jaspa, whereas the maximum number visited at depth 0.60 m, in the depth experiment, was two.

4.3.11. The relative frequency of hide visits under the various current conditions

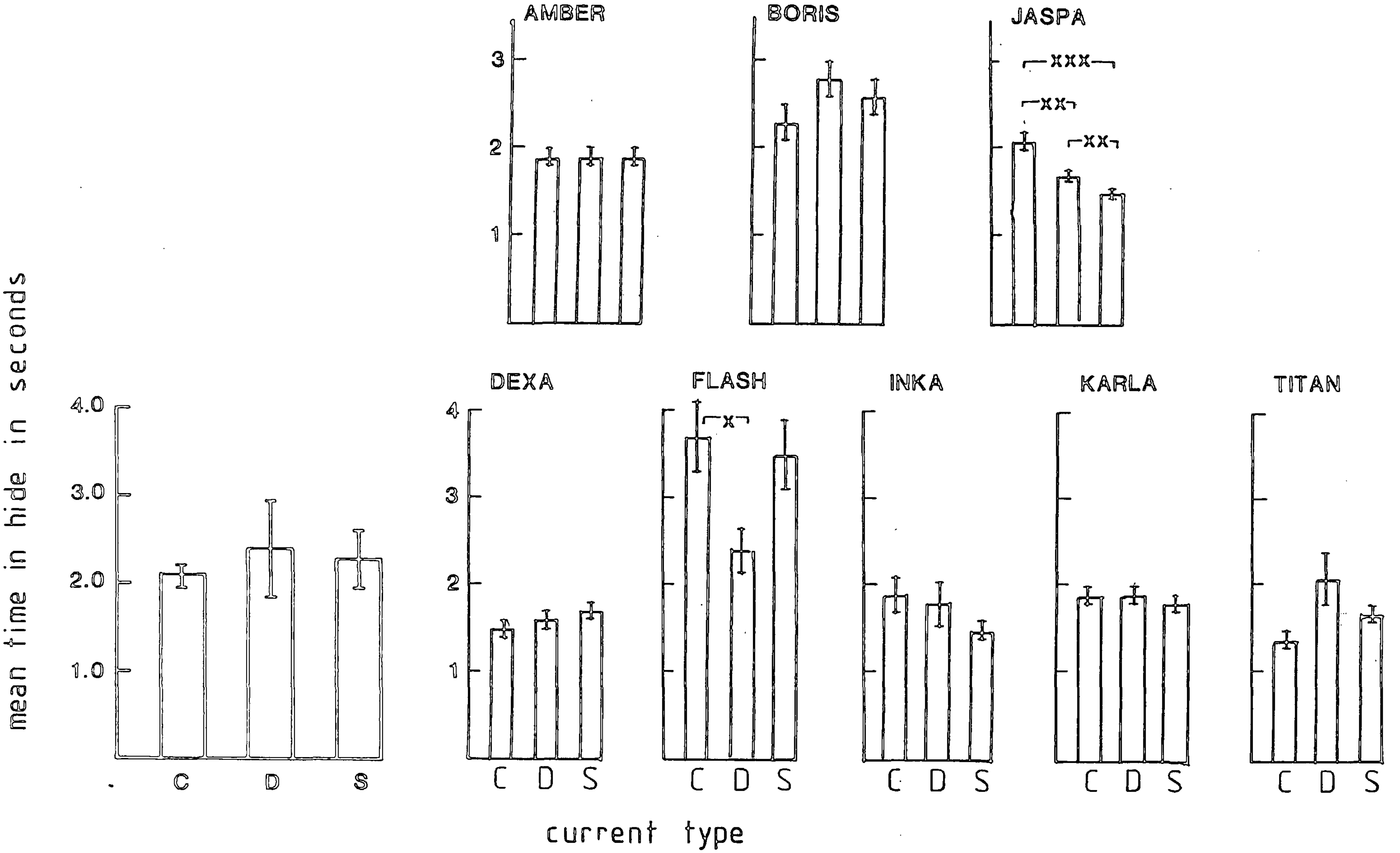
The inter-animal variability in mean number of hides visited per dive under different current conditions is demonstrated in Fig. 4.10. This shows the % frequency of dives involving 0,1,2,3,4 and 5 or more hide visits for control, deep current and surface current conditions. In this case data for all dives have been combined. One point to note is that, generally, for All Animals and individuals, the proportion of dives in which no hides were visited is approximately the same, regardless of current condition or control, although the actual values vary between animals. Most dives visiting hides, searched either one or two hides, but occasionally three hides were visited per dive. Finally, in contrast to the previous experiment at the same depth, some dives involved as many as seven hide visits per dive.


ALL
AMBER
BORIS
JASPA
FLASH
KARLA
DEXA
INKA
TITAN
% FREQUENCY
50
40
30
20
10
80
40
0 1 2 3 4 >5
hides / dive
C
D
S
CURRENT TYPE

4.3.12. Mean Time in Hide

Generally, this behaviour lasts for one to two seconds, and is the period during which an animal pushes open the door of a hide, scans the interior and removes the food reward, if it is present. In the results of the previous experiment, it was shown that mean time in hide was greater for successful visits, and this could be explained by the extra time required to remove the food reward from the hide. However, it is possible that even during searches of hides which are not baited, animals may alter the amount of time spent 'checking' to ensure that there is no food reward present. This would be expected, particularly if environmental conditions were such that the cost in terms of energy expenditure were great. Here, it might be expected that animals would increase the amount of time spent in hide to ensure that hides were thoroughly searched.

To investigate this, data for unsuccessful hide visits only were analysed. Mean time in hide ± S.E. was calculated for All Animals and individuals, as is illustrated in Fig. 4.11. It can be seen that the only significant results are for male Jaspa and female Flash. For Jaspa, mean time in hide was about 0.5 s greater in the control, compared to either of the experimental conditions. Thus, control compared to deep current: $t= 2.95$, $df = 127$, $p<0.01$; control compared to surface current: $t= 5.12$, $df = 133$, $p<0.001$. Also, for deep compared to surface current: $t= 2.66$, $df = 190$, $p<0.01$, and here mean time in hide was slightly greater when deep current flowing. Similarly, for female Flash, mean time in hide was greater in the control than in the experimental conditions, but the difference was only significant in control compared to deep current: $t= 2.22$, $df = 34$, $p<0.05$, where the animal spent roughly one second longer in each hide in the control. For the remaining individuals, it can be seen that whilst the differences are not statistically significant, in many cases mean time in hide is slightly greater in the control compared to the experimental conditions, although S.E. bars show that there may be considerable overlap.



mean time in hide in seconds
4.0
3.0
2.0
1.0
C
D
S
AMBER
BORIS
JASPA
3
2
1
xxx
xx
xx
DEXA
FLASH
INKA
KARLA
TITAN
4
3
2
1
x
C D S
C D S
C D S
C D S
C D S
current type

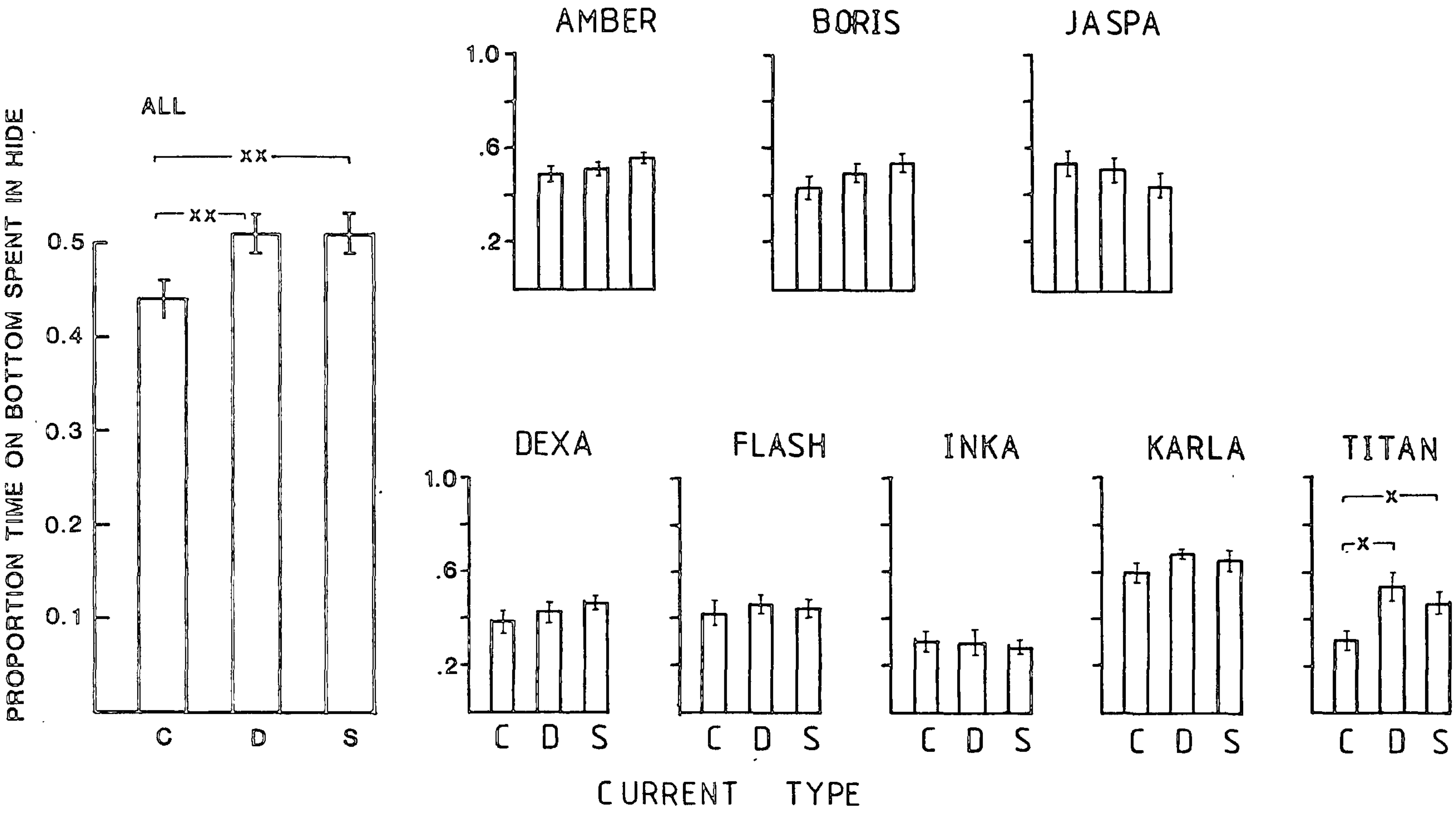
It must be noted that although, generally, the differences in mean time in hide are only of the order of 0.5 s, since mean time on bottom is, generally, approximately 8 s, this represents 6% of the available foraging time. If the animal were to visit three hides, for instance, and search each of them for 0.5 s longer than usual, this would account for roughly 18% of the foraging time, and would presumably result in dive durations being extended.

4.3.13. Proportion of Time on Bottom spent Hide Searching

Since the time spent hide searching and on the bottom are small, (a few seconds only), changes in behaviour between the control and experimental situations may not be clearly apparent, particularly in view of the great individual variations in behaviour. Thus, the proportion of time on bottom spent hide searching was calculated for unsuccessful dives as outlined in 3.3.13. Fig. 4.12 illustrates the results and significant t-test analyses between the three conditions. It can be seen that there are significant differences in the proportion of time spent hide searching in the control and experimental conditions only for All Animals and for the female Titan. Thus, control compared to deep current: All Animals: t= -2.73, df = 220, $p<0.01$; Titan: t= -2.69, df = 16, $p<0.05$. For control compared to surface current: All Animals: t=-2.83, df = 255, $p<0.01$; Titan: t= -2.26, df = 17, $p<0.05$). There were no significant differences when the two current conditions were compared.

4.3.14. Distance Travelled

The distance travelled was obtained using the digitiser and tracking arm (see 2.4.). The data were calculated only for that section of a dive when the animal was foraging on the


ALL
PROPORTION TIME ON BOTTOM SPENT IN HIDE
0.5
0.4
0.3
0.2
0.1
xx
xx
C
D
S
AMBER
BORIS
JASPA
1.0
.6
.2
DEXA
FLASH
INKA
KARLA
TITAN
1.0
.6
.2
x
x
C D S
C D S
C D S
C D S
C D S
CURRENT TYPE

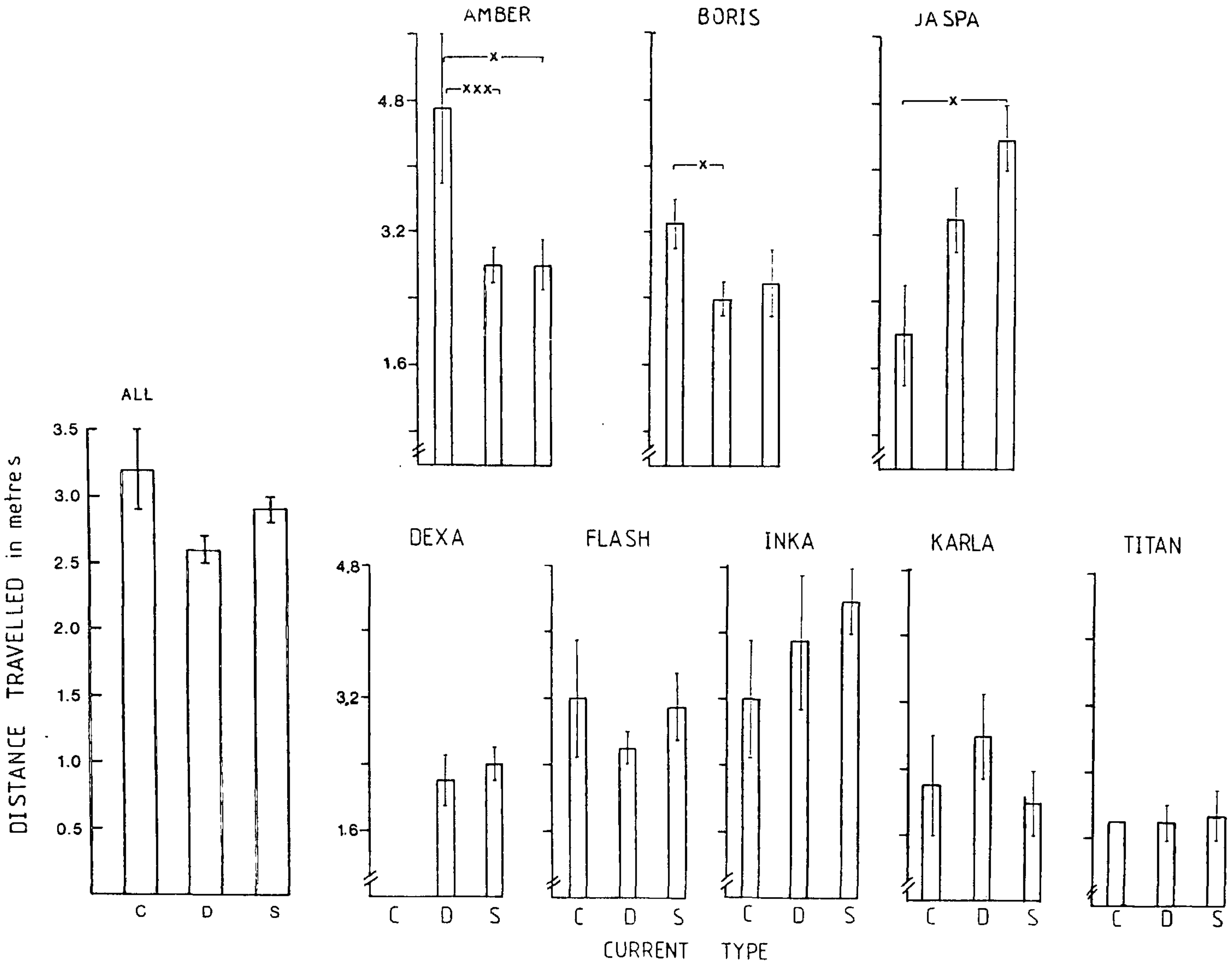
bottom of the pool. Mean values for distance travelled ± Standard Error are illustrated in Fig. 4.13.

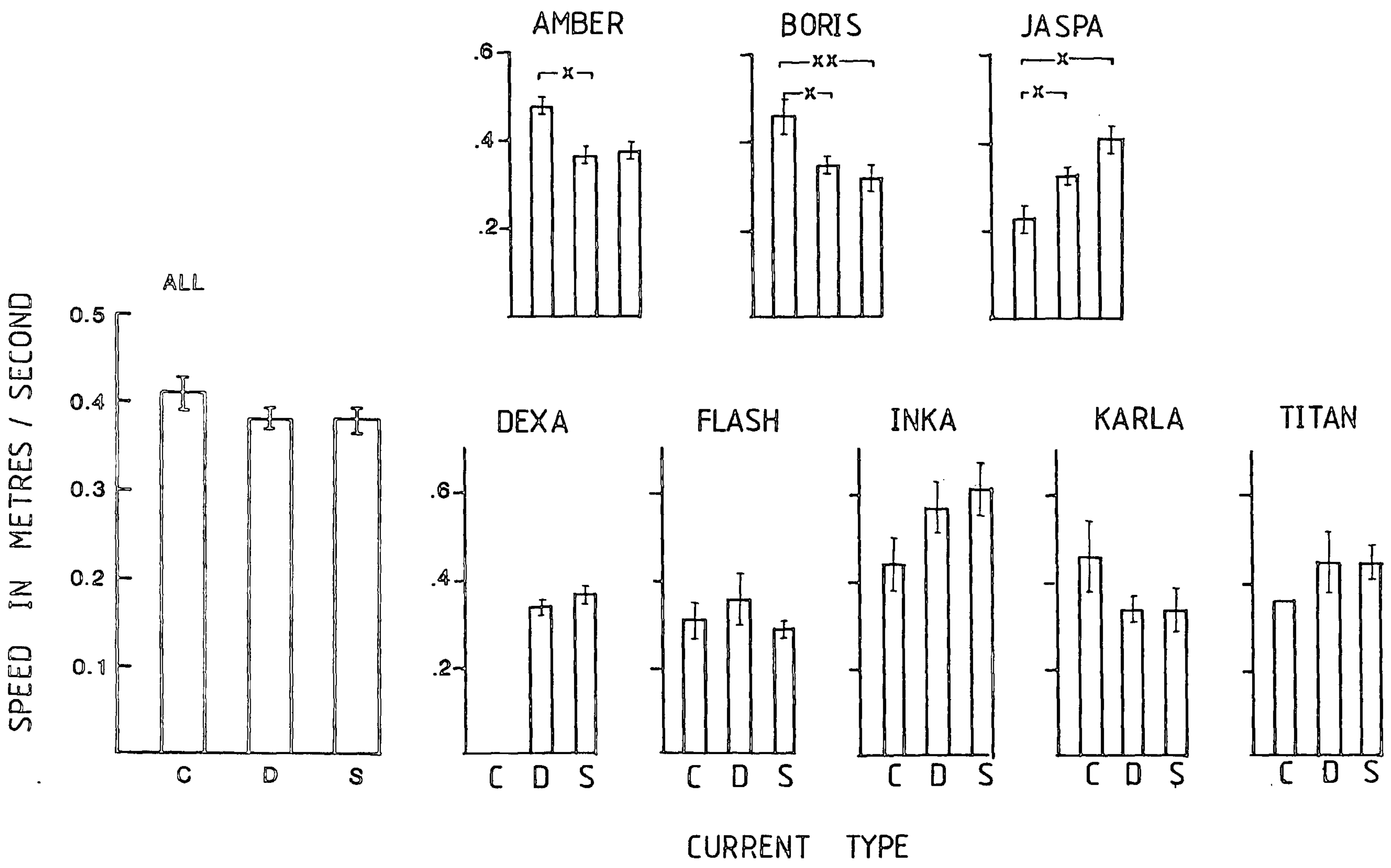
It can be seen that there are only significant differences amongst individual males. Thus, for comparison of the control and deep current conditions, significant results were obtained for Amber: t= -3.72, df = 40, p<0.001, and Boris: t= -2.62, df = 32, p<0.05. In each case mean distance travelled was greater in the control. Comparison of the control and surface current gave significant results for Amber: t= -2.65, df = 34, p<0.05 and Jaspa: t= -2.68, df = 16, p<0.05. However, these results are difficult to interpret since for Amber distance travelled on bottom is much greater in the control compared to surface condition, but the reverse is true for Jaspa. Similar variability is shown by the data for individual females, although none of the results are statistically significant. Finally, there were no significant results when deep and surface current conditions were compared, although from Fig. 4.13, it does appear that, generally, the mean value for distance travelled was greater when surface current was operating.

4.4.15. Speed of Travel on Bottom

This was calculated for each successful dive by dividing total distance travelled on the bottom in metres by total duration of time on bottom in seconds. From this a mean value for speed could be calculated for all animals and each individual under the three current conditions. Fig.4.14 illustrates theresults for mean speed ± S.E. and significant t-test analyses.

It can be seen that there are no significant differences for All Animals or for individual females, between the current conditions. Significant results were obtained for comparison of control and deep current for: Amber: t= -2.60, df = 40, p<0.05, Boris: t= -2.63, df =


AMBER
BORIS
JASPA
x
xxx
x
x
4.8
3.2
1.6
ALL
3.5
3.0
2.5
2.0
1.5
1.0
0.5
DISTANCE TRAVELLED in metres
C
D
S
DEXA
FLASH
INKA
KARLA
TITAN
4.8
3.2
1.6
C
D
S
C
D
S
C
D
S
C
D
S
C
D
S
CURRENT TYPE


AMBER
BORIS
JASPA
ALL
DEXA
FLASH
INKA
KARLA
TITAN
SPEED IN METRES / SECOND
0.5
0.4
0.3
0.2
0.1
.6
.4
.2
x
xx
C
D
S
CURRENT TYPE

32, $p<.0.05$ and Jaspa: $t= 2.27$, $df = 14$, $p<0.05$. In all cases, except Jaspa, mean speed of travel was greater (by about 0.1 $m\ s^{-1}$) in the control condition. When control and surface current were compared, significant results were obtained for Boris: $t= 2.91$, $df = 34$, $p<0.01$ (where speed was greater in the control) and Jaspa: $t= -2.85$, $df = 16$, $p<0.05$ (where speed was greater when surface current was operating). There were no significant differences in mean speed of travel when deep and surface current results were compared.

Finally, in most cases, the mean speed was less than 0.4 $m\ s^{-1}$,regardless of whether a current was flowing, or not.

4.4.16. Directionality of Dives

One variable which might indicate whether current flow has an energetic effect on the foraging behaviour of mink is the directionality of dives, i.e. whether mink swim with or against the current flow when foraging on the pool bottom. This will only really be of any significance when a deep current is flowing, but it is possible that even when a surface current is operating this may influence the direction in which mink dive. Data were obtained from the plotter outputs generated by the Behpath programme, (see Fig. 2.3). Dives were scored as being 'With' or 'Against' the direction of flow of the current. In many cases, animals dived to the pool bottom, swam directly to a hide and then either surfaced, or returned directly to the base of the rostrum. Such dives were not included. Similarly, many dives were made where animals simply circled the rostrum, and again these were not included. Finally, any dives where the direction could not easily be ascertained, e.g. if there were several dives overlying one another on the 'Behpath' plot, such that although the end-points of the dives could be seen, the outward and return stages could not be identified, were also excluded from the analysis. As a result data were examined for a total of 621 dives. The results of number of dives 'With' and 'Against' the current flow, for deep and surface currents are given in Table 4.19. A Chi-Squared analysis was carried out to see if animals favoured swimming with or against the current. The results are also given in Table 4.19, from which it can be seen that for all animals, except Dexa, there was no significant difference in the number of dives 'With' or 'Against' the current flow when either deep or surface current was flowing. For Dexa, it can be seen that she performed significantly more dives 'Against' the direction of flow of the current, when a deep current was operating.

4.4.17. Revisiting of Hides

In this experiment, there were 30 hides of which only ten were baited at the start of each trial, i.e. prey density was 33%. It has been noted above that the proportion of successful hide visits to total hide visits was, in some cases as much as 40%. If, during a trial, an animal searched each hide once, a proportion of 33% would be expected. Since only three trials out of a total of 121 trials, under all conditions, involved more than 30 hide visits, it might be expected that the proportion of successful hides visited would be lower than 33%. However, the food rewards were distributed in a random fashion, and were not replenished during a trial. Thus, the greatest degree of success should be achieved, if mink followed a foraging strategy whereby they did not revisit hides that had already been investigated. To investigate this, the number of 'new' hides visited during a trial was scored as well as the number of 'revisits'. However, since very few animals searched 30 hides during a trial, simply scoring new or revisit for each hide visit during a trial would lead to a bias in favour of new. In order to compensate for this the 15th hide visit was examined for each trial, since then there is a 50:50 chance of that particular visit being to a new hide or being a revisit. In order to obtain more data, it was decided to examine the 12th to 18th hide visit inclusive. Visits were scored as being to new hides or revisits, and the results are given in Table 4.20. The null hypothesis is that there is an equal chance of

Table 4.19: Directionality of dives when current flowing.

		DEEP	SURFACE
All	W	158 (167.5)	141 (143)
	A	177 (167.5)	145 (143)
	χ^2	1.08 p = ns	0.06 p = ns
Amber	W	22 (21.5)	11 (12.5)
	A	21 (21.5)	14 (12.5)
	χ^2	0.02 p = ns	0.36 p = ns
Boris	W	23 (25.5)	22 (22.5)
	A	28 (25.5)	23 (22.5)
	χ^2	0.49 p = ns	0.02 p = ns
Jaspa	W	23 (20.5)	12 (16.5)
	A	18 (20.5)	21 (16.5)
	χ^2	0.61 p = ns	2.45 p = ns
Dexa	W	6 (10.5)	14 (14.5)
	A	15 (10.5)	15 (14.5)
	χ^2	3.86 $p<0.05$	0.03 p = ns
Flash	W	19 (22)	22 (21.5)
	A	25 (22)	21 (21.5)
	χ^2	0.82 p = ns	0.02 p = ns
Inka	W	32 (32)	28 (26)
	A	32 (32)	24 (26)
	χ^2	0.00 p = ns	0.31 p = ns
Karla	W	12 (13)	7 (7.5)
	A	14 (13)	8 (7.5)
	χ^2	0.15 p = ns	0.07 p = ns
Titan	W	21 (22.5)	25 (22)
	A	24 (22.5)	19 (22)
	χ^2	0.20 p = ns	0.82 p = ns

W = number of dives 'with' current flow. (n) = expected number for Chi-square test.
A = number of dives 'against' current flow. df = 1 in all cases.

Table 4.20: Number of New hide visits and Revisits for 12th to 18th hide visit of each trial

		CONTROL	DEEP CURRENT	SURFACE CURRENT
All	N	39 (31.5)	56 (43.5)	59 (40.5)
	R	24 (31.5)	31 (43.5)	22 (40.5)
	χ^2	3.57 p = ns	7.18 $p<0.01$	16.90 $p<0.01$
Amber	N	4 (3.5)	23 (14.5)	21 (14.5)
	R	3 (3.5)	6 (14.5)	8 (14.5)
	χ^2	insufficient data	9.97 $p<0.01$	5.83 $p<0.05$
Boris	N	- (-)	- (-)	1 (2.5)
	R	- (-)	- (-)	4 (2.5)
	χ^2	-	-	insufficient data
Jaspa	N	14 (8.5)	23 (21)	24 (15)
	R	3 (8.5)	19 (21)	6 (15)
	χ^2	7.12 $p<0.01$	0.38 p = ns	10.80 $p<0.01$
Dexa	N	- (-)	- (-)	3 (1.5)
	R	- (-)	- (-)	0 (1.5)
	χ^2	-	-	insufficient data
Flash	N	0 (3.5)	- (-)	- (-)
	R	7 (3.5)	- (-)	- (-)
	χ^2	insufficient data	-	-
Inka	In no trial did Inka visit 12 hides.			
Karla	N	21 (16)	10 (8)	10 (7)
	R	11 (16)	6 (8)	4 (7)
	χ^2	3.13 p = ns	1.00 p = ns	2.57 p = ns
Titan	In no trial did Titan visit 12 hides.			

N = number of new hides visited.
R = number of revisited hides.
(n) = expected number for Chi-square test.
df = 1 in all cases.

these visits being to either new or old hides. A Chi-Square analysis was carried out and the results are also given in Table 4.20.

There are several points to note. Firstly, it can be seen that in several cases animals did not visit as many as 12 hides during a trial, under any conditions, hence this analysis could not be carried out. Further, in some cases where 12 or more hides had been visited, the data were still insufficient for a Chi-Square analysis to be carried out as the expected value was less than five. Secondly, of the 11 results which could be analysed, six were significant and five not. Of the significant results, it can be seen that in all cases, the bias of hide visits is towards visiting new hides. Thus, within each trial, animals seem to be capable of remembering which hides have already been searched and avoiding them in subsequent dives. This is the case regardless of current condition.

4.5. Discussion

Since mink are known to live on river banks (e.g. Mech, 1965; Birks and Linn, 1982), they will obviously have to cope with a current flow when foraging. This experiment attempted to study the effect that a current flowing on the water surface, and a current flowing near the pool bottom, might have on the foraging strategy and efficiency of mink hunting for dead prey underwater. Before attempting to interpret the results obtained, it is necessary to consider what the likely effects of a current flow might be.

It might be expected that having a deep current flowing would increase the energetic cost of a dive, particularly if animals were swimming into the current. Williams (1983a) measured the maximum surface swimming speed of mink, by forcing them to swim against a current in an enclosed chamber. She recorded a maximum swimming speed of 0.70 m s^{-1} as determined by the behaviour of the mink, i.e. the animals refused to swim against a current of greater speed. In this experiment, the speed of the current at the outflow was between 0.84 and 0.86 m s^{-1}, (depending on the direction of current flow), and from Williams' results, this would clearly be expected to have an effect on the energetics of a dive. However, it must also be noted that the speed of the current decreased dramatically with distance from the outflow pipe, and for dives in the region of 'C' (Fig. 4.2), current flow might well have had a minimal effect. Nevertheless, dives into other regions of the pool, would have to contend with a substantial current flow, and it would be expected that energy expenditure, and hence oxygen consumption, would be increased leading to changes in dive duration. This is similar to what was expected as water depth was increased, and it might be expected that similar changes in behaviour would occur. Thus, with a deep current flowing, animals might be expected to make fewer dives per minute, because of the higher energy cost needing a longer recovery period.

Animals might also be expected to increase dive duration to try and maximise the number of prey encounters (by visiting more hides per dive), if overall dive rate was decreased. Alternatively, it is possible that swimming against a current would cause such a great increase in energy consumption that animals were not able to increase dive duration to any appreciable extent. In such a case, animals might adopt a particular search strategy to make the most efficient use of time available underwater. Thus, it would seem that energy expenditure could be reduced if animals chose to swim with, rather than against the current. Further, since 33% of hides were baited, and food was not replenished during a trial, the 'optimum' strategy would seem to be one whereby animals did not revisit hides, particularly those where the search had been rewarded. Thus, animals should try and increase the number of hides searched during a dive, provided that each hide visited was a 'new' hide.

When a surface current was operating, the mink were faced with a different problem. The velocity of the current at the outflow was still considerable (0.60 to 0.63 m s^{-1}, depending on direction), but again speed decreased dramatically with distance from the outflow. In this case the problem was more one of hide location, rather than swimming energetics. Poole and Dunstone (1976) showed that mink prefer aerial location of prey. When a surface current was operating the disturbance to the water surface was considerable, particularly in the region of the outflow, with waves found over all the water surface. Mink might therefore be expected to increase dive duration in order to provide extra time for locating hides on the pool bottom. Again, a non-revisit strategy would seem to be appropriate. Although current flow underwater would be negligible, it might still be expected that mink would not dive into the current particularly at the outflow. Williams (1983a) showed that when swimming underwater, the elongated shape of the mink reduced body drag, and hence reduced energy expenditure. However, it is possible that the strong surface current at the outflow would increase friction (and hence drag) at least until mink were completely underwater. As a result, mink might be expected to avoid diving in this area of the pool. In view of these points the results obtained will now be evaluated.

It might be expected that dive rate would be lower when a current was flowing. The results however (Fig. 4.3), showed that where differences were significant, there were a greater number of dives per minute performed when either deep or surface current was operating. It is possible that the energetic effect is not as great as originally thought, and that in fact a current flow has a certain 'novelty value', resulting in mink performing more dives per minute. This would seem to be supported by the observation that many dives when deep current was operating, were directed to the current outflow pipe, and did not involve any hide visits. When a surface current was operating, there may also have been an element of 'novelty value', but it is also possible that animals were performing more dives per minute in order to locate hides which could not be seen from out of the water, because of the surface disturbance.

If current flow did have an effect on the energetics of diving, it might be expected that mink would visit hides during every dive to maximise prey encounter rate, but if current simply had a 'novelty value' effect this would not necessarily be the case. The results for hide visit dive rate (Fig. 4.4), do show that, generally, there was little difference between the control and experimental conditions. Differences were only significant for three cases when control and surface conditions were compared, and in each case, hide visit dive rate was higher when the current was flowing. However, in view of the fact that, generally, overall dive rate was greater in the experimental conditions, it is possible that the proportion of total dives visiting hides is changing significantly, and this will be discussed below.

First, the results for successful dive rate will be briefly discussed. This parameter can be used to give a rough guide to foraging efficiency. In general, there were few significant differences in mean successful dive rate between the various conditions. Where differences were significant, in some cases mean successful dive rate was greater in the experimental conditions compared to the control, in others the reverse was true. However, since many dives did not involve hide visits, this parameter is not really a good measure of foraging success. Its usefulness lies more in its value for comparison of the general number of successful dives per minute across experiments. In this case, mink generally achieved one successful dive every four minutes.

A better measure of foraging efficiency for this study, is the proportion of dives visiting a hide. These results (Fig. 4.5), appeared to suggest that although there was a higher dive rate in the experimental conditions, a smaller proportion of them visited a hide, supporting the view that more of the dives were used either for investigating the current flow, or for exploring the pool bottom to locate hides. Again in the majority of cases, there was no significant difference between control and experimental conditions. The final point to be made is that in most cases at least 40% of dives involved hide visits, and occasionally the proportion was as great as 95%. This was true for all conditions, and generally, (in 14 out of 27 results) the proportion of dives visiting hides was greater than 50%.

In view of this variability in the number of dives involving hide visits, a more accurate guide to foraging efficiency would be the proportion of successful hide visits to total hide visits. From Fig. 4.6 it can be seen that there were, generally, no significant differences between control and experimental conditions, and the proportion was usually less than 40%. It must be noted that there is considerable individual variation in behaviour as shown by differences in dive rate, proportion of dives etc. However, since many animals are achieving similar efficiency ratios, this implies that individuals may be adopting different foraging strategies.

From Fig. 4.5 it can be seen that, on average, 60% of dives involve a hide visit, and from Fig. 4.6 it can be seen that approximately 40% of hide visits are successful. Since prey density was only 33%, this indicates that mink are not searching randomly, but are using some strategy to improve their foraging success. The questions are, what is this strategy, and how is it affected by current flow? The most obvious method by which a mink could alter its foraging success would be to increase the number of hides visited per dive. Thus, it is possible that in the experimental situations, although it appears that mink perform fewer dives that visit hides, those that do may visit a greater number of hides, and therefore would be of longer duration. It would be expected that dives in which no food is found would be prolonged to the limit of the mink's diving ability. Thus, only unsuccessful dives were examined for most of the subsequent analyses.

It was however, found that in fact there was little difference in mean dive duration for control or experimental conditions (Fig. 4.7). However, there were individual differences. For individual females, dive duration was, generally, greater in the control compared to experimental sessions, whereas for males, duration was, generally, greater when a surface current was operating. It is possible that the females were performing more dives per minute in the experimental situation but each dive was of shorter duration than those in the control. This may be related to the fact that the water surface was disturbed by the current, thus animals were actually having to 'search' the pool whilst underwater to locate hides. Dunstone and O'Connor (1979b) examined the relationship between the 'search' and 'pursuit' durations of mink dives and found a strong negative correlation, i.e. as 'search' duration increased so 'pursuit' duration decreased. In this experiment mink were not required to pursue prey, but they did have to investigate hides once they had been located. Thus, mink may have been extending the 'search' phase of dives when surface current was flowing (i.e. searching the pool to locate hides), to such an extent that the 'hide search' phase was abandoned. This might then lead to a lower dive duration overall.

If this were the case, it might be reflected in the results for mean number of hides visited per dive etc., and will be examined below. Firstly, from above, mean dive duration for individual males tended to be greater when a surface current was flowing compared to control. The males used in this experiment were larger than the females. Stahl (1967) showed that larger animals have proportionately bigger lungs, blood volume etc., and since dive endurance ability would be expected to be related to oxygen storage capacity, it may be that male mink are using a different foraging strategy to females when a surface current is flowing. Thus, males also perform a greater number of dives per minute in the experimental compared to the control situation. However, a smaller proportion of those dives visit hides when a surface current is operating, even though mean dive duration is greater. Thus, it could be that when a surface current is flowing, male mink also extend the 'search' phase of their dives to explore the pool and locate hides, but having a possibly greater oxygen storage capacity than females, they 'choose' to also extend the hide search duration and search as many hides as possible once they have been located.

From the point of view of foraging strategy, time on bottom may be more important than dive duration in determining how many hides can be visited etc. In this experiment, however, water depth was constant, and hence travel time to the pool bottom would be expected to be constant for all conditions. However, current flow may affect the drag operating on a diving mink, and this might lead to a reduction in time on bottom in the experimental conditions. From Fig. 4.8, it can be seen that, generally, there were no significant differences in mean time on bottom between control and experimental conditions. This suggests that current flow did not have much effect on friction or drag. Generally, the results indicated that travel time was constant for control and experimental conditions. Thus, it could be concluded that changes in total dive duration do reflect changes in the amount of time being allocated for foraging activity. Thus, individual females were, generally, spending longer on the bottom in the control versus experimental conditions, whereas males, generally, spent longer on the pool bottom when surface current was flowing, and least time in the control.

In this study, all prey items were located in hides, therefore if mink are to maximize their foraging efficiency, they should always search at least one hide per dive, or preferably as many hides as possible per dive until a food reward was located. When the results for mean number of hides visited per dive are examined, (Fig. 4.9) it can be seen that, generally, there appears to be little change in the values for mean number of hides visited per dive between the control and experimental conditions. Thus, it does not appear that females may have longer mean dive durations during control conditions, because location of hides was easier and more hides were visited per dive. However, for Jaspa, significantly more hides were visited per dive when surface current was operating, and this can be related to a significant difference in both mean dive duration and mean time on bottom in surface compared to control conditions. However, for the remaining males, the longer dive duration noted when surface current was operating does not seem to lead to an increase in mean number of hides visited per dive. One point to note is that on average most dives involved one to two hide visits. This can be compared to the results for the depth experiment where most dives visited one hide and no dives visited more than three hides. Another important point is that (from Fig. 4.10), generally, at least 25% of dives in all conditions involved no hide visits, but often the proportion of such dives was greater in the experimental compared to control conditions. This indicates that perhaps more dives during experimental conditions were simply 'exploring' the pool and locating hides.

Since changes in mean time on bottom between the control and experimental conditions could not readily be explained by changes in the mean number of hides visited per dive, perhaps animals were adopting a different foraging tactic, namely searching individual hides more thoroughly. Results for mean time in hide during unsuccessful searches (Fig. 4.11) indicated that in fact there was little difference in the mean time in hide for control and experimental conditions. The results were only significant for the male Jaspa, where mean time in hide was greater in the control, (although Jaspa spent significantly longer on the pool bottom when surface current was flowing compared to control), and female Flash (who had anomalously large values for mean dive duration and time on bottom compared to the other females). On the whole mean time in hide is roughly 2 s, but for Flash the values are as high as 3.5 s in the control. This is very interesting in view of the fact that Flash has a mean dive duration in the control of over 12 s, yet on average she visits only one hide per dive and has the lowest successful dive rate of all the females. It appears from this that Flash is by no means an efficent forager underwater particularly in the control situation. Her performance does seem to improve, particularly when deep current is operating.

Generally, it does not seem that differences in dive duration in control and experimental situations could be explained by differences in techniques of hide searching. It is possible, since the durations involved are so small, and the variation in individual behaviour is great, that biologically significant differences are present but are being masked by this variation. Thus, the proportion of time on bottom spent hide searching was also examined (Fig. 4.12). Interestingly, where results were significant, the proportion of time on bottom spent hide searching was lower in the control compared to the experimental conditions. For the remaining results, the lack of any significant differences simply reflect the variations already noted in time on bottom, number of hides visited per dive etc., and do not suggest that there is any significant difference in foraging strategy between control and experimental conditions.

If the surface current was affecting the ability of mink to locate hides from out of the water, it might be expected that the animals would be forced to locate hides underwater. Mean distance travelled might then be expected to increase in the surface conditions. Thus, the parameters of distance travelled and speed were examined. Significant differences were only found for the individual male results, and, generally, (except for Jaspa) the distance travelled per dive was greater during the control situations. For Jaspa, it appears that the longer dive durations recorded during surface trials, may in fact be due to travelling further on the pool bottom. However, for the other males, mean dive duration was not significantly different, yet in each case distance travelled was significantly greater in the control, especially when compared to deep conditions (Fig. 4.13). In the control sessions, it would be expected that animals would easily be able to locate hides aerially and could then swim directly to them. If the first hide was empty, animals should move to another hide, and so on. This would be expected to give rise to an increase in mean distance travelled per dive, but also to a rise in mean number of hides visited per dive which was not seen. Similarly, when a surface current was operating, if mink have difficulty in locating hides aerially they would then be forced to dive and search for hides underwater. This might result in a lower value for mean number of hides visited per dive, but would be expected to produce a larger value for mean distance travelled compared to the control. This was not the case. Finally, with a deep current flowing, it is possible that although hides could be easily located aerially (there was no surface disturbance visible to the observer) once animals dived and encountered the current their foraging behaviour was disrupted. Thus, in control conditions, it is possible, since mink are considered to be opportunistic predators, that some of the dive duration was spent in exploring the pool bottom in an attempt to find other more accessible prey items, although in fact there never were any items located outside hides once an experiment was begun, but loose food was used during initial training.

When the results for mean speed of travel are examined (Fig. 4.14), comparisons are again only significant for individual male results. Here mean speed of travel was greater for the control compared to experimental conditions, for all except Jaspa. In view of the shorter dive durations and longer distances travelled by Amber and Boris this is not surprising. The final point to note is that generally mean speed was roughly 0.4 m s^{-1} regardless of individual or current condition. This will be discussed further in Chapter 7 where the implications of such a slow underwater speed will be considered in relation to the known facts about aquatic components of mink diet and their habits.

The final parameters to be studied were the directionality of dives and the amount of revisiting. If current, particularly deep current, had an effect on the energetics of diving, it might be expected that animals would prefer to swim with, rather than against, the current. The results however (Table 4.19), showed that in all except one case, there was no significant difference in the number of dives with, or against, the current flow. This certainly implies that current flow (at the velocities investigated) did not affect the diving behaviour. However, it must also be remembered that as distance from the outflow pipe increased, the velocity of the current flow dropped dramatically. Many dives involved foraging in parts of the pool where the current flow would be weak, but equally, on many occasions animals dived directly to the outflow pipe.

Finally, with regard to the foraging strategy used by mink, an analysis of the amount of hide revisiting was carried out. Since baited hides were not replenished during a trial, the optimum strategy would seem to be one of visiting new hides, particularly in view of the fact that the proportion of dives visiting hides appeared to be lower in the experimental conditions, yet successful dive rate was similar for all conditions. The results of this analysis (Table 4.20) showed that where there were significant differences, in all cases, animals did seem to be adopting a 'search new hides' strategy.

Thus, in conclusion, the results obtained show that, generally, the mink's behaviour was unaffected by the presence or absence of a current. It must be noted that the current speed used in this experiment was considerably less than what a mink might experience in the wild, e.g. Chanin and Linn (1980) record measurements of the current flow in the River Teign, of 1.3 $m^3 s^{-1}$, although the authors did think that mink probably concentrated their efforts in the quieter stretches. The water depth where current flow was measured varied between 0.1 m and 2.4 m during their study. Finally, there are some indications from the results of this experiment that surface disturbance does inhibit foraging abilities to some extent, but, generally, the mink seemed able to cope quite adequately with the conditions provided, despite the results of Williams (1983a) on maximum surface swimming speeds.

CHAPTER 5

THE EFFECT OF PREY DENSITY AND ENVIRONMENTAL COMPLEXITY ON THE UNDERWATER FORAGING BEHAVIOUR OF THE MINK

5.1. Introduction

This experiment attempts to investigate the effect of changes in prey density and environmental complexity, on the underwater foraging behaviour of the mink. Pyke (1984) in his review of Optimal Foraging Theory, outlines a number of criteria which he feels should be met by studies attempting to investigate the foraging behaviour of an animal, in relation to predictions made by Optimal Foraging Theory (O.F.T.). This experiment was not designed to provide quantitative data for testing predictions made by O.F.T., rather it was designed to study how changes in the foraging environment affected the foraging strategies employed by mink. It was hoped, however, that qualitative information would be obtained which could then be related to the broad predictions of O.F.T. Thus, Pyke felt that laboratory studies should mimic natural foraging situations as closely as possible. This was clearly not the case in these experiments. For instance, tests were not carried out under a system of 'closed foraging economics' (Pierce, 1985), i.e. animals did not depend on the food rewards obtained during the experiment for their daily energy intake.

This experiment investigates the underwater foraging behaviour of the mink at each of three hide arrangements, and at each of four prey densities, thus allowing comparisons of foraging behaviour at a given density, but under different hide distribution conditions and vice versa.

5.2. Materials and Methods

5.2.1. Subjects

Six animals were used, three females (Flash, Inka, Titan) and three males (Amber, Bill, Boris). All except Bill, had been used in previous experiments, (see Appendix I) and were familiar with the experimental arena and hide searching.

5.2.2.Maintenance

All animals were mature by the beginning of this experiment in July 1983. By this time, the two females Inka and Titan were approximately 38 months old. The remaining female, Flash, and the two males, Amber and Boris, were approximately 26 months old, while the remaining male, Bill, was 14 months. All animals had undergone a strict training regime (see General Materials and Methods: 2.6. Preliminary Training) to ensure proficiency in swimming, diving and hide searching.

For a week prior to the start of the experiment, all the animals to be used were brought into the experimental arena for a period of refamiliarization. Ten hides (all baited) were distributed randomly throughout the pool. A resting place was provided in each half of the pool and water depth was 0.60 m.

After this period, the arena was prepared for this experiment, and data collection began. In this experiment animals were tested between 14.00 and 20.00 hours, and received 75% of their maintenance diet on their return to their 'home' cage. The remainder was made up of food rewards obtained during the experiment, and additional eel given if necessary on return to the 'home' cage. As before, excess food was removed by high pressure hosing at 0900 hours each day. Animals had thus been deprived of food for between 5-9 hours prior to the start of their experimental trial. Order of testing animals was varied at random daily, to avoid the same animal being consistently deprived for a long or short period prior to the experimental trial.

5.2.3. Experimental Arena

Prior to the start of this experiment, the bottom of the 'deep' end was raised, such that the floor level was now equal to that in the 'shallow' end, i.e. water depth would now be the same throughout the pool. The experiment was carried out with the water depth at 0.60 m.

5.2.4. Experimental Procedure

For this experiment 32 hides were used, 16 in each half of the pool. One resting place was provided as near to the centre as possible. Access to the pool was provided by a removable wooden ramp, and the position of entry of the mink to the rostrum was varied for each individual and for each trial.

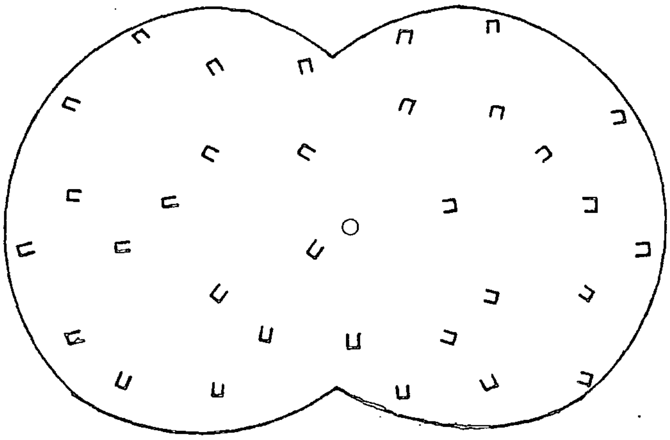
Four prey densities were used:-

25% - 8 hides baited (4 in each half)
50% - 16 hides baited (8 in each half)
75% - 24 hides baited (12 in each half)
100% - 32 hides baited (16 in each half)

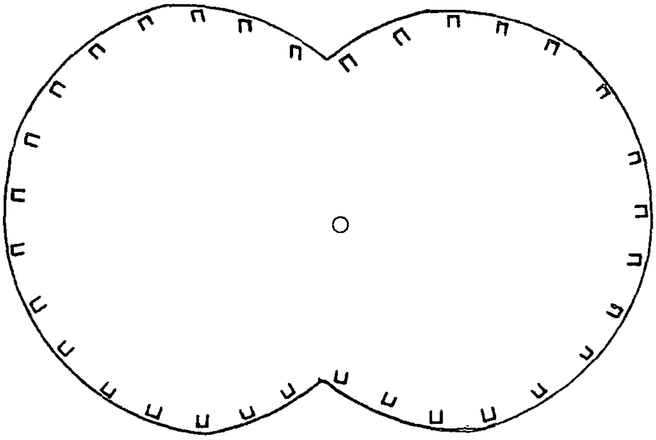
The hides were also arranged according to one of three distrbution patterns (Fig. 5.1), namely:-

Regular : hides arranged around edge of pool.
Random : hides scattered throughout pool.
Clumped : 4 clumps of 4 hides in each half of pool.

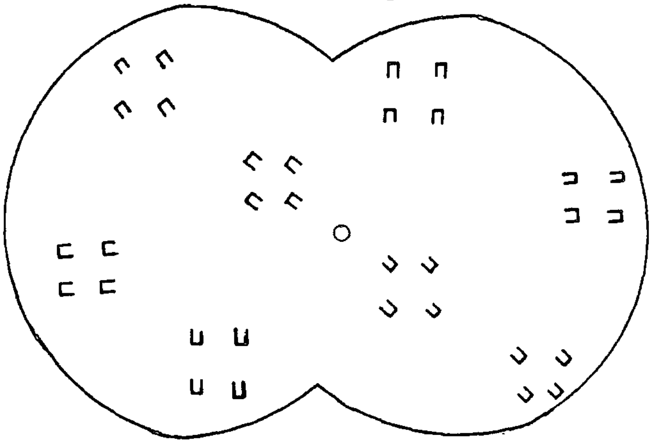
RANDOM



REGULAR



CLUMPED



For prey densities less than 100%, a random number table was used at the beginning of each session to determine which hides should be baited. The hides chosen to be baited remained fixed for all trials within that session. During a trial, hides which were emptied by the mink were not refilled, but bait was replenished prior to the start of the next trial. Detailed records were kept of the position of baited hides and modifications were made if the random number tables indicated that the same hide was to be baited for several consecutive sessions. Changes were also made if all baited hides were, e.g. close to the rostrum in the regular distribution. Finally, for the clumped distribution, the number of hides to be baited within each clump was equal, i.e. at 25% prey density, four hides were to be baited in each half of the pool, one hide in each clump. In this case, the observer decided which hides to bait and changed them accordingly for each session. Thus, it was hoped that mink would not develop any position tendencies with regard to baited hides.

It was also hoped that the three hide arrangements would represent some change in the complexity of the minks' hunting environment, with the clumped distribution analagous to food patches. The random and regular distributions would represent a more evenly distributed food source, especially at the higher prey densities. For this reason, in the analysis of results, the hide arrangement is referred to as the 'habitat complexity' parameter.

Each animal was given one trial per day under a particular set of conditions. Trials were repeated on subsequent days until all animals had achieved a minimum of 30 hide visit dives under that set of conditions. Thus, the total number of dives recorded was generally greater than 30. However, due to lack of time, if an animal was given six trials under a particular set of conditions, and failed to provide the required number of hide visit dives, trials were discontinued for that animal under those conditions. The order of presentation of the different densities and distribution patterns is given in Table 5.1. A trial was timed to last for 10 min or until the animal had completed a total of 20 dives, whichever was soonest. From Table 5.1, it can be seen that, on average, each combination of density and hide arrangement took five days to complete. In many cases a gap of approximately 10 days followed, during which data were transcribed from videotapes. For two days prior to the start of a new series animals were given only 75% of maintenance diet. Table 5.2 gives details on the total number of dives, and number of hide visit dives recorded for each animal under each of the 12 conditions.

The videotape data were transcribed using the Event and Behpath programmes onto an Apple II microcomputer. However, a problem arose, since now the entire pool was being used for the experiment, but the videocameras could only cover one half. This was overcome by using the videomixer which allowed the observer to switch from one camera to another as appropriate. However, when data were transcribed using Behpath, a code had to be added to indicate when the animal moved from Left to Right or vice versa, and the programme reset each time. This meant that when data were analysed using a Listplot programme, it was possible to obtain a complete pictorial representation of the movements of the mink (see Fig. 2.3), but it was found that the two cameras were somewhat out of alignment. Some correction could be made, but it was felt that data of distance travelled would have too great an error factor and hence it was not examined. Data on a total of 3,407 dives were obtained for analysis.

5.3. Results

Previous experiments had shown that there was often considerable variation in individual behaviour under the same conditions. Foraging success was also shown to contribute greatly to differences in the behaviour of an individual under any particular condition.

TABLE 5.1: Sequence of hide arrangements and prey densities used to investigate the effects of habitat complexity and prey density on underwater foraging behaviour of mink.

Dates	Hide Arrangement	Prey Density
3. 7.83 - 10. 7.83	REGULAR	50%
17. 7.83 - 20. 7.83	CLUMPED	50%
29. 7.83 - 4. 8.83	RANDOM	50%
29. 8.83 - 15. 9.83	REGULAR	100%
4.10.83 - 9.10.83	CLUMPED	100%
13.10.83 - 16.10.83	RANDOM	100%
20.10.83 - 27.10.83	REGULAR	25%
28.10.83 - 1.11.83	CLUMPED	75%
6.11.83 - 13.11.83	RANDOM	25%
29.11.83 - 5.12.83	REGULAR	75%
6.12.83 - 10.12.83	CLUMPED	25%
11.12.83 - 16.12.83	RANDOM	75%

TABLE 5.2: Number of dives and hide visit dives, (in brackets) recorded for each animal under each condition.

Condition	Amber	Boris	Bill	Flash	Inka	Titan	Total
25% REG	41 (36)	39 (38)	24 (19)	55 (12)	40 (35)	56 (31)	255 (171)
25% CL	63 (37)	58 (34)	57 (36)	60 (37)	58 (45)	61 (44)	357 (233)
25% RAN	47 (39)	48 (41)	39 (35)	52 (16)	42 (37)	69 (41)	297 (209)
50% REG	46 (31)	78 (27)	69 (18)	52 (34)	38 (17)	38 (35)	321 (162)
50% CL	45 (35)	64 (46)	45 (34)	37 (35)	36 (28)	15 (14)	242 (192)
50% RAN	30 (22)	51 (38)	43 (36)	38 (36)	32 (28)	40 (36)	234 (196)
75% REG	58 (27)	51 (34)	60 (30)	59 (28)	34 (17)	72 (25)	334 (161)
75% CL	41 (39)	41 (40)	41 (37)	71 (29)	45 (35)	50 (39)	289 (219)
75% RAN	42 (36)	53 (35)	45 (39)	47 (35)	38 (30)	48 (35)	273 (210)
100% REG	63 (46)	66 (37)	54 (39)	44 (35)	45 (41)	46 (40)	318 (238)
100% CL	40 (34)	50 (44)	46 (39)	38 (34)	40 (40)	40 (39)	254 (230)
100% RAN	42 (41)	41 (38)	42 (41)	30 (19)	41 (40)	37 (36)	233 (215)
TOTAL	558 (423)	640 (452)	565 (403)	583 (350)	489 (393)	572 (415)	3407 (2436)

Further, in this experiment, the aim was to investigate the effects not only of changes in prey density, but also of different habitat complexities. A series of Analysis of Variance tests were therefore carried out in an attempt to find out which factors were the most important in influencing changes in the underwater foraging behaviour of the mink.

5.3.1. Analysis of Variance

Anova tests were carried out on dive duration, time on bottom and total time in hide, with independent variables, Animal, Prey Density, Habitat Complexity and Success. The results of these Anova tests are given in Tables 5.3 to 5.5 but a summary can be outlined as follows:-

	Significant Main Effects	Sig.2 way Interactions	Sig.3 way Interactions
a) Dive duration	A,D,C,S	A x D, A x S, D x S, C x S.	A x D x C
b) Time on bottom	A,D,C,S	A x D, A x S, D x S, C x S.	A x D x C
c) Total time in hide	A,D,C	A x D, D x C,	-

There were no significant 4-way interactions.
A = Animal, D = Prey Density, C = Habitat Complexity, S = Foraging Success.

The main point to emerge from this preliminary analysis is that, for dive duration and time on bottom, all the variables tested had a significant effect, i.e. changes in dive duration were due both to individuals behaving differently under the same conditions of density and complexity, and to changes in behaviour of all animals as conditions of density and complexity were altered. Foraging success was also an important factor. If the results for total time in hide are considered, they are very interesting. Here, dives which did not visit any hides (roughly 30% of all dives) were obviously excluded from the Anova calculation. The result is that foraging success is apparently not a cause of changes in total time spent in hides, i.e. it did not matter if overall the dive had been scored as

TABLE 5.3: Anova of dive duration by Animal, Density, Complexity and Success.

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main Effects	10042.346	12	836.862	138.214	0.0001
Animal	3758.312	5	751.662	124.142	0.0001
Density	777.628	3	259.209	42.810	0.0001
Complexity	800.857	2	400.428	66.134	0.0001
Success	5560.707	2	2780.354	459.195	0.0001
2-Way Interactions	2989.802	51	58.624	9.682	0.0001
Animal Density	518.390	15	34.559	5.708	0.0001
Animal Complexity	117.633	10	11.763	1.943	0.036
Animal Success	1148.142	10	114.814	18.962	0.0001
Density Complexity	128.337	6	21.389	3.533	0.002
Density Success	171.290	6	28.548	4.715	0.0001
Complexity Success	663.260	4	165.815	27.385	0.0001
3-Way Interactions	994.032	92	10.805	1.784	0.0001
Animal Density Complexity	392.950	30	13.098	2.163	0.0001
Animal Density Success	295.914	30	9.864	1.629	0.017
Animal Complexity Success	122.022	20	6.101	1.008	0.499
Density Complexity Success	112.540	12	9.378	1.549	0.100
4-Way Interactions	509.324	59	8.633	1.426	0.019
Animal Density Complexity Success	509.324	59	8.633	1.426	0.019
Explained	14535.504	214	67.923	11.218	0.0001
Residual	19327.062	3192	6.055		
Total	33862.566	3406	9.942		

3407 Cases were processed.
0 Cases (0.0%) were missing.

TABLE 5.4: Anova of time on bottom by Animal, Density, Complexity and Success.

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	9440.633	12	786.719	139.283	0.0001
Animal	3787.009	5	757.402	134.092	0.0001
Density	654.404	3	218.135	38.619	0.0001
Complexity	745.391	2	372.696	65.983	0.0001
Success	5007.268	2	2503.634	443.250	0.0001
2-Way Interactions	2635.089	51	51.668	9.148	0.0001
Animal Density	444.797	15	29.653	5.250	0.0001
Animal Complexity	141.851	10	14.185	2.511	0.005
Animal Success	992.523	10	99.252	17.572	0.0001
Density Complexity	94.784	6	15.797	2.797	0.010
Density Success	164.942	6	27.490	4.867	0.0001
Complexity Success	544.231	4	136.058	24.088	0.0001
3-Way Interactions	931.959	92	10.130	1.793	0.0001
Animal Density Complexity	359.241	30	11.975	2.120	0.0001
Animal Density Success	260.741	30	8.691	1.539	0.031
Animal Complexity Success	130.445	20	6.522	1.155	0.285
Density Complexity Success	116.724	12	9.727	1.722	0.056
4-Way Interactions	465.411	59	7.888	1.397	0.025
Animal Density Complexity Success	465.411	59	7.888	1.397	0.025
Explained	13473.092	214	62.958	11.146	0.0001
Residual	18029.567	3192	5.648		
Total	31502.659	3406	9.942		

3407 Cases were processed.
0 Cases (0.0%) were missing.

TABLE 5.5: Anova of total time in hide by Animal, Density, Complexity and Success.

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	424.225	11	38.566	26.289	0.0001
Animal	250.294	5	50.059	34.124	0.0001
Density	76.562	3	25.521	17.397	0.0001
Complexity	107.368	2	53.684	36.595	0.0001
Success	0.466	1	0.466	0.317	0.573
2-Way Interactions	279.236	41	6.811	4.643	0.0001
Animal Density	103.391	15	6.893	4.699	0.0001
Animal Complexity	28.895	10	2.890	1.970	0.033
Animal Success	28.620	5	5.724	3.902	0.002
Density Complexity	76.056	6	12.676	8.641	0.0001
Density Success	15.446	3	5.149	3.510	0.015
Complexity Success	7.098	2	3.549	2.419	0.089
3-Way Interactions	134.734	61	2.209	1.506	0.007
Animal Density Complexity	76.038	30	2.535	1.728	0.008
Animal Density Success	21.531	15	1.435	0.978	0.475
Animal Complexity Success	20.702	10	2.070	1.411	0.169
Density Complexity Success	16.600	6	2.767	1.886	0.079
4-Way Interactions	55.790	30	1.860	1.268	0.151
Animal Density Complexity Success	55.790	30	1.860	1.268	0.151
Explained	893.984	143	6.252	4.262	0.0001
Residual	3357.908	2289	1.467		
Total	4251.893	2432	1.748		

3407 Cases were processed.
974 Cases (28.6%) were missing. (Non hide visit dives, and data lost during transcription of videotapes).

successful or not. But, it is found that not only do animals behave differently under the same conditions, but there is an important interaction between prey density and habitat complexity (Table 5.5). Thus, individual behaviour will vary with density, depending on which hide arrangement is being used, etc.

The situation is obviously complex. To investigate it further, a second series of Anova tests were perfomed. This time data were selected for analysis on the basis of foraging success. Thus, the effects of Animal, Prey Density and Habitat Complexity were investigated for successful and unsuccessful dives which visited hides. Dives which did not visit hides were not included in the analysis, as it was not possible to be sure whether animals were using these dives to explore the pool bottom, to obtain information on hide positions, (and therefore potential position of food rewards), or whether animals were just playing, as had been seen in previous experiments. The results are given in Tables 5.6 to 5.8 and the main points are summarised below:-

	Significant Main Effects	Significant 2-way Interactions
a) Dive duration		
(i) Successful dives	A,D,C	-
(ii) Unsuccessful dives	A,D,C	A x D
b) Time on bottom		
(i) Successful dives	A,D,C	-
(ii) Unsuccessful dives	A,D,C	A x D
c) Total time in hide		
(i) Successful dives	A,D,C,	D x C
(ii) Unsuccessful dives	A,D,C,	A x D

There were no significant 3-way interactions.
A = Animal, D = Prey Density, C = Habitat Complexity

There are several points to be made from these results. All three parameters, Animal, Prey Density and Habitat Complexity, influenced changes in behaviour, i.e. individuals were behaving differently when tested under the same conditions of density and complexity.

TABLE 5.6: Anova of dive duration by Animal, Prey Density and Habitat Complexity.

(i) Successful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	1433.858	10	143.386	25.237	0.0001
Animal	667.257	5	133.451	23.488	0.0001
Density	300.539	3	100.180	17.632	0.0001
Complexity	507.169	2	253.584	44.632	0.0001
2-Way Interactions	415.694	31	13.409	2.360	0.0001
Animal Density	204.875	15	13.658	2.404	0.002
Animal Complexity	78.567	10	7.857	1.383	0.183
Density Complexity	133.230	6	22.205	3.908	0.001
3-Way Interactions	279.263	30	9.309	1.638	0.017
Animal Density Complexity	279.263	30	9.309	1.638	0.017
Explained	2128.815	71	29.983	5.277	0.0001
Residual	5954.336	1048	5.682		
Total	8083.152	1119	7.224		

1120 Cases were processed.
0 Cases (0%) were missing.

(ii) Unsuccessful hide visit dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	4885.543	10	488.554	75.306	0.0001
Animal	3764.755	5	752.951	116.060	0.0001
Density	360.015	3	120.005	18.498	0.0001
Complexity	858.762	2	429.381	66.185	0.0001
2-Way Interactions	577.881	31	18.641	2.873	0.0001
Animal Density	405.701	15	27.047	4.169	0.0001
Animal Complexity	99.819	10	9.982	1.539	0.120
Density Complexity	50.767	6	8.461	1.304	0.252
3-Way Interactions	347.801	30	11.593	1.787	0.006
Animal Density Complexity	347.801	30	11.593	1.787	0.006
Explained	5811.225	71	81.848	12.616	0.0001
Residual	8180.875	1261	6.488		
Total	13992.100	1332	10.505		

1333 Cases were processed.
0 Cases (0%) were missing.

TABLE 5.7: Anova of time on bottom by Animal, Prey Density and Habitat Complexity.

(i) <u>Successful dives</u>

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	1590.541	10	159.054	30.313	0.0001
Animal	903.352	5	180.670	34.433	0.0001
Density	290.517	3	96.839	18.456	0.0001
Complexity	432.562	2	216.281	41.220	0.0001
2-Way Interactions	369.609	31	11.923	2.272	0.0001
Animal Density	176.360	15	11.757	2.241	0.004
Animal Complexity	87.077	10	8.708	1.660	0.085
Density Complexity	109.808	6	18.301	3.488	0.002
3-Way Interactions	234.513	30	7.817	1.490	0.044
Animal Density Complexity	234.513	30	7.817	1.490	0.044
Explained	2194.663	71	30.911	5.891	0.0001
Residual	5498.901	1048	5.247		
Total	7693.564	1119	6.875		

1120 Cases were processed.
0 Cases (0%) were missing.

(ii) <u>Unsuccessful hide visit dives</u>

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	4549.558	10	454.956	73.064	0.0001
Animal	3547.802	5	709.560	113.953	0.0001
Density	305.581	3	101.860	16.358	0.0001
Complexity	789.031	2	394.516	63.358	0.0001
2-Way Interactions	542.050	31	17.485	2.808	0.0001
Animal Density	364.790	15	24.319	3.906	0.0001
Animal Complexity	107.996	10	10.800	1.734	0.068
Density Complexity	54.519	6	9.086	1.459	0.189
3-Way Interactions	335.879	30	11.196	1.798	0.005
Animal Density Complexity	335.879	30	11.196	1.798	0.005
Explained	5427.487	71	76.443	12.277	0.0001
Residual	7851.958	1261	6.227		
Total	3279.446	1332	9.970		

1333 Cases were processed.
0 Cases (0%) were missing.

TABLE 5.8: Anova of total time in hide by Animal, Prey Density and Habitat Complexity.

(i) Successful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	127.519	10	12.752	11.504	0.0001
Animal	46.196	5	9.239	8.335	0.0001
Density	70.920	3	23.640	21.326	0.0001
Complexity	18.042	2	9.021	8.138	0.0001
2-Way Interactions	96.752	31	3.121	2.816	0.0001
Animal Density	42.613	15	2.841	2.563	0.001
Animal Complexity	26.624	10	2.662	2.402	0.008
Density Complexity	34.467	6	5.744	5.182	0.0001
3-Way Interactions	40.631	30	1.354	1.222	0.192
Animal Density Complexity	40.631	30	1.354	1.222	0.192
Explained	264.902	71	3.731	3.366	0.0001
Residual	1140.631	1029	1.108		
Total	1405.534	1100	1.278		

1120 Cases were processed.
19 Cases (1.7%) were missing. (Data lost during transcription of videotapes).

(ii) Unsuccessful hide visit dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	376.999	10	37.700	21.423	0.0001
Animal	248.853	5	49.771	28.283	0.0001
Density	35.539	3	11.846	6.732	0.0001
Complexity	100.373	2	50.186	28.519	0.0001
2-Way Interactions	159.959	31	5.160	2.932	0.0001
Animal Density	82.805	15	5.520	3.137	0.0001
Animal Complexity	28.428	10	2.843	1.615	0.097
Density Complexity	59.295	6	9.882	5.616	0.0001
3-Way Interactions	91.196	30	3.040	1.727	0.009
Animal Density Complexity	91.196	30	3.040	1.727	0.009
Explained	628.153	71	8.847	5.028	0.0001
Residual	2217.277	1260	1.760		
Total	2845.431	1331	2.138		

1333 Cases were processed.
1 Case (0.1%) was missing. (Data lost during transcription of videotapes).

However, there were also a number of significant two-way interactions. From these it can be seen that density has a greater influence on behavioural changes, than does complexity, as there were a number of significant interactions between density and animal. This implies that although individuals behave differently under any given condition of prey density, a change in density will cause a change in the behaviour of each individual. There are no significant interactions between complexity and animal, but there is one between density and complexity. Thus, if the behaviour of animals is studied when density is constant, this significant interaction suggests that there will be changes in individual behaviour between the three hide arrangements.

In this experiment, three male and three female animals were used. Mink are highly sexually dimorphic, and sex has been shown to be important in determining differences in diet and habitat use of mink in the wild (see 1.2.3). It is, therefore, possible that the individual variation in behaviour noted in the previous Anova tests, may actually be a reflection of sex-related differences in behaviour. A final series of Anova tests were carried out to investigate this. Data were selected for analysis on the basis of foraging success. Data for dive duration, time on bottom and total time in hide were tested against Prey Density, Habitat Complexity and Sex. The results are given in Tables 5.9 to 5.11, but the main points are summarised below:-

	Significant Main Effects	Significant 2-way Interactions
a) Dive duration		
(i) Successful dives	SX,D,C	-
(ii) Unsuccessful dives	SX,D,C	SX x D
b) Time on bottom		
(i) Successful dives	SX,D,C	-
(ii) Unsuccessful dives	SX,D,C	SX x D
c) Total time in hide		
(i) Successful dives	- ,D,-	SX x D
(ii) Unsuccessful dives	SX,-,C,	-

TABLE 5.9: Anova of dive duration by Sex, Prey Density and Habitat Complexity.

(i) Successful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	940.562	6	156.760	24.855	0.0001
Sex	173.960	1	173.960	27.583	0.0001
Density	299.729	3	99.910	15.841	0.0001
Complexity	484.734	2	242.367	38.429	0.0001
2-Way Interactions	159.759	11	14.524	2.303	0.009
Sex Density	38.459	3	12.820	2.033	0.108
Sex Complexity	0.878	2	0.439	0.070	0.933
Density Complexity	120.732	6	20.122	3.190	0.004
3-Way Interactions	70.501	6	11.750	1.863	0.084
Sex Density Complexity	70.501	6	11.750	1.863	0.084
Explained	1170.823	23	50.905	8.071	0.0001
Residual	6912.329	1096	6.307		
Total	8083.152	1119	7.224		

1120 Cases were processed.
0 Cases (0%) were missing.

(ii) Unsuccessful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	2007.164	6	334.527	38.374	0.0001
Sex	886.376	1	886.376	101.678	0.0001
Density	252.009	3	84.003	9.636	0.0001
Complexity	842.662	2	421.331	48.332	0.0001
2-Way Interactions	449.239	11	40.840	4.685	0.0001
Sex Density	330.583	3	110.194	12.641	0.0001
Sex Complexity	69.773	2	34.886	4.002	0.019
Density Complexity	78.638	6	13.106	1.503	0.173
3-Way Interactions	124.535	6	20.756	2.381	0.027
Sex Density Complexity	124.535	6	20.756	2.381	0.027
Explained	2580.937	23	112.215	12.872	0.0001
Residual	11411.163	1309	8.717		
Total	13992.100	1332	10.505		

1333 Cases were processed.
0 Cases (0%) were missing.

TABLE 5.10: Anova of time on bottom by Sex, Prey Density and Habitat Complexity.

(i) Successful dives

Source of variation		Sum of squares	df	Mean Square	F	Signif. of F
Main effects		878.931	6	146.489	24.284	0.0001
Sex		191.743	1	191.743	31.786	0.0001
Density		293.351	3	97.784	16.210	0.0001
Complexity		410.323	2	205.161	34.011	0.0001
2-Way Interactions		138.075	11	12.552	2.081	0.019
Sex	Density	37.362	3	12.454	2.065	0.103
Sex	Complexity	0.417	2	0.209	0.035	0.966
Density	Complexity	99.279	6	16.546	2.743	0.012
3-Way Interactions		65.243	6	10.874	1.803	0.095
Sex Density Complexity		65.243	6	10.874	1.803	0.095
Explained		1082.250	23	47.054	7.801	0.0001
Residual		6611.314	1096	6.032		
Total		7693.564	1119	6.875		

1120 Cases were processed.
0 Cases (0%) were missing.

(ii) Unsuccessful dives

Source of variation		Sum of squares	df	Mean Square	F	Signif. of F
Main effects		1913.820	6	318.970	38.665	0.0001
Sex		912.064	1	912.064	110.559	0.0001
Density		200.940	3	66.980	8.119	0.0001
Complexity		773.990	2	386.995	46.911	0.0001
2-Way Interactions		470.141	11	42.740	5.181	0.0001
Sex	Density	331.640	3	110.547	13.400	0.0001
Sex	Complexity	76.375	2	38.188	4.629	0.010
Density	Complexity	93.201	6	15.534	1.883	0.080
3-Way Interactions		96.881	6	16.135	1.956	0.069
Sex Density Complexity		96.881	6	16.135	1.956	0.069
Explained		2480.772	23	107.860	13.075	0.0001
Residual		10798.674	1309	8.250		
Total		13279.446	1332	9.970		

1333 Cases were processed.
0 Cases (0%) were missing.

TABLE 5.11: Anova of total time in hide by Sex, Prey Density and Habitat Complexity.

(i) Successful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	85.232	6	14.205	11.991	0.0001
Sex	3.908	1	3.908	3.299	0.070
Density	64.727	3	21.576	18.213	0.0001
Complexity	17.566	2	8.783	7.414	0.001
2-Way Interactions	35.374	11	3.216	2.715	0.002
Sex Density	5.947	3	1.982	1.673	0.171
Sex Complexity	0.144	2	0.072	0.061	0.941
Density Complexity	28.443	6	4.741	4.002	0.001
3-Way Interactions	9.079	6	1.513	1.277	0.265
Sex Density Complexity	9.079	6	1.513	1.277	0.265
Explained	129.685	23	5.638	4.760	0.0001
Residual	1275.848	1077	1.185		
Total	1405.534	1110	1.278		

1120 Cases were processed.
19 Cases (1.7%) were missing. (Data lost during transcription of videotapes).

(ii) Unsuccessful dives

Source of variation	Sum of squares	df	Mean Square	F	Signif. of F
Main effects	195.702	6	32.617	17.016	0.0001
Sex	67.556	1	67.556	35.244	0.0001
Density	22.827	3	7.609	3.970	0.008
Complexity	108.921	2	54.461	28.412	0.0001
2-Way Interactions	105.900	11	9.627	5.023	0.0001
Sex Density	56.907	3	18.969	9.896	0.0001
Sex Complexity	10.565	2	5.283	2.756	0.064
Density Complexity	42.129	6	7.022	3.663	0.001
3-Way Interactions	36.636	6	6.106	3.186	0.004
Sex Density Complexity	36.636	6	6.106	3.186	0.004
Explained	338.238	23	14.706	7.672	0.0001
Residual	2507.192	1308	1.917		
Total	2845.431	1331	2.138		

1333 Cases were processed.
1 Case (0.1%) was missing. (Data lost during transcription of videotapes).

There were no significant 3-way interactions.
SX = Sex of Animal, D = Prey Density, C = Habitat Complexity

The results show that the sex of an animal does appear to be an important influence on behaviour under different conditions of complexity and prey density, irrespective of success. Again density and complexity also have a significant main effect, but the most interesting result is the fact that the only significant two-way interactions (at the 0.1% level) are between sex and density. Thus, it appears that the different sexes will behave differently at the same density, and further, behaviour will also change with changes in density. From the above analysis, it appears that changes in habitat complexity are not important in explaining changes in the behaviour of the sexes, although from previous analyses, complexity did seem to affect individual behaviour. However, it was decided not to analyse data on the basis of Sex: (a) because the number of animals used was so small, and (b) there was no overlap in the size, in terms of body weight, between the males and females used, and thus sexual differences in behaviour may actually have been the result of the differences in size between the animals.

In order to separate the effects of density and complexity, more detailed analyses need to be carried out on various aspects of the foraging behaviour of the mink. Data for All Animals are presented, and, where possible, data for individuals are included for comparison. The effects of prey density were investigated by examining data for each of the four prey densities under each condition of hide distribution pattern, to see how, for a given situation, behaviour changed. It was then decided to investigate the data for habitat complexity by comparing the results obtained when hides were distributed in a random, regular or clumped manner, with prey density at 50%. This density was chosen as it was the same as the prey density used in the investigation of the effect of depth on the underwater foraging behaviour and hence would allow comparisons to be made. The results for these two approaches will be presented separately, although the behavioural parameters investigated (e.g. dive rate, dive duration etc.) will be the same.

5.4. Results : Prey Density

It could be predicted that as density increases, the probability that the first hide visited would contain food, would increase. Thus, an increase in measures of success rate would be expected. Further, since each trial lasted for a fixed period, if animals are more successful at high densities, more time will be taken up handling the prey, and it would be expected that dive rate would level off. Also, the mean number of hides visited per dive would be expected to be lower at greater prey densities. Dunstone and O'Connor (1979b) further predict that at higher prey encounter rates, i.e. at higher densities, Giving-Up Time (equivalent to mean unsuccessful dive duration) should be lower. Thus, if the first hide searched is not baited, animals should terminate the dive and try again elsewhere. At lower densities, a better strategy would be to extend the dive for as long as possible and try to search as many hides as possible, then resurface and try again in a different area. However, there are a number of problems with this idea. First, the animal has to make a number of dives before it can obtain any idea of the prey density. Secondly, when hides are arranged in clumps, at high prey density, even if the first hide searched was not baited, there are three other hides, in close proximity, where there is a very high probability that one or more is baited. In this case the best strategy would seem to be one where the dive was extended, at least to include searching one more hide. The results obtained will be discussed in the light of these predictions.

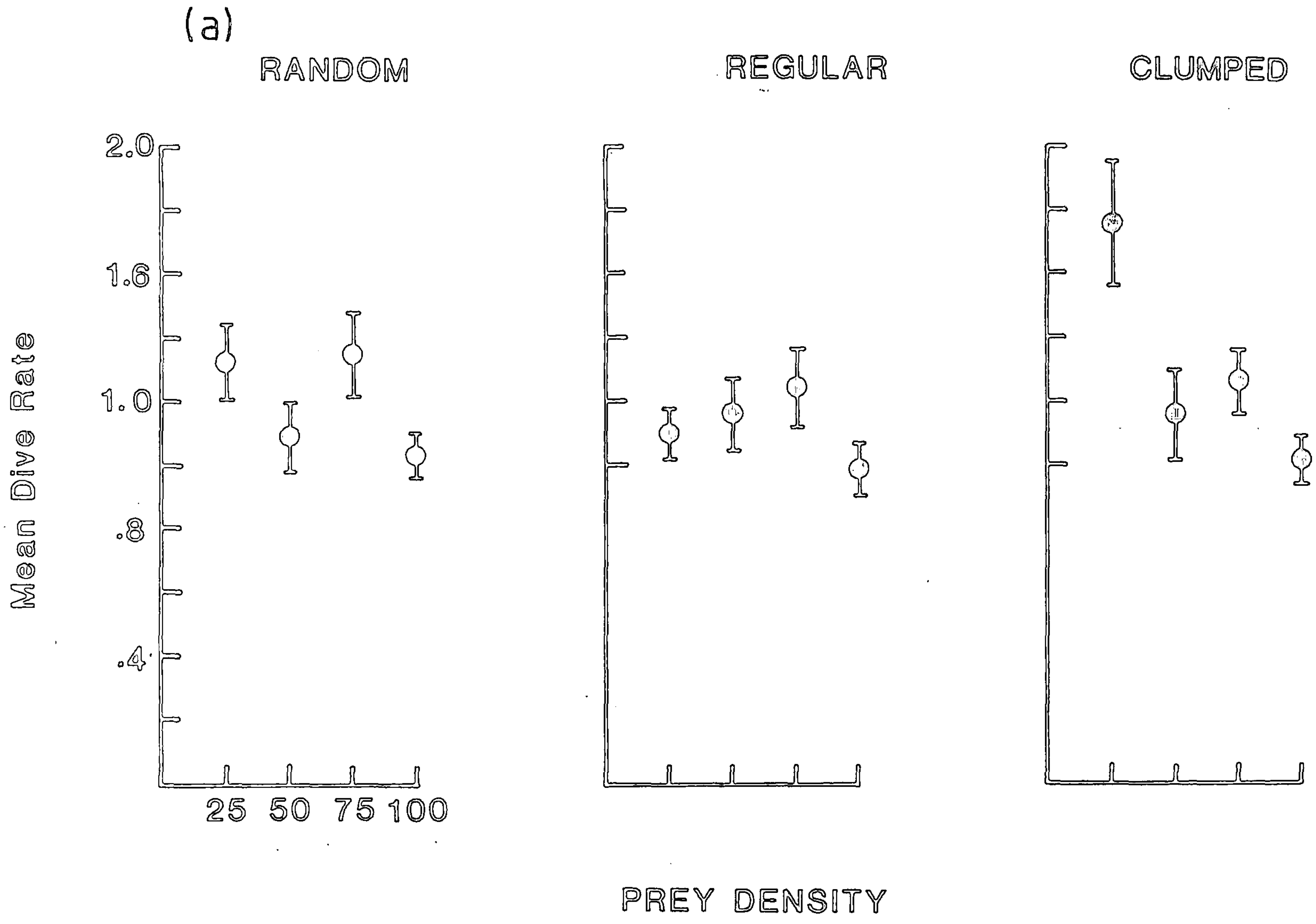
Before reporting the results obtained, it is neccessary to discuss the statistical analysis used. Data were first plotted as 'scattergrams', to determine if the relationship was linear. In some cases it did seem that there may be a linear relationship between the variables, hence linear regression analysis was carried out, using all data for the dependent variables. In some cases, the regression line was not significant, and here further analysis was carried out, again using all of the data. If regression analysis showed that there was a significant relationship between the variables, this would mean that further predictions of the expected behaviour at a given prey density could be made. It should be noted however, that although only four densities were used, any significant result (especially at 0.1% level) can be considered as reflecting a change in the behaviour of the mink as 'prey density' changes, since density could only vary between 0-100% and the conditions of density studied were evenly spread over this range. Finally, where linear regression analysis was not significant, it appeared in many cases that the relationship between the variables might be curvilinear. In these cases curvilinear analysis (a special case of multiple linear regression analysis) was carried out using the Forced Entry method with independent variables Density, $(\text{Density})^2$ and $(\text{Density})^3$. Where curvilinear analysis showed that there were significant quadratic or cubic results, a random selection of a small number of results were chosen, and the lines of best fit, as given by the equations, were plottted on the appropriate graph. These results are illustrated on the graphs for mean dive rate and mean dive duration for unsuccessful dives. The results plotted in the graphs are mean values only, and in some cases the lines of best fit produced by curvilinear analysis using all of the data do not fit the mean points well. There are two explanations for this, one is that in some cases the values for the coefficients of the quadratic and cubic terms are extremely small, indicating that although these terms contribute significantly to the equations, they are not very different from zero and hence do not greatly influence the shape of the curve. Secondly, in some cases, it is possible that at the higher densities there were fewer points in the equation than at the lower densities, and this again would influence the shape of the curve, such that a line described by a cubic equation, may actually plot out as being very close to a straight line, with only.minor curving

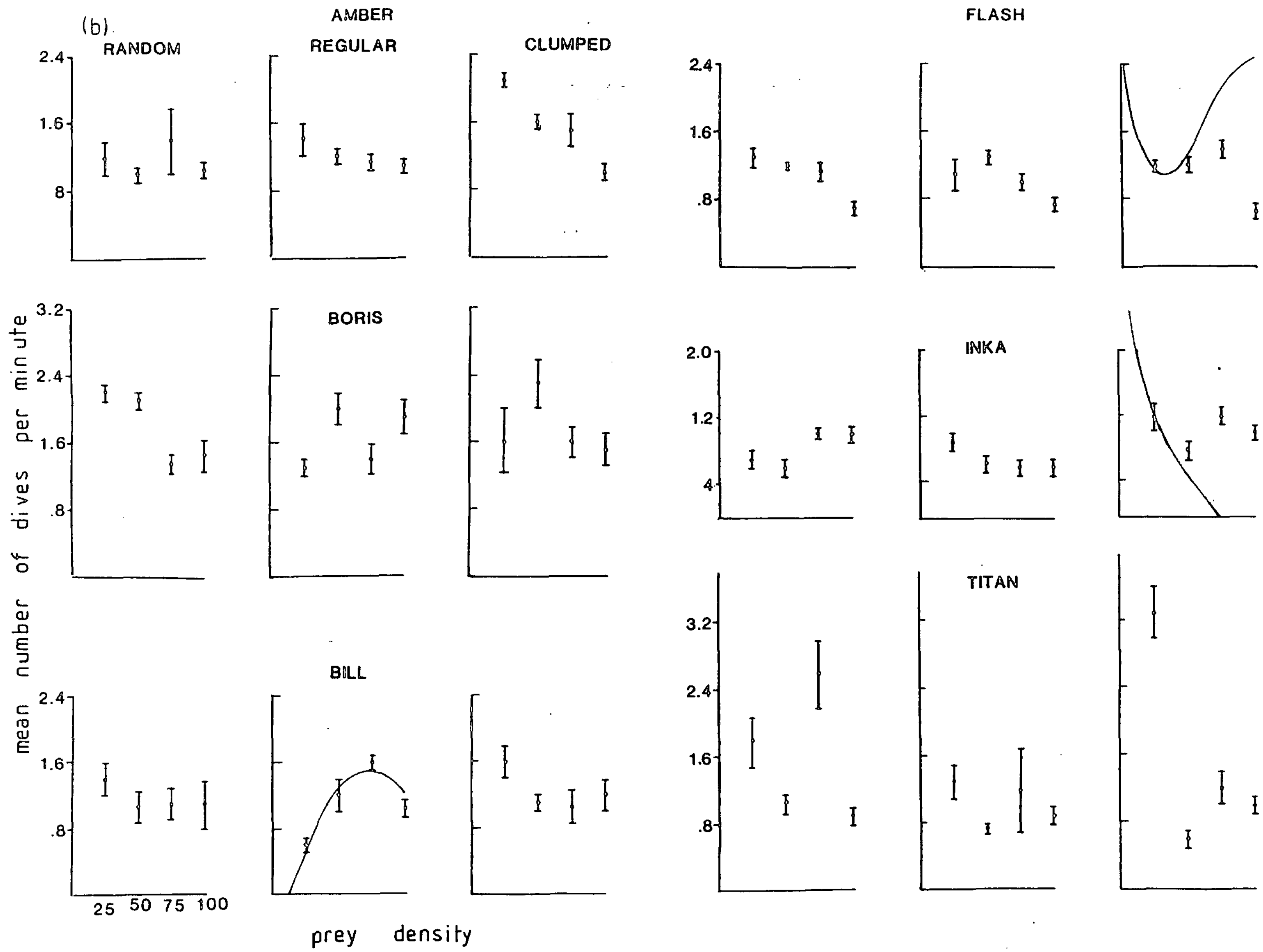
5.4.1. Dive Rate

Mean values for dive rate per minute were calculated for each condition of prey density and complexity. The results are given in Fig. 5.2a (All animals) and Fig. 5.2b (individual results).

Linear regression analysis of the combined data shows that there is one significant correlation, for All:Clumped ($r = -0.38$, $df = 97$, $p<0.001$). When the results for individuals are examined, eight results showed a significant linear correlation. Thus: Boris:Random ($r = -0.81$, $df = 11$, $p<0.001$) Flash:Random ($r = -0.64$, $df = 15$, $p<0.01$), Inka:Random ($r = 0.59$, $df = 18$, $p<0.01$), Amber:Regular ($r = -0.46$, $df = 17$, $p<0.05$), Flash:Regular ($r = -0.52$, $df = 19$, $p<0.05$), Inka:Regular ($r = -0.43$, $df = 21$, $p<0.05$) and Amber:Clumped ($r = -0.72$, $df = 12$, $p<0.001$). In most cases the correlation is negative, showing that dive rate decreases as prey density increases, but for Inka:Random the reverse is true.

Thus, most results showed that there was no significant linear relationship between dive rate and density, regardless of the hide arrangement used. Curvilinear analysis was carried out on the data for All animals and individuals. In some cases, significant results were obtained when the linear and quadratic terms were included in the regression equation, in others, results were only significant when the cubic term was also included in the regression equation. The equations relating to these results are given in Fig. 5.2.


(a)
RANDOM
REGULAR
CLUMPED
Mean Dive Rate
2.0
1.6
1.0
.8
.4
25
50
75
100
PREY DENSITY


(b)
AMBER
RANDOM
REGULAR
CLUMPED
FLASH
BORIS
INKA
BILL
TITAN
2.4
1.6
8
2.4
1.6
.8
3.2
2.4
1.6
.8
2.0
1.2
4
2.4
1.6
.8
3.2
2.4
1.6
.8
mean number of dives per minute
25 50 75 100
prey density

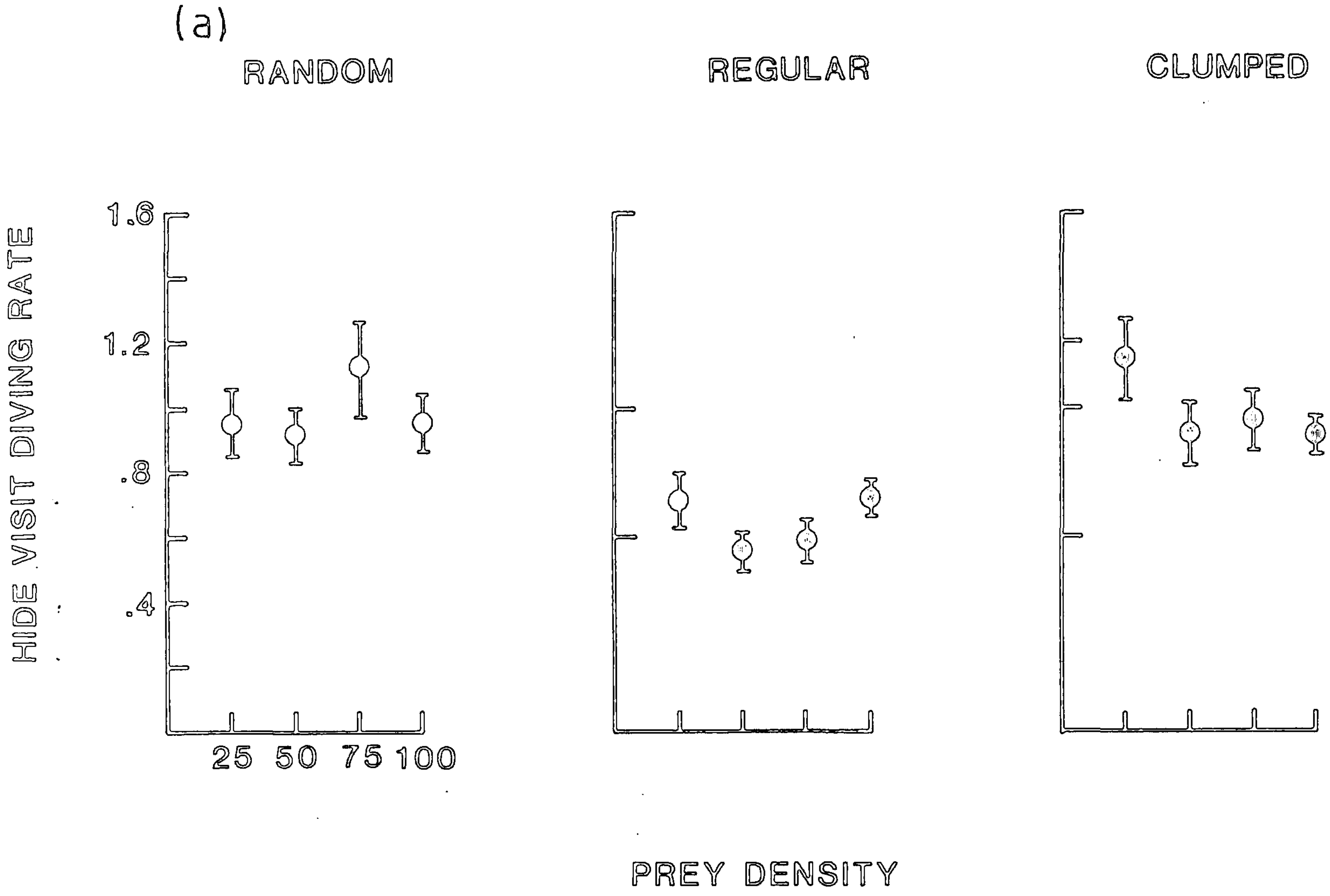
Interpretation of the results obtained is very difficult. In some cases, e.g. Inka:Random, there is a straight-forward increase in dive rate with increasing density. In other cases, a quadratic curve supplies the best fit, e.g. Bill:Regular. Finally, in many cases, e.g. Boris:Regular, Titan:Random, a cubic curve gave the best fit. From the equations given in the Figure legend, it can be seen that in some cases dive rate initially declines with density, then increases again, but the reverse is also true.

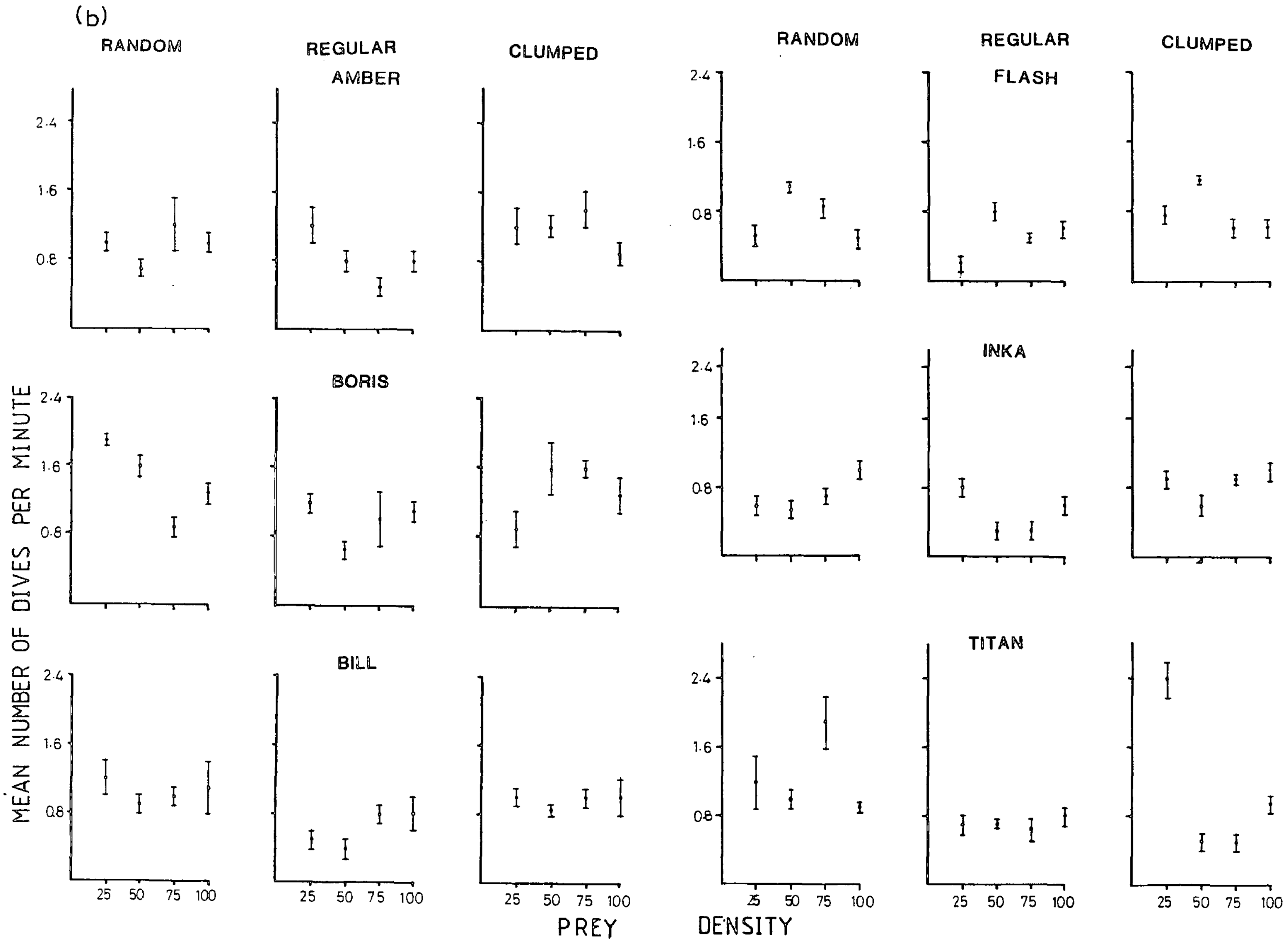
Since the changes in behaviour are not consistent between the different hide arrangements used, this implies that perhaps complexity has a greater effect than was thought. This point will be dealt with in more detail in the appropriate section.

5.4.2. Hide Visit Dive Rate

As in previous experiments the number of successful dives in a trial can be considered as a measure of foraging efficiency. However, animals occasionally failed to search any hides during a dive and obviously these dives could not be successful.

Thus, an examination of the hide visit dive rate with increasing food supply was carried out. The results for All Animals are given in Fig. 5.3a, and individual results in Fig. 5.3b. There were no significant linear correlations between the two variables under any conditions for the combined data, and only for Inka:Random ($r = 0.59$, $df = 18$, $p<0.01$) amongst the individual results. However, when curvilinear analysis was carried out, there were a number of significant results among individuals. Again, in some cases a quadratic curve gave the best fit, whereas in others a cubic curve was the best. In many of these cases, it appears that the hide visit dive rate initially declines with density, then increases again at the maximum density, but the reverse also occurs.


(a)
RANDOM
REGULAR
CLUMPED
HIDE VISIT DIVING RATE
1.6
1.2
.8
.4
25
50
75
100
PREY DENSITY

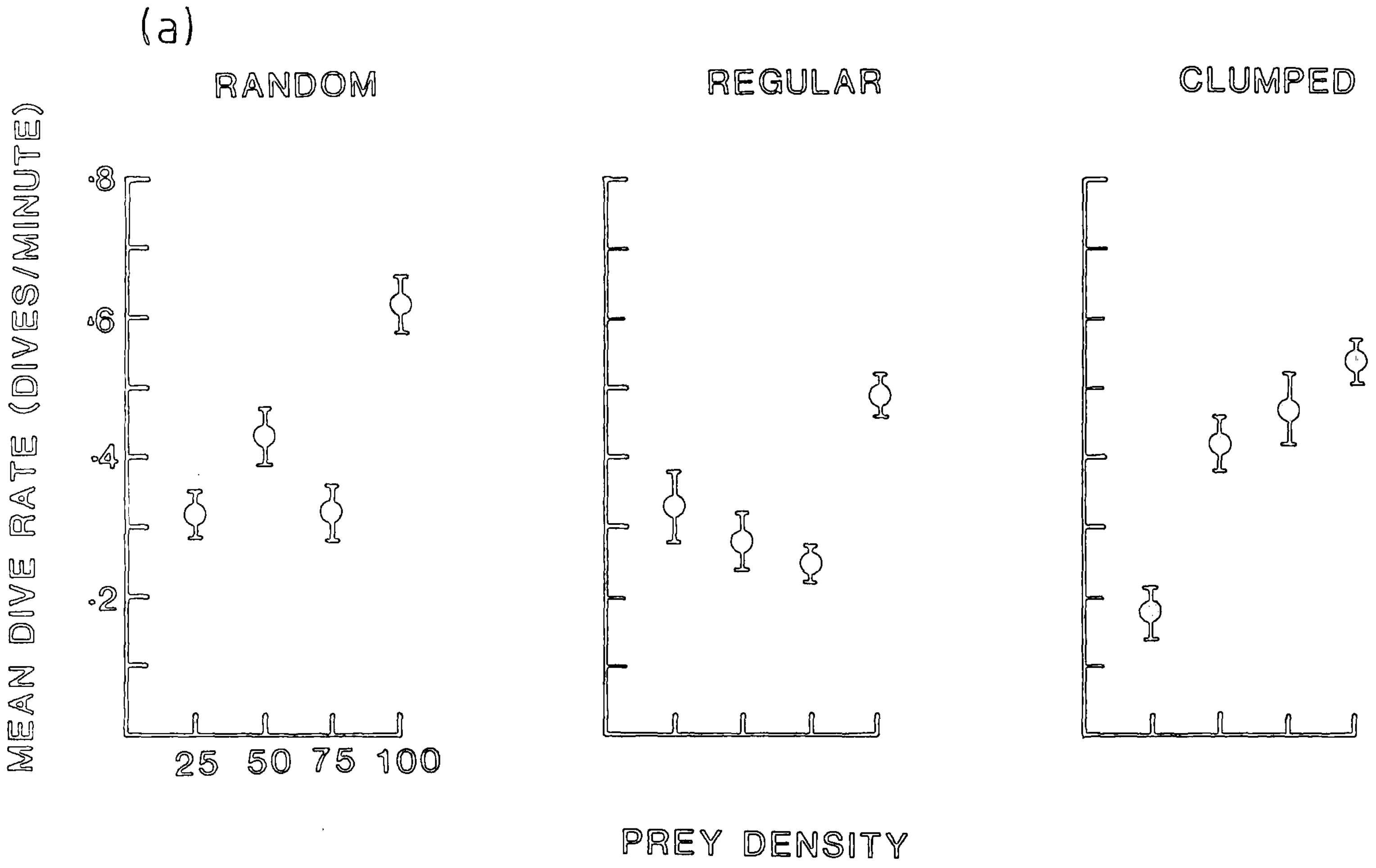

(b)
RANDOM
REGULAR
CLUMPED
AMBER
BORIS
BILL
RANDOM
REGULAR
CLUMPED
FLASH
INKA
TITAN
MEAN NUMBER OF DIVES PER MINUTE
2·4
1·6
0·8
25
50
75
100
PREY DENSITY

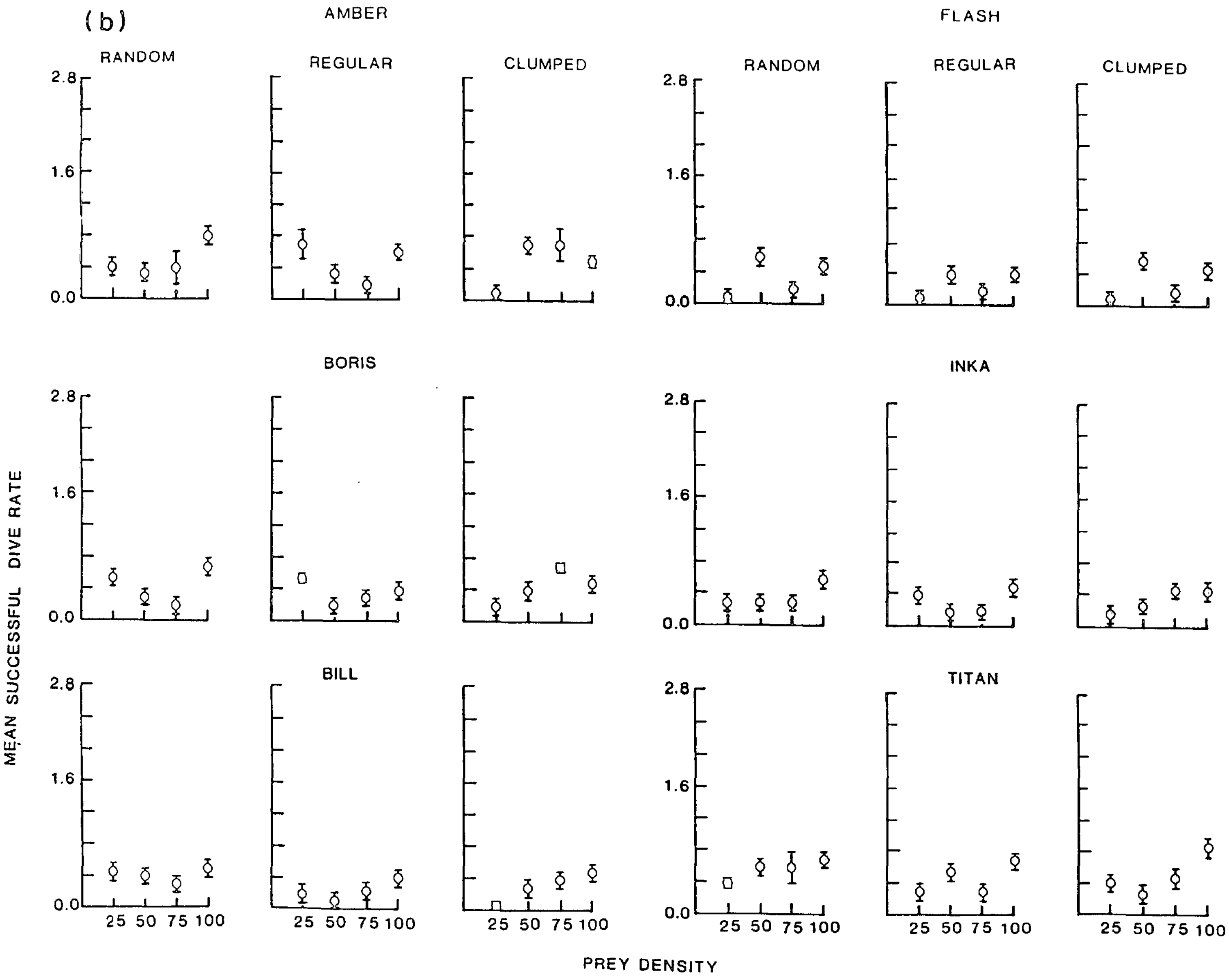
The main point to note from all results is that the value of mean hide visit dive rate varies between approximately 0.5 (i.e. one hide visit dive per 2 min) to around 2.0 (i.e. two hide visit dives per min).

On the whole it is very difficult to interpret these results. It might be thought that as the amount of food available increases there is a greater probability that a hide visit dive would lead to the animal obtaining a food reward. From this it might have been expected that animals would, therefore, be encouraged to investigate hides each time they dived, and that this would lead to an increase in hide visit dive rate as density increased. However, since dive rate did not show any clear relationship with density, any significant changes in hide visit dive rate may be masked.

5.4.3. Successful dive rate

Values for mean successful dive rate were calculated for each individual, and for All Animals, under each hide distribution and prey density condition. The results are illustrated in Fig. 5.4a (All Animals) and Fig. 5.4b (individual results). The values for successful dive rate are generally very low. For All Animals, 80% of the results are below a mean value of 0.5 (i.e. less than one successful dive in every 2 min). For individual results, 70% are below a mean value of 0.5. The lowest value of all is that for the female Flash, when density was 25% and hides were distributed regularly, where a mean successful dive rate of 0.08 (i.e. less than one successful dive in 10 min) was observed. At the opposite extreme, the female Titan managed a mean successful dive rate of 0.85 (i.e. nearly one successful dive per min), when density was 100% and hides were clumped. These results are somewhat different to those obtained in the depth experiment for example, when all the mean values for successful dive rate were less than 0.5.


(a)
RANDOM
REGULAR
CLUMPED
MEAN DIVE RATE (DIVES/MINUTE)
·2
·4
·6
·8
25
50
75
100
PREY DENSITY


(b)
AMBER
FLASH
RANDOM
REGULAR
CLUMPED
RANDOM
REGULAR
CLUMPED
BORIS
INKA
BILL
TITAN
2.8
1.6
0.0
MEAN SUCCESSFUL DIVE RATE
25 50 75 100
PREY DENSITY

The second point concerns the relationship between mean successful dive rate and prey density. From Fig. 5.4a it can be seen that there is a significant linear correlation between the two variables for All:Clumped ($r = 0.53$, $df=97$, $p<0.001$). When individual results (Fig. 5.4b) are examined, significant linear correlations were obtained in six cases: Inka:Random ($r = 0.60$, $df = 18$, $p<0.01$), Titan:Random ($r = 0.63$, $df = 13$ $p<0.05$), Bill:Regular ($r = 0.57$, $df = 18$, $p<0.01$), Bill:Clumped ($r = 0.77$, $df = 14$, $p<0.001$), Inka:Clumped ($r = 0.76$, $df = 16$, $p< 0.001$) and Titan:Clumped ($r = 0.67$, $df = 15$, $p<0.01$). However, from the Figures, it appears that there may also be a curvilinear relationship in many cases. Curvilinear analysis was carried out using the forced entry method, and a number of significant results were obtained. The equations describing these relationships are given in the Figure legends. The majority of significant results show that a quadratic curve produced the best fit, but for some results, notably for female Flash, a cubic curve gave the best fit to the data.

Again individual behaviour varies considerably. However, the general trend does seem to be one of ultimately increasing successful dive rate with increasing prey density, although in many cases, there is initially a decline. This result is not totally unexpected, since, as the amount of food available increases it would be expected that even if the number of hide visit dives were constant for all conditions, more of these dives would visit baited hides and would then have the possibility of being successful.

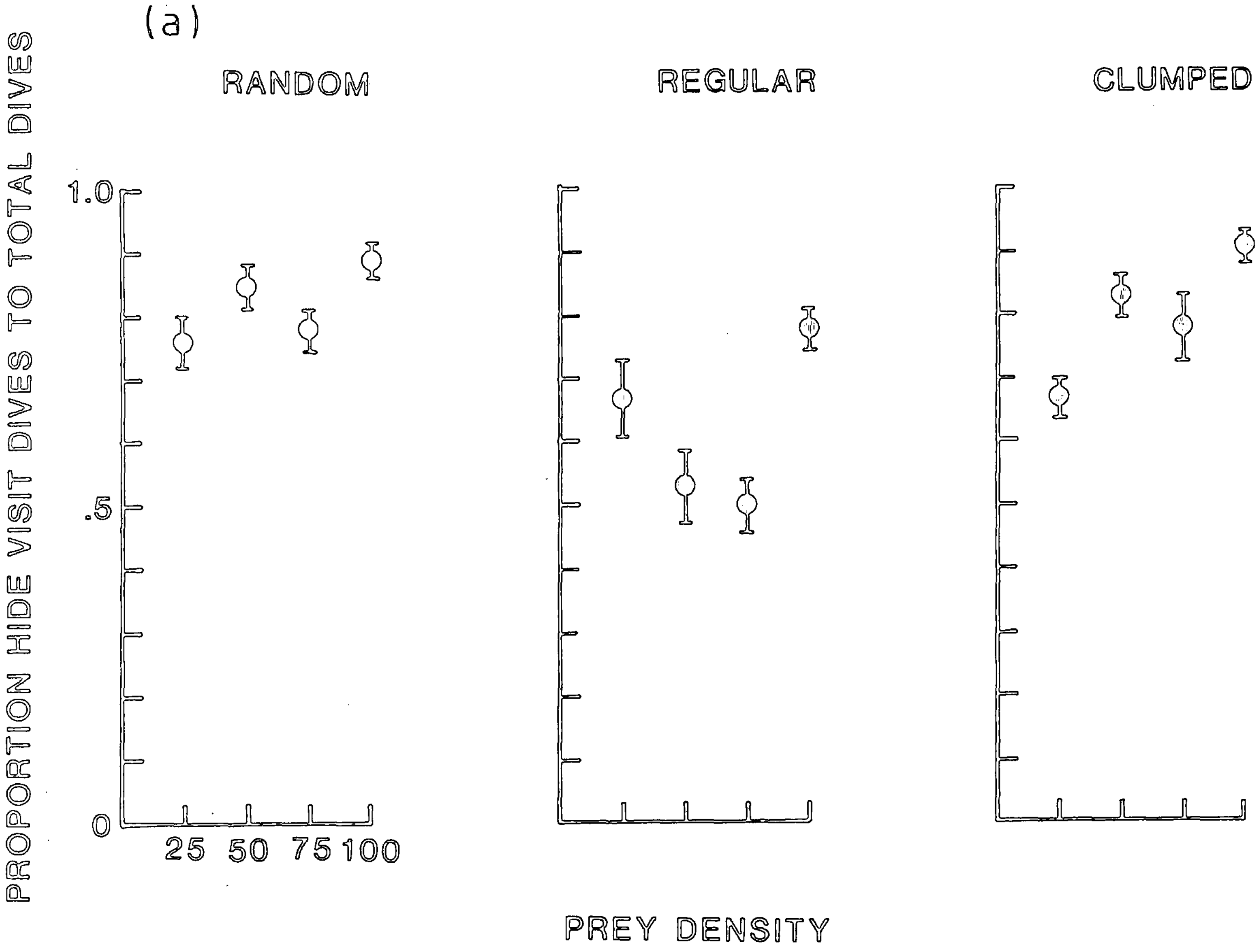
5.4.4. Proportion of dives visiting a hide

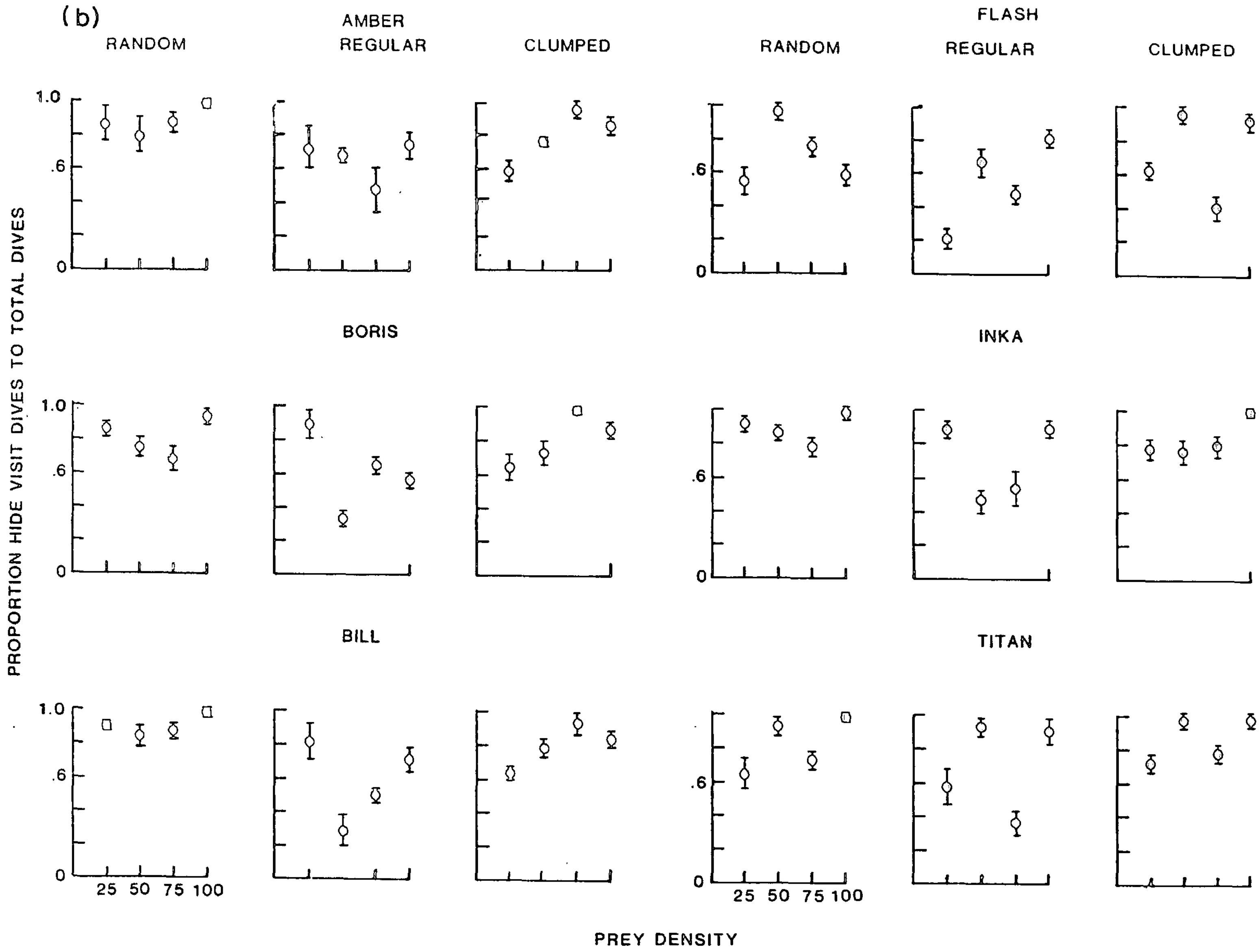
From the previous analyses, there are some indications that dive rate decreased as food availability increased. Further, there were some significant positive correlations between hide visit dive rate and density, although there were also some results where the reverse was true. However, when successful dive rate was examined the results showed a clearer correlation between increase in food availability and increased success. Since not all dives involve hide visits, relationships between foraging success and food availability may become clearer if the changes in the proportion of dives which visit a hide are investigated. The mean and Standard Error for proportion of dives visiting a hide for all animals and individuals, under each condition of hide distribution and density, was calculated as previously described in Section 3.3.5. Results are shown in Figs. 5.5a (All Animals) and 5.5b (individual data).

Linear regression analysis reveals that there are significant linear correlations between the two variables for All:Clumped ($r = 0.45$, $df = 97$, $p<0.001$), Boris:Clumped ($r = 0.63$, $df=13$, $p<0.05$), and Inka:Clumped ($r = 0.50$, $df=16$, $p<0.05$). Curvilinear analysis, however, reveals that there are a greater number of significant correlations, and the equations describing the relationships are given in the Figure legend.

From Figs. 5.5a and b, it can be seen that behaviour is again very variable, and there seem to be no consistent changes in the proportion of dives visiting hides when the results for the same hide arrangement are compared for different individuals and All Animals. Thus, in some cases, the proportion of dives visiting hides increases, but then declines as the maximum density is reached, i.e. following a positive quadratic relationship, whereas in other cases the reverse is true. Further, in other cases the relationship is cubic in form, with the proportion of dives visiting hides rising and falling with density.

One further point to note is that in the majority (79%) of cases, the proportion of dives visiting a hide is in excess of 0.6, regardless of conditions of density and hide arrangement, i.e. on average six out of every ten dives involved a hide visit. (A case is


(a)
RANDOM
REGULAR
CLUMPED
PROPORTION HIDE VISIT DIVES TO TOTAL DIVES
1.0
.5
0
25
50
75
100
PREY DENSITY


(b)
AMBER
RANDOM
REGULAR
CLUMPED
FLASH
RANDOM
REGULAR
CLUMPED
BORIS
INKA
BILL
TITAN
1.0
.6
0
25
50
75
100
PROPORTION HIDE VISIT DIVES TO TOTAL DIVES
PREY DENSITY

one result at any given density and hide arrangement, either for individual or All Animals. Therefore, there are 84 cases in all.) In the depth experiment, only 67.5% of cases had a value for proportion of dives visiting hides greater than 0.6. However, in the depth experiment, the maximum value recorded was 0.9 (i.e. nine out of ten dives visiting a hide), whereas for this experiment 24% of cases scored a value of 0.9 or higher. Of this 24%, more than half (65%) occurred when prey density was 75% or 100%.

Thus, from these results there is some suggestion that at higher prey densities animals are making fewer non-hide visit dives.

5.4.5. Proportion of successful dives

In the previous experiments the proportion of successful to total hide visit dives was examined as a measure of foraging efficiency. However, dives scored as 'hide visit' often involved visits to more than one hide, but only one of these hide visits (the last) would actually be successful. Thus, it was considered that a better measure of foraging efficiency would be the relationship between the number of positive hide searches and total number of hide searches under different conditions of habitat complexity and prey density. Thus, for this experiment, an analysis of the proportion of successful dives to total hide visit dives was not carried out.

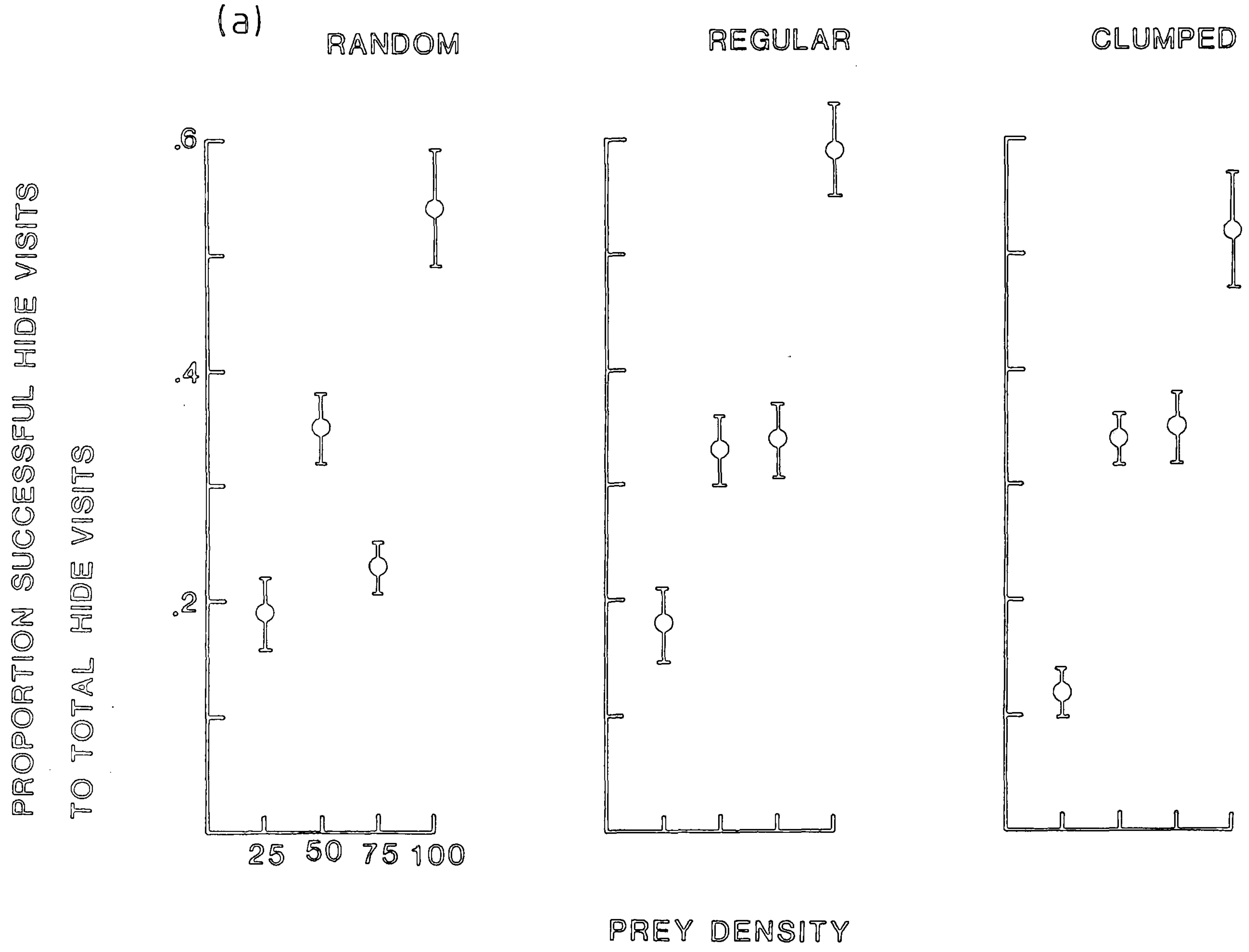
5.4.6. Proportion of successful hide visits to total number of hide visits

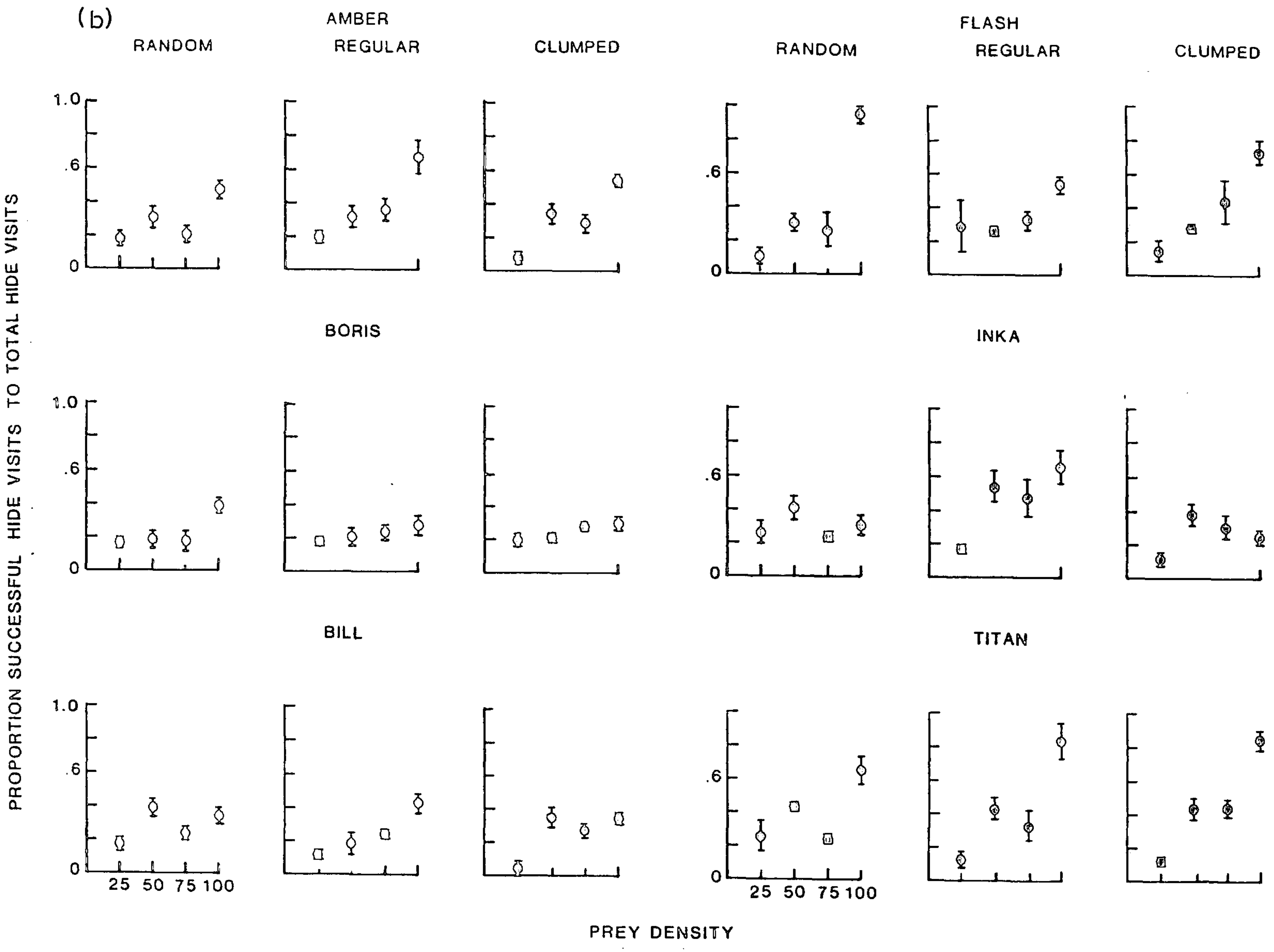
Values for mean proportion of successful hide visits to total number of hide visits were calculated according to the formula given previously (see 3.3.7.). Trials in which no hides were visited were excluded from the analysis, but trials in which hides were visited but none of the visits were successful (i.e. giving a proportion value of 0.0) were included.

The results are plotted in Figs. 5.6a (All Animals) and 5.6b (individuals) and linear regression analysis was carried out for all. There were a number of significant linear correlations. When hides are random, there was a single positive correlation for Boris ($r = 0.60$, df=11, $p<0.05$). When hides are regular, there are five positive correlations: All ($r = 0.55$, df = 114, $p<0.001$), Amber ($r = 0.72$,df = 16, $p<0.001$) and Bill ($r = 0.70$, df = 16, $p<0.01$), Flash ($r = 0.46$, df =18, $p<0.05$) and Inka ($r = 0.51$, df = 21, $p<0.05$). When hides are clumped, there are three significant correlations, for Boris ($r = 0.65$, df = 13, $p<0.01$), Flash ($r = 0.78$, df = 17, $p<0.001$) and Titan ($r = 0.89$, df = 15, $p<0.001$). In each case the slope of the line was less than 0.01, indicating that the change in proportion of successful hide visits with density was really very small. There were no significant negative linear correlations, which was as expected, since increasing food density would be expected to lead to an increase in success, i.e. at higher densities the probability is much higher that the first hide visited will contain food.

Curvilinear analysis was also carried out, as in many cases it appeared that there might be a curvilinear relationship between the two variables. A number of significant results were obtained, and in most of these a cubic curve gave the best fit. The equations describing these relationships are given in the legend to Fig. 5.6. Again, the general picture is that the proportion of successful hide visits is greater when prey density is greater. It can also be seen that there are considerable differences in the behaviour of individuals, particularly when the same hide arrangement conditions are compared. It is possible that there are considerable differences in the foraging strategies used by individuals under different conditions which will account for this.

Thus, the overall picture obtained from these results is that, generally, the proportion of successful hide visits increases with density.


(a)
RANDOM
REGULAR
CLUMPED
PROPORTION SUCCESSFUL HIDE VISITS
TO TOTAL HIDE VISITS
.6
.4
.2
25
50
75
100
PREY DENSITY

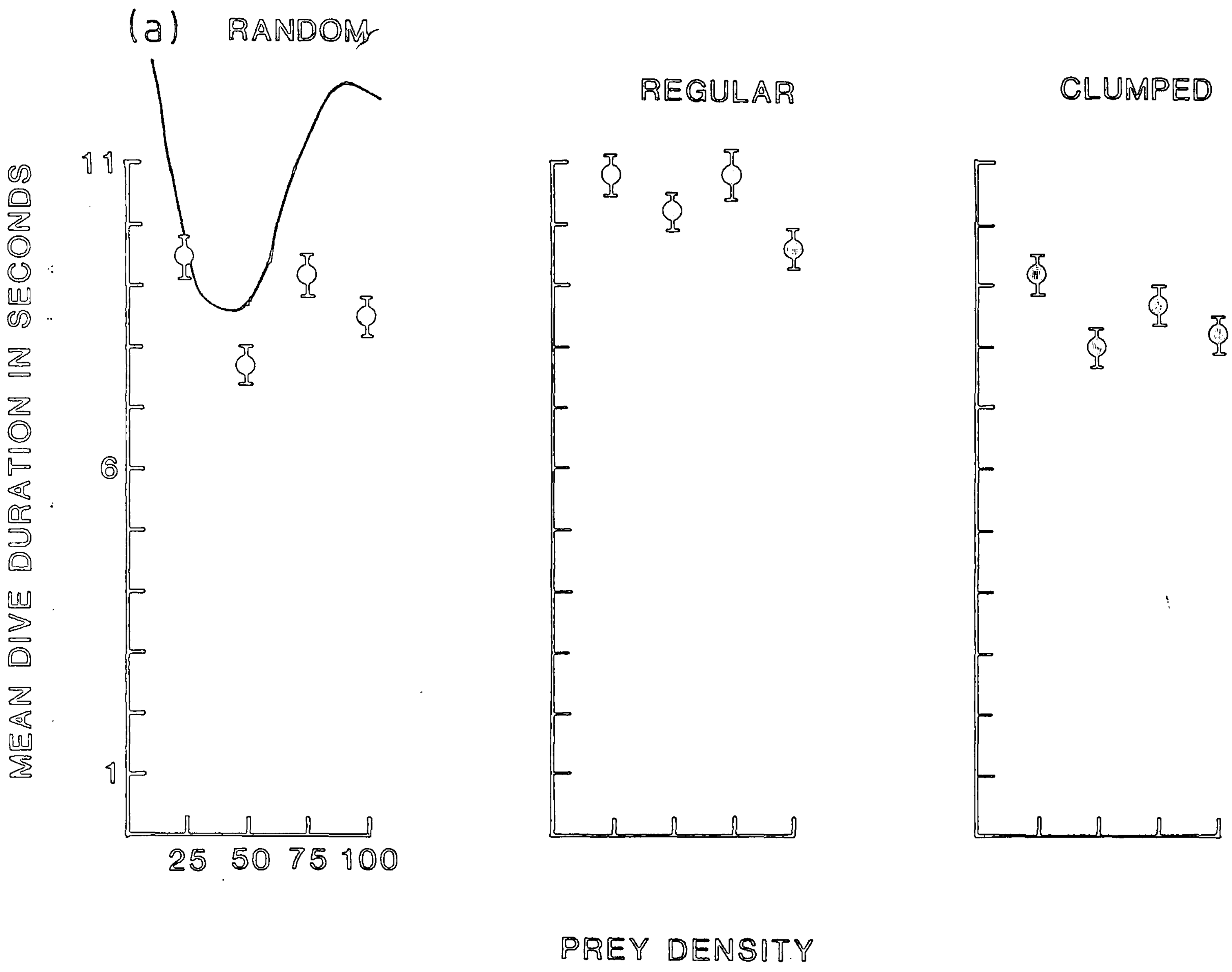

(b)
AMBER
RANDOM
REGULAR
CLUMPED
FLASH
RANDOM
REGULAR
CLUMPED
BORIS
INKA
BILL
TITAN
1.0
.6
0
25 50 75 100
PROPORTION SUCCESSFUL HIDE VISITS TO TOTAL HIDE VISITS
PREY DENSITY

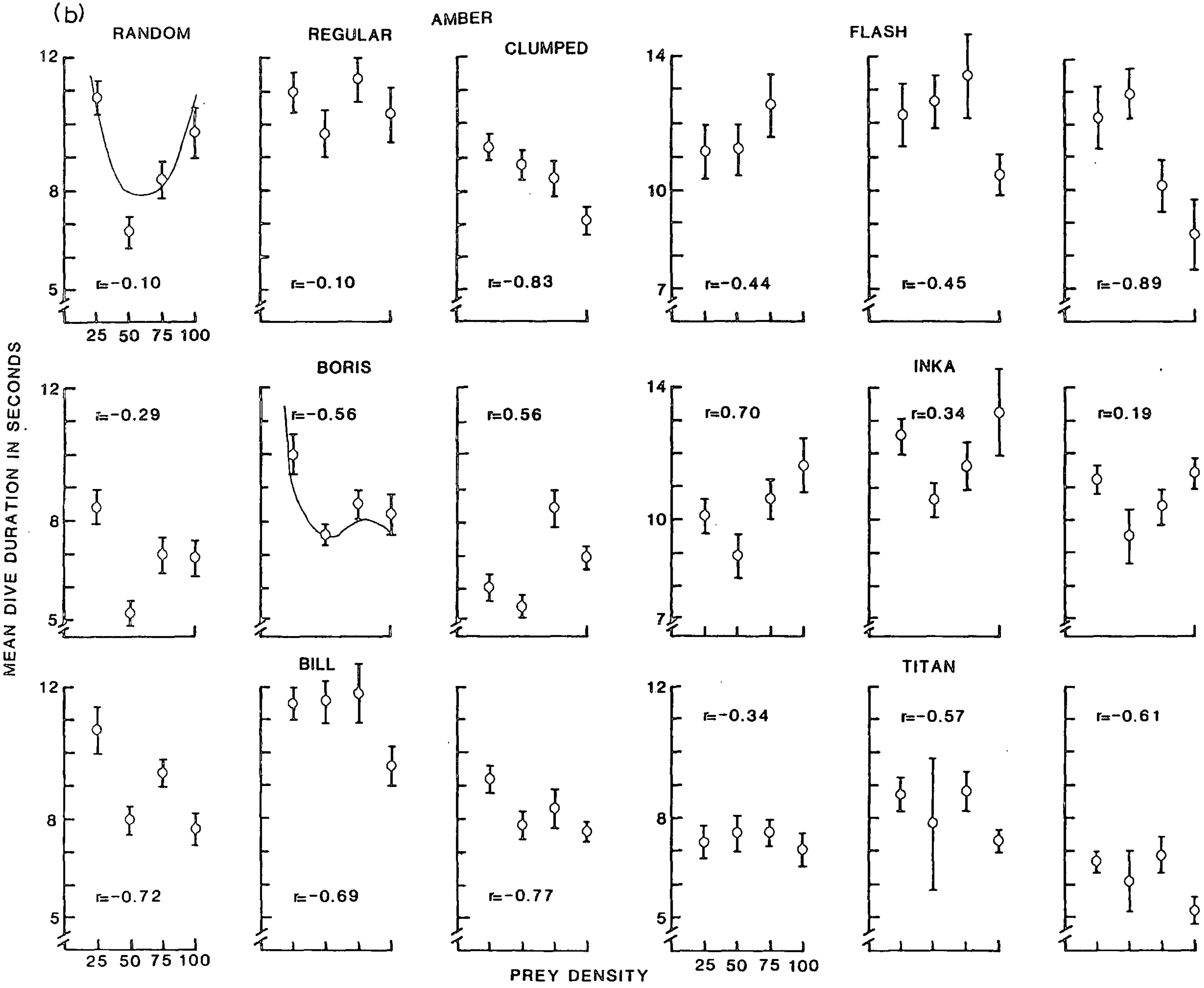
Tables 5.3-5.6 give the results of Analysis of Variance tests of various parameters by Animal, Density, Habitat Completity and Foraging Success. The results show that generally Foraging Success is important in explaining changes in behaviours such as dive duration, time on bottom etc., both between animals under the same conditions and for an individual under varying conditions. For this reason, from this point on, successful and unsuccessful dives have been analysed separately (unless otherwise stated). Also, unless otherwise stated, dives in which no hides were visited (954 cases) were excluded from further analysis. Thus, the analyses were conducted on data obtained from 1120 successful dives and 1333 unsuccessful dives.

5.4.7. Dive duration

Mean dive duration was calculated for unsuccessful and successful dives as explained previously (see 3.3.8). Fig. 5.7a presents data for unsuccessful dives for All Animals, and Fig. 5.7b gives individual results. Figs. 5.8a and b illustrate data for successful dive duration. Linear regression analyses were carried out to see if there was a correlation between the variables. If there was a significant correlation, this would mean that it would be possible to predict the expected dive duration under any condition of prey density, provided habitat complexity was also known.

The results of the regression analysis for unsuccessful dive duration showed that there were five significant correlations between the two variables. Thus, Bill:Random ($r = -0.32$, $df = 89$, $p<0.01$), All:Regular ($r = -0.11$, $df = 353$, $p<0.05$), Amber:Clumped ($r= -0.31$, $df = 78$, $p<0.01$), Bill:Clumped ($r = -0.24$, $df = 98$, $p<0.05$) and Flash:Clumped ($r = -0.27$, $df = 68$, $p<0.05$). In each case dive duration declines with density. From Figs. 5.7a and b, it can be seen that there is great variation in behaviour, both within

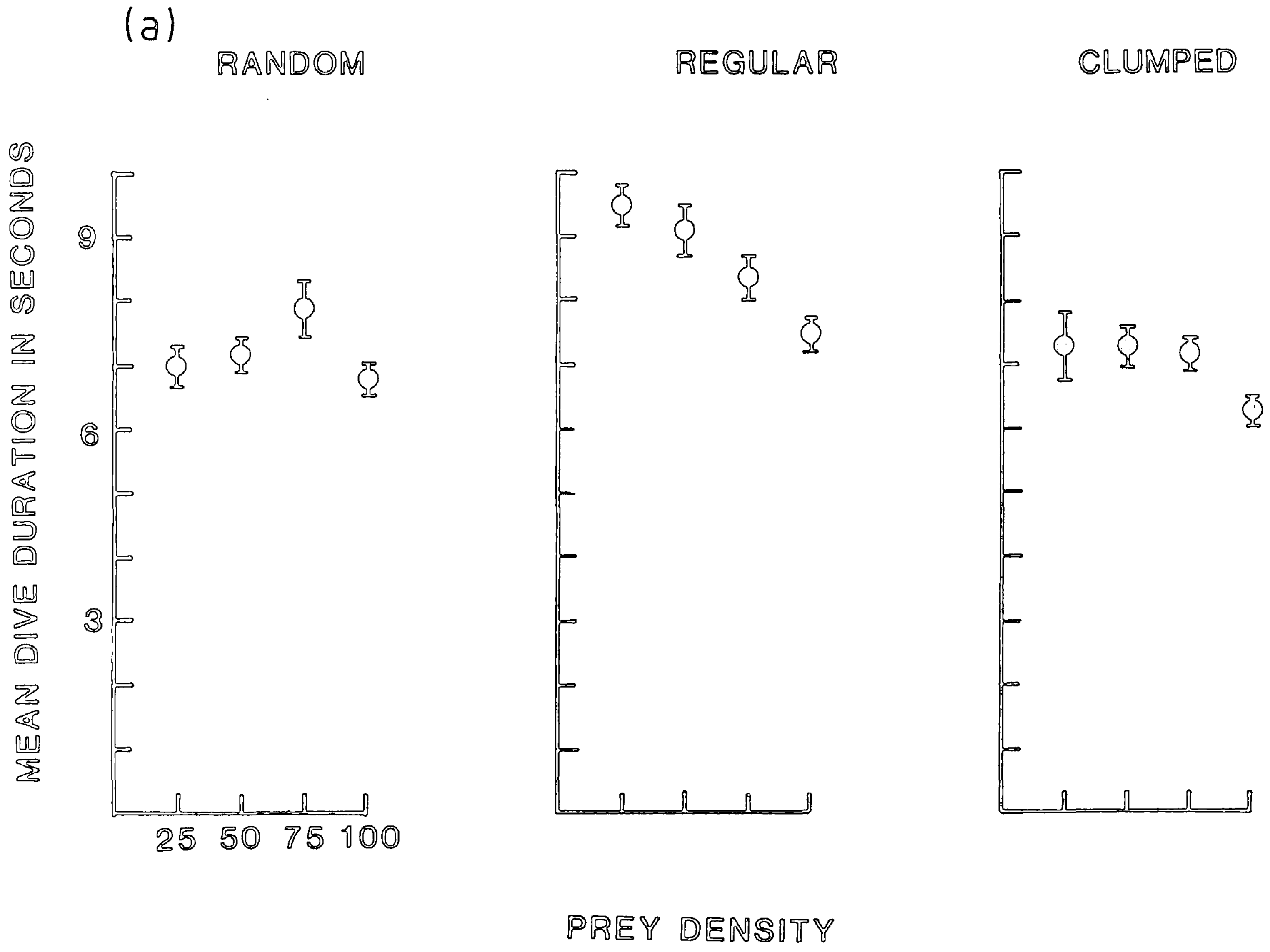

(a)
RANDOM
REGULAR
CLUMPED
MEAN DIVE DURATION IN SECONDS
11
6
1
25
50
75
100
PREY DENSITY

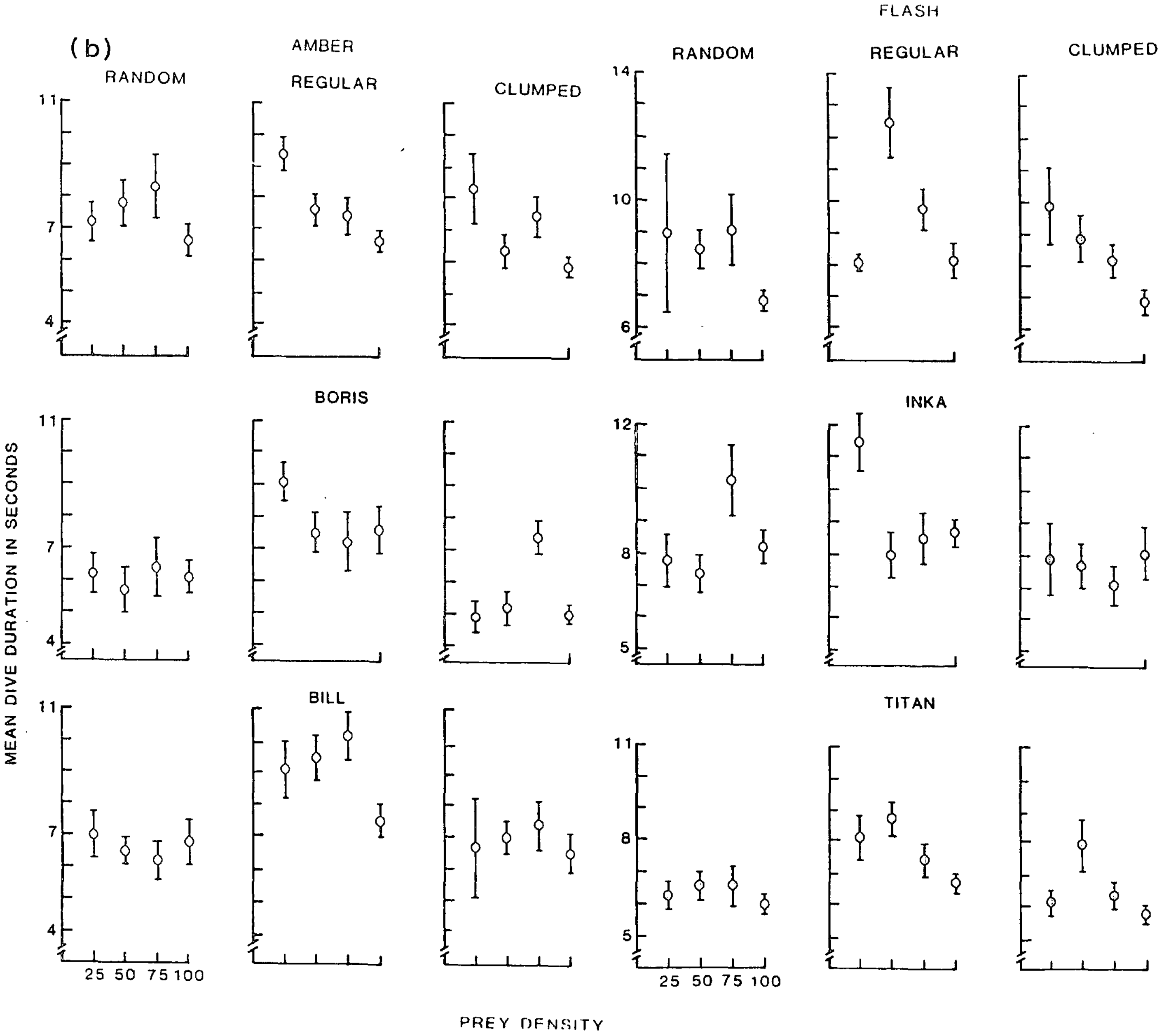

(b)
AMBER
RANDOM
REGULAR
CLUMPED
FLASH
BORIS
INKA
BILL
TITAN
MEAN DIVE DURATION IN SECONDS
PREY DENSITY
12
8
5
14
10
7
25 50 75 100
r=-0.10
r=-0.10
r=-0.83
r=-0.44
r=-0.45
r=-0.89
r=-0.29
r=-0.56
r=0.56
r=0.70
r=0.34
r=0.19
r=-0.72
r=-0.69
r=-0.77
r=-0.34
r=-0.57
r=-0.61

individual results for the different hide arrangements, and between individuals when the results for the same hide arrangement are considered. Curvilinear analysis revealed that, in five cases, there was a significant cubic relationship, and in one case a significant quadratic relationship. The equations are given in the Figure legend. These are more complex to interpret, but again, generally, mean dive duration at the maximum density was less than that at the minimum density.

The results for successful dive duration are given in Fig. 5.8a (All Animals) and Fig. 5.8b (individual data). Linear regression analysis shows that in five cases there were significant negative correlations, between mean successful dive duration and density: All:Regular ($r = -0.29$, $df = 384$, $p<0.001$), Amber:Regular ($r = -0.47$, $df = 80$, $p<0.001$), Titan:Regular ($r = -0.32$, $df = 86$, $p<0.01$), All:Clumped ($r = -0.16$, $df = 361$, $p<0.01$) and Flash:Clumped, ($r = -0.40$, $df = 63$, $p<0.01$), although the slopes indicate that as density increases from 0 to 100%, dive duration drops by between 2 and 4 s, depending on the animal and condition. Again, it can be seen from the graphs that there is considerable variation both within and between individuals, although overall, the suggestion is that animals are finding food faster as density increases. Again, curvilinear analysis shows that in two cases there is a significant quadratic relationship between the variables, and in three cases, there is a significant cubic relationship. Again the general trend is for mean successful dive duration to be lowest at the maximum density.

There are a number of points to be noted when the results for mean unsuccessful and sucessful dive duration are compared. If individual data for a given hide arrangement are compared, it can be seen that often the sort of change recorded is very different, e.g. Flash:Regular. For unsuccessful dives, mean dive duration seems to increase slightly until a density of 75% is reached, then it drops sharply, but there is no significant relationship.


(a)
RANDOM
REGULAR
CLUMPED
MEAN DIVE DURATION IN SECONDS
9
6
3
25
50
75
100
PREY DENSITY


(b)
AMBER
FLASH
RANDOM
REGULAR
CLUMPED
RANDOM
REGULAR
CLUMPED
BORIS
INKA
BILL
TITAN
MEAN DIVE DURATION IN SECONDS
11
7
4
11
7
4
11
7
4
14
10
6
12
8
5
11
8
5
25 50 75 100
25 50 75 100
PREY DENSITY

When mean successful dive duration is considered, duration increases sharply as density rises from 25% to 50%, then declines, and there is a significant cubic relationship between the two variables. Such changes make it very difficult to discern consistent trends in the data. Further, it can be seen that even where there is a significant correlation, the actual values for mean durations vary by only a few seconds. In all cases the maximum mean duration was 13.5 s (Flash:Regular unsuccessful) and the minimum mean was 5.0 s (Boris:Clumped successful). The final point to note from Figs. 5.7 and 5.8 is that, on the whole, mean successful dive durations are less than the corresponding values for mean unsuccessful dive durations. However, Standard Error bars do show that in many cases there is overlap, and in a few instances mean unsuccessful dive duration is less than the corresponding mean successful duration. Nevertheless, on the whole this result is consistent with that observed in the previous experiments. Since it would be expected that successful dives would be terminated by prey capture, (and hence would be shorter than unsuccessful dives), analyses were carried out, generally, on data from unsuccessful dives only from this point on.

5.4.8. Time on bottom

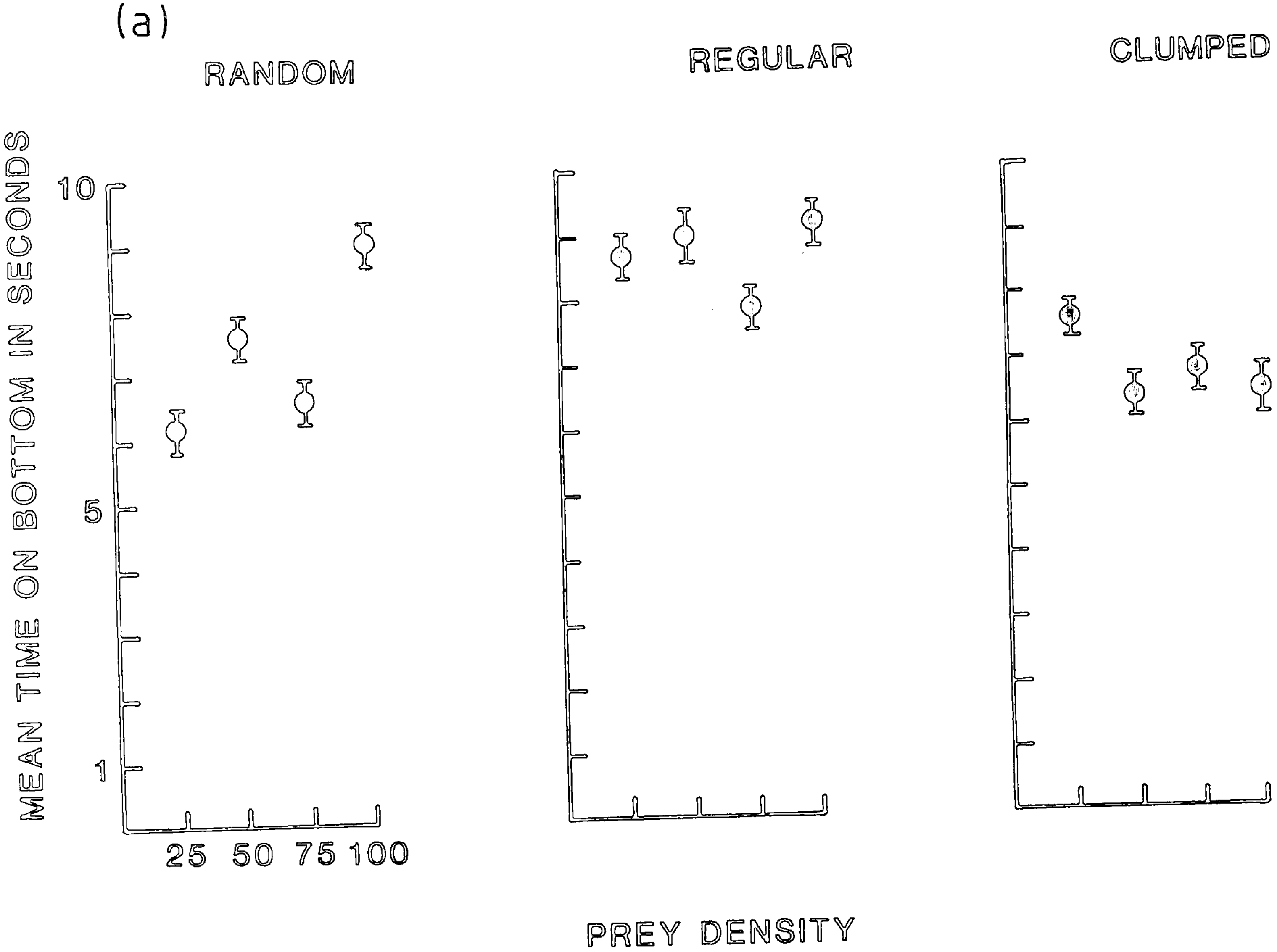
Dive duration is a measure of the total time spent underwater, but this is not necessarily equal to the total time available for foraging behaviour, since some time is taken up by travel to and from the pool bottom. It was noted that mink would sometimes dive vertically to the pool bottom, at other times they would dive at a shallow angle and reach the pool bottom a few metres from their entry point, etc. It was therefore felt that a more appropriate measure of the time available for mink to search for prey was mean time on bottom, since some of the differences in mean dive duration with depth could be due to longer travel times, especially at the lower densities, particularly if animals were not concentrating solely on the foraging task.

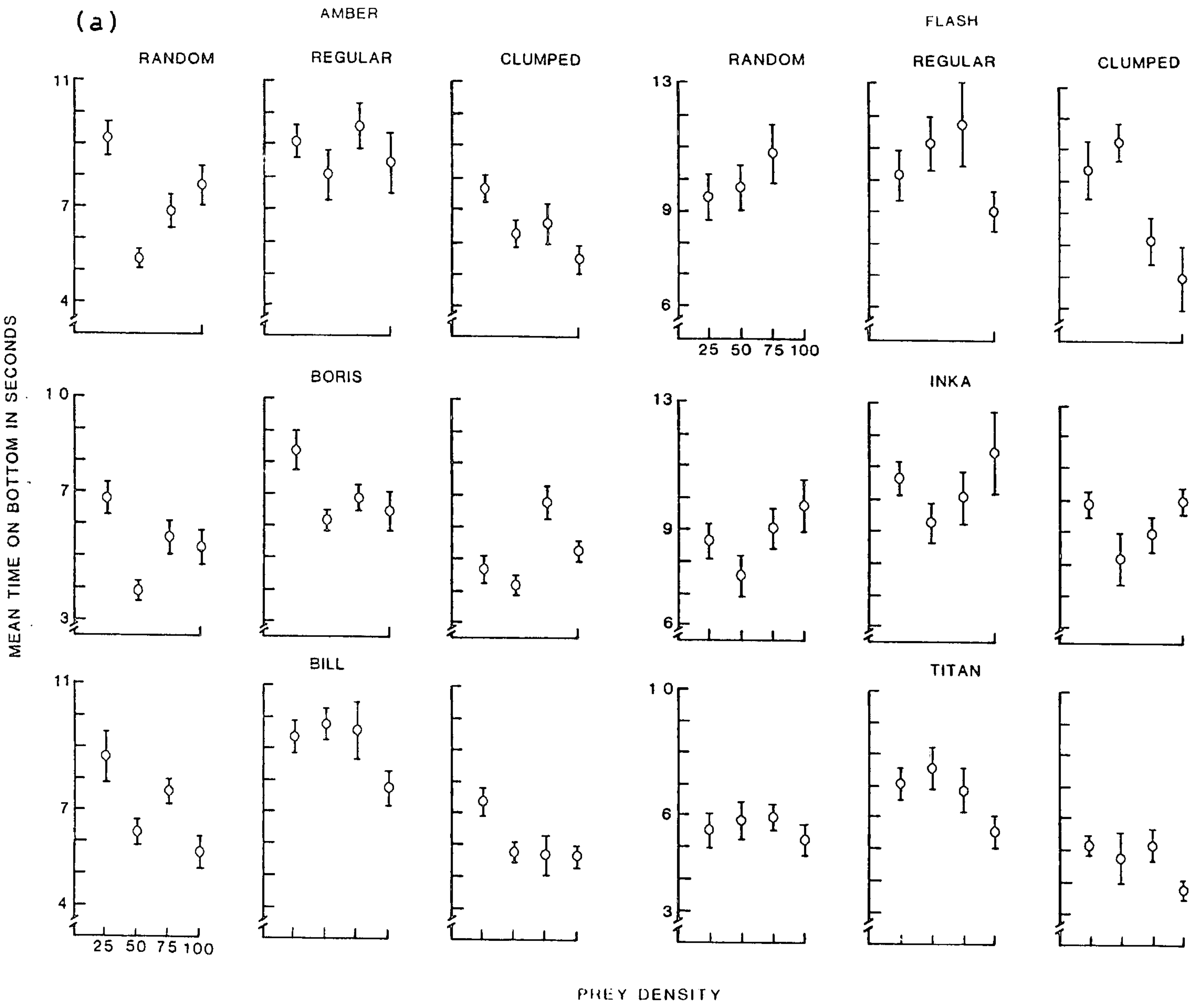
Mean time on bottom for All Animals and individuals, under the different conditions of density and complexity, was calculated for unsuccessful dives from the formula outlined in section 3.3.9. The results are illustrated in Fig. 5.9a (All Animals) and Fig. 5.9b (Individuals).

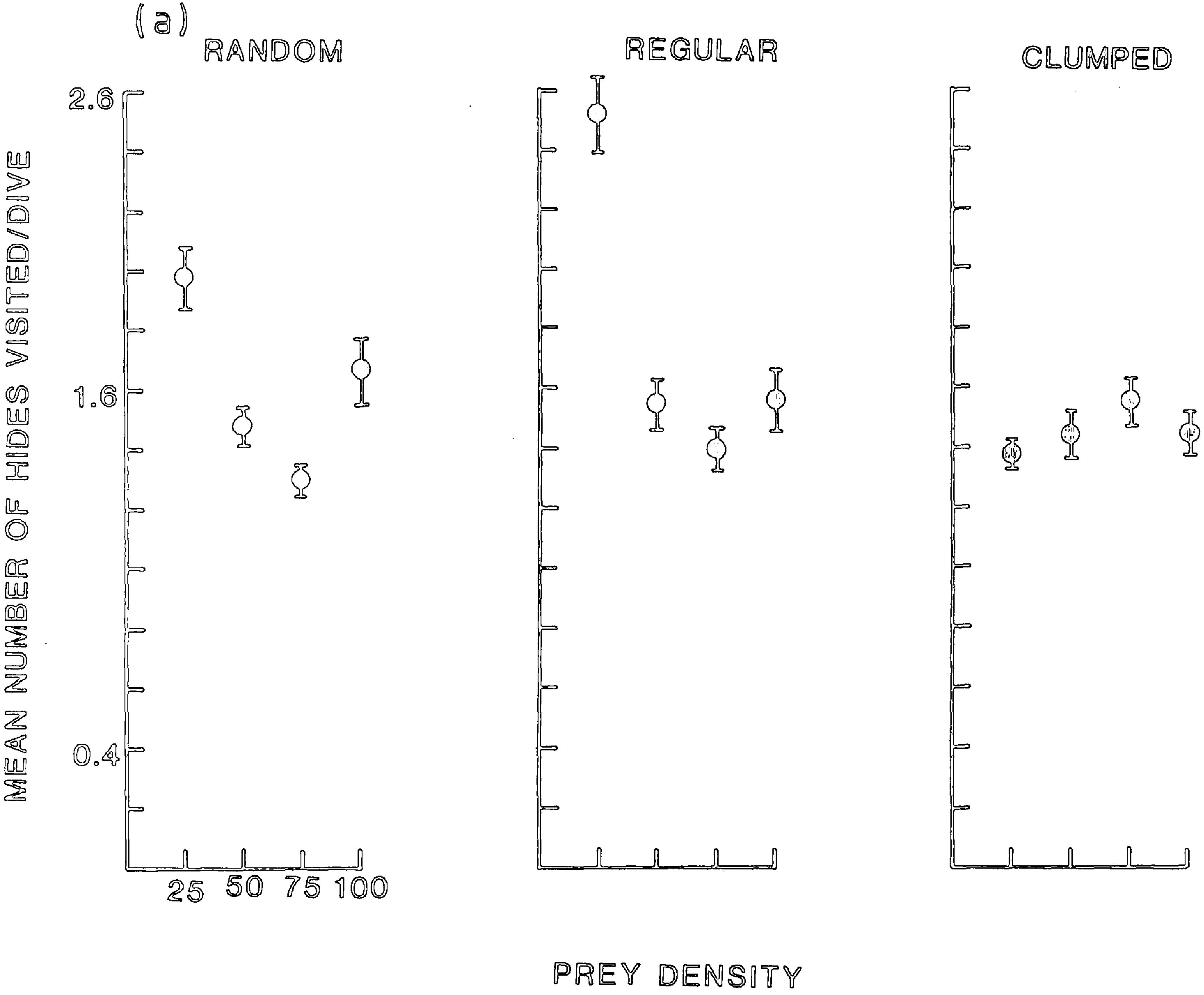
Linear regression analysis revealed that there were six statistically significant correlations between the two variables, all negative. These were: All:Regular ($r = -0.11$, $df = 353$, $p<0.05$), Boris:Regular ($r = -0.23$, $df = 88$, $p<0.05$), All:Clumped ($r = -0.12$, $df = 512$, $p<0.01$), Amber:Clumped ($r = -0.34$, $df = 78$, $p<0.01$), Bill:Clumped ($r = -0.31$, $df = 98$, $p<0.01$) and Flash:Clumped ($r = -0.29$, $df = 68$, $p<0.05$). Curvilinear analysis showed that in five cases, there was a significant cubic relationship. In each case this was the same type of relationship as that found for mean unsuccessful dive duration, and again the general trend was for mean time on bottom to decrease with density, thus reflecting the decrease in dive duration. Perhaps not surprisingly, the various patterns shown in these graphs closely follow those of the corresponding dive duration graphs, (but the values are generally of the order of 1-2 s less), indicating that travel time was not an important factor in determining changes in mean dive duration with density.

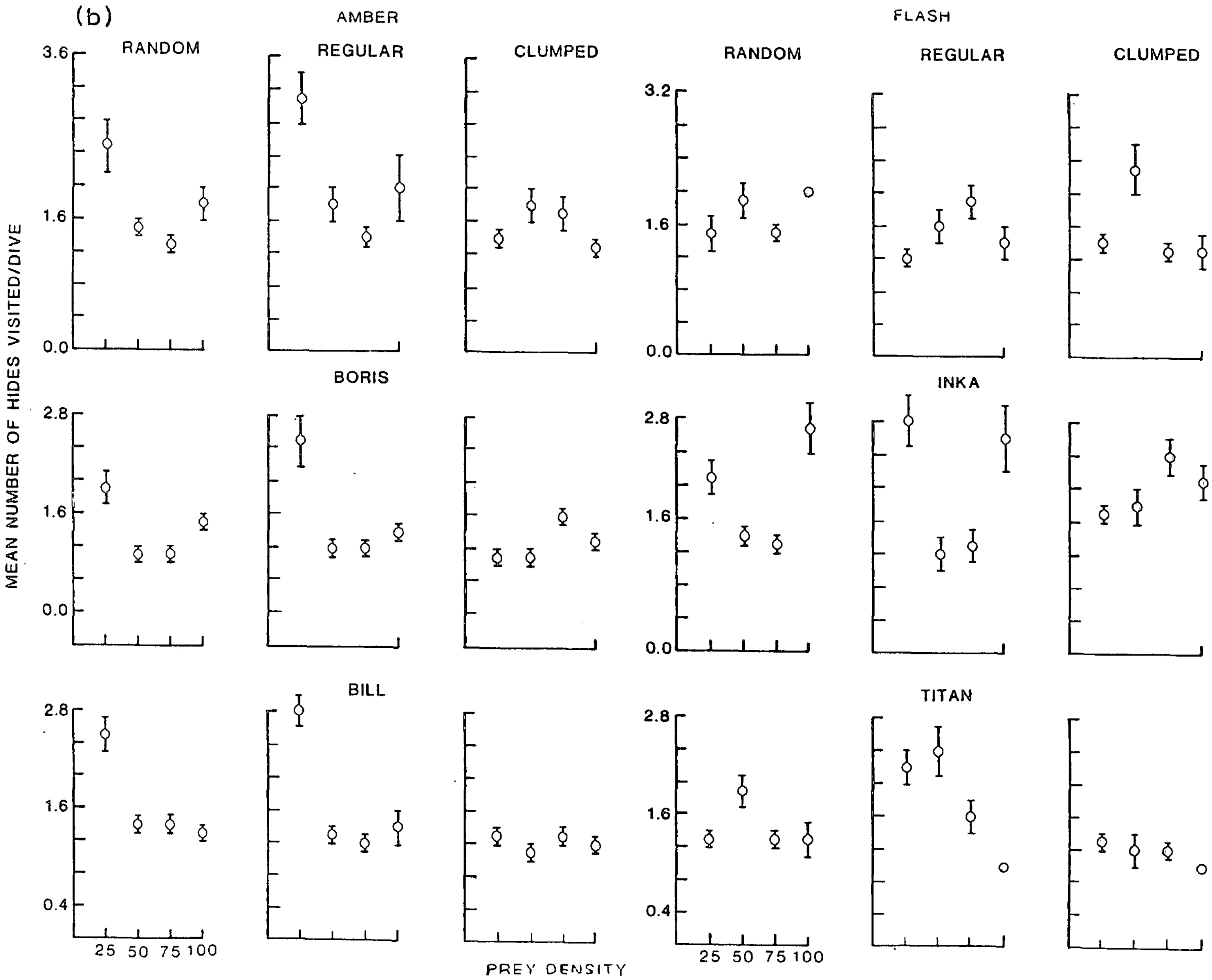
5.4.9. Mean number of hides visited per dive

The mean number of hides visited per dive was calculated for individuals and All Animals over each condition of density and complexity using the formula outlined in section 3.3.10. Data for unsuccessful dives are illustrated in Fig. 5.10a (All Animals) and Fig. 5.10b (individual data).


(a)
RANDOM
REGULAR
CLUMPED
MEAN TIME ON BOTTOM IN SECONDS
10
5
1
25
50
75
100
PREY DENSITY


(a)
AMBER
FLASH
RANDOM
REGULAR
CLUMPED
RANDOM
REGULAR
CLUMPED
BORIS
INKA
BILL
TITAN
MEAN TIME ON BOTTOM IN SECONDS
PREY DENSITY
11
7
4
10
7
3
11
7
4
13
9
6
13
9
6
10
6
3
25 50 75 100
25 50 75 100


(a)
RANDOM
REGULAR
CLUMPED
MEAN NUMBER OF HIDES VISITED/DIVE
2.6
1.6
0.4
25
50
75
100
PREY DENSITY


(b)
AMBER
FLASH
RANDOM
REGULAR
CLUMPED
RANDOM
REGULAR
CLUMPED
3.6
1.6
0.0
3.2
1.6
0.0
BORIS
INKA
2.8
1.6
0.0
2.8
1.6
0.0
BILL
TITAN
2.8
1.6
0.4
2.8
1.6
0.4
MEAN NUMBER OF HIDES VISITED/DIVE
25 50 75 100
25 50 75 100
PREY DENSITY

Linear regression analysis of the data showed that in two cases, there was a significant relationship between the two variables. For Titan:Regular ($r = -0.40$, $df = 41$, $p<0.01$) and number of hides visited per dive decreased with density, although the slope of the regression line indicated that the decrease was very small (only 0.01 hides per dive for each 1% change in density). For Inka:Clumped, there was a significant positive relationship ($r = 0.29$, $df = 86$, $p<0.01$), but again the slope showed that the increase was very small. The size of the Standard Error bars indicates that the results for All Animals are greatly influenced by individual variation, and results for individuals show that animals are behaving differently between trials under the same conditions. Curvilinear analysis showed that in 11 cases there was a significant quadratic relationship between the two variables, and, generally, the mean number of hides visited declined with density, although for the female Inka mean number of hides visited tended to increase with density, regardless of hide arrangement. In three cases there was a significant cubic relationship.

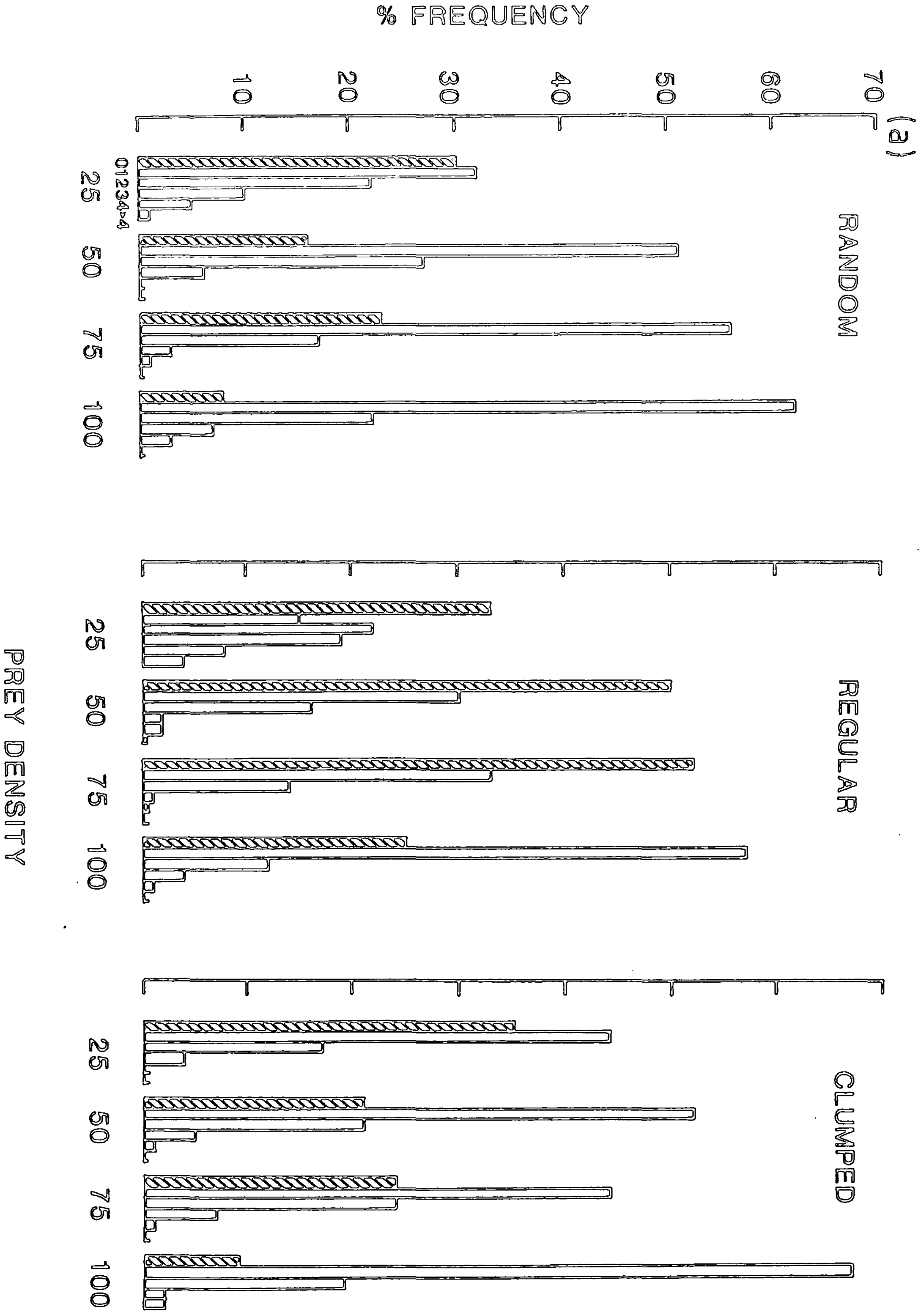
The most interesting point to emerge from these results concerns the actual values for mean number of hides visited per unsuccessful dive under the various conditions. Results for All Animals range from a minimum mean value of 1.30 hides/dive at 75% (random) to a maximum of 2.53 at 25% (regular). This contrasts with results obtained in the depth experiment, where the mean number of hides visited per unsuccessful dive at the equivalent depth, i.e. 0.60 m, was 1.13. Generally, results for individuals agree with the above, with mean values of two or more hides visited per dive recorded at a density of 25%, regardless of hide arrangement. Since non-hide visit dives were excluded, the mean number of hides visited per dive never falls below 1.0, but it does reach this value for female Titan under conditions of 100% density when hides are either arranged regularly or in clumps.

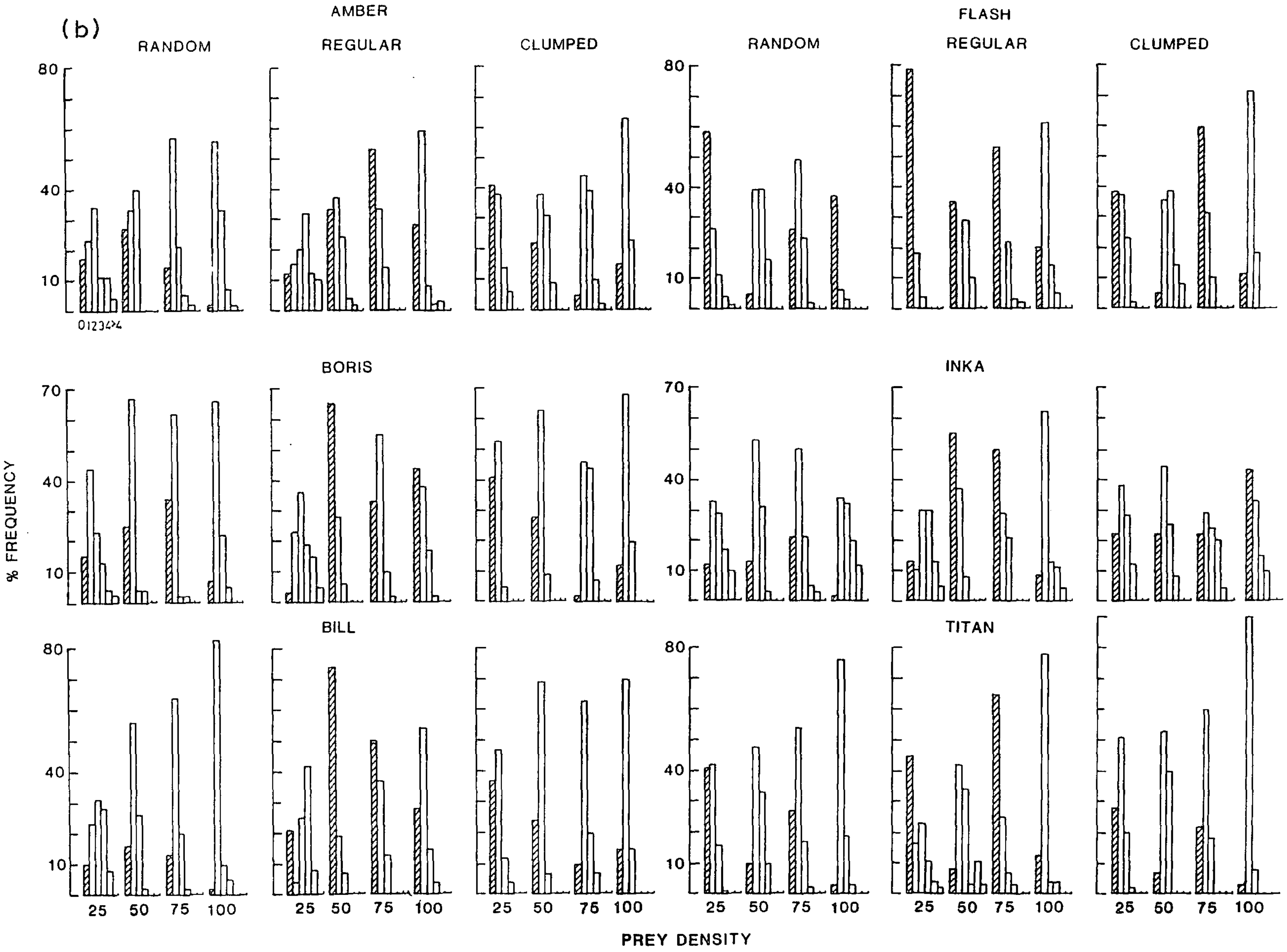
Overall then there does seem to be a correlation between mean number of hides visited per unsuccessful dive and density, with the trend being for higher values of number of hides visited per dive to occur at the lower densities.

5.4.10. The relative frequency of hide visits under the various conditions

The individual variation in mean number of hides visited per dive, under different conditions, can be clearly seen if the data are presented in the form of histograms. Further, this will allow comparison with results obtained in previous experiments. Data from successful, unsuccessful and non-hide visit dives have been combined and the results are illustrated in Fig. 5.11a (All Animals) and Fig. 5.11b (individual data).

From these histograms several points can be noted. Firstly, it can be seen that in some cases, at low densities, (e.g. Flash: 25% regular, Bill: 50% regular) a very large proportion of dives (up to 80% for Flash) did not visit any hides, but in the majority (27 out of 42 cases at densities of 25% and 50%) less than 30% of dives failed to visit any hides. Secondly, as already indicated in the previous analysis, there is a general trend at the lower densities (25% and 50%) for a greater proportion of dives to involve visits to 2,3,4 and more hides. The highest figure was 7 hides for Inka: 25% regular. At prey densities of 75% and 100% there are no records of any dives visiting more than 4 hides per dive and, generally (especially at 100% density), the majority of dives visit only one hide. Also, in half the results (21 out of 42 cases at densities 75% and 100%) less than 20% of dives fail to visit any hides, although there is some variation between individuals, which is reflected in the results for All Animals. However, when the results are examined with regard to hide arrangement, it can be seen that when hides are clumped, there are no records, at any density, for dives involving more than 4 hide visits, and in the majority of


(a)
% FREQUENCY
10
20
30
40
50
60
70
RANDOM
REGULAR
CLUMPED
0 1 2 3 4 >4
25
50
75
100
PREY DENSITY


(b)
AMBER
RANDOM
REGULAR
CLUMPED
FLASH
RANDOM
REGULAR
CLUMPED
80
40
10
80
40
10
01234>4
BORIS
INKA
70
40
10
70
40
10
BILL
TITAN
80
40
10
80
40
10
% FREQUENCY
25 50 75 100
25 50 75 100
25 50 75 100
25 50 75 100
25 50 75 100
25 50 75 100
PREY DENSITY

results (22 out of 28 cases at all densities), there are no records of dives visiting more than 3 hides per dive. This is very interesting in view of the fact that each 'clump' comprised 4 hides, and will be considered further below. Also, there is some indication that, at the lower densities, it is more common for individuals to visit more than 4 hides per dive when hides are arranged in a regular manner, compared to random.

The final point is that in contrast to the depth experiment (where prey density was 50%) where no animal visited more than 3 hides during a dive, there are, as noted, several records of dives involving 4 or more visits when density is 25 or 50%. Also, in the depth experiment, at least 25% (and frequently the figure was higher) of dives did not visit a hide. This contrasts with these results where there are 19 cases (out of 84) of less than 10% of dives visiting no hides.

The general conclusion from this analysis is that as density increases, fewer hides are visited per dive, but fewer dives fail to visit any hides. Since successful dive rate shows a tendency to increase as density increases this would seem to support the idea that as more prey is available, so the probability of the first hide searched being baited increases, hence animals visit one hide per dive more often at higher prey densities. This might lead to a decline in dive duration and time on bottom as density increases, particularly for successful dives.

5.4.11. Mean time in hide

It has been shown in previous experiments, that this behaviour generally lasts for one to two seconds, and that successful visits are longer than unsuccessful ones. It was suggested in the previous experiments, that if the changing conditions in the experiment had an effect on the energetics of diving, then it was possible that mink would alter the amount of time spent searching an individual hide, i.e. animals should spend longer 'in hide' to ensure that it was not baited. In this experiment, conditions of water depth are constant, but it is possible that mean time in hide may alter as density changes, and it would be expected therefore that mean time in hide for unsuccessful visits, should be greater at the lower densities. However, it was found in the previous experiments that, generally, there was little change in the mean time spent in hide as foraging conditions were altered. Further, it was noted in previous experiments, that even where there were statistically significant changes in the mean time spent in hide, these changes were, generally, of the order of less than a second in duration. Consequently, it was decided not to investigate time in hide for this experiment.

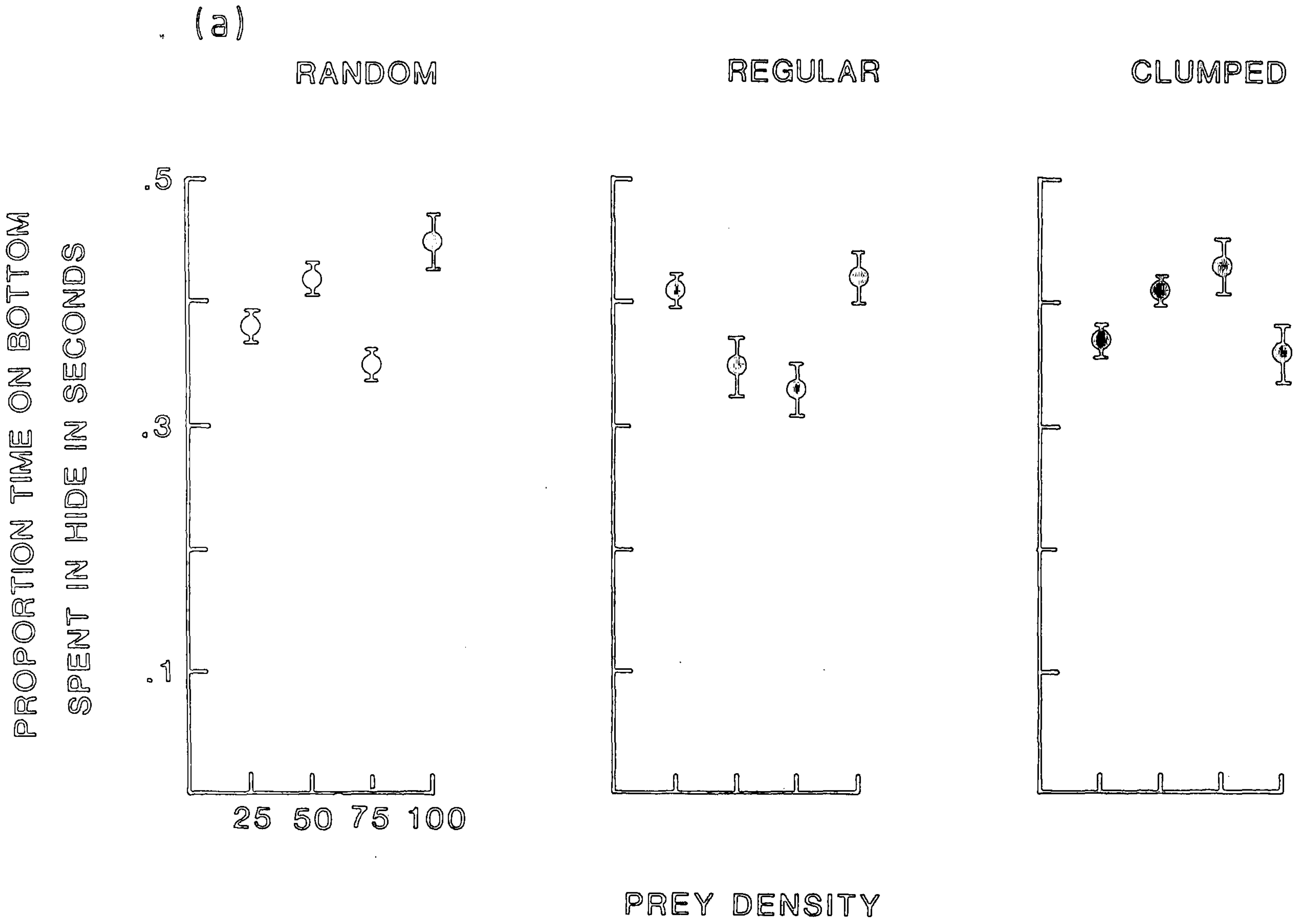
5.4.12. Proportion of time on bottom spent in hide

Since the durations involved in behaviours such as 'hide searching', 'time on bottom' and 'dive duration' are generally small, e.g. from previous experiments, total time hide searching lasted, on average, 1-2 s only, and individual variation in behaviour is considerable, significant changes in behaviour under different conditions of density and complexity may not be readily apparent. Thus, in an effort to investigate changes in foraging behaviour as density increases ,the proportion of time on bottom spent hide searching was calculated for each individual and All Animals, for each condition of density and complexity. If time in hide is being altered slightly as foraging conditions change, and since number of hides visited per dive varies with the different conditions, changes in the overall foraging strategy may be seen more clearly by examining any differences in the proportion of time underwater allocated to hide searching under the various foraging conditions. Further, this parameter will also give a better idea of whether travel time on the pool bottom is changing, which might again indicate whether animals are following different searching strategies.This point will be considered in more detail in the section on revisiting. For now, previous analyses have shown that at low densities, more hides were visited per dive. Also, as density increased, time on bottom showed some tendency to decline. An analysis of the proportion of time on bottom spent hide searching, should, therefore, indicate whether animals are changing their foraging strategies in terms of allocation of time to actually searching hides, regardless of density.

Data were calculated for unsuccessful dives using the formula outlined in section 3.3.13. The results for mean proportion of time on bottom spent hide searching ± Standard Error are illustrated in Fig. 5.12a (All Animals) and Fig. 5.12b (Individual results).

Linear regression analysis was carried out on the data, and it was found that there were no significant correlations between the two variables. Curvilinear analysis however, revealed that in eight cases there was a significant quadratic relationship, and in three cases a significant cubic relationship (Fig. 5.12). The general trend is for proportion of time on bottom spent hide searching to decline with density up to 75%, and then to increase again, although the reverse is occasionally true when hides are clumped. Most values lie within the range of 30-50% of bottom time spent in hides.

Thus, at low densities, dive duration and time on bottom tend to be greater than at the higher densities. But, mink are visiting more hides per dive at low densities. Thus, since the mean proportion of time on bottom spent hide searching appears to stay within a fairly narrow limit despite changes in environmental conditions, this indicates that mean time spent in hide was relatively unchanged under the various foraging conditions provided.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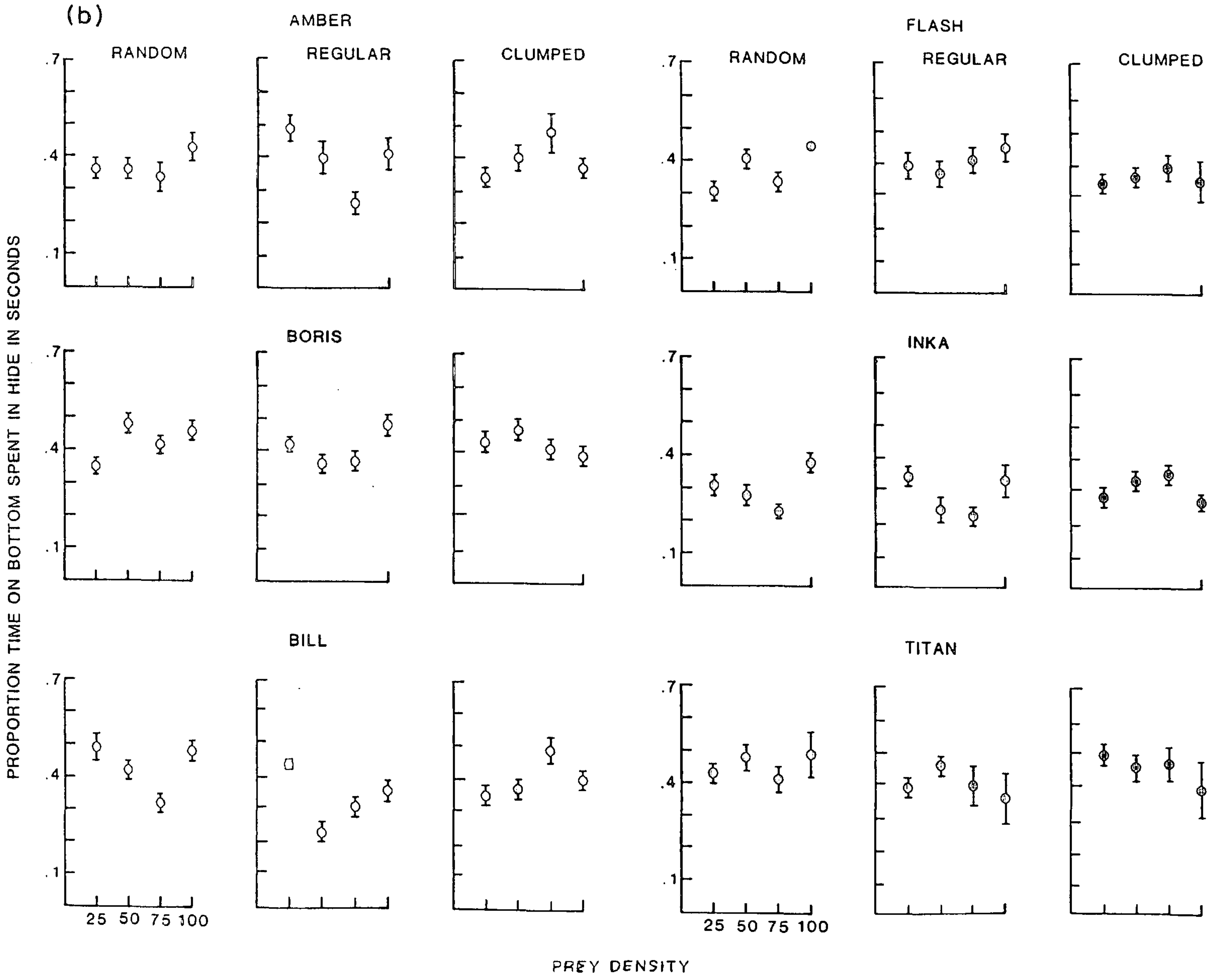
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PROPORTION TIME ON BOTTOM SPENT IN HIDE IN SECONDS
PREY DENSITY

5.4.13. Hide revisiting

The final parameter to be investigated is revisiting of hides. Since hides are not replenished during a trial, revisiting may be important at all densities, but is especially important at low prey densities, when the most efficient strategy would be to search new hides and not revisit old ones, particularly those which have already been successfully searched. Since significantly more hides per dive are visited at the lower densities, this does suggest that mink are attempting to forage as efficiently as possible, and this analysis will investigate whether this additional search effort is directed towards visiting new hides.

Since, in this experiment, 32 hides were provided, it was decided to investigate the 16th hide visit during a trial, since there would then be a 50% chance of this visit being to a 'new' hide, if the mink was following a random foraging strategy. However, in many cases animals did not visit 16 hides during a trial, so it was decided to score results for the 13th to 19th hide visit inclusive to obtain more data. This does mean that where the animals visited fewer than 16 hides per trial, the results would still be biased in favour of visiting 'new' hides, if animals were foraging randomly. Thus, the results must be interpreted with caution.

Hide visits were scored as being to 'new' or 'old' hides. Table 5.12 presents the results for each individual and All Animals, for all combinations of prey density and hide arrangement conditions. The null hypothesis is that there is an equal probability of these visits being to either old or new hides. A Chi-square analysis was carried out and the results are also given in Table 5.12.

TABLE 5.12: Number of new hide visits and revisits for 13th to 18th hide visit of each trial.

		100% Random	100% Regular	100% Clumped
All	N	45 (31.5)	14 (11.5)	23 (17)
	R	18 (31.5)	9 (11.5)	11 (17)
	χ^2	11.57 $p<0.01$	1.08 p = ns	4.24 $p<0.05$
Amber	N	11 (7.5)	5 (3.5)	- (-)
	R	4 (7.5)	2 (3.5)	- (-)
	χ^2	3.27 p = ns	-	-
Boris	N	12 (7.5)	3 (2.5)	5 (3.5)
	R	3 (7.5)	2 (2.5)	2 (3.5)
	χ^2	5.40 $p<0.05$	-	-
Bill	N	6 (3)	3 (2)	4 (2.5)
	R	0 (3)	1 (2)	1 (2.5)
	χ^2	-	-	-
Flash	In no trial did Flash visit 13 hides.			
Inka	N	16 (13.5)	3 (3.5)	13 (10.5)
	R	11 (13.5)	4 (3.5)	8 (10.5)
	χ^2	0.93 p = ns	-	1.19 p = ns
Titan	N	- (-)	- (-)	1 (0.5)
	R	- (-)	- (-)	0 (0.5)
	χ^2	-	-	-

N = number of new hides visited.
R = number of revisited hides
(n) = expected number for Chi-square test.

TABLE 5.12: (Contd.)

		75% Random	75% Regular	75% Clumped
All	N	22 (16)	2 (1.5)	40 (34)
	R	10 (16)	1 (1.5)	28 (34)
	χ^2	4.05 $p<0.05$	-	2.12 p = ns
Amber	N	6 (4)	- (-)	10 (10)
	R	2 (4)	- (-)	10 (10)
	χ^2	-	-	0.00 p = ns
Boris	N	- (-)	2 (1.5)	17 (9.5)
	R	- (-)	1 (1.5)	2 (9.5)
	χ^2	-	-	11.84 $p<0.01$
Bill	N	4 (3.5)	- (-)	6 (4)
	R	3 (3.5)	- (-)	2 (4)
	χ^2	-	-	-
Flash	N	4 (2.5)	- (-)	- (-)
	R	1 (2.5)	- (-)	- (-)
	χ^2	-	-	-
Inka	N	3 (1.5)	- (-)	7 (10.5)
	R	0 (1.5)	- (-)	14 (10.5)
	χ^2	-	-	2.33 p = ns
Titan	N	5 (4.5)	- (-)	- (-)
	R	4 (4.5)	- (-)	- (-)
	χ^2	-	-	-

TABLE 5.12: (Contd.)

		50% Random	50% Regular	50% Clumped
All	N	36 (23.5)	18 (13)	35 (28.5)
	R	11 (23.5)	8 (13)	22 (28.5)
	χ^2	13.30 $p<0.01$	3.84 $p<0.05$	2.96 p = ns
Amber	N	1 (1)	6 (3.5)	12 (9)
	R	1 (1)	1 (3.5)	6 (9)
	χ^2	-	-	2.00 p = ns
Boris	N	6 (4)	- (-)	6 (6.5)
	R	2 (4)	- (-)	7 (6.5)
	χ^2	-	-	0.08 p = ns
Bill	N	4 (3.5)	- (-)	- (-)
	R	3 (3.5)	- (-)	- (-)
	χ^2	-	-	-
Flash	N	15 (9.5)	6 (6)	2 (2)
	R	4 (9.5)	6 (6)	2 (2)
	χ^2	6.37 $p<0.05$	0.00 p = ns	-
Inka	N	- (-)	- (-)	15 (11)
	R	- (-)	- (-)	7 (11)
	χ^2	-	-	2.91 p = ns
Titan	N	10 (5.5)	6 (3.5)	- (-)
	R	1 (5.5)	1 (3.5)	- (-)
	χ^2	7.36 $p<0.01$	-	-

TABLE 5.12: (Contd.)

		25% Random	25% Regular	25% Clumped
All	N	62 (44)	60 (40.5)	28 (20)
	R	26 (44)	21 (40.5)	12 (20)
	χ^2	14.72 $p<0.01$	18.78 $p<0.01$	6.40 $p<0.05$
Amber	N	17 (12)	15 (10.5)	6 (4)
	R	7 (12)	6 (10.5)	2 (4)
	χ^2	4.17 $p<0.05$	3.86 $p<0.05$	-
Boris	N	16 (10.5)	19 (10.5)	- (-)
	R	5 (10.5)	6 (10.5)	- (-)
	χ^2	5.76 $p<0.05$	13.76 $p<0.01$	-
Bill	N	15 (10.5)	4 (3.5)	1 (1)
	R	6 (10.5)	3 (3.5)	1 (1)
	χ^2	3.86 $p<0.05$	-	-
Flash	N	- (-)	- (-)	4 (2.5)
	R	- (-)	- (-)	1 (2.5)
	χ^2	-	-	-
Inka	N	8 (7)	15 (12.5)	11 (7.5)
	R	6 (7)	10 (12.5)	4 (7.5)
	χ^2	0.29 $p = ns$	1.00 $p = ns$	3.27 $p = ns$
Titan	N	6 (4)	7 (3.5)	6 (5)
	R	2 (4)	0 (3.5)	4 (5)
	χ^2	-	-	0.40 $p = ns$

The first point to note is that, in several cases, particularly at the higher densities, animals failed to visit even 13 hides in a trial. This was especially true when density was 75%. Further, in many more cases the expected values were less than five, and it was not possible to carry out a Chi-square analysis. The results show great variations, both between individuals, between prey density conditions and between hide arrangement conditions. The results for All Animals will be considered first. When density is 100%, there are two significant results, when hides are random and clumped. In each case the results suggest that the animals do not revisit hides. When hides were arranged regularly, there was no significant difference, suggesting that animals are foraging randomly and that revisiting does occur. However, it must be noted that the actual numbers of hide visits scored was very low, i.e. generally animals were searching less than 16 hides per trial under these conditions. At 75% density, only the result when hides were random was significant, and again showed that revisiting did not occur. When density was 50% there were two significant results, when hides were random and regular, and when density was 25%, results were significant for each hide arrangement. In each case, the results showed that animals did not revisit hides.

When the data for individuals are examined, a similar picture can be seen, i.e. whenever results are significant they indicate that hides are not revisited. One other point to note is that several individuals, particularly Flash and Titan, often failed to reach the criterion level of 13 hide visits per trial, and this indicates that there may be differences in foraging strategies between individuals. The effects of density can be outlined as follows. When density is 100% or 75%, significant results occur only when hides are arranged randomly or in clumps, and only for individual males. In some cases, this reflects the fact that fewer hide visits are made per trial at these densities, but in others, e.g. Inka: 100% Random, it suggests that the animals are searching in a random manner. When density is

50%, there are two significant results when hides are arranged randomly, both for individual females, and at density 25%, significant results are found only when hides were arranged in a random or regular pattern, this time only for individual males.

Thus, the general picture is that at the higher densities, so few hides are visited per trial, because the encounter rate is so high, it was not possible to see if animals, particularly females, were using any systematic foraging strategy to increase success, or were simply searching at random. At lower densities, animals are visiting more hides per trial, and there is some evidence that where a systematic strategy is being used, particularly among males, this is biased towards not revisiting previously searched hides. There is some evidence that hide arrangement plays an important part in this.

5.5. Results : Habitat Complexity

An initial investigation into the effect of habitat complexity was carried out using Analysis of Variance tests on dive duration, time on bottom and total time in hide (Tables 5.3-5.5). It was found that complexity, density and animal were all important variables, and there were several significant interactions between complexity and foraging success. A second series of Anova tests separated the data on the basis of foraging success (Tables 5.6-5.8), and it was found that only in one case (Table 5.8) was there a significant interaction between complexity and density, although complexity was a Main Effect in all cases. The animal factor was thought to be a possible reflection of sex differences in behaviour, and a final series of Anova tests were conducted (Tables 5.9-5.11), to investigate the effects of sex, complexity and density. The results revealed that complexity was only important as a Main Effect.

Thus, complexity did seem to be important in explaining behaviour of individuals and sexes, under different prey density conditions. Further, when data are analysed on the basis of foraging success, there is only one significant interaction, between prey density and complexity, suggesting that changes in behaviour at different hide arrangements are not influenced by changes in prey density. However, in view of the small number of animals used in the experiment, and the fact that there was no overlap in size between the males and females, it was decided not to separate data for the two sexes. Instead, data are provided for All Animals with individual results given for comparison.

One further point concerns the statistical analyses used. Firstly, as mentioned previously, it was decided to investigate the effect of complexity, only for a prey density of 50%, since this would allow comparisons to be made with results from other experiments, particularly those from the depth experiment. The results for the various behaviours examined have been presented as a series of histograms. To investigate whether behaviour is different under various conditions of complexity, t-test analyses were carried out. However, for some behaviours, it was possible to investigate the effect of complexity using Oneway Analysis of Variance, incorporating a Multiple Range Test (Scheffe's Procedure), with complexity being the only independent variable.

5.5.1. Scheffe's procedure

Data for unsuccessful dives only were analysed, since successful dives are terminated once food is located, and therefore may not vary between conditions. The results of Anova tests reported previously (Tables 5.3-5.8) had shown that there was considerable individual variation, hence these tests were only carried out on data for individuals. The variables, dive duration, time on bottom and total time in hide, were tested against the three habitat complexities. The results for the between group tests are expressed as an F ratio, with associated probability values. These probability values are shown in Table 5.13. To investigate changes in behaviour between the hide arrangements in more detail, the Scheffe's Procedure analysis was carried out at a significance level of 1% (i.e. $\alpha = 0.01$). This analysis produces a matrix where the mean values of, e.g. dive duration, are compared between the three hide arrangements. The results are also given in Table 5.13, and it can be seen that there were a number of cases where there were significant differences between the mean values of, e.g. dive duration, between different habitat complexities.

The results in Table 5.13 show that there is a considerable difference in the behaviour of individual male and female mink. It can be seen that there are no significant differences in behaviour for each of the three females between each of the habitat complexity situations. For the three males, on the other hand, it would appear that while behaviour under random and clumped conditions is similar, behaviour when hides are arranged regularly is often significantly different to that observed when hides are arranged randomly, or in clumps.

Thus, more detailed analyses need to be carried out to determine exactly what these changes in behaviour are. However, in this case only those behaviour parameters that might show that the foraging strategy of the mink was changing as habitat complexity was altered, were studied.

5.5.2. Dive rate

Fig. 5.13 shows the results for mean dive rate for All Animals and each individual, over the three hide arrangement conditions, when prey density was 50%. A series of t-tests

TABLE 5.13: Summary of results of Oneway Anova (giving values of probability of F) and results of the matrix comparison produced by Scheffe's Procedure. (Only unsuccessful dives were considered).

		Dive Duration	Time on Bottom	Total time in Hide
Amber	Prob. of F	0.001	0.002	0.013
	Scheffe	Reg x Ran	Reg x Ran	ns
Boris	Prob. of F	0.00001	0.00001	0.075
	Scheffe	Reg x Ran Reg x Cl	Reg x Ran Reg x Cl	ns
Bill	Prob. of F	0.00001	0.00001	0.178
	Scheffe	Reg x Ran Reg x Cl	Reg x Ran Reg x Cl	ns
Flash	Prob. of F	0.246	0.264	0.989
	Scheffe	ns	ns	ns
Inka	Prob. of F	0.394	0.404	0.228
	Scheffe	ns	ns	ns
Titan	Prob. of F	0.024	0.044	0.135
	Scheffe	ns	ns	ns

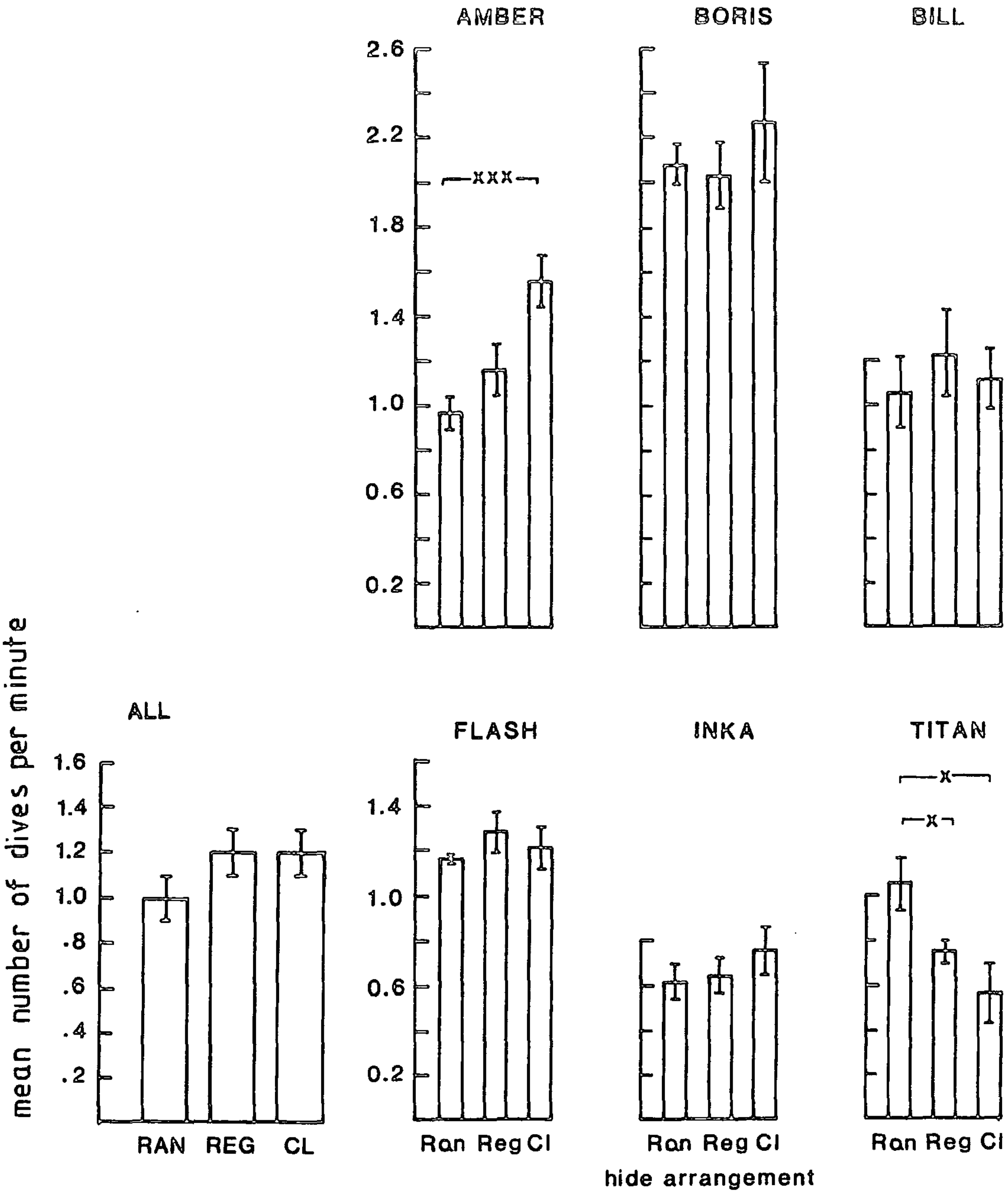
were carried out to investigate whether there were any significant differences in behaviour between the three hide arrangement conditions.

It can be seen from Fig. 5.13 that in only three cases were there significant differences in the mean number of dives per minute. Thus, for male Amber, dive rate was significantly higher when hides were clumped compared to when hides were random ($t = -4.25$, $df = 5$, $p<0.001$). For female Titan, mean dive rate is greatest (1.06 dives per min) when hides are arranged randomly. There are significant differences between dive rate when the results for regular distribution are compared to random, ($t = 2.40$, $df = 7$, $p<0.05$) and when clumped results are compared to random, ($t = 2.56$, $df = 6$, $p<0.05$), but there were no significant differences between the results for regular and clumped conditions.

The conclusion from these results is that, generally, there is little difference in mean dive rate between the three hide arrangement conditions. However, where the results are significant, the two animals concerned (Amber and Titan) would appear to be adopting completely opposite foraging strategies. There are also differences in the actual mean values recorded. Thus, generally for the individual females, mean dive rates vary between 0.6 and 1.3 dives per min, but for individual males, the mean values range from around 1.0 to 2.3 dives per min. Generally, individual males perform more dives per min than individual females.

5.5.3. Hide visit dive rate

If the spatial position of hides is an important factor in determining the foraging strategy employed, then it might be expected that the number of hides visiting dives would vary with habitat complexity. The data for mean hide visit dive rate for individuals and All Animals are given in Fig. 5.14, together with the significant results of t-test analyses.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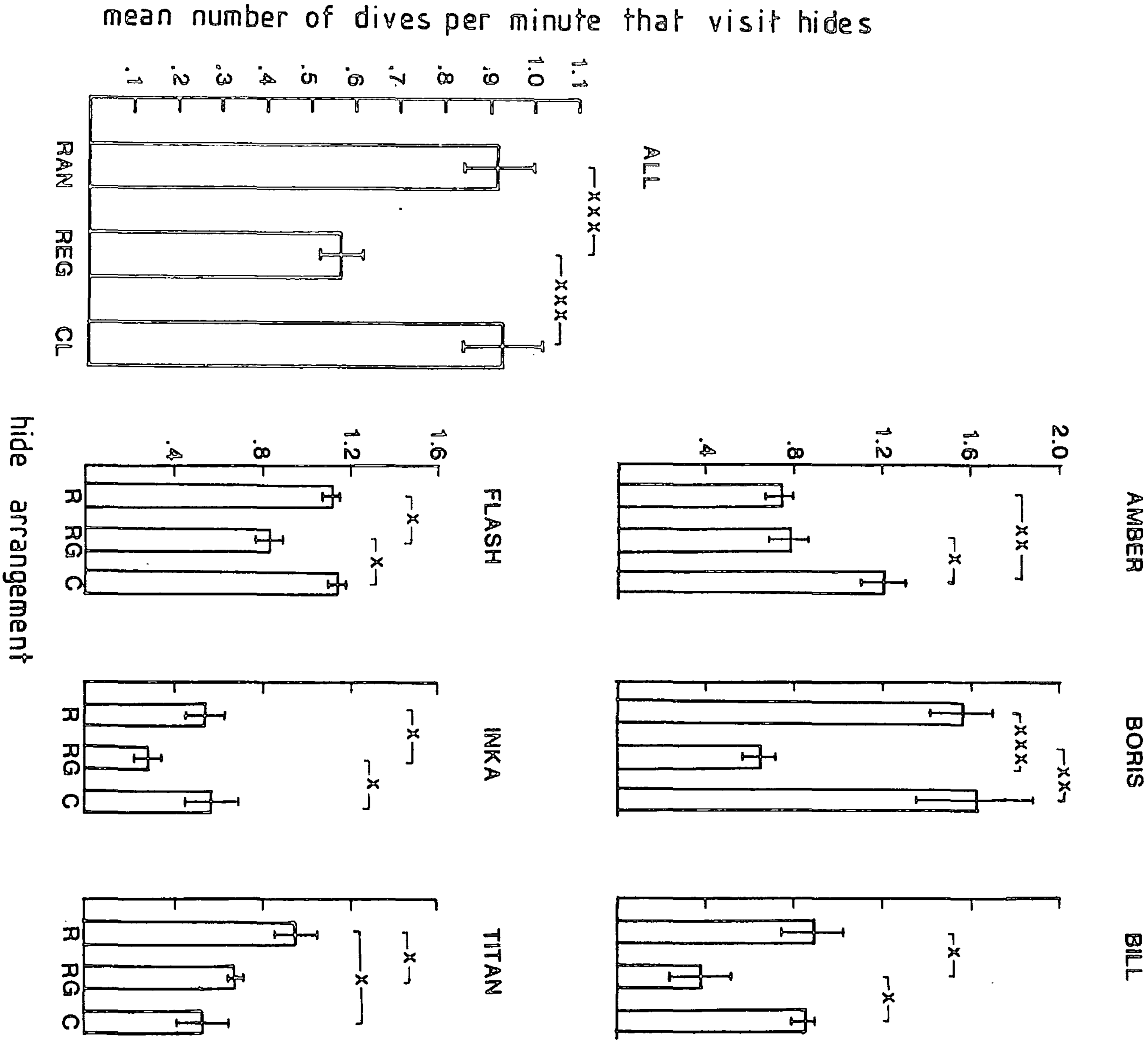
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When the results are examined, it can be seen that there are a number of significant differences. Generally, there are significant differences between the mean hide visit dive rates when hides are randomly arranged compared to regular, (All Animals: t= 4.02, df = 52, $p<0.001$, Boris: t = 6.58, df = 6, $p<0.001$, Bill: t = 2.43, df = 9, $p<0.05$, Flash: t= 3.46, df = 5, $p<0.05$, Inka: t= 2.46, df = 9, $p<0.05$, Titan: t= 2.98, df = 7, $p<0.05$). In all cases hide visit dive rate is significantly greater when hides are arranged randomly. There are also significant differences between regular and clumped arrangements, and hide visit dive rate is greater in all cases when hides are clumped, (All Animals: t = -3.64, df = 51, $p<0.001$, Amber: t= -3.31, df = 5, $p<0.05$, Boris: t= -4.62, df = 6, $p<0.05$, Bill: t= -2.50, df = 9, $p<0.05$, Flash: t= -3.94, df = 5, $p<0.05$, Inka: t= -2.30, df = 7, $p<0.05$). There are two further significant results, when random and clumped conditions are compared. For Amber, (t= -4.33, df = 5, $p<0.01$), and mean hide visit dive rate is significantly greater when hides are clumped. For Titan, however, (t= 2.82, df = 6, $p<0.05$), the reverse is true.

The general picture, therefore, is that mean hide visit dive rate is lowest when hides are arranged regularly, and highest when hides are either randomly arranged or clumped, there being little difference between these two conditions.

The results for Amber and Titan mirror those for mean dive rate. For the remaining animals, there were no significant differences in mean dive rate under any of the habitat conditions, but there are very great differences in the mean hide visit dive rates recorded, particularly when hides are arranged regularly. As for dive rate, females generally have lower mean hide visit dive rates than males under the equivalent condition, although when hides are regular, hide visit dive rates for all individuals vary only between 0.4 and 0.8

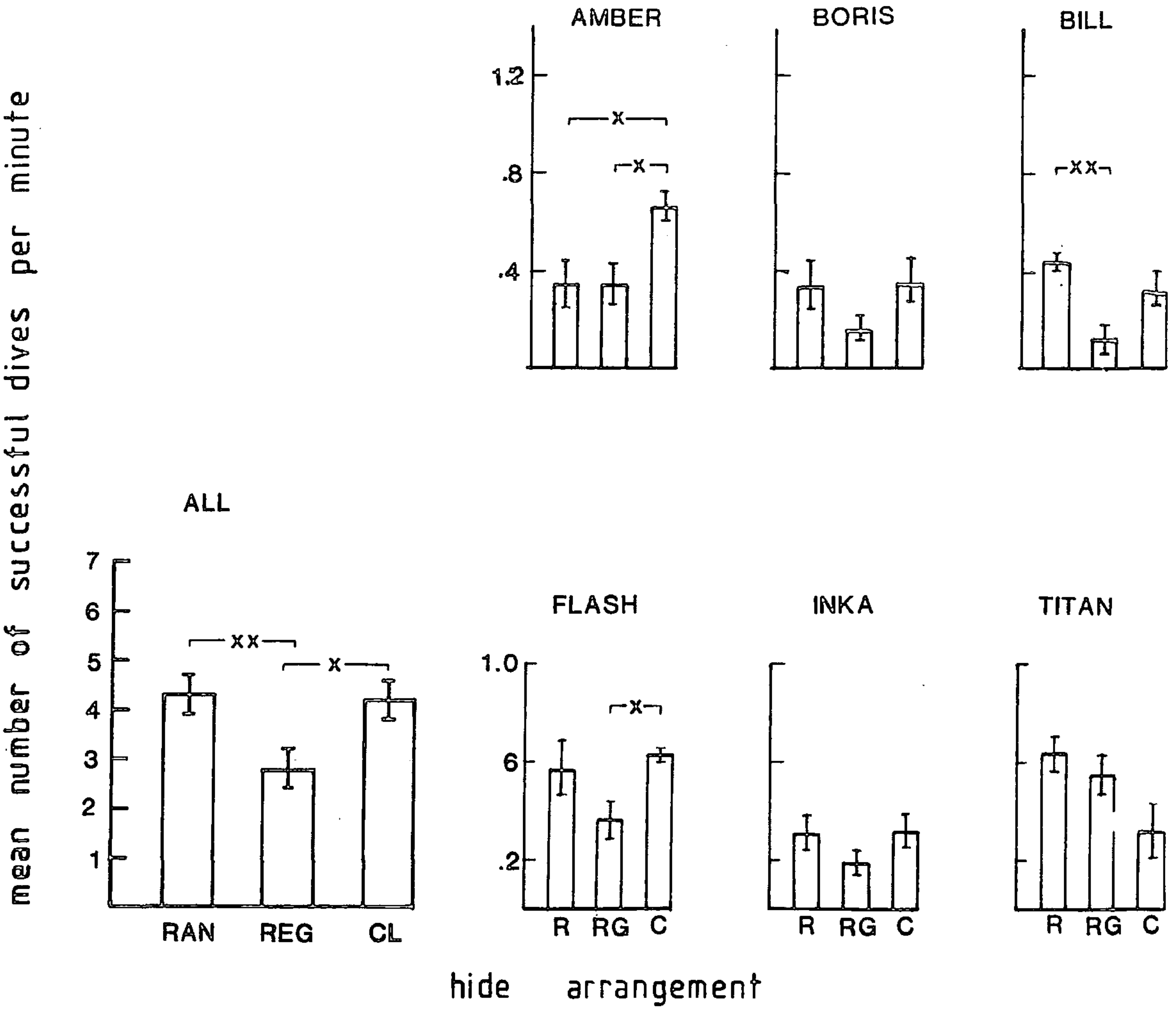
dives per min. For random and clumped conditions, mean hide visit dive rate for individual males varies from 0.75 to 1.6 dives per min, and for individual females from 0.55 to 1.15 dives per min.

5.5.4. Successful dive rate

The rate of successful dives can be used to give some measure of the foraging efficiency of the mink under different conditions. The results for mean successful dive rate are shown in Fig. 5.15, together with the significant results of t-test analyses.

The results, show that there are a small number of significant differences, and generally, mean successful dive rate is lowest when hides are arranged regularly. The mean values are higher when hides are either random or clumped, and there are no significant differences between these two conditions, except for male Amber (t= -2.73, df = 5, $p<0.05$), when sucessful dive rate is greater when hides are clumped. The other significant results occur when either, random and regular conditions are compared: All (t= 2.84, df = 52, $p<0.01$) and Bill (t= 3.78, df = 9, $p<0.01$), when successful dive rate is greater when hides are random, or when regular and clumped are compared: All (t= -2.56, df = 51, $p<0.05$), Amber (t= -3.00, df = 5, $p<0.05$) and Flash (t= -2.79, df = 5, $p<0.05$), when successful dive rate is greater when hides are clumped.

A further point is that the actual values for mean successful dive rate are low, generally less than 0.4 dives per min (i.e. roughly four successful dives per 10 min) for random and clumped arrangements, and about half this value when hides are arranged regularly. The result for Boris is particularly interesting, since his results for dive rate and hide visit dive rate, particularly when hides were random or clumped, were considerably higher than those for the other males.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mean number of successful dives per minute
hide arrangement

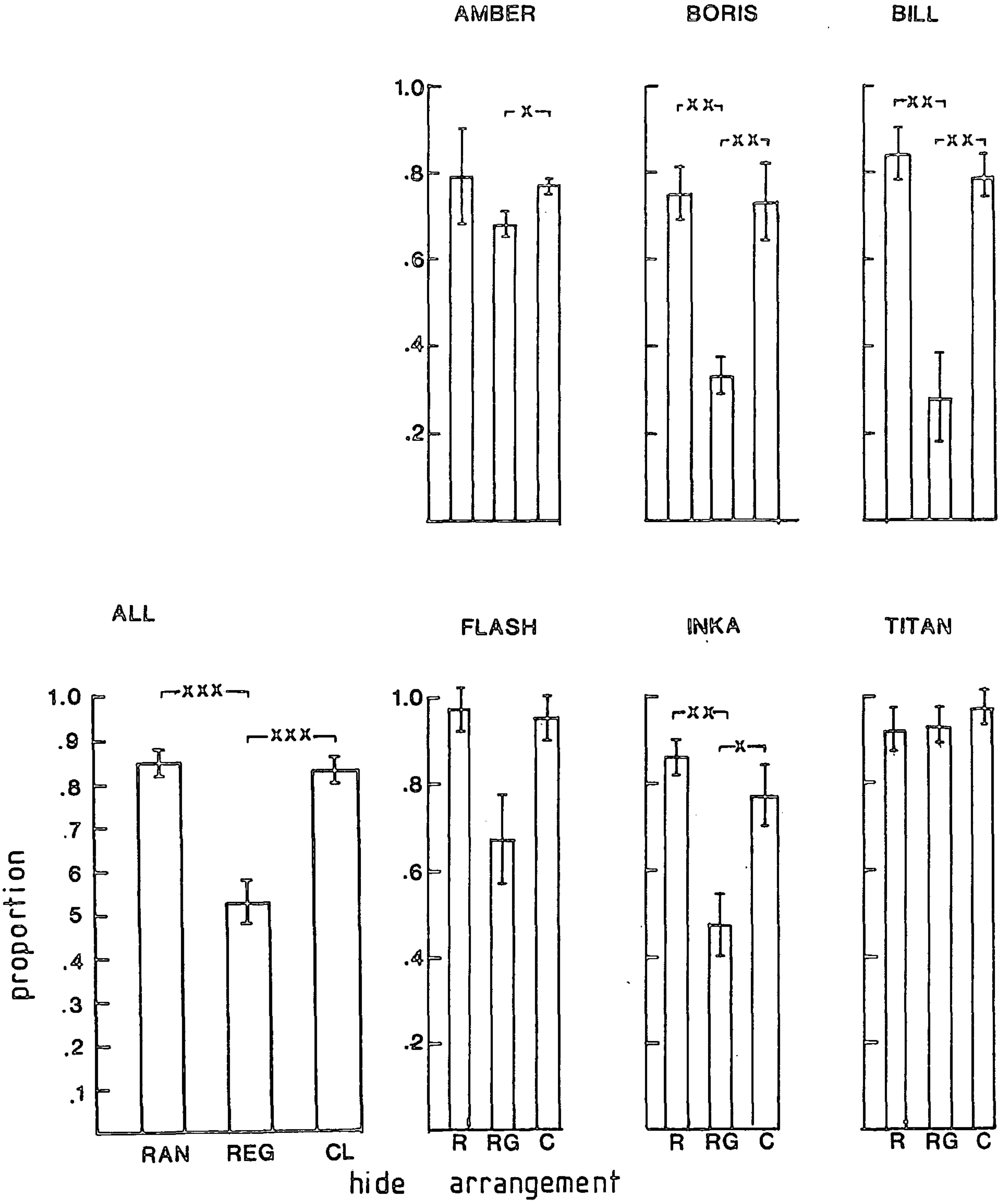
The final point to emerge from the above analysis is that generally the mean successful dive rate for individual females is greater than that for individual males under equivalent conditions, yet mean hide visit dive rate was lower. This implies that females may be using a different foraging strategy to males, which leads to a higher reward rate, i.e. females are searching more efficiently than males. This may also explain why there is little difference in mean successful dive rate for females between conditions, although there were significant differences in mean hide visit dive rate between conditions.

5.5.5. Proportion of dives visiting a hide

From the above, it has been noted that although in many cases there were no significant differences in mean dive rate, there were significant differences in mean hide visit dive rate, suggesting that there were changes in the proportion of dives visiting hides. It might be expected that if a habitat was judged by the mink to be 'complex', the best strategy would be to attempt to search a hide during each dive. If a habitat was considered to be less 'complex', e.g. it was easier to remember which hides had already been searched, then mink may choose not to search hides during each dive, but to explore the pool instead, in case food items could be found outside hides.

Data were calculated for each trial of each animal, for each hide arrangement. Fig. 5.16 illustrates the mean proportion of hide visit dives ± S.E. for each individual and All Animals, and presents the results of t-test analysis between all combinations of hide arrangements.

When the data are examined, it can be seen that there are a number of significant differences. When random and regular conditions are compared, there are significant



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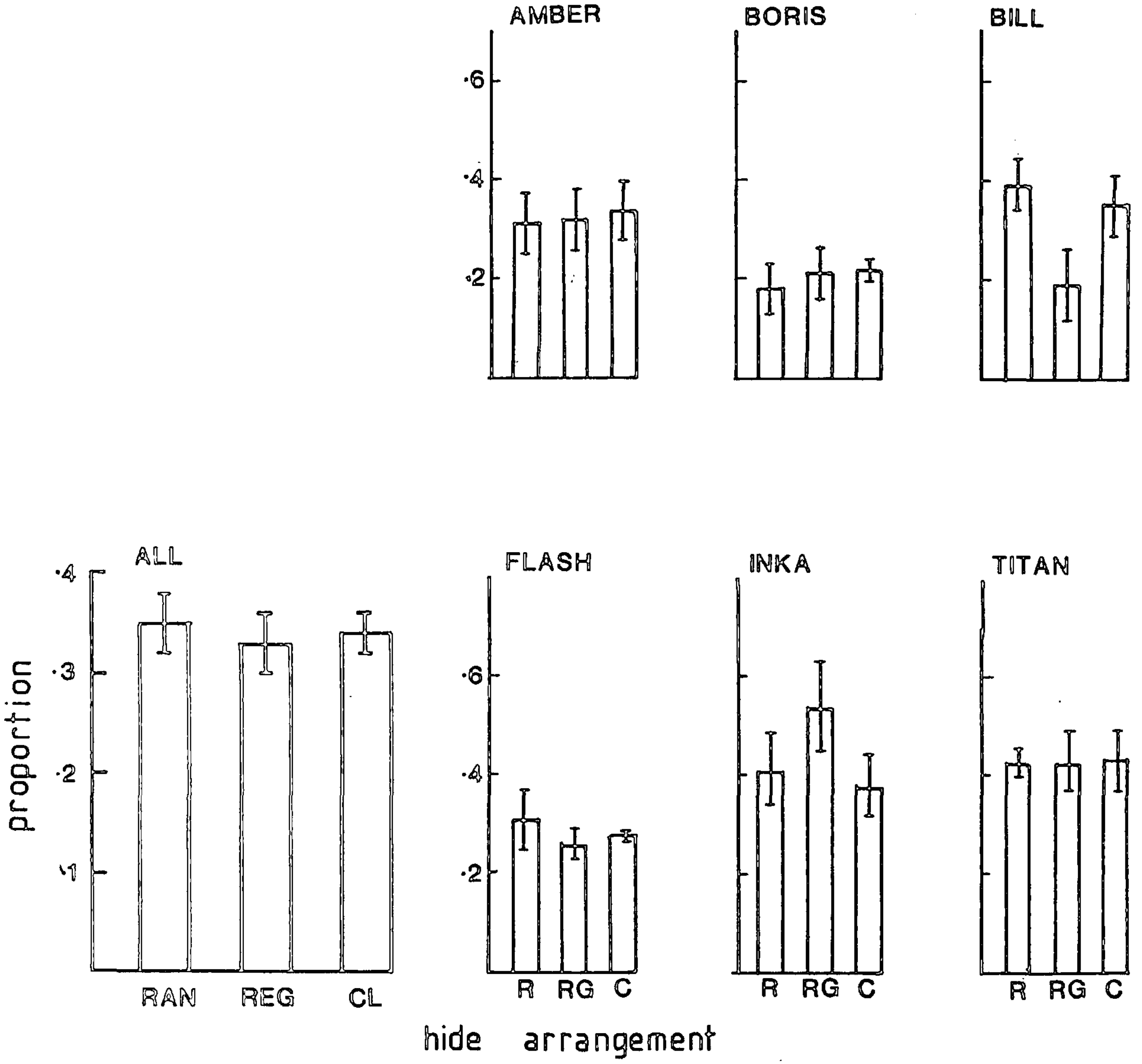
C
hide arrangement

differences for: All (t= 5.08, df = 52, p<0.001), Boris (t= 5.92, df = 6, p<0.01), Bill (t= 3.87, df = 9, p<0.01), and Inka (t= 4.68, df = 9, p<0.01). In all cases the proportion is lower when hides are arranged regularly. When regular and clumped hide distributions are examined, there are significant differences for: All (t= -4.62, df = 51, p<0.001), Amber (t= -2.73, df = 5, p<0.05), Boris (t= -4.82, df = 6, p<0.01), Bill (t= -3.59, df = 9, p<0.01) and Inka (t= -2.99, df = 9, p<0.05). In all these cases, the proportion is again lower when hides are arranged regularly. When data for random and clumped are compared there are no significant differences.

The overall picture suggests that the proportion of dives visiting hides is lower when hides are regular, and there is no difference when random and clumped are compared. This was as expected from the results for dive rate and mean hide visit dive rate. Since there is little difference in the mean number of successful dives per min, this suggests that animals are employing a different foraging strategy when hides are regularly arranged, which allows a moderate success rate despite apparently fewer foraging opportunities. The final point concerns the actual values for mean proportion of dives visiting hides. When hides are arranged either randomly or in clumps, more than 70% of dives visit a hide, and this can be as high as 90% or more for individual females. When hides are arranged regularly, the proportion is always less than 70%, and in half of the cases, the proportion is less than 40%

5.5.6. Proportion of successful hide visits to total number of hide visits

Since dives often involve visits to more than one hide, another measure of foraging efficiency is the proportion of successful hide visits to total number of hide visits. Data were calculated over each of the three hide arrangement conditions when density was 50%. The results are illustrated in Fig. 5.17. A series of t-test analyses were carried out to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hide arrangement

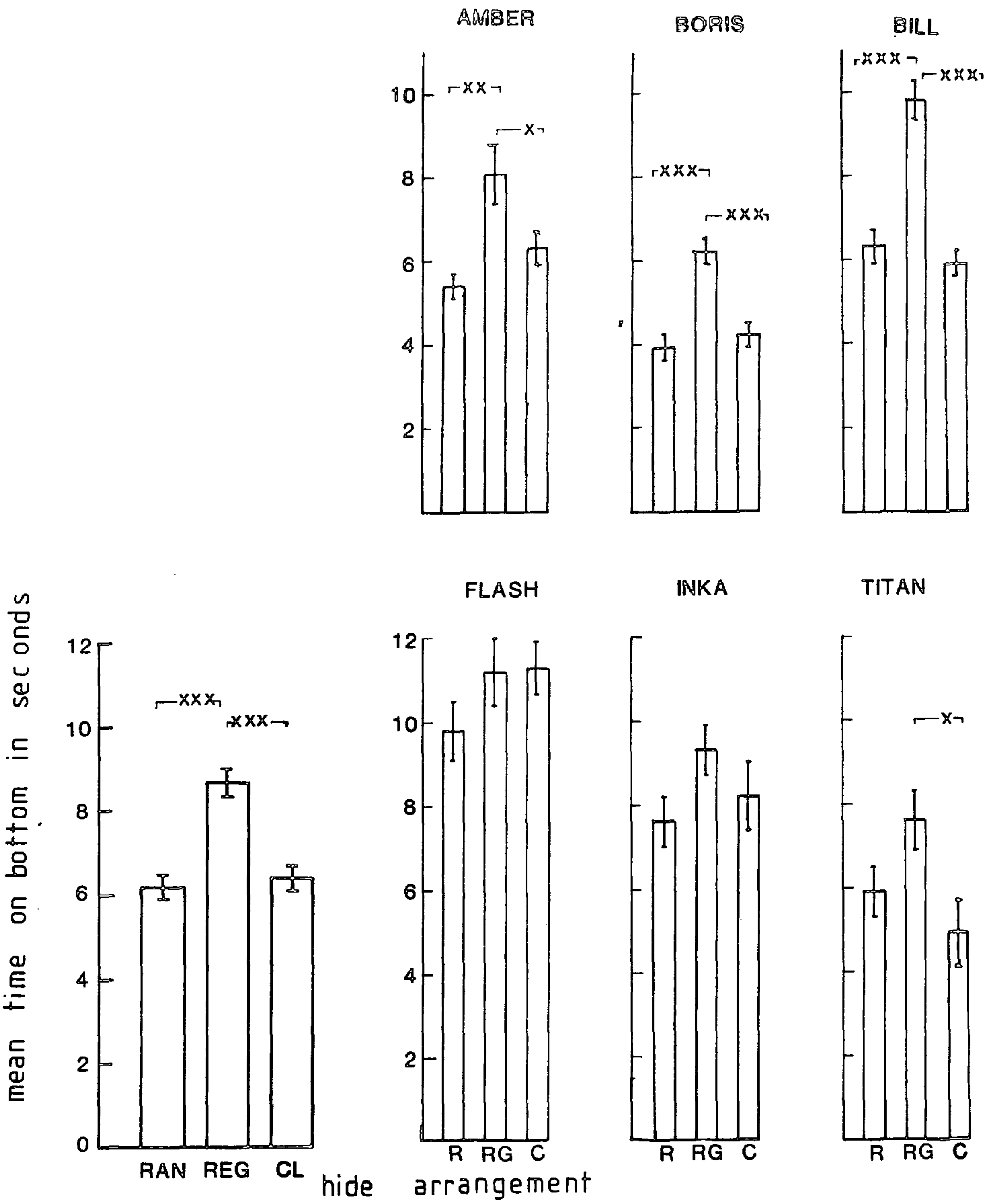
investigate differences between the various conditions. The results showed that there were no significant differences in proportion of successful hide visits, either for All Animals or individuals between any combination of hide arrangement conditions.

If animals visited every hide once during a trial, the expected proportion would be 50%, since prey density was 50%. The actual values vary with the individual, but in one case (Inka:Regular) the proportion is 54%, suggesting either chance, or an efficient foraging strategy. Generally, the values for proportion of successful dives are slightly higher for individual females compared to the males. Generally, female results show that around 40% of hide visits are successful, while for males around 30% are successful.

5.5.7. Time on bottom

If animals are adopting different foraging strategies under different conditions of hide arrangements, it might be expected that dive duration would vary. However, dive duration includes travel time to and from the pool bottom. Thus, a better measure of the actual time available for foraging is mean time on bottom. Analysis of Variance tests (Table 5.3) had shown that foraging success was an important factor influencing dive duration (and therefore time on bottom), thus, data were only examined for unsuccessful dives.

Mean time on bottom was calculated for each individual and All Animals, over each condition of hide arrangement. The results are illustrated in Fig. 5.18, together with significant results of t-test analysis. The results show that there are considerable differences in the behaviour of individual males and females. When the data are examined, it is found that when results for random and regular hide distributions are compared, there are a significant differences for: All (t= -6.00, df = 182, p<0.001),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Amber (t= -3.26, df = 28, p<0.01), Boris (t= -5.27, df = 48, p<0.001) and Bill (t= -5.77, df = 29, p<0.001), with mean time on bottom being greater when hides were arranged regularly. When the results for regular and clumped distributions were compared, there were significant differences for: All (t= 5.09, df = 187, p<0.001), Amber (t= 2.36, df = 31, p<0.05), Boris (t= 4.65, df = 53, p<0.001), Bill (t= 7.22, df = 32, p<0.001), and Titan (t= 2.66, df = 10, p<0.05). Again, mean time on bottom was significantly greater when hides were arranged regularly in all cases. There were no significant differences between mean time on bottom when hides were arranged randomly or in clumps.

The actual values for mean time on bottom appeared to be shorter for individual males than those for females. Generally, for males, when hides were either random or clumped, mean time on bottom was roughly 4-6 s, depending on the individual, whereas when hides were regular, mean time on bottom was around 6-9 s, depending on the individual. For females, mean time on bottom for unsuccessful dives varied with individual, but results were between 5-11 s. However, apart from female Titan, females showed no significant differences in mean time on bottom between the various hide arrangement conditions.

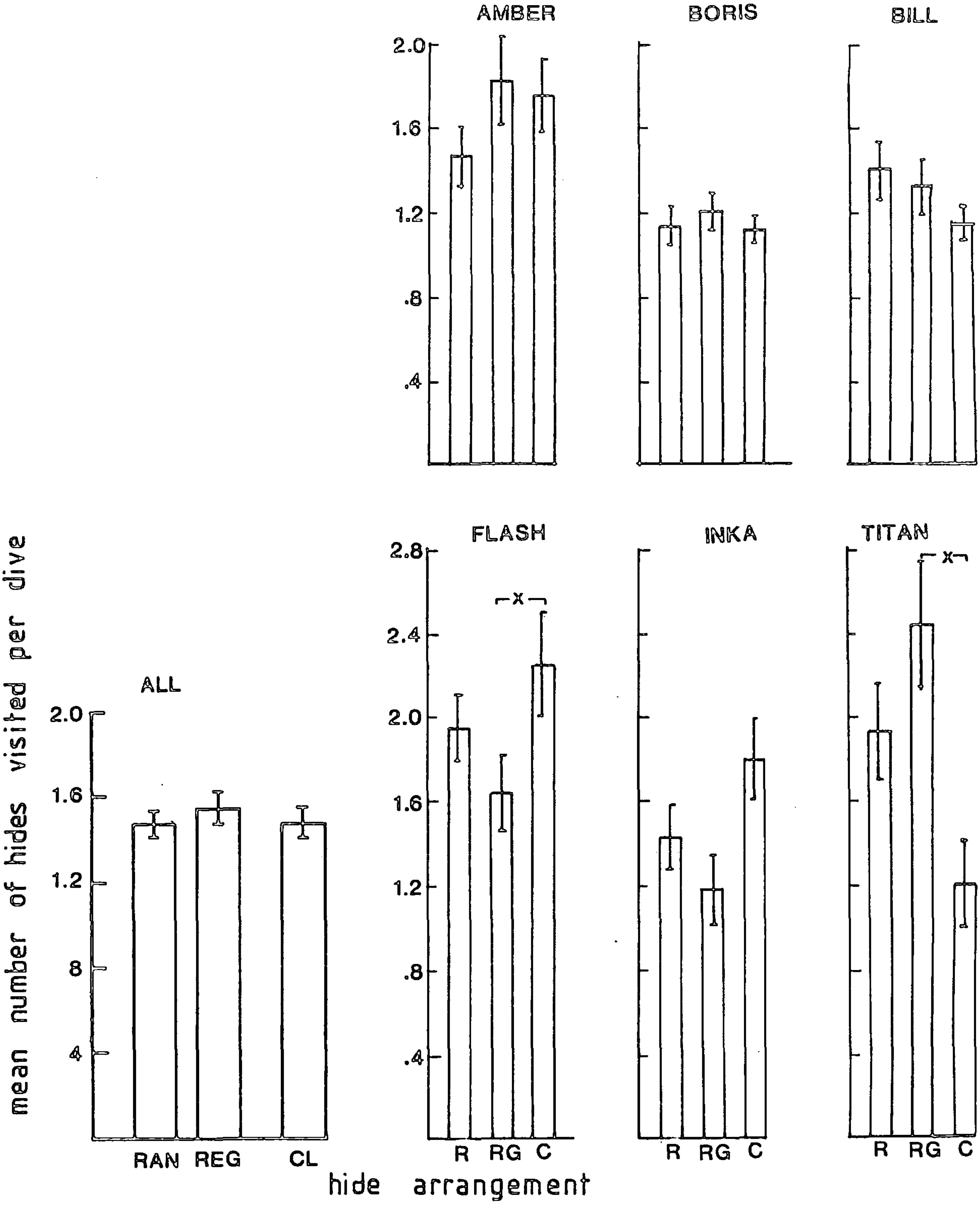
5.5.8. Mean number of hides visited per dive

The foraging efficiency of the mink will depend on the number of different hides searched for prey items. If the different hide arrangements do represent differences in the complexity of the mink's foraging environment, then differences in the mean number of hides visited per dive may reflect this.

To investigate this, the mean number of hides visited per unsuccessful dive was calculated for each individual and for All Animals, for the three hide arrangement conditions. The results are given in Fig. 5.19, together with significant results from t-test analyses. It can be seen that there are only two significant results. These both concern comparison of regular and clumped arrangements. They are: Flash ($t= -2.08$, $df = 33$, $p<0.05$) where mean number of hides visited per dive is greater when hides are clumped, and Titan ($t= 3.12$, $df = 10$, $p<0.05$) where the reverse is true. For all animals, there is considerable individual variation, but it appears that for individual females, a higher proportion of hide visit dives involve visits to more than one hide, whereas for individual males, the results indicate that, generally, dives involve a visit to one or two hides per dive regardless of hide arrangement.

5.5.9. The relative frequency of hide visits under the various hide arrangement conditions

The inter-animal variability in mean number of hides visited per dive under different conditions is shown in Fig. 5.20. In this case data for all dives have been combined. One point to note is that the proportion of dives in which no hides are visited, is generally greater when hides are regularly distributed, than in either of the other two conditions. The second point is that, for individual males, it can generally be seen that, regardless of hide arrangement, the proportion of dives visiting one hide was considerably greater than the proportion visiting two or more. The maximum number of hides visited in a dive was four, for Amber:Regular. For individual females, it can be seen that, generally, the proportions of dives visiting either one or two hides per dive, are similar, regardless of hide arrangement. In some cases, the proportion visiting two is greater. The maximum number of hides visited in a dive was five, for Titan:Regular.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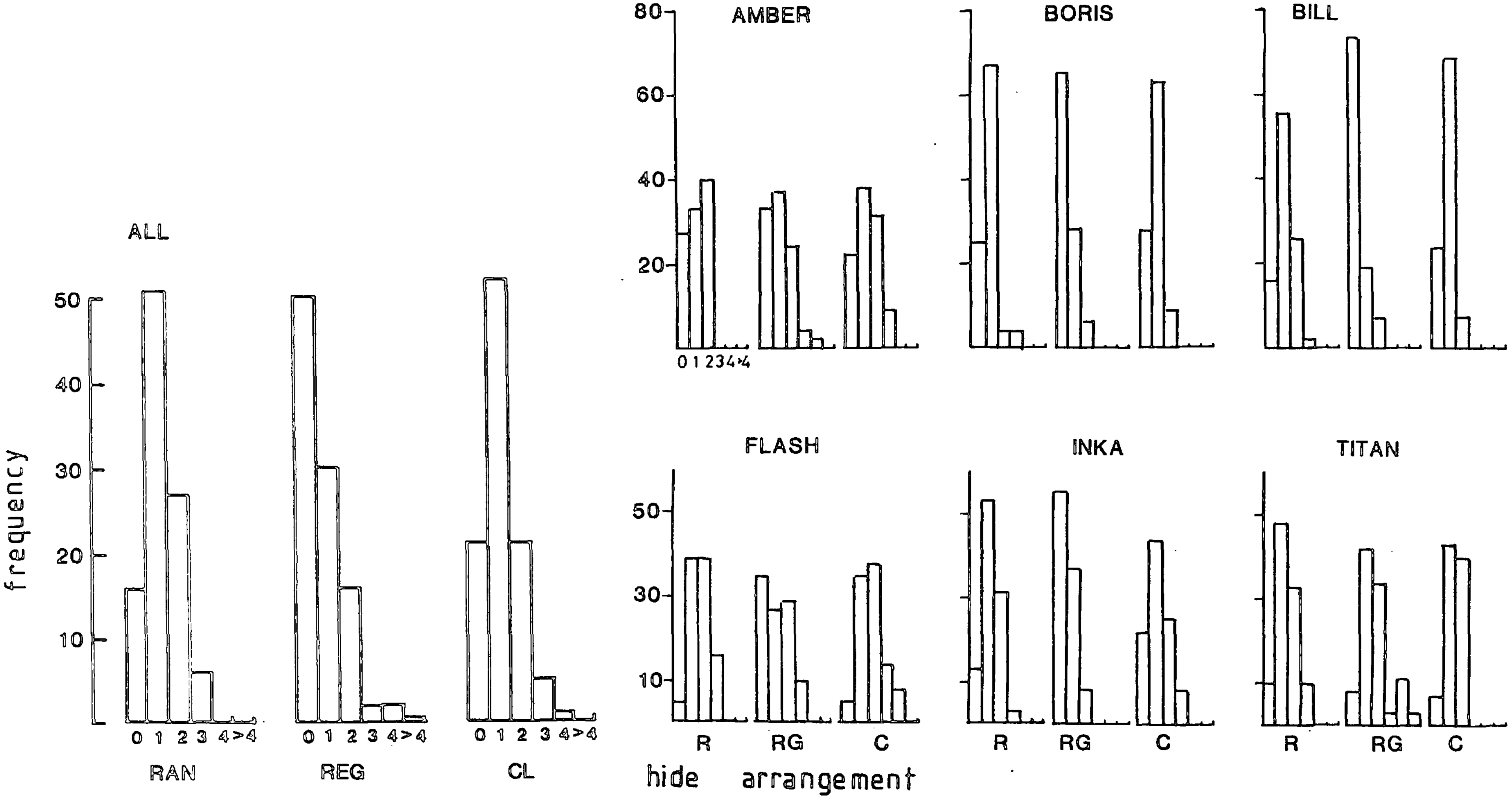
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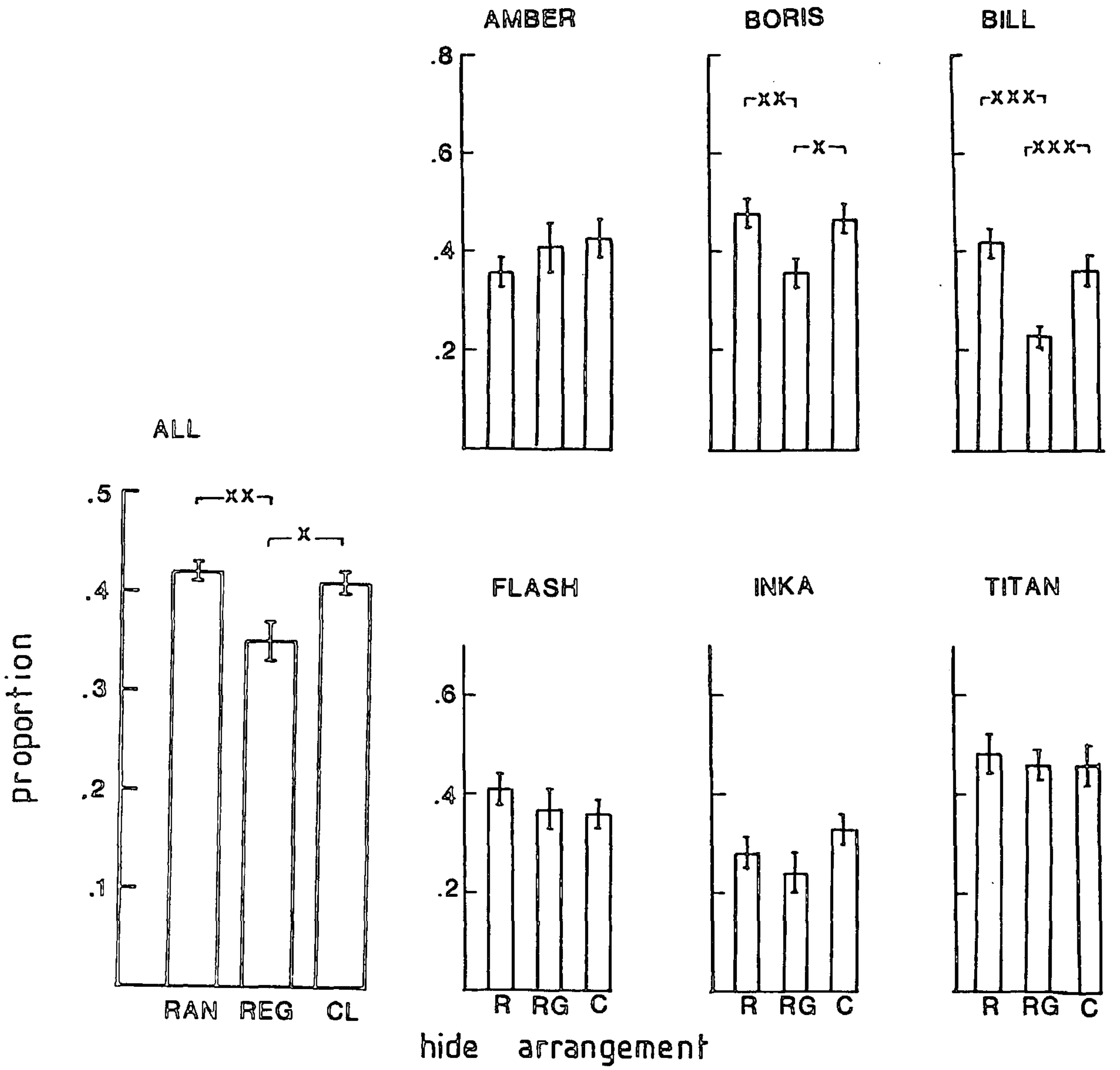
5.5.10. Proportion of time on bottom spent hide searching

This parameter was examined in order to investigate the foraging strategies employed under different hide arrangements. Previous analyses had shown that mean time on bottom did vary between some conditions, e.g. between random and regular conditions for some individuals. However, analysis of the mean number of hides visited per unsuccessful dive did not show much change, although there was an indication that individuals were behaving differently. Previous analysis (see section 5.4.11) has shown that there is generally little change in the mean time spent in a hide by the mink. From this it follows that the proportion of time on bottom spent hide searching will be a function of the number of hides visited during a dive.

The results for individuals and All Animals are given in Fig. 5.21. It can be seen that there are a number of significant results. When random and regular conditions are compared, there are three significant results: All ($t= 3.06$, $df = 181$, $p<0.01$), Boris ($t= 2.97$, $df = 28$, $p<0.01$) and Bill ($t= 5.21$, $df = 29$, $p<0.001$), and in each case proportion of time on bottom spent hide searching is greater when hides are arranged randomly. When regular and clumped results are compared, significant results are obtained for: All ($t= -2.49$, $df = 186$, $p<0.05$), Boris ($t= -2.61$, $df = 52$, $p<0.05$) and Bill ($t= -3.69$, $df = 32$, $p<0.001$). In each case proportion of time on bottom spent hide searching is greater when hides are clumped. There were no significant differences when data for random and clumped arrangements were compared.

5.5.11. Revisiting of hides

In this experiment there were 32 hides. For the investigation of the effects of hide arrangement, only data when prey density was 50% was studied, thus, only 16 of the available hides were baited at the start of each trial. In no trial did an animal search 32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hides, yet the proportion of successful hide visits to total hide visits was often 40% or even more. Since the food rewards were distributed at random and were not replenished during a trial, the greatest degree of success would be achieved if animals followed a strategy of not revisiting hides which had already been searched. Further, habitat complexity would be expected to influence this. Thus, if the hide arrangement was 'complex' the mink may have greater difficulty in remembering which hides had already been searched and vice versa if the hide arrangement was 'easy'. Since no animal searched 32 hides during a trial, simply scoring 'new' or 'revisit' for each hide visit during a trial would lead to a bias in favour of 'new'. To compensate for this, it was decided to examine the 16th hide visit in each trial, since then there would be a 50:50 chance of that visit being to a 'new' or 'old' hide. In order to obtain more data it was decided to examine the 13th to 19th hide visit, although again in trials where animals only searched 15 or 16 hides, this might lead to a bias in favour of 'new'. Visits were scored as being to 'new' or 'old' hides and the results are given in Table 5.12 together with the results for the other prey density conditions. The null hypothesis is that there is an equal chance of these visits being to either 'new' or 'old' hides. A Chi-square analysis was carried out and the results are also given in Table 5.12.

From Table 5.12, several points can be noted. Firstly, in several cases when hides were arranged regularly, the animals did not visit as many as 13 hides during a trial. Secondly, of the results which could be analysed, significant results were obtained in only five cases. These were for All, Flash and Titan, when hides were arranged randomly, and for All when hides were either regular or clumped. In each case the results showed that animals were tending to visit 'new' hides. There were no significant results for any individual males under any condition, suggesting that males were visiting both new and old hides at random.

5.6. Discussion

Animals can be adapted to their environments by means of their inherited morphology and behavioural repertoire, enabling them to exploit successfully a certain range of habitats. They may also inherit the ability to modify their behaviour to exploit a larger number of environments (Smith, 1974b). Mink are very interesting as they are able to forage in a wide variety of habitats. Smith (1974b) suggested that for blackbirds, (*Turdus merula*) the diversity of diet obtained from different feeding situations will place a premium on searching behaviour which is adaptively variable. Many studies have investigated how predators vary their foraging sites and prey types at least on a seasonal basis, e.g. Dunstone and Birks (1987) on mink, Kruuk (1972b) on spotted hyaenas (*Crocuta crocuta*) and Goss-Custard (1969) on redshank (*Tringa totanus*). However, there have been few studies which examine how predators respond to short-term variations in food supply, i.e. prey density. Some studies including those of Smith (1974a, b) and Pierce (1987), have concentrated on the searching behaviour of the predator within the foraging area. In many studies, the ability of the predator to detect prey, and therefore assess density, had an important effect on its foraging strategy, and certainly Optimal Foraging Theory assumes that the time spent in a patch will be heavily dependent on the net rate of energy gain (i.e. the number of food items obtained) from that patch (Charnov, 1976; Pyke, 1984).

In the natural state, potential prey items may be difficult to detect at a distance by the predator. Various workers have shown that the mink's visual capabilities are severely impaired when searching underwater, (Sinclair et al., 1974; Dunstone and Clements, 1979). Similarly, I have demonstrated that disturbance of the water surface by a current flow may also affect the mink's ability to locate potential prey sites (i.e. hides). In the natural state, ponds and lakes are usually very turbid. Green (1977) showed that otters hunting in murky water had reduced hunting success (particularly when vibrissae were removed) compared to when they hunted for live fish prey in clear water. Under such conditions it is possible that the mink have to spend much longer searching for potential prey items than in situations where prey could be easily located aerially. Thus, in murky conditions in the field, animals would not be able to assess prey density as a result of direct observation, but would have to rely on foraging success as a measure of density and alter their behaviour accordingly.

In this experiment, mink were presented with a fixed number of hides (32), and the prey density was varied by baiting a different proportion, 25%, 50%, 75% and 100%. Hide positions were varied between random, regular and clumped arrangements, and position of baited hides were varied daily in the hope that animals would not develop position tendencies. It was hoped that this experimental situation would be analagous to mink hunting in the field, since animals were not able to see directly how many prey items were available, but had to rely on sampling hides to obtain information on the prey density.

There was a great deal of variation in behaviour between individuals. However, in this case, there was also a difference in behaviour between the sexes. From Appendix I, it can be seen that the mean weights of the males and females differ, hence the sex variable may reflect the size difference between animals. In view of the fact that only a small number of animals of each sex were used in this experiment, it was therefore decided not to separate the data on the basis of sex. Finally, it was clear from Anova tests (Tables 5.3-5.6) that changes in behaviour were influenced by the interaction of prey density and habitat complexity variables. In order to investigate these changes in more detail, the results for each of the four prey densities were considered for each hide arrangement, and results for each hide arrangement were compared when density was 50%. The results obtained in each of these two sections will be discussed separately.

When the results for prey density are examined, a number of points emerge. Firstly, it was noted that as prey density increased, the number of dives per minute generally decreased, although significant linear correlations were obtained only for some individual results. This was not unexpected since as prey density increases, it would be expected that the probability of a dive being successful would also increase, and thus more of the time available would be occupied with eating, and hence less time would be available for underwater foraging. The difference in individual results however, cannot be explained, and suggests that the animals are employing different foraging strategies. This will be discussed more fully below.

Further, it would be expected that mean successful dive rate would increase with density. There were, in fact, seven significant positive linear correlations, and further, in a number of cases, curvilinear analysis showed that there were significant curvilinear relationships, and that the tendency was for mean successful dive rate to increase with density. The most interesting point concerns the actual values of mean successful dive rate, which were generally very low, less than 0.5 dives per min. The results obtained when density was 25% and 50% can be compared to the results obtained in the current experiment, where the hides were also arranged regularly. Thus, in this experiment, mean successful diving rate for All Animals (density 25%: regular hide distribution) was 0.33 dives per min, and at density 50% it was 0.28. For the current experiment, density was 33%, and the mean successful dive rate for All Animals varied from 0.20 (control), to 0.25 (deep current) and 0.24 (surface current). This suggests that in this experiment, as density increases, animals are slightly more successful than might have been expected, however, the results are not strictly comparable. Nevertheless, they give some indication that as density increases, success rate does change (and may, in fact, increase).

Finally, the relationship between density and mean number of dives which visited a hide, was investigated. It was noted that in many cases, animals dived to the pool bottom, but did not visit any hides. It might have been expected, from Optimal Foraging Theory, that mean hide visit dive rate would increase with density. This is because if an animal is attempting to maximise it's net rate of energy intake (Pyke, 1984), then as density increases, the best strategy would be to search at least one hide during each dive, since the probability of locating a baited hide would increase with increasing density. However, the actual results show that there was only one significant linear correlation between density and hide visit dive rate, for female Inka:Random. Possibly then, since mink are considered to be 'opportunistic' predators (i.e. they will take whatever prey is available according to its vulnerability to predation, (Chanin and Linn, 1980)), although density of food within hides was increasing, mink were continuing to use some dives to search the pool floor. Croxhall (pers. comm.) suggested that this might be in order to locate hides which could not be seen from out of the water, but in the depth experiment, mink had not appeared to have difficulties locating hides at the depth used in this experiment (0.60 m). However, occasionally, animals would retrieve a food reward, return to the rostrum and then drop the food back into the water. Generally, these animals would immediately dive and retrieve the food, but occasionally this did not happen, and later in the trial, the food item would be found 'accidentally' during a dive. This was, however, a very rare occurrence. It is, however, possible that in some cases mink were continuing to use 'pool search' dives, even at high prey densities, since prey items found 'loose' would be easier to obtain (although less likely to be found) than prey items located inside a hide which required the door to be opened before the prey could be taken. Thus, any prey found loose in the pool would represent a higher net energy intake per unit effort for the mink. A further problem is that this is a 'rate', i.e it is the number of dives per min which would visit hides, thus if the overall number of dives per min is declining with depth, if each of these dives visited a hide, the hide visit dive rate would also decline with density.

In order to investigate this further, the proportion of dives visiting a hide with density was examined. Here, there were three significant positive linear correlations, and in several cases curvilinear analysis indicated that the proportion of dives visiting a hide did increase with density. Further, the proportion of dives visiting a hide was generally greater than 60%, and the maximum values of 90% were obtained at the higher densities. This suggests that the lack of correlation between mean hide visit dive rate and density, may be due, in part, to the considerable individual variation in results both between conditions, and between trials under the same conditions, and in part, to the fact that mean dive rate declined with density. The conclusion however, is that there does appear to be some slight change in foraging strategy as density increases, leading to more dives visiting hides.

Although there appear to be changes in the number of dives visiting hides as density increases, the previous results do not show whether the efficiency of the mink is altering with density. A measure of search efficiency is given by the relationship between the number of successful hide searches and the total number of hide searches, under any given set of conditions. The results (Fig.5.6) showed that there were several significant positive linear correlations, particularly when hides were either regular or clumped. This shows that as density increased, so search efficiency increased, suggesting that there may be changes in foraging strategy with density. Thus, as density increases a higher proportion of dives visit hides and the probability of the first hide searched being baited will also increase with density. But at lower densities, it might be expected that mink will also attempt to maximise their efficiency, by searching more hides per dive. Thus a measure of foraging efficiency based on the number of successful dives to total dives might have shown that efficiency did not alter with density. It is possible, that on a finer scale, changes in prey density do induce changes in foraging strategy, i.e. mink may change their dive durations, the number of hides visited per dive etc.

Since in the depth and current experiments, and in this experiment, it was shown that changes in behaviour were related to foraging success, data for successful and unsucessful dives were considered separately. When mean dive duration for successful dives was analysed, it was found that in five cases there was a significant linear decrease in dive duration with density. This is as expected, since as density increases to 100% there is an increasing probability that the first hide visited during a dive will contain food and the dive will be terminated, i.e. animals are finding food faster. Therefore, it would be more interesting to examine the data for unsuccessful dives. Here, the results showed that there were also five significant negative linear correlations, and a number of significant curvilinear correlations. However, the patterns shown by individuals were very variable, some animals showing an increase in mean dive duration with density, others a decrease. These results are more difficult to interpret.

It is an underlying concept of O.F.T. (e.g. Pyke, 1984), that animals forage in such a way as to maximise their 'net rate of energy intake'. Hence, it might have been expected that unsuccessful dives would be prolonged to try and maximize encounters with potential prey. However, Dunstone and O'Connor (1979a) suggested that increasing the overall rate of prey encounters (i.e. increasing prey density) should lead to shorter 'pursuit' durations. In other words the Giving-up Time will be less at high density, since the likelihood of encountering prey on subsequent dives is very high. Thus, the expected outcome in this experiment, would be a decrease in mean unsuccessful dive duration with increasing density. Since, in some cases mean unsuccessful dive duration appeared to increase with density, while in others it seemed to decrease with density, it is possible that individual mink are adopting different foraging strategies under the same conditions. Thus, instead of trying to prolong each individual dive to maximise prey encounters, animals may have adopted the rule 'if the first hide searched is empty, abandon the dive'. This would then allow animals to switch their searching effort to a different area of the pool. Further, it might be expected that short duration dives would be physiologically less stressful than longer dives which approached the dive limit. It must be noted that the mean dive durations recorded are considerably below the dive limit of mink. The mean values range from 7 to 13.5 s, depending on the individual and the conditions (see Fig. 5.7). When the durations for individual dives are examined, it is found that the maximum recorded duration was 27.4 s, for female Flash (density 75%, regular), and dives frequently exceeded 15 s. Thus, some animals may opt for a strategy of many short duration dives, whereas other animals adopt the strategy of fewer dives of longer duration. In both cases the aim would seem to be to maximise prey encounter rate.

These differences can be investigated in more detail. To see if the amount of time actually available for foraging varies with the different conditions, mean time spent on bottom during unsuccessful dives was examined. There were six significant negative linear correlations, and there were a number of significant curvilinear relationships. The general trend did seem to be towards a decrease in time on bottom with density, especially for individual males. Thus, there is some evidence that mink may be opting for dives of shorter duration as density increases.

One final point arises if the equivalent results for mean dive duration and mean time on bottom are compared. It can be seen that generally the difference between them is of the order of 1.5-2.0 s. This is the travel time required to reach the pool bottom and to resurface at the end of a dive. However, it must be noted that this travel time does seem to vary, even though the water depth was constant throughout the experiment. Animals did not always dive directly to the pool floor, some would dive at a very shallow angle to the water surface, thus taking 3-4 s before reaching the pool bottom, while others would dive vertically from the rostrum to the pool floor. Further, individuals would vary their techniques and this no doubt accounts for the variations in travel times. It is possible that dives to hides located more than 1.0 m from the rostrum may have been of the 'shallow angle' type, but this could not be determined from the data. Stephenson et al. (1988) noted that mink making deep dives (to depths of nearly 2 m) would use objects within the experimental tank to push off from, thus increasing their initial velocity, and reducing energy expenditure. It is possible that in this experiment vertical dives from the rostrum, would be used either to search hides situated near to the rostrum, or else having dived rapidly using less energy, this might allow dive durations to be extended and more hides to be searched per dive. This might then account for the lack of any pattern between change in travel time, density and hide arrangement.

When the results for mean number of hides visited per dive during unsuccessful dives are studied (Fig. 5.10), it is found that in fact there are two significant linear correlations For Titan:Regular, the mean number of hides visited per dive decreases with density, but for Inka:Clumped, the reverse is true. Curvilinear analysis.results were very variable, but generally there was an initial decrease in mean number of hides visited per dive with density. The main point to note from these results is that generally the mean value is around 1.4 hides visited per dive, but this increases up to as much as 3.0 hides visited per dive especially at lower prey densities, i.e. the animals do seem to be working harder at lower densities. It is possible that there are so few significant linear regression results, because of the great individual variation. This was more clearly illustrated in Fig. 5.11, from which it can be seen that, at the lower densities, a greater proportion of dives do not visit any hide, while at the maximum density, generally, the greatest proportion of dives involve a visit to one hide only. Secondly, only at the lowest density (25%) do any dives involve visits to 5 or more hides. Also at the lower densities a greater proportion of dives which involve hide visits search 2,3 or more hides per dive. This does suggest that at the higher densities, as would be expected, the first hide visited may well yield a prey item and the dive is terminated, but further, animals have an 'expectation' that this is so and hence abandon the dive after one hide search, even if it was not successful. This is perhaps surprising, since at high densities, there would be a very high probability that a second hide searched during a dive would contain food.

The measure of efficiency defined by Dunstone (1978) involves a relationship between the number of successful searches and the total number of searches, but in this study (as in Dunstone's) mink are foraging underwater and other constraints, e g. oxygen limitation, are acting on them. In this case, mink may be able to maximize their foraging efficiency by reducing the time spent searching individual hides. This would mean that they could choose either (i) to search more hides per dive, or (ii) to search just one hide, and therefore to have dives of shorter duration than expected per dive. Option (i) might be less 'efficient' if each hide search is counted as 'one search' for Dunstone's definition, but if it leads to more dives being successful and efficiency is restated as the number of successful dives to total number of dives, this could lead ultimately to an increase in the defined measure of efficiency.

From the results for mean number of hides visited per dive, it does appear that at low densities mink may be searching more hides per dive. If the mink adopts Option (ii) instead, i.e. shorter time in hide and fewer hide searches per dive, then dive duration would be expected to be shorter. As noted earlier, it is probable that dives of shorter duration would not be as physiologically stressful as dives of longer duration. Presumably shorter dives would require a shorter recovery period, and more dives per minute could be performed. It might be expected that mink would choose Option (ii) at high prey densities when there is a high probability that any single hide searched will be baited. However, it has previously been suggested that at greater depths, animals may search individual hides more carefully in an attempt to maximise prey encounter rate. In this experiment, it is possible that at the maximum densities, where animals are 'expecting' a high reward rate, they may 'decide' to search single hides more thoroughly. This would be reflected in an increase in mean time spent in hide. However, since results of previous experiments had shown that there was little change in time in hide with changes in foraging conditions, this parameter was not directly investigated in this experiment.

Instead, since the durations involved in all underwater activities are very small, and the variation between individuals is considerable, the proportion of time on bottom spent hide searching was calculated. The results (Fig. 5.12) showed that there were no significant linear correlations, although there were significant curvilinear relationships. The general trend was for a decline in the proportion of time on bottom spent hide searching up to a density of 75%, followed by a slight increase. Since previous results had shown that the mean number of hides visited per dive decreased with density, the results for mean proportion of time on bottom suggested that there was, in fact, little change in tthe amount of time spent in each hide. The actual values for proortion of time on bottom spent hide searching vary only between 20-50%, with most results being between 30-45%, regardless of individual or condition. Thus, at least 50% of the foraging time is spent either travelling, locating the hide when underwater, or searching the pool bottom.

The general picture is that as density increases most dives visit just one hide, although in some cases 20% or more, dives involve visits to 2 or more hides even at 100% density. It is likely that the reason for this (at 100% density) is that the first hide searched had been emptied during a previous dive, and under the experimental regime it would not be refilled during the trial. Thus, the animal might choose to move on to another hide to see if it would be successful there. A point here is that the optimal strategy for mink would be not to revisit hides, especially if they had been successfully emptied. Then at the highest density it might have been expected that all dives would either search one hide successfully, or no hides, i.e. animals would be 'searching' the tank instead, looking for other possible food sources. This is obviously not the case, and it implies either (i) that mink cannot remember where they have already searched or (ii) if they were successful, they chose to return to see if more prey were available and, if not, they then opt to try and maximize their foraging success by moving on to another hide.

The number of revisits might shed light on this problem. The results (Table 5.12) showed that where there was a significant difference between the number of 'new' and 'old' hides visited, it was always biased in favour of 'new' hides. However, the results varied both between individuals and All Animals, and depended on the conditions of density and hide arrangement. Generally, however, there were no significant differences when density was 100% This mainly reflected the fact that animals often did not visit as many as 13 hides per trial and revisiting could not be scored. This simply shows that at high density, it was easier to obtain food, hence fewer dives were made, and each dive visited fewer hides, and it was not possible to ascertain whether animals were foraging systematically or randomly. At the lowest density, however, animals visited more hides during a trial, and it was found that there were a number of sigificant results, although only for males. These results did suggest that mink were capable of 'remembering' which hides had been visited, and of altering their foraging strategy accordingly. For individual females, it did appear that generally they foraged in a random manner, with 'new' and 'old' hides being searched equally. This difference between the sexes cannot be explained.

Thus, the final conclusion that can be drawn from the above is that mink do appear to be altering their foraging strategies as density increases. Also, these changes do seem to provide qualitative evidence that mink obey at least the more general predictions of Optimal Foraging Theory, in that the changes in their foraging strategy can be interpreted as changes that are attempting to maximise net rate of energy intake per unit effort (Pyke, 1984).

The results from the second part of this experiment, namely the effect of habitat complexity will now be discussed. It was hoped that the three hide arrangements provided would represent different degrees of complexity for the mink hunting underwater. Before discussing the results, it is first necessary to try and predict which of the hide arrangements would represent the most complex environment and which the least. Since hides were not replenished during a trial, the most efficient strategy would be one where animals did not revisit hides. It has already been noted that revisiting of hides not only depended on the prey density available, but also on the hide arrangement, which gives some idea that the mink did find differences in the complexity of the habitats. It is, therefore, predicted that the regular arrangement would be the least complex. Once a hide was located from the aerial vantage point of the rostrum, the mink could dive to it, and after searching, move on to a neighbouring hide, since each hide was only roughly 0.5 m from its nearest neighbour (see Fig. 5.1). An animal had only to use some cue, external to the pool if necessary, e.g. position of hide in relation to the window, radiator, etc., remember this, and on the next dive it would be able to direct its search effort to another hide. It is considered that the clumped arrangement would provide the next least complex environment. This is because a group of four hides provides a larger 'target' for mink to aim at. Further, once mink had searched one box in each clump, there would be three others close by, and even at the lowest density, at least one box in each clump would be baited. Presumably, since there were only eight clumps in all and they did not vary in position throughout the experiment, it might actually be easier for animals to remember which clump had been visited. However, it was then also necessary to remember which hides within the clump had been previously searched. Finally, it was felt that the random arrangement would be the most complex from the point of view of 'remembering' which hides had been previously searched. Also, when actually seaching a hide, if this was unbaited, the distance to the next nearest neighbour varied, (Fig. 5.1). However, it must also be noted that for both random and clumped arrangements, a number of hides were to be found at only 0.5 m from the rostrum, whereas for the regular arrangement, the nearest hide was 1.5 m from the rostrum.

Based on the hypothesis of which hide arrangement provides the most complex environment for the hunting mink, a number of predictions concerning changes in the foraging behaviour can be made. Thus, if regular or clumped hides are easier to locate underwater, it would be expected that animals would try to search as many hides per dive as possible, particularly at the lower densities. Hence, mean number of hides searched per dive would be greater, and correspondingly mean dive duration and mean time on bottom would also be greater than when hides were arranged randomly. Further, when hides are arranged randomly, if the first hide visit was not successful,animals could choose to return to the rostrum and try in another area, thus resulting in a lower dive duration. Finally, it might be expected that revisiting of hides would be greater when hides were arranged randomly, if this is considered to be the most complex environment. However, revisiting may also occur when hides are clumped, since here animals may choose to revisit clumps, especially if density was greater than 25%, and they may then revisit previously searched hides.Thus, the lowest amount of revisiting could be expected when hides are arranged regularly.

The results for habitat complexity were considered only for the data obtained when prey density was 50%. The reason for this was that this density would allow comparisons to be made with results from the depth experiment when density was also 50%. Further, Smith (1974b) investigated the food searching behaviour of the blackbird and the song thrush (*Turdus philomelos*) hunting for artificial prey at high or low densities, and arranged either in random, regular or clumped distributions in a meadow. He found that at the high density there was no change in food searching behaviour after a prey capture, regardless of prey distribution. At low density similar changes occurred after a prey capture in each of the three prey arrangements. Here, changes occurred in either the search path or the time spent searching, such that searching effort was increased in the area surrounding the capture site.

Similar parameters to those investigated in the results for prey density were analysed for habitat complexity. If search duration varies between hide arrangement conditions, it might be expected that this would be reflected in differences in the mean number of dives per min. However, mean dive rate (Fig. 5.13), generally, did not differ between the conditions. In the two cases where differences were significant, it appeared that opposite strategies were being used. Thus, for Amber, mean dive rate increased such that random < regular < clumped, while for Titan the reverse was true. However, the remaining individual results showed similar (though not significant) trends to that shown by Amber. The most interesting point was that, generally, individual males performed more dives per min than individual females, regardless of hide conditions.

If the mink are capable of perceiving differences in habitat complexity, it might be expected that this would be reflected in the way mink concentrated their searching behaviour. Thus, animals may either choose to concentrate on searching a hide thoroughly, and possibly investigating the pool bottom, if the environment is 'complex', or alternatively, they may search more hides if the environment is 'simple'. However, there was little difference in the number of hide visit dives per min (Fig. 5.14), when hides were random or clumped, but far fewer hide visit dives were made when hides were regular. However, since there had, generally, been little difference in dive rate with complexity, these changes in hide visit dive rate suggest that there are variations in the proportion of dives visiting a hide. The results (Fig. 5.16) show that this is, in fact, the case. Generally, when hides were arranged regularly, as few as 30% of dives involve hide visits. By contrast, when hides were arranged randomly or in clumps, more than 70% of dives involved hide visits for all animals. Thus, it appears that if the regular habitat is considered to be the simplest, mink are actually making fewer hide visit dives. This is the opposite to what was predicted above. This is a good point and serves as an illustration of a point raised by Pyke (1984) regarding Optimal Foraging Theory, where he points out that assumptions generally have to be made about the level of information available to the forager, and its ability to store and process this information. Here, the assumptions made would seem to be incorrect, and it appears that if the environment is simple, mink may be able to avoid revisiting, and perhaps obtain more food in fewer hide searches, generally resulting in a lower dive rate.

The results for successful dive rate (Fig. 5.15), however, show that, where differences were significant, mean successful dive rate was lower when hides were regular, with, generally, little difference between random and clumped. Since most of the significant results were obtained for individual males, this suggests that males may be using a similar strategy for each hide arrangement in terms of number of hides visited, revisiting etc., but that because fewer dives visit hides when they are regularly positioned, the overall result is that mean successful dive rate is decreased. For individual females, however, it appears that they may be altering their foraging strategy in some way, such that a similar degree of success is achieved regardless of the habitat complexity. Further, when the actual values for successful dive rates are compared, it is found that, generally, those for females are higher than those for males under corresponding conditions. Yet, male hide visit dive rates were, generally, higher than the equivalent values for females. This implies that the females are foraging more efficiently.

Since dives often involved visits to more than one hide, another measure of foraging efficiency relates the number of successful hide visits to the total number of hide visits. When these results were examined (Fig. 5.17), it was found that there were no significant differences between any of the hide arrangement conditions. Generally, however, the results for individual males show that 20-35% of hide visits are successful, regardless of hide arrangement, whereas 25-50% of hide visits performed by individual females are successful, and this again suggests that there are differences in the foraging strategies employed by individual males and females.

To investigate the foraging strategies in more detail, the mean time on bottom for unsuccessful dives, was examined for each hide arrangement. The results (Fig. 5.18) showed that there were individual differences. For the males and female Titan, the mean time on bottom was significantly greater when hides were arranged regularly. There was little difference between mean time on bottom when hides were either arranged randomly or in clumps. Although, there were individual differences in the actual mean values, generally, most animals spent 4-8 s on the bottom when hides were random or clumped, but spent between 6-11 s when hides were regular. Thus, some individuals seemed to be using a strategy of fewer, longer dives when hides are arranged regularly. For other individuals, especially amongst the females, there was, generally, little significant difference between mean time on bottom for the three hide arrangements, although again there was some indication that dives were of longer duration when hides were regular. Also, generally, the mean time on bottom is greater for some individuals (especially females) compared to that for other individuals (particularly males) when equivalent conditions are compared, but there are individual variations within each sex.

It is possible that these differences in mean time on bottom reflect differences in the search strategies in terms of number of hides visited per dive. However, the results of mean number of hides visited per dive (Fig. 5.19) showed that, generally, there was little difference between hide conditions. On average, most dives visited 1-2 hides per dive, depending on the individual animal. Thus, it does not seem that for individual males the longer time on bottom when hides are arranged regularly is being used to visit more hides per dive. Therefore, this may simply be a reflection of the fact that the nearest hides to the rostrum are 1.5 m distant, compared to 0.5 m for the other hide arrangements. For the individual females, there were two significant results, when more hides were visited per dive when hides were clumped (Flash) or regular (Titan). However, the mean values for individual females were, generally, higher than the corresponding values for males, and it appeared that more dives would visit two or more hides, regardless of condition. From Fig. 5.20 it does appear that two of the females have adopted a strategy of trying to visit several hides per dive. This would account for the higher values for mean time on bottom, and may also explain how females achieve a similar rate for successful dives to that of males, despite having lower overall dive rates to males. However, male Amber also appears to be visiting several hides per dive, whereas female Inka has a strategy of fewer hide visits. Thus, differences in behaviour are not consistent between the sexes.

When the proportion of time on bottom spent hide searching was examined (Fig. 5.21), it was found for males that there were a number of significant differences. Generally, the proportion of time on bottom spent in hide was less for the regular arrangement, while there was little difference between the values for random and clumped. This supports the idea that because the hides are farther from the rostrum when hides are arranged regularly, more of the time on bottom is spent simply travelling to the first hide. A similar number of hides are searched by males during a dive regardless of hide arrangement, and this leads to the mean value for time on bottom being greater when hides are regular. For females, there were no significant differences in the proportion of time on bottom spent hide searching, which was roughly 40% regardless of condition. Since females visited similar numbers of hides per dive regardless of hide arrangement conditions, this result suggests that when hides are arranged randomly or in clumps, females may not be opting to visit those hides closest to the rostrum, but may be choosing to move on to hides that are farther away, with the result that the proportion of time on bottom spent hide searching is similar to that observed when hides are arranged regularly. This was investigated by examining the amount of revisiting performed under the different conditions.

The results of the analysis of revisiting (Table 5.12), showed that for males, animals appeared to be foraging in a random manner regardless of the conditions of habitat complexity. However, for females, the results showed that when hides were arranged randomly, animals were foraging in such a way that hides which had been searched were not revisited. This may account for the low proportion of time on bottom spent in hides, since animals may well search hides closest to the rostrum and then move out to search hides further away, so that travel time on the pool bottom increases.

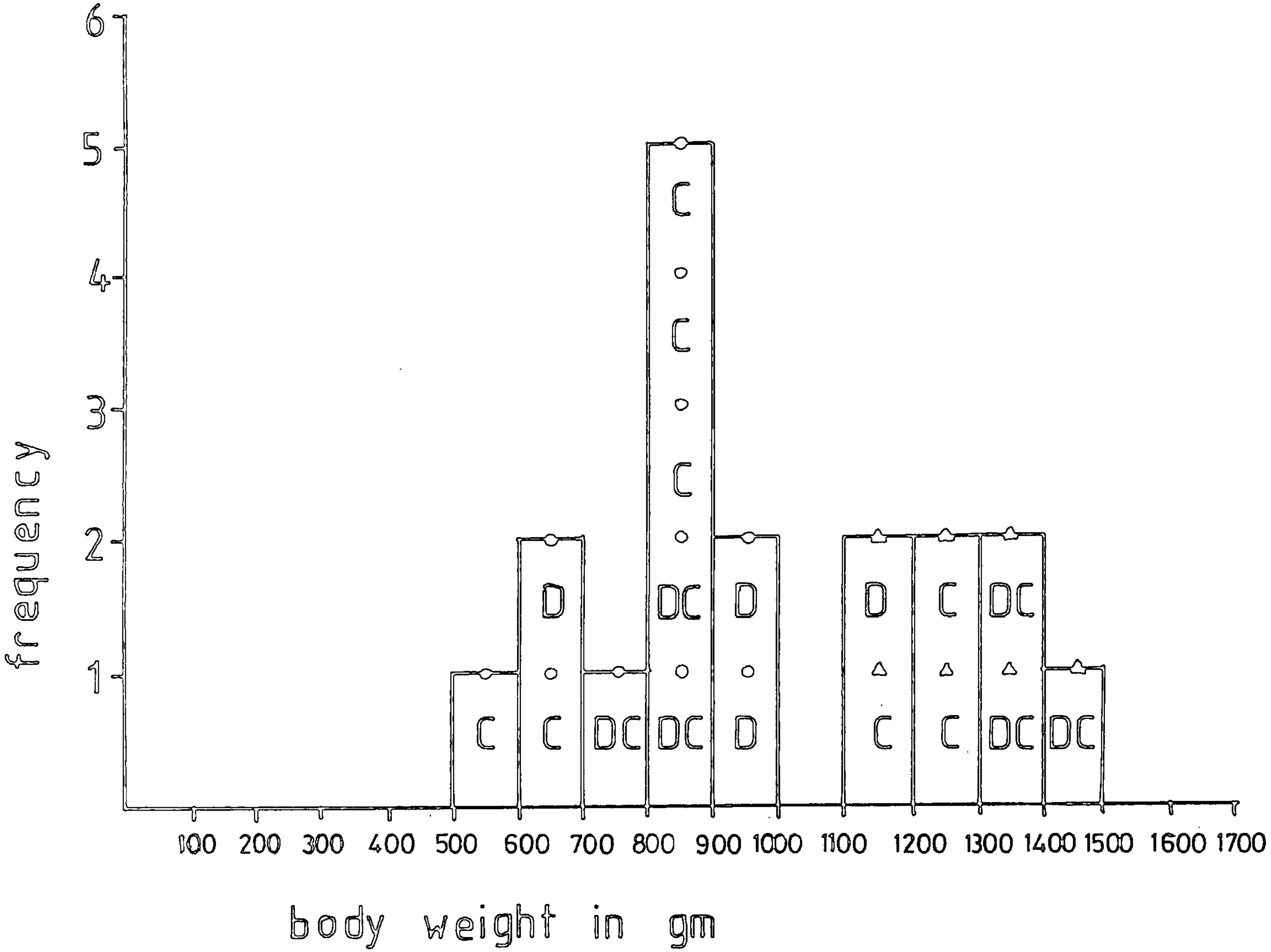
With regard to the complexity of the habitats, the results do show that the different hide arrangements do have some effect on the foraging behaviour. However, the predictions made earlier concerning which hide arrangement was the most complex do not seem to have been supported. It was suggested for example, that if the random arrangement was the most complex, animals would not be able to remember which hides had been visited and revisiting would occur. In fact, the opposite seems to be true, and it is only when hides are randomly arranged that foraging behaviour was biased in favour of searching new hides. The main conclusions that emerged from this analysis is that some animals do seem to have adopted a different foraging strategy to others. Thus, some females seem to visit more hides per dive, hence mean time on bottom is greater, but they perform fewer dives overall per min than some of the males. Also, generally, the females appeared to be the more efficient foragers. Smith (1974b) also found sex differences in the behaviour of his thrushes which he was unable to explain. In this experiment, due to the small number of individuals used, it was not really possible to show whether these differences in the behaviour of males and females, reflected a true difference in the behaviour of the sexes. Further work, using a larger number of animals of each sex, is needed before any definite conclusions about sexual differences in diving behaviour could be drawn.

CHAPTER 6

INDIVIDUAL STRATEGIES

Among the mustelids, mink are known to be one of the more sexually dimorphic species (Moors, 1980). This is thought to have important consequences regarding niche separation, e.g. Birks and Dunstone (1985) found considerable differences in the annual diets of male and female mink in Scotland, which could be related to differences in body size.

In the three experiments carried out, it was frequently observed that there was considerable variation in the responses of individual animals to changes in the foraging environment. In the experiments on the effect of current flow and prey density, there were some indications that there were differences in behaviour between the two sexes, but insufficient animals were tested to satisfactorily demonstrate this. In fact, any sexual differences in behaviour may well have simply been a reflection of differences in body weight (see Fig. 6.1). Some animals were used in several experiments, and their mean body weights varied between experiments (Appendix I), hence they may contribute several points to Fig. 6.1, but the legend denotes which size classes of males and females were used in each experiment. It can be seen that in no experiment was there any overlap between the mean weights of males and females, although for the depth experiment, only one size class separated the single male from the females. The most marked separation occurred for the density / complexity experiment, where each of the three males used weighed 1300 g or more, while each of the three females weighed less than 900 g. Perhaps not surprisingly, Analysis of Variance tests indicated that there were significant differences between the behaviour of males and females in this experiment, but the data were insufficient to show whether this was due to sex or size.


frequency
1
2
3
4
5
6
C
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D
C
C
DC
DC
DC
100
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1300
1400
1500
1600
1700
body weight in gm

In this section, however, the differences in individual strategy will be examined. Since a number of animals were used in several experiments, it is possible to look at aspects of their foraging strategies, and to examine whether there are any consistent changes in strategy in response to changing environmental conditions. Thus, are there animals who are consistently more efficient foragers, or animals who are consistently less efficient. This was examined by looking at the mean dive duration, the mean number of hides visited per dive and mean total dive rate, for each animal and each experimental condition. In each experiment, animals were ranked in decreasing order for each variable. The results are given in Tables 6.1 (dive durations), 6.2 (mean number of hides visited per dive) and 6.3 (mean total dive rate).

The following animals were used in more than one experiment: Females: Inka (three), Titan (three), Dexa (two) and Flash (two); Males: Amber (two), and Boris (two). From the results it would appear that the female, Titan, is using a strategy of many short duration dives, during which, generally, few hides are visited. This seems to be true regardless of the experimental conditions, although at high prey densities, her dive rate also declines. It is possible that she uses a strategy of non-revisiting, but the data (Table 5.12) were insufficient to show this.

The female Inka, on the other hand, seems to have employed a more variable strategy, at least in terms of the rank achieved compared to the other animals in the experiments. However, she does seem to be adopting a strategy of longer duration dives than Titan, with generally more hides visited per dive, especially when density was 100%, and this leads to a generally lower dive rate than that achieved by Titan. Since the mean weights of these two animals was similar throughout the experiments (both ranged between 850-950

TABLE 6.1: Rank of animals for mean unsuccessful dive duration, across all experiments. Longest mean dive duration is given the highest rank

1) DEPTH EXPERIMENT.

0.30 m	0.60 m	0.75 m	1.00 m	1.05 m	1.20 m	1.45 m	1.65 m
Dexa	Inka	Inka	Dexa	Dexa	Dexa	Dexa	Inka
Titan	Dexa	Raja	Inka	Raja	Inka	Inka	Dexa
Raja	Raja	Titan	Titan	Inka	Titan	Titan	Titan
Inka	Titan	Dexa	Raja	Titan	Raja	Raja	Raja

2) CURRENT EXPERIMENT. (depth = 0.60 m)

Control	Deep Current	Surface Current
Flash	Jaspa	Jaspa
Amber	Flash	Flash
Jaspa	Karla	Boris
Karla	Amber	Amber
Inka	Boris	Inka
Dexa	Inka	Dexa
Boris	Dexa	Karla
Titan	Titan	Titan

3) DENSITY EXPERIMENT. (depth = 0.60 m)

25%Ran.	25%Reg.	25%Cl.	50%Ran.	50%Reg.	50%Cl.
Flash	Inka	Flash	Flash	Flash	Flash
Amber	Flash	Inka	Inka	Bill	Inka
Bill	Bill	Amber	Bill	Inka	Bill
Inka	Amber	Bill	Titan	Amber	Amber
Boris	Boris	Titan	Amber	Titan	Titan
Titan	Titan	Boris	Boris	Boris	Boris

75%Ran.	75%Reg.	75%Cl.	100%Ran.	100%Reg.	100%Cl.
Flash	Flash	Inka	Inka	Inka	Inka
Inka	Bill	Flash	Amber	Flash	Flash
Bill	Inka	Boris	Flash	Amber	Bill
Amber	Amber	Amber	Bill	Bill	Amber
Titan	Titan	Bill	Titan	Boris	Boris
Boris	Boris	Titan	Boris	Titan	Titan

TABLE 6.2: Rank of animals for mean number of hides visited per dive, across all experiments. Maximum value for mean number of hides visited per dive is given the highest rank.

1) DEPTH EXPERIMENT.

0.30 m	0.60 m	0.75 m	1.00 m	1.05 m	1.20 m	1.45 m	1.65 m
Titan	Raja	Raja	Inka	Raja	Dexa	Dexa	Inka*
Raja	Inka	Dexa	Dexa*	Dexa	Inka	Raja	Dexa*
Dexa	Dexa	Inka	Raja*	Titan	Raja	Inka	Raja
Inka	Titan	Titan	Titan	Inka	Titan	Titan	Titan

2) CURRENT EXPERIMENT. (depth = 0.6 m)

Control	Deep Current	Surface Current
Karla	Jaspa	Jaspa
Jaspa	Karla	Karla
Amber	Amber	Amber
Dexa	Flash	Dexa
Boris	Dexa	Boris
Flash	Boris	Flash
Inka	Titan	Inka
Titan	Inka	Titan

3) DENSITY EXPERIMENT. (depth = 0.6 m)

25%Ran	25%Reg.	25%Cl.	50%Ran.	50%Reg.	50%Cl.
Bill	Amber	Inka	Flash	Titan	Flash
Amber	Inka	Flash	Titan	Amber	Inka
Inka	Bill	Amber	Amber	Flash	Amber
Boris	Boris	Bill	Inka	Bill	Titan
Flash	Titan	Titan	Bill	Boris	Bill
Titan	Flash	Boris	Boris	Inka	Boris

75%Ran.	75%Reg.	75%Cl.	100%Ran.	100%Reg.	100%Cl.
Flash	Flash	Inka	Inka	Inka	Inka
Bill	Titan	Amber	Flash	Amber	Flash
Inka	Amber	Boris	Amber	Boris	Boris
Titan	Inka	Flash	Boris	Flash	Amber
Amber	Bill	Bill	Titan	Bill	Bill
Boris	Boris	Titan	Bill	Titan	Titan

* denotes a tie in Rank.

TABLE 6.3: Rank of animals for mean dive rate, across all experiments. Maximum mean dive rate is given the highest rank.

1) DEPTH EXPERIMENT.

Level I	Level II	Level III	Level IV
Titan	Titan	Titan	Titan
Inka	Inka	Raja	Inka
Raja	Raja	Inka	Dexa
Dexa	Dexa	Dexa	Raja

2) CURRENT EXPERIMENT. (depth = 0.6 m)

Control	Deep Current	Surface Current
Boris	Boris	Boris
Titan	Titan	Titan
Flash	Inka	Inka
Inka	Flash	Flash
Karla	Amber	Amber
Amber	Jaspa	Karla
Jaspa	Karla	Jaspa
Dexa	Dexa	Dexa

3) DENSITY EXPERIMENT. (depth = 0.6 m)

25%Ran.	25%Reg.	25%Cl.	50%Ran.	50%Reg.	50%Cl.
Boris	Amber	Titan	Boris	Boris	Boris
Titan	Titan	Amber	Flash	Flash	Amber
Bill	Boris	Boris	Titan*	Bill	Flash
Flash	Flash	Bill	Bill *	Amber	Bill
Amber	Inka	Flash	Amber	Titan	Inka
Inka	Bill	Inka	Inka	Inka	Titan

75%Ran.	75%Reg.	75%Cl.	100%Ran.	100%Reg.	100%Cl.
Titan	Bill	Boris	Boris	Boris	Boris
Amber	Boris	Amber	Bill	Amber	Bill
Boris	Titan	Flash	Amber	Bill	Inka
Flash	Amber	Titan	Inka	Titan	Amber
Bill	Flash	Inka	Titan	Flash	Titan
Inka	Inka	Bill	Flash	Inka	Flash

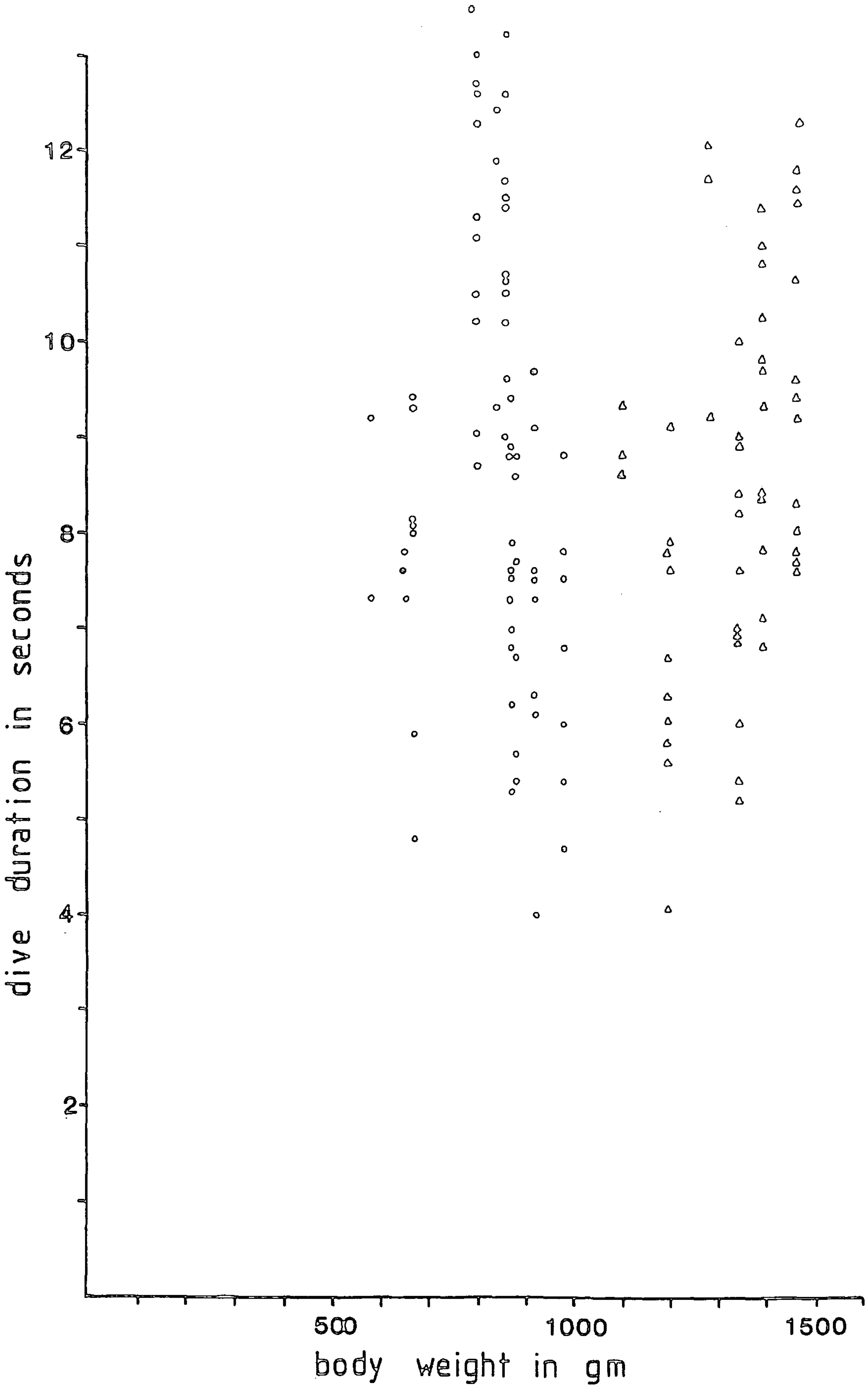
*denotes a tie in rank.

g), these differences obviously do not reflect differences in body size, but must reflect actual individual foraging preferences.

In the depth experiment, the female Dexa appeared to have a foraging strategy similar to that of Inka, i.e. few dives per minute, each of fairly long duration, and visiting one or more hides per dive. In the current experiment, she was consistently ranked at the bottom for mean dive rate, and it appeared that her dives were also of shorter durations than previously. Since she died shortly after completion of the current experiment, these results may reflect the fact that since these experiments were not carried out under a 'closed foraging economics' system, Dexa may have been opting for a strategy giving her some returns for minimum effort.

When the results for the males Amber and Boris are considered, it can be seen that they are frequently ranked close to one another. However, in terms of the number of hides visited per dive, Amber is consistently ranked higher than Boris, whereas in terms of mean dive rate, Boris is generally ranked higher than Amber. When mean dive duration of unsuccessful dives is considered, Amber is again, generally, ranked higher than Boris. Thus, it appears that, like Inka, Amber's strategy may be one of few, longer duration dives, visiting one or more hides per dive, whereas Boris has opted for many short duration dives, generally visiting one hide only.

The most interesting point to emerge from the above results is that there appears to be no division between the sexes in terms of the type of foraging strategy used. This is illustrated even more clearly in Fig. 6.2. This is a graph of mean unsuccessful dive duration against body weight, for all experimental conditions combined. Again, animals used in more than one experiment will have results for each experiment. Data for males



12
10
8
6
4
2
dive duration in seconds
500
1000
1500
body weight in gm

and females are coded separately. From this it can be seen that there does not seem to be any relationship between mean body weight and dive duration. Thus, females with body weights around 800-900 g, have mean dive durations which are similar too, and in some cases greater than, the mean dive durations for males with body weights of more than 1300 g. This implies that whilst some sexual differences in foraging behaviour may well be a consequence of size differences, much of the differences do in fact reflect individual preferences, regardless of body size.

These results may not have universal applicability to all diving vertebrates. For example, it is interesting to note that in the smooth newt (*Triturus vulgaris*) there are a number of subspecies. A new subspecies, *T.v. schmidtleri,* has recently been described from Turkey (Raxworthy, 1988). One of the main features is that this appears to be a dwarf subpecies, compared to the nominate subspecies, *T.v. vulgaris*. It was noted (Raxworthy, 1988), that breathing ascents during courtship were considerably less frequent in *T.v. schmidtleri* displays compared to *T.v. vulgaris*. It was suggested that the smaller size of the *schmidtleri* males might allow a greater uptake of dissolved oxygen from the water. However, it was also noted that *schmidtleri* displays included much longer fan durations than *vulgaris* displays, which may aerate the skin of the male, or may even be energetically less costly than the whip and wave displays also shown during courtship of this species. Although courtship in newts is not strictly comparable to foraging underwater in mink, the above information does lead to some interesting speculations. It would be interesting to examine the diving behaviour of different subspecies of mink, particularly those from the more southern U.S.A.(small subspecies), compared to, e.g. Alaskan mink (large subspecies), to see if behaviour is in anyway different. It has been noted in this study that individual males and females behave differently, although the different foraging strategies used could not be related to differences in body size.

CHAPTER 7

SWIMMING SPEED AND FISHING BEHAVIOUR

7.1. Introduction

Much work has been carried out on the diet of mink both in North America and Europe, particularly in Britain. The results have basically shown that mink will take whatever prey is locally abundant in relation to its vulnerability to capture. Prey items are generally very varied and include small mammals, e.g. lagomorphs and rodents, which are mainly terrestrial, birds, including both gamebirds and waterfowl, and fish, including coarse fish, marine species and salmonids. There have been many reports of mink decimating local waterfowl stocks (e.g. Gudmunsson, 1952) and rodents (e.g. Schnell, 1964; Platt, 1968), but little information on their impact on fish stocks. Despite this, there have been claims that mink, especially feral mink in Europe, pose a grave threat to local faunas. As a result in Britain, for example, the mink was registered as a pest species, and all mink farms were required in 1962 to be licensed under the Mink (Importation and Keeping) Order (Thompson, 1967). This point will be discussed more fully below. Studies of mink diet in different localities and during different seasons have shown that fish could form as much as 70% of the diet (Cuthbert, 1979). Tables 1.2 and 1.3 give a list of the fish families and species recorded in the diet of mink in Europe and North America. From these tables it can be seen that a wide range of species are taken as prey.

This study was concerned with the underwater foraging behaviour of mink, and the results obtained can be considered in view of knowledge of what fish mink generally prey upon, and how the habits of these fish may make them more, or less, vulnerable to predation by mink.However, an important point here concerns the relative swimming speeds of predator and prey. Measurements have been made previously of the swimming speed of mink whilst on the water surface (e.g. Dunstone, 1981; Williams, 1983a) and underwater when pursuing live prey (Poole and Dunstone, 1976; Dunstone, 1981).

Measurements were obtained for the speed of underwater travel in the current experiment. However, animals were not pursuing prey in this experiment, and the results obtained may not give a true picture of the capabilities of mink when pursuing live prey. Thus, four animals were also tested for 'maximum' underwater swimming speed. The results obtained will be discussed with reference to data on the known swimming speed of fish taken as prey by the mink, and to known details of the general habits of these fish.

7.2. Materials and Methods

7.2.1. Subjects

Four animals were used in this experiment, two males (Amber and Boris) and two females (Flash and Titan). All had been used in previous experiments and were familiar with the experimental arena.

7.2.2. Experimental Procedure

The experiments were carried out in the grid-marked pool. A resting place was provided at one end of the pool. There were no hides, and water depth was 0.75 m throughout. Prior to the start of the experiment, the distance between each grid line was checked to ensure equality.

A piece of eel, 5 cm long, was attached to the end of a long pole. Animals were required to chase this bait, underwater, from one end of the pool. At the start of each chase, animals were resting on the rostrum. The pole was then held close to the animal, and once interest had been shown in the bait, the pole was quickly submerged. If the animal dived in after the bait, a second observer started a stop watch, whilst the first observer ran the length of the pool until either the animal gave up the chase and surfaced, or until the farther wall of the pool was reached. In either case the first observer signaled, and the stopwatch was stopped. The first observer noted the position of the animal in relation to the grid, and the distance travelled could then be calculated. Distance travelled and time taken were noted and speed of swimming could then be obtained.

This procedure was repeated at least five times for each animal, and each animal (except Flash) received at least two trials. A number of measurements were also made when animals were swimming on the water surface, or just below it (sub-surface) but where they were not considered to be completely submerged, and hence this was not recorded as a dive.

7.3. Results

7.3.1. Maximum swimming speed underwater

The results obtained for maximum swimming speed are given in Table 7.1. It can be seen that most results were between 70-80 cm s^{-1}, but the maximum speeds reached varied for each animal, and were:-

Flash (wt= 800 gm) 76.7 cm s^{-1} for 4.47 s.
Titan (wt= 825 gm) 82.3 cm s^{-1} for 6.54 s.
Amber (wt=1375 gm) 103.6 cm s^{-1} for 6.14 s
Boris (wt=1413 gm) 88.6 cm s^{-1} for 6.63 s.

From this it can be seen that the smaller females may not be able to swim as fast as the larger males, but the values for Titan and Boris are very close. Since individual behaviour has been shown to be very variable, this point could be resolved by obtaining data for a larger number of individuals of both sexes and of varying weights.

Table 7.1 Distance travelled, duration and maximum speed underwater.

Date	Animal	Sex	Weight in gm.	Duration in s.	Distance in cm.	Speed in cm s^{-1}
5/2/84	Titan	Female	850	7.46	489.5	65.6
				7.34	562.9	76.7
				6.73	440.6	65.5
				5.65	342.7	60.6
				7.48	587.4	78.5
				5.57	391.6	70.3
				4.41	293.7	66.6
				4.65	342.7	73.7
	Boris	Male	1450	3.50	269.2	76.9
				4.67	367.1	78.6
				6.63	587.4	88.6
				3.67	195.8	53.4
				5.24	342.7	65.4
				3.26	244.8	75.1
				5.47	391.6	71.6
	Flash	Female	800	8.27	293.7	35.5
				6.00	293.7	49.0
				4.47	342.7	76.7
				5.31	244.8	46.1
				8.71	440.6	50.6
				7.49	440.6	58.8
				6.05	293.7	48.5
	Amber	Male	1450	2.67	195.8	73.3
				7.04	416.1	59.1
				7.50	636.4	84.9
				6.14	636.4	103.6
				7.40	465.0	62.8
				6.15	636.4	103.5
				6.22	293.7	47.2
14/2/84	Boris	Male	1360	2.32	171.3	73.2
				5.88	391.6	66.6
				3.37	244.8	72.6
				4.09	269.2	65.8
				2.19	159.1	72.6
				2.82	97.1	34.7
14/2/84	Amber	Male	1300	6.09	391.6	64.3
				3.94	318.2	80.8
				6.28	489.5	77.9

Table 7.1(Contd.) **Distance travelled, duration and maximum speed underwater and when surface swimming.**

Date	Animal	Sex	Weight in gm.	Duration in s.	Distance in cm.	Speed in cm s^{-1}
14/2/84	Amber	Male	1300	6.97	562.9	80.8
				5.41	342.7	63.3
				8.66	636.4	73.5
				8.44	636.4	75.4
				6.04	416.1	68.9
				3.35	293.7	87.7
				6.50	636.4	97.9
				4.24	342.6	80.8
	Titan	Female	800	6.54	538.4	82.3
				7.19	587.4	81.7
				5.44	440.6	81.0
				4.58	342.7	74.8
				4.50	305.9	68.0
16/2/84	Boris	Male	1430	4.93	293.7	59.6
				4.40	293.7	66.8
				5.65	416.1	73.6
SURFACE SWIMMING						
5/2/84	Titan	Female	850	4.97	293.7	59.1
				7.47	587.4	78.6 (subsf)
	Boris	Male	1450	8.16	636.4	78.0
	Flash	Female	800	7.59	636.4	83.8
				6.34	489.5	77.2
14/2/84	Boris	Male	1360	4.11	342.7	83.4 (subsf)
	Amber	Male	1300	7.04	636.4	90.4 (subsf)
				7.50	636.4	84.8
				6.63	636.4	96.0
				7.50	636.4	84.8
	Titan	Female	800	8.01	587.4	73.3
				6.20	501.7	80.9
				4.20	318.2	75.8
				7.40	636.4	86.0
				6.61	636.4	96.3
16/2/84	Boris	Male	1430	7.82	636.4	81.4

The limitations in length of the pool did not allow a full investigation into how long a mink could maintain its maximum speed underwater although the longest dive was of 8.66 s for male Amber, when speed was 73.5 cm s^{-1}. Thus, it was not possible to see if an animal could maintain an underwater speed of, say, 80 cm s^{-1} for 20 s.

7.3.2. Maximum underwater swimming speeds measured in current experiment

Only data for unsuccessful dives were considered, since it was felt that in these cases, particularly where animals attempted to visit more than one hide per dive, the resulting speed of travel might give some idea of the capability of the mink. Three males and five females were used in the current experiment. The speed of travel was measured as an average over the whole dive duration, i.e. including hide visits. Table 7.2 gives the values for the maximum speed recorded during any single dive, the minimum and the range, for each individual under the three conditions of the experiment.

From this it can be seen that for the males, maximum swimming speed varies between roughly 62-70 cm s^{-1}, depending on the animal and the condition. For the females, maximum swimming speed varied between roughly 52-100 cm s^{-1}, depending on the animal and the condition. There is a problem in that the measure for speed of travel during a dive was an average and included a certain time when the animal was stationary, i.e. when investigating a hide. Therefore, it is possible that during pursuit of prey, mink may be able to achieve even faster speeds. What is not known is how long such speeds could be maintained. Nevertheless, these results can provide some idea of the sort of speeds mink can attain when searching for a stationary target. Again, there is considerable individual variation, and in this case the maximum speeds of some females are considerably higher than those for males under the same conditions.

Table 7.2: Maximum, minimum and range of speed of underwater travel, in cm s^{-1}, recorded in current experiment.

Animal	Sex	Mean Weight in gm.	Control Max.	Control Min.	Control Range	Deep Max.	Deep Min.	Deep Range	Surface Max.	Surface Min.	Surface Range
Amber	M	1103	59	42	17	67	23	44	65	18	47
Boris	M	1210	70	20	50	51	19	32	60	4	56
Jaspa	M	1276	29	18	11	43	21	22	62	18	44
Dexa	F	654	no data			48	24	24	52	24	28
Flash	F	841	52	17	35	71	26	45	48	6	42
Inka	F	882	64	26	38	82	31	51	74	46	28
Karla	F	577	72	30	42	48	15	33	79	13	66
Titan	F	881	36	36	-	100	24	76	61	17	44

N.B. Each value is the mean speed recorded during any one dive.

Table 7.3 Data of maximum swimming speeds recorded in other studies.

Reference	Speed in cm s^{-1}	Comments
Dagg and Windsor, 1972	83.3	
Poole and Dunstone, 1976	60.0	Underwater search for live fish
	76.0	Underwater pursuit of live fish
Dunstone, 1981	42.0	Surface swimming
	49.0	Underwater search
	59.0	Underwater pursuit
Williams, 1983a	70.0	Surface swimming

7.3.3. Results of swimming speed obtained in other studies

A number of workers have investigated the swimming and diving capabiities of mink. Some have examined the energetics of swimming (e.g. Williams, 1983a), while others investigated the underwater predatory behaviour of the mink (e.g. Poole and Dunstone, 1976). The results of these studies are give in Table 7.3., and it can be seen that, although there is a wide variation in the published speeds, the maximum seems to be over 80 cm s^{-1}.

These figures can be compared to the underwater speeds for otter which can be as fast as 278-330 cm s^{-1} (Mason and Macdonald, 1986).

7.3.4. Known swimming speeds and habits of fish species preyed on by mink

Poole and Dunstone (1976), record the maximum swimming speed of the minnow, when performing level flight, as 114 cm s^{-1}, and of the goldfish as 100 cm s^{-1}.

Bainbridge (1958a,b) recorded the swimming speeds of dace (*Leuciscus leuciscus*), trout, and goldfish of different sizes. He found that the maximum speed was related to the size of the fish. From his data, it can be seen that for a dace of 9 cm length, maximum speed recorded was roughly 170 cm s^{-1}, while for a 24 cm specimen, maximum speed was 225 cm s^{-1}. For trout, maximum speed for a 29 cm specimen was over 300 cm s^{-1}, and for a 13.5 cm fish it was roughly 225 cm s^{-1}. Finally, for goldfish, maximum speed for a 22.5 cm fish was roughly 80 cm s^{-1}, and for a 7 cm fish, nearly 70 cm s^{-1}. Bainbridge (1958a) also gave a table of swimming speed data, compiled from the literature, for a number of other fish species. However, he felt that in some cases, measurements may not have been accurate, and also may not represent the maximum speed of the fish concerned.

Nevertheless, the data for species known to be preyed on by mink will be included here for comparison. All results are in cm s^{-1}: bleak (50), perch (66), rudd (114), pike (148), salmon (600)

Wardle (1975) reports data for a number of marine fish. Many of these were not known to be preyed upon by mink, but some results are included for comparison. He found that small (seawater) salmon (25-28 cm length) could reach 250 cm s^{-1} (10 body lengths s^{-1}), in the laboratory. Similarly, smaller fish, e.g. 10 cm haddock (*Melanogrammus aeglefinus*) and sprats (*Sprattus sprattus*) had maximum swimming speeds of 260 cm s^{-1} (or 26 body lengths s^{-1}). Larger fish, e.g. 73 cm cod (*Gadus morhua*) were measured at 280 cm s^{-1}, but it was thought that this was an underestimate due to the laboratory conditions, since it is reported in the literature that large cod of around 100 cm length could reach speeds of 400 cm s^{-1} (i.e. four body lengths s^{-1}) (Wardle, 1975).

Finally, Table 7.4. summarises the known habits of fish predated by mink, both in Europe and North America, (from Sterba, 1962; Wheeler, 1968). From this it appears that the majority of freshwater fish predated by mink, are found in shallow, slow-moving water. Further, many are bottom dwellers and lead relatively sedentary lives, whilst the majority of marine fish recorded in mink diets, are commonly found in rock pools.

7.4. Discussion

During the course of the investigations into changes in the underwater foraging behaviour of the mink in response to changes in environmental conditions, a number of general conclusions have been made. Thus, mink generally locate potential prey items aerially (Poole and Dunstone, 1976). They are capable of diving to depths of at least 1.9 m (Stephenson et al., 1988) and searching for prey underwater, where they will readily

Table 7.4 Habits of fish species predated by mink

Fish species	Habits
Freshwater species	
Ameiurus sp. (Catfishes)	Slow flowing and standing waters generally shallow depth. Predatory, bottom dwellers, hide amongst vegetation, roots and stones. Most species spawn in shallow depressions. Size up to 45 cm, but generally smaller.
Anguilla anguilla (Eel)	Standing and flowing water. Predatory, bottom dwellers, especially on sandy beds where eel will 'dig in' especially in winter. Spawns in the ocean, elvers return to freshwater habitats about 3 years after hatching. Size up to 150 cm.
Catastomus sp. (suckers)	No information.
Centrarchidae (Sunfishes and Basses)	Clear slow flowing stream waters, over rocky or sandy bottom and lakes especially in quiet, weedy shallows. Predatory. Ambush prey from among roots or between stones. Sizes up to 70 cm.
Cottidae (Bull heads and Sea Scorpions)	Mostly marine but some species live in freshwater, in clear mountain and lowland streams, especially those with stony beds. Some are found in brackish water. Fish can be found in water of 10 cm to 9 m but prefer the shallow regions. Predatory but hides under rocks and stones during the day and hunts at night for crustaceans and bottom living insect larvae. May eat salmon and trout eggs. Spawns March-May in cavities excavated beneath stones. Size up to 17 cm but usually smaller.
Cyprinidae (Carp and Carp-like fish)	European species. Slow flowing rivers and streams, also clear lakes and ponds. Some species like densely vegetated areas. Most are predatory. Some, e.g. Bream and Roach live in deepwater but Bream move into thickly weeded shallows near banks to spawn (May-July). Some species, e.g. Bream, Bleak and Minnows shoal. A few, e.g. Ide and Minnow live in upper layers of flowing waters and lakes. Others, e.g. Tench and Bream, are bottom feeders. Sizes vary up to 70 cm. North American species Clear, flowing water, most prefer slow moving streams or lakes but some live in moderately fast flowing rivers. Most prefer clear water. Most are predatory, some take plant material also some species school, some feed in midwater, others on bottom - many species spawn in shallows.
Cyprinodontidae (Tooth-Carps)	Rivers, streams and brackish water. Some are surface livers, but those recorded in mink diet are bottom dwellers. Prefer fairly deep water, thick plant growth. Size up to 15 cm.
Esocidae (Pikes)	Found in fresh and brackish water in Northern hemisphere. Predatory. Ambush prey preferably from amongst vegetation near water surface. Spawn (February to May) in shallows over banks. Size up to 70 cm.
Gadidae (Codfish)	The Burbot is the only freshwater codfish. Prefers lowland rivers, lakes but also found in brackish water. Predatory but has a sedentary life style, usually hides among roots, in crevices, under banks during day and hunts at night. Size can be up to 1 m but generally 50 cm.

Table 7.4 Habits of fish species predated by mink (cont'd.)

Fish species	Habits
Gasterosteidae (Sticklebacks)	Fresh water andmarine species,standing and flowing water. Active swimmers. Predatory. Prefers shallows of 0-1 m depth. Some species prefer densely vegetated sites. Build 'nests' on bottom during breeding season (April-June) Size up to 10 cm.
Percidae (True Perches)	Perch - *Perca fluviatilis*. Clear and turbid flowing waters, ponds, lakes and brackish waters. Predatory. Prefers weedy margins and young shoal. Spawn March to July. Up to 25 cm. Darters - *Characidium fasciatum*. Wide variety of water, lives under stones and 'digs in' when attacked. Also very fast swimmer. Spawning occurs under stones in spring. Size up to 6.5 cm.
Salmonidae	Fresh, brackish often fast-flowing running water, ranging from mountain streams to estuaries. Many migrate to the sea. Predatory. Some are territorial e.g. Brown trout which spawn (October-January) in shallow areas with gravelly bottom. Brook trout spawn in the swift gravelly reaches of streams. Mature salmon hunt mainly in coastal waters and migrate upstream to spawn (November to December) in shallow waters, young remain 2-4 years in freshwater before migrating back to the sea. Size up to 40 cm for trout, 1.5 m for salmon.
Thymallidae (Grayling)	Clear running water, mainly rivers but also lakes. Predatory mainly on bottom living insects, crustaceans and molluscs. Spawn in spring on gravelly shallows.
Umbridae (Mudminnows)	Freshwater ponds, streams - slow moving water, thickly weeded. Predatory on bottom living insects etc. Tolerant of cold. Size up to 20 cm.
<u>Marine species</u>	
Blenniidae (Blennies)	Common shore fish, especially on rocky coast. Found in rock pools, but also in sandy and muddy pools provided they contain stones. Predatory, mostly on bottom living species. In the sea found to depths of 30 m (Blenny) or 100 m (Butterfish).
Heterosomata (Flatfish)	Bottom dwellers generally in the sea but young of some species may be common in tidal pools.
Gadidae (Cod fish)	Five-bearded rockling. Commonly found in intertidal zone on all shores, especially in rock pools, but can live down to 20 m. Predatory on crustacea and small fish.
Gobiidae (Gobies)	Difficult to identify, but of the *Gobius* species the larger gobies (12 cm or more) live on rocky shores and inshore waters. Medium gobies (7-11 cm) live on stony shores and inshore. All small gobies (less than 8 cm) belong to other genera. Many feed on algae but others are predatory.

enter confined spaces, but dive rate per min was much greater in shallower depths, i.e. up to 0.60 m. Overall dive durations tend to be short, of the order of 5-15 s, but dives of 25-30 s duration were also recorded. Male and female mink tended to behave differently and, generally, females made fewer longer duration dives than males. From observations, mink appeared to be very agile underwater and were able to turn sharply whilst swimming. In view of these conclusions and the information obtained on the swimming speeds of mink and fish, the question arises "How do mink manage to catch fish?". There are several points which need to be considered in order to answer this question.

Firstly, it is obvious that the size of fish taken as prey will be important, since it can be seen that smaller fish do swim more slowly. Wise et al. (1981) examined the diet of mink and otter in southern England. They also estimated the lengths of fish prey taken by the two predators (from remains in scats), and compared these results to the frequency distribution of different fish sizes as shown by electrofishing in two habitat types. The main fish prey taken on the Rivers Webburn and Dart were salmonids and eel. The proportion of fish in mink diet varied seasonally, most being caught in winter. Salmonids were most important and most fish caught were less than 15 cm long, although there were a few records of salmonids as large as 40 cm having been taken. Eels were next in importance, and most captured by mink were less than 40 cm in length, although again there were a few records for eels up to 55 cm having been consumed. At Slapton Ley, there was no seasonal variation in the proportion of fish taken by mink. The most important fish prey here were Cyprinids (namely roach and rudd) and most were less than 15 cm long. Eels were also important and most were again less than 40 cm in length. Finally, perch and pike were of some importance and most specimens captured by mink were less than 20 cm and 70 cm in length respectively. Electrofishing data showed that there was no apparent size selection by mink at either site.

From the work of Wise et al. (1981), it can be seen that mink do take a wide size range of prey, which are therefore capable of swimming at a range of speeds underwater. In all known cases the maximum swimming speed of the fish is considerably greater than that recorded for mink. Thus, there must be other factors involved. Since fish are poikilothermic, water temperature is very important and can have a dramatic effect on fish swimming speed. Wardle (1975) states that a 73 cm cod would be expected to reach a speed of 660 cm s^{-1} at 20°C but only 430 cm s^{-1} at 0°C. Similarly, Chanin (1985) cites work by Rowe-Rowe, showing that captive clawless otters (*Aonyx capensis*) took four times as long to catch *Tilapia* (of the same length) when water temperature was 27°C compared to 17°C. Further, Rowe-Rowe also found that when clawless otters were offered a variety of fish species, they caught them in inverse proportion to the fishes' swimming ability: small fish were captured more readily than large fish (cited in Mason and Macdonald, 1986). This may explain why the proportion of fish in mink diet often increases in winter (e.g. Wise et al., 1981; Birks and Dunstone, 1985; Dunstone and Birks, 1987), i.e. the reduction in fish swiming speed may facilitate capture by mink.

Erlinge (1968) found that captive otters (*Lutra lutra*) caught fish with damaged fins much more quickly than healthy fish of the same size and species. It is unknown whether otters in the wild might prey preferentially on weak or sickly fish, but as Chanin (1985) points out, diseased fish and those 'spent' after spawning are no doubt particularly vulnerable. It is therefore probable that the same applies to mink, e.g. Hamilton (1959) noted that Brook trout and Brown trout eggs and remains were found in the stomachs of mink trapped in early November in the Adirondacks. He further notes that these fish spawn in late October/early November and they select shallow water over gravel, where they are presumably vulnerable to predation. Similarly, Gerell (1967b) notes that on the River Ronnea in Sweden, the proportion of fish in mink diet increases during winter/spring. He suggested this was due to increased vulnerability of the fish since the lower water temperature decreases their activity and agility. He further notes that many freshwater fishes form aggregations during the cold months which may further increase their vulnerability.

This leads on to the final point, which is that the behaviour of the fish may well increase their vulnerability to mink predation, despite their advantage in terms of swimming speed. This certainly seems to be true for otter predation. Chanin (1985), for example, points out that pike normally lie in wait in vegetation and consequently, being inactive, may not be noticed by an otter who is attracted by more mobile prey. Similarly, a shoal may be more detectable than a single fish, but if the shoal breaks up the predator may be greatly confused by fish darting in all directions.

To investigate whether those fish species taken as prey by mink are more susceptible, their known habits can be examined. The fish species recorded as mink prey can be divided into marine and freshwater. Migratory fish such as eel and salmon will be considered as freshwater since they are mainly taken by mink in rivers. The details of the known habits of fish preyed on by mink are given in Table 7.4. From this, it can be seen that most of the marine fish taken by mink are found in rock pools, and certainly the observations of mink foraging in coastal habitats (Dunstone and Birks, 1983, and pers.comm.), suggest that mink do concentrate their efforts on the rock pools rather than the sea itself. Here it is immaterial whether the fish are slow moving bottom dwellers or fast pelagic species, since rock pools are generally of limited dimensions and mink should be able to locate prey aerially and use all of the available dive time for pursuit and capture.

In freshwater habitats the situation is more difficult. Nevertheless, from Table 7.4 it can be seen that a large number of the fish species taken as prey are generally found in shallow, slow moving water or lake margins, (e.g. catfishes, sunfishes, cyprinids). Many are bottom dwellers (e.g. catfishes, mudminnows, burbot) and lead relatively sedentary lives. The majority of fish prefer clear water which will make aerial detection easier for mink; however, many also prefer densely vegetated parts (e.g. pike, some sticklebacks) which would be expected to hinder predation by mink. Nevertheless, sedentary bottom-dwellers would presumably be easy targets for mink provided they were located aerially. If species are camouflaged or, like the "Miller's thumb", *Cottus gobio*, they hide under stones, mink may be forced to dive and search underwater, and especially under stones. However, this may actually increase their vulnerability, since this study has shown that mink will readily enter confined spaces underwater. This particular species is known to freeze once its protective stone is overturned and this would presumably convey an added advantage to the hunting mink, unless its immobility fails to attract the predator. Some species lead more active lives in faster flowing waters. However, many of these species shoal (e.g. minnows (Pitcher, 1973)), and presumably a shoal, being a larger 'target', would be more conspicuous (Poole and Dunstone, 1976), and therefore easier to locate aerially, than a single sedentary individual. Having located a shoal, a mink may then be able to direct its dive towards a particular individual, and spend all the available dive time in pursuit of the prey, rather than search then pursuit.

Thus, it appears that despite the apparent limitations of mink for underwater foraging, the animal has adopted strategies which allow it to make the best use of its resources namely:- (a) Preferentially locates prey aerially, (b) Hunts in shallow water and lake margins, (c) Concentrates on sedentary bottom dwelling fish or shoals in shallows, (d) Presumably takes larger fish, e.g. salmon, when they are diseased, or 'spent' after spawning (Hamilton, 1959; Wise et al., 1981). The latter noted that salmonids were more important in mink diet during winter, i.e. the spawning season.

It now remains to examine the percieved harmful effects of mink in the light of the results and ideas discussed above. During the past 60 years, the North American mink has been introduced, either deliberately or accidentally, into many parts of Europe and Russia, where it has spread rapidly, and is now common in many parts. The presence of feral mink has aroused much controversy, e.g. Thompson (1971) cites reports of otters failing to breed in areas where mink populations are dense, and of the disappearance of moorhens in areas where mink had recently been introduced. Similarly, Lever (1977) states that in Scandinavia and Iceland, feral mink are reported to have caused considerable damage to domestic poultry, game birds, fisheries and wild water birds. He further states that in Britain it might be tempting to regard mink as an interesting addition, but in fact they "present a very real threat to many species of native wildlife". The main reason for supposing mink to be a threat to native wildlife is, of course, the fact that it is a carnivore. Furthermore, it is unusual, especially in British and European faunas, in having a very broad-based diet which includes both terrestrial and aquatic items, and this may lead to reduced competition with native carnivores, thus allowing mink to establish itself and spread. The opposing view to that of Thompson and Lever was proposed by Linn and Chanin (1978a,b). These authors conclude that because mink are generalized carnivores, they should be able to coexist with native carnivores, e.g. otters. Further, they suggest that the evidence indicates that otters are the superior competitors for aquatic food items. However, their general conclusion is that mink may have a beneficial effect in killing some grain pest mammals, but may have a detrimental effect on fish stocks. Overall they believe that mink will have a neutral effect but may be a nuisance on a small scale at some times.

Because the mink is an introduced carnivore, there is much concern over its potential effects on both 'wild' prey stocks and domestic stocks, especially amongst poultry and game farmers, fish nursery owners and water bailiffs concerned with fish stocks in rivers. Furthermore, many carnivores are known to 'surplus kill' in the wild (Kruuk, 1972a; Chanin, 1985). There have been some instances reported where it is thought that mink were responsible for attacks in hen houses (Hill, 1964). Also, Disney (pers. comm.) observed that after the arrival of mink on the Malham Tarn estate, birds, especially gulls (*Larus* sp.), coots and, occasionally, great crested grebes (*Podiceps cristatus*) and moorhens, were often found pushed into the heather surrounding the Tarn, especially during winter. It is possible that the mink had killed excess birds and were trying to 'cache' them.

However, it must be noted that although there are fears by anglers etc., that mink may cause damage to commercially valuable fish stocks in rivers, i.e. salmon, trout etc., it should also be noted that if mink are removing 'spent' or diseased fish, they may actually help to improve fisheries. Furthermore, some of the other fish taken by mink are known to eat salmon and trout eggs and in this way, if mink have a substantial impact on these populations they may actually assist a larger proportion of salmon/trout eggs to survive to hatching. Whether this would be beneficial in the long run is unknown, since mink are also taking fish that would be potential prey items for older salmon. However, Cott

(1961) showed that the Nile Crocodile, *Crocodilus niloticus*, feeds mainly on fish which in themselves are of little commercial value, but which are known to feed on eggs, fry and adults of the commercially important species such as *Tilapia*. He showed that in areas where crocodiles had declined in numbers, the *Tilapia* fishery was suffering due to increased predation by these bottom feeding fish, e.g. barbel (*Heterobranchus* sp.), which had previously formed a major component of the crocodile diet. It is also interesting to note that previous ignorance of the crocodile's precise feeding habits led to its extermination in large parts of its range because of fears that it would cause great damage to the commercial fisheries. Since Cott's study revealed the opposite was true, this case should be taken as a warning not to relegate a species to pest status too readily.

CHAPTER 8

GENERAL DISCUSSION

All studies have shown that mink not only live in habitats associated with water (Mech, 1965), but that they actively hunt for aquatic prey items (e.g. Melquist et al., 1980; Wise et al., 1981; Dunstone and Birks, 1987), which may form as much as 70% of the diet (e.g. Cuthbert, 1979), depending on season, sex and locality. However, mink are considered to have evolved very few specialised anatomical or morphological adaptations to enhance their ability to hunt underwater (Stephenson et al., 1988).

The results of this study have shown that mink are capable of altering their underwater foraging strategy in response to changes in the environmental conditions. Further, it was found that there were considerable differences in individual behaviour under the same environmental conditions. Mink are extremely sexually dimorphic, especially in terms of body weight. There was some evidence that there might also be sexual differences in behaviour, but the sample sizes of animals were so small, and there was no overlap in body size between the males and females used, that it was not possible to determine if there was a true sexual difference, or whether it was merely an expression of the size differences between animals. The general changes in foraging strategy will be discussed first, with reference to individual differences in behaviour.

Since this study involved the mink in searching underwater for prey located in 'hides', it was found that the main behavioural change involved dive duration. Since trial times were fixed, changes in dive duration would be expected to influence dive rate. Further, if dive duration were altered, this would be expected to influence the number of hides visited during a dive, which in turn might affect mean distance travelled and so on. The main finding in all three experiments was that mink were able to lengthen their mean dive duration, particularly for unsuccessful dives, as conditions were altered. Thus, as depth was increased from 0.3 m to 1.65 m, mean dive duration for unsuccessful dives increased (Fig. 3.7). However, the most interesting point concerns individual results for dive duration.

Examples of the sort of changes recorded in this study are: mean unsuccessful dive duration for four animals at depth 0.30 m, prey density 50%, was 4.45 s, but at depth 1.65 m for the same animals, the figure was 8.25 s, nearly twice the duration. Similarly, in the investigation of the effect of habitat complexity, at a constant depth of 0.6 m, and prey density of 50%, mean dive duration of unsuccesful dives for All Animals, varied from 7.66 s (random hide arrangement) and 7.96 s (clumped hides), to 10.22 s (regular arrangement). The minimum mean unsuccessful dive duration recorded for All Animals, was the 4.45 ± 0.16s in the depth experiment, and the maximum mean value was 10.84 ± 0.27s recorded at a depth of 0.60 m, prey density 25%, regular hide arrangement. On an individual level there were even greater extremes, e.g. for Inka (female) the lowest unsuccessful dive duration recorded was 1.5 s at a depth of 0.3 m, depth expteriment, 50% prey density. Her maximum unsuccessful dive duration was 20.8 s recorded in the density experiment, at depth 0.60 m, 100% density, regular hide distribution.

From the above, and the remaining experimental results, it was found that although most dives (successful and unsuccessful) were of less than 10 s duration, many dives, particularly in the density experiment, were between 10 - 15 s and the maximum time recorded was 27.2 s for female Flash: 75% density, random hides, unsuccessful dive. Such changes in dive duration will obviously have important effects on the foraging strategies employed by animals underwater, e.g. the number of hides visited per dive, distance travelled etc. Therefore, it is of great importance to examine how mink decide when to terminate a dive, and how, physiologically, they can achieve extended dives.

Thus, the question arises as to whether increases in dive duration are within the aerobic diving limits of the mink, and that other constraints act to normally keep dive durations low, or whether mink are forced to switch to anaerobic metabolism in order to increase dive durations, i.e. to be 'stressing' themselves. The implications for foraging behaviour arising from both the above strategies will be discussed.

During this study, no physiological measurements were made, but from the behaviour of the animals under different conditions, several general points were noted which may indicate the rules that mink use to 'decide' dive duration. The first point is that, as mean dive duration increased for any particular set of conditions, so mean dive rate decreased. This is only to be expected since trials were of a fixed time limit, but if dives of longer duration require a switch to anaerobic metabolism they may also need a longer interdive recovery period leading to reduced dive rate. Results from the depth experiment where trials were terminated if animals completed 20 dives, or spent 10 min in the arena, show that at the lowest water level (i.e. depths 0.30 m and 0.75 m) 18 out of 22 trials were of less than 10 min duration, because the mink completed the required 20 dives. By contrast at water level IV (depths 1.20 m and 1.65 m), only 5 out of 47 trials were of less than 10 min duration. In each case the animals had not completed the required 20 dives, but the trials were stopped because of technical problems. From the results given previously (see above), mean dive duration at the maximum depth was roughly twice that at the minimum depth, but at the lower depths, animals often completed 20 dives in 7-10 min. Thus, if dives of longer duration did require a longer recovery period, it would be expected that at the maximum depths, if dive duration is twice that at the shallowest depth, recovery time would also be increased, and animals should complete fewer dives in 10 min. When the raw data for each trial is considered, it is found that in 35 trials out of 42, less than 10 dives were completed within the 10 min allowed, and the mean number of dives per trial was only 4.42. This does indicate that longer dives do require a longer recovery period.

Data for recovery time between dives was not analysed since, if animals were successful it was noted that there was great variation between individuals in the time taken to eat a similar sized prey item. Thus, female Dexa, for example, was often noted to spend betweeen 1-2 min consuming a piece of eel, whereas the male Boris generally required less than 20 s. Secondly, some individuals, e.g. female Titan, tended to eat each food item as soon as they had regained the rostrum, whereas others, e.g. female Flash, tended to 'stockpile' prey items and then eat several in one long feeding bout. Finally, animals sometimes engaged in grooming bouts between dives (especially during the depth experiment at maximum depth) or bouts of prolonged surface swimming between dives. Thus, from the behaviour it was not possible to assess whether a mink was physiologically incapable of diving again, or was engaged in alternative activities such as grooming, swimming etc., or if the animal was still recovering before the next dive. Recovery might be slower than expected because animals were expending some energy in these other activities. Surface swimming in particular is considered by Williams (1983a) to be a very energetically costly form of aquatic locomotion for mink.

Nevertheless, the fact remains that mink are able to vary the duration of dives in response to varying conditions underwater. Kramer (1988), using principles of economic design, produced a "theory of optimal breathing" for air breathing aquatic mammals. He considered the relevance of optimal foraging principles to the uptake of oxygen by air breathing aquatic organisms. He stated that if the principle of optimal exploitation of diving resources was applied to the aquisition of oxygen at the water surface by diving animals, this principle would predict that with increasing distance to feeding sites or other areas of resource gain, bout lengths of surface time and dive time would increase. This is exactly what was seen in the results from this study for effect of depth. Kramer also predicted that as distance to feeding sites increased, the amount of oxygen carried in the lungs, blood and muscle at the start of a dive should be greater. Since larger oxygen stores should permit greater time away from the surface, dive durations should also be longer. Some experimental work has been carried out on the effects of different oxygen availabilities on diving behaviour. Jones and Larigakis (1988) found that cormorants (*Phalacrocorax auritis*) forced to dive, had heart rates that were significantly elevated if they had breathed oxygen before diving, compared to those breathing air. Thus, onset of bradycardia was delayed, and was not as deep as in those birds breathing air. Similarly, Halliday (1977) investigated the effect of breathing various gases, namely nitrogen, compressed air and oxygen, on the sexual behaviour of the smooth newt (*Triturus vulgaris*). The approximate partial pressure of oxygen was 9, 150 and 750 mm Hg under nitrogen, air and oxygen respectively. It was found that variations in oxygen supply produced marked differences in the frequency of breathing ascents. Thus, as oxygen availability increased, the number of breathing ascents decreased and first inter-breathe interval increased. Males also slighlty speeded up their sexual behaviour under reduced oxygen, thus partly compensating for the fact that less time could be devoted to sexual behaviour under such conditions.

Thus, this is one method by which mink could increase dive duration, i.e. by taking up more oxygen at the surface between dives, but other available physiological information for diving mammals and birds, and in particular data for mink, will also be considered. A general review of diving physiology was given in section 1.3, but a brief summary of the relevant details will be given here. The conclusions reached were that highly adapted aquatic species have evolved a number of adaptations to cope with periods of prolonged apnoea whilst diving. These include morphological adaptations, e.g. it is possible that diving mammals may have proportionately larger lungs (Stahl, 1967), and physiological adaptations, e.g. development of mechanisms which trigger bradycardia at the start of a long dive thus helping to conserve oxygen stores. It now remains to review the available physiological data for mink to see how these animals compare.

Stephenson et al. (1988) investigated heart rate and oxygen consumption for two freely diving female mink, performing normal foraging dives at the University of Birmingham (unfamiliar) and the University of Durham (familiar). Dive durations were also measured, but data are only given for deep dives, and the results were as follows:-

	Durham 1.9 m depth	Birmingham more than 1.0 m
650 g female	8.1 ± 0.4 s	9.8 ± 0.9 s
1000 g female	6.5 ± 0.3 s	6.3 ± 0.5 s

Similar data were obtained in the present study, whereby female Dexa (approximate mean weight 600 g), and female Titan (approximate mean weight 1000 g), gave mean unsuccessful dive durations, at 1.65 m depth of 9.38 ± 0.68 s (mean ± S.E.) and 7.76 ± 0.28 s respectively. It can be seen that in both cases the larger animal has a lower mean dive duration. However, during this study the mean unsuccessful dive durations are longer at 1.65 m than those reported in Stephenson et al. (1988) for mink diving to 1.9 m. This is probably because the dives in this study involved multiple hide visits whereas those in Stephenson's work involved one. This will be discussed in more detail below. The point to be noted here is that during these deep dives recorded by Stephenson et al., at both Durham and Birmingham, heart rate was similar to, or above, that recorded during normal resting exhalation, and this was lower than the heart rate recorded when animals were sleeping. West and van Vliet (1986) demonstrated that lung deflation, especially when coupled with water in the trachea of their anaesthetized mink, was important in initiating bradycardia. Stephenson et al. (1988) noted that their mink sometimes exhaled at the start of a dive. Exhalation, followed by apnoea may then cause a drop in heart rate. Finally, a pronounced bradycardia was only recorded by Stephenson et al. during pipe searching dives, at Durham, to depths of 0.3 m. The mean duration of these dives was much greater than for non-pipe visit shallow dives:

	pipe visit dives	non-pipe visit shallow dives
650 g female	11.9 ± 1.43	3.3 ± 0.34
1000 g female	7.0 ± 0.44	4.6 ± 0.29

In this study the duration of mean unsuccessful hide visit dives at depth 0.3 m for females Dexa and Titan were as follows:

Dexa (approx. 600 g)	4.78 ± 0.26
Titan (approx. 1000 g)	4.70 ± 0.31

However, these results were obtained in an experiment where there were a very small number of hides available and where, on average, each dive visited just one hide. In Stephenson et al.'s (1988) study, there was only one 'hide', a piece of pipe, available in Durham, but in Birmingham, the hides used were identical to those used in this study. Other experiments carried out in this study used a higher number of hides available for searching, but the depth of water used is not comparable to that in Stephenson et al. (1988). However, as these authors point out, the occurrence of a pronounced bradycardia during 'hide search' dives only, suggests that the mink are invoking physiological adjustments to increase breath-hold endurance times. They also point out that since Dunstone and O'Connor (1979a) showed that giving-up time was inversely related to fish encounter rate in mink, it would be interesting to see if the physiological adjustments during hide-search dives were affected by prey encounter rate. The question arises as to whether the occurrence of a bradycardia was a mechanism to increase breath-hold endurance when food availability was low, or whether it was an effect of being in an enclosed space when submerged, and being unable to easily reach the water surface. They show, in fact, that both mechanisms may operate under the appropriate circumstances. However, in this study all food items were located in enclosed spaces (hides) and it would not be possible to separate the effects of low food density and enclosed spaces. Nevertheless, one indication that low food density is of importance comes from the results for unsuccessful dive duration in the experiment investigating effects of prey density. Here, depth and number of hides were constant throughout, but the number of hides baited varied between: 8,16,24 and 32 out of 32 (i.e. 25%, 50%, 75%, 100%). The female Titan (mean weight approximatley 1000 g) was used in this experiment and, from Fig. 5.7, when hides were arranged regularly, it can be seen that mean unsuccessful dive duration is greatest at the lowest prey density. This suggests that when food availability is low, mink may try to prolong the dive duration, under the conditions of this study, in order to visit more hides. It would be interesting, therefore, to see if a bradycardia had developed during prolonged dives when prey density was 25%.

As well as measuring heart rate, Stephenson et al. (1988) also made measurements on gas exchange (i.e. oxygen uptake, VO_2, and carbon dioxide production, VCO_2) but only during dives made at Birmingham University. Similar measures were made by Williams (1983a,b) for mink surface swimming and running on a treadmill. Such measurements are useful in estimating the metabolic costs of various activities to mink, and Williams (1983a) demonstrated that surface swimming was a very energetically expensive form of aquatic locomotion, due to poor swimming efficiency (resulting from the small surface area of paws, which does not allow efficient thrust generation), use of hindpaws to supplement forepaw propulsion, and high stroke frequency (around 200 strokes min^{-1}). The implications of the above results are that surface swimming and diving are energetically very costly to mink, a species that already has an unusually high metabolic rate (Iversen, 1972). This would imply that if the oxygen storage capacity of mink body oxygen reserves are similar to that of other similarly sized mammals, e.g. muskrat, then mink would be able endure apnoea for a much shorter time than muskrats. Stephenson et al. (1986) cited work which suggested that naturally diving animals should be capable of maintaining aerobic metabolism in all tissues for the duration of a normal dive - this was based on measurements of oxygen storage capacities and estimated rates of oxygen consumption during spontaneous diving activity. Woakes (1988) showed that for tufted ducks and Humboldt penguins, this was indeed the case. Stephenson et al. (1988) have measured oxygen consumption during diving, but I have been unable to find any estimates for oxygen storage capacities in mink, although Butler (1988) estimated that normal foraging dives in mink would be aerobic in nature.

However, Gilbert and Gofton (1982a) noted that mink became unconscious, roughly 2 min after being submerged, and brain death occurred after about 4.5 min. What is not known, is how long mink could remain underwater before having to switch to anaerobic metabolism, but presumably the occurence of a bradycardia at the onset of a dive would lower the metabolic demands of diving and allow mink to remain submerged for longer periods before anaerobiosis would become necessary. It would be interesting to see if there is any evidence of anaerobic respiration in mink which have voluntarily performed very long (i.e. over 20 s) foraging dives, e.g. by measuring lactic acid levels in the blood, (as was done by Kooyman et al. (1980) on Weddell seals), and whether a bradycardia is invoked even if these long dives are within the aerobic capabilities of mink. Furthermore, as mentioned above, Stephenson et al. (1988) noted that mink exhale at the start of deep dives. This would mean even lower oxygen reserves available for aerobic respiration. However, from the work of West and van Vliet (1986), lung deflation appeared to assist in the development of a bradycardia, and Stephenson et al. did note that heart rate dropped in these cases.

The main point to arise from the above studies is that diving would seem to be a metabolically extremely costly activity for mink, and morphologically mink do not appear to be well adapted to it, e.g. they have small paws. However, laboratory work and field studies have shown that mink can, and do, catch aquatic prey, e.g. fish and crustaceans, underwater. In this study, and that of Stephenson et al. (1988), mink were observed to use structures within the tanks to propel themselves into the water using the hind limbs to provide thrust. This would enable animals to achieve greater velocities and so save energy expenditure. Brown and Lasiewski (1972) have suggested that the elongate body form of mustelids (whilst being energetically inefficient) might be adaptive for increasing the ability to capture prey in confined spaces. Thus, mink may have evolved behavioural mechanisms to capture prey underwater, e.g. by searching refuges. From the data on the known habits of fish species preyed on by mink (Table 7.4), this would seem to be the case. Also Birks and Dunstone (1985) noted that during terrestrial hunting mink will readily enter confined spaces, and in the laboratory studies of Dunstone (1978), Dunstone and O'Connor (1979a) and this study, mink were adept at entering 'hides' (i.e. confined spaces) to search for prey.

Thus, it appears that mink may have evolved some physiological mechanisms (principally the bradycardial response), to increase breath-hold endurance during diving. It would be interesting to see if terrestrial mustelid species such as stoats or polecats, also develop bradycardia when submerged, although in their case submergence would be involuntary and bradycardia might then be the result of a fear response. It might perhaps be better to examine blood lactic acid concentration or oxygen consumption. Similarly, such studies would be interesting if carried out on otters, as some clues might then be produced which would help to elucidate the phylogenetic relationships of these mustelids, and would perhaps give some further evidence as to whether mink should be regarded as primitive otters, or highly advanced mustelids undergoing convergent evolution with otters in the use of the aquatic niche. Certainly, amongst the Anatidae (ducks), work by Johnsgard (1960, 1961, 1962) using behavioural characteristics has indicated that the trends in diving have been from a semi-terrestrial existence where diving is rarely, if ever, performed, to one where adaptations for diving have precluded life on dry land (e.g. the stiff-tailed ducks). Much work has been done on the physiological responses of the tufted duck (*Aythya fuligula*), a diving duck. Its responses appear to be similar to that of the mink, but it has dive durations which are more of the order of those seen in otters, e.g. Stephenson et al. (1986) found that maximum dive duration recorded was 46.3 s and most dives were between 15-25 s duration. Johnsgard (1961, 1962) suggests that the *Aythya* genus is a relatively recent one and that within the genus, the species *fuligula* is also fairly recent.

The suggestion from this is that perhaps mink evolved as exploiters of both terrestrial and aquatic habitats, i.e. they are not advanced mustelids evolving convergently with otters, but rather highly 'specialized' mustelids who are adept at exploiting many habitats. The elongate body, whilst being metabolically inefficient, allows access to confined spaces on land and underwater. The small paws prevent awkwardness when running, but result in inefficient thrust generation in water. Furthermore, the observed foraging strategy of locating underwater prey aerially (Dunstone, 1978; Melquist et al., 1980; this study), allows mink to use a strategy of 'dive-chases' (Dunstone and O'Connor, 1979a). Here, extra velocity is provided by pushing off with the hind legs when diving. The animals reach their general goal more quickly, with less energy expenditure, allowing more of their limited dive time to be used for pursuit of prey. Finally, the mink has evolved physiological mechanisms which are under both voluntary and involuntary control to help increase breath-hold endurance (Stephenson et al., 1988), although from Gilbert and Gofton's (1982a) work on terminal dives, the indications are that mink may not easily be able to switch to anaerobic metabolism as do other species which are considered to be much more highly specialized divers. Further work is required on the physiological mechanisms involved in diving in the mink, particularly measurements of VO_2 and VCO_2 during diving only, and measurements of blood lactic acid concentrations to indicate the occurence of anaerobic respiration. It would also be interesting to investigate dives where bradycardia would be expected to be initiated, e.g. dives to great depths with low food availability, to see if such dives require a longer recovery time, or if, having triggered a bradycardia, mink are able to conserve their oxygen resources to a sufficient extent that even a long dive duration does not result in the development of a large oxygen debt requiring a long recovery period.

Although at first sight the mink may not appear to be well adapted to diving, the above work shows that, under the circumstances in which it dives, the mink's morphology and physiology are adequate to cope with the pressures and stresses it is likely to meet in nature. The final question that remains to be answered is, since the initiation of bradycardia can be under voluntary control, what factors influence the decision of an animal to increase its dive duration by triggering this reflex?

One factor which may have an important effect here is water depth. Field studies using tufted ducks (Draulens, 1982) showed that mean diving times increased as depth increased from 2-4 m, but with little change as depth increased further to 6 m. Similarly, Hobson (1969) has noted that marine iguanas (*Amblyrhynchus cristatus*) probably increase their dive time as depth increases. Kramer (1988) suggested that theoretically, dive time should increase with depth. Increasing dive times with increasing depth have been found in northern fur seals (*Callorhinus ursinus*) and South African fur seals (*Arctocephalus pusillus*) fitted with time-depth recorders (Gentry et al., 1986; Kooyman and Gentry, 1986). A positive relationship between dive times and depth was also found for leatherback sea turtles (*Dermochelys coriacea*) fitted with time-depth recorders (Eckert et al., 1986). Finally, Wanless et al. (1988) suggested that for their radio-tracked guillemots (*Uria aalge*), puffin (*Fratercula arctica*) and razorbill (*Alca torda*), increased dive durations meant that birds could potentially dive to deeper depths. This study has shown that when water depth increases from 0.3 m to 1.65 m mean dive duration increases.

It has been suggested that the changes in hydrostatic pressure associated with an increase in depth may be important, since increased pressure will result in reduced bouyancy by compressing the body gases. Compression of the air in the lungs would also result in increased uptake of lung oxygen stores to the blood (Hobson, 1965; Watson, 1986; Stephenson et al., 1988). Reduced bouyancy would lower the oxygen cost of locomotion during longer dives (Stephenson et al., 1988), and if the animal can exert sufficient force at the start of a dive to take the excess air in the lungs down to a given depth, then locomotion at depth should be less costly energetically than in shallow water (Watson, 1986). In the case of the mink, the depths involved are not very great, and furthermore if the animal exhales before diving there is less bouyancy due to the presence of extra oxygen in the lungs, to overcome. Again a 'dive-chase' strategy would seem most sensible. However, pressure changes may be sufficient to trigger bradycardia during diving, thus enhancing the animal's breath-hold endurance. From this study, the average time taken to travel from the water surface to a depth of 1.65 m was around 1 s. E.K.G. recordings made by Stephenson et al. (1988) for a female mink diving to 1.9 m, show that the onset of bradycardia is gradual, i.e. it is possible that changes in hydrostatic pressure act as a signal to the mink of the depth reached, inducing the animal to prolong dive duration for as long as possible, in order to maximize prey encounter rate. Bradycardia and the effects of increased depth in reducing bouyancy would assist in this.

However, changes in dive duration are also seen when water depth is kept constant, but other factors such as prey density, distribution of possible prey locations (i.e. hides) are altered. In this case mink appear to be acting more in agreement with Optimal Foraging Theory, by attempting to maximize the rate of energy intake. Thus, it would be expected that the initial dives under any conditions may, as well as resulting in prey capture, be providing information on prey encounter rate. This would probably affect the length of time the animal allocates to underwater searching behaviour on a subsequent dive. Dunstone and O'Connor (1979a) showed that the behaviour of mink foraging for live fish prey at different densities was broadly consistent with predictions derived from the Marginal Value Theorem (Charnov, 1976), after allowing for constraints imposed on the mink because of their limited underwater endurance. As expected, Dunstone and O'Connor found that as prey density increased, duration of dive-chases decreased, giving-up time (i.e. duration of search phase of a dive) and pursuit duration decreased, as did the frequency of search dives. In this study also, dive duration for hide visit dives, was greater at the lowest prey density (25%) than at the highest (100%). It would be interesting to see if mink do initiate bradycardia for these longer dives, but in this study the difference was only a few seconds.

Thus, the conclusions to be reached from the above review are that mink are highly versatile, opportunistic mustelids, well adapted for their semi-aquatic, semi-terrestrial life style. They have evolved a few physiological mechanisms to assist their breath-hold endurance underwater, and these mechanisms can be initiated voluntarily in response to environmental conditions of water depth and prey availability.

Much work has been done on the underwater foraging behaviour of another aquatic mustelid, the otter. It is interesting to compare the data for dive times for the two species. Thus, Hewson (1973), recorded mean dive durations of 12.45 s and 16.36 s, for otters hunting in a freshwater loch, in water depths generally up to 2.8 m. The longest dive he recorded was 20 s. This is very similar to the results obtained for the mink. However, Kruuk and Hewson (1978), obtained mean values of 15.9 s for successful dives, and 24.8 s for unsuccessful dives, for otters foraging in the sea, off the coast of Scotland. The maximum durations recorded were between 31-35 s for unsuccessful dives. Kruuk et al. (1985) investigated the effect of depth on the foraging behaviour of otters hunting off the coast of the Shetlands. They found that dive duration increased with depth, and recorded unsuccessful dives of up to 50 s at depths of 10+ m. Watson (1986) working on the Shetlands, obtained means of 25.4 s for successful dives and 32.7 s for unsuccessful dives, and a maximum unsuccessful dive lasting between 61-65 s. Finally, Conroy and Jenkins (1986) studying otters foraging in freshwater lochs and off the coast of the Shetlands, recorded mean dive durations of 13.1 s (successful) and 12.7 s (unsuccessful) in the freshwater lochs, and 13.3 s (successful) and 22.7 s (unsuccessful) in the marine habitat.

From the above results, it can be seen that in freshwater habitats, otters seem to forage underwater for similar durations to those observed during this study on mink. However, when otters foraging in marine environments are observed, their dive durations appear to be considerably longer than those normally recorded for mink. However, as seen from the work of Kruuk et al. (1985), water depth does seem to be important. The problem with all of these studies is that data were collected in the field, and it is possible that otters might have been surfacing more frequently, and that sometimes sightings were missed. However, Erlinge's (1968) study of captive otters, recorded dives that were, generally, of less than 30 s duration. There is a considerable size difference between individual otters, where males can weigh from 4-13 kg (Mason and Macdonald, 1986), depending on body length, whereas mink males are generally around 1.5 kg (Birks, 1984). From Stahl's (1967) work on the scaling of respiratory variables, it might have been expected that otters would have a much greater capacity for longer duration dives than mink. It appears however, that although otters are potentially capable of diving for periods of up to a minute, the favoured durations are less than 30 s. This is a similar principle to that observed in the mink, where animals did perform dives of 25+ s, but generally dives were 10-15 s duration.

From the point of view of foraging behaviour, the overall length of a dive is not as important as the time on bottom, since this is a measure of the actual time available for foraging. Kruuk and Hewson (1978) proposed a model to calculate time on bottom, for otters foraging in the field, where the only data available were for overall dive duration and water depth. They proposed that using data for successful and unsuccessful dives, it would be possible to estimate the amount of time that an otter spent travelling between the surface and the bottom, during an average dive, and hence calculate the time on bottom available for foraging. The model was expressed algebraically as:-

$$S_- = D + F_- + U \qquad (1)$$

$$S_+ = D + F_+ + U^1 \qquad (2)$$

where S_- = total time underwater, unsuccessful.

S_+ = total time underwater, successful.

D = time spent travelling down, for all dives.

U = time spent travelling up, for unsuccessful dives.

U^1 = time spent travelling up, for successful dives.

F_+ = time spent foraging on bottom, with success.

F_- = time spent foraging on bottom, without success.

They assumed that on average, $U = U^1$. Further, it was assumed that an otter had an equal likelihood of encoutering a prey at any time during its foraging on the bottom, then F_+ would equal half F_-. Thus:-

$$S_+ = D + 1/2F_- + U \qquad (3)$$

Subtracting (3) from (1) :-

$$S_- - S_+ = 1/2F_- \qquad (4)$$

Using their observed results for mean dive durations for successful and unsuccessful dives, Kruuk and Hewson calculated that 28% of the total dive time was spent in travelling to and from the water surface. The water depth in this case was estimated to be between 2-3 m. In this study, measurements were made of the total dive duration and mean time on bottom, for successful and unsuccessful dives. The results obtained for All Animals in the depth experiment can be substituted into equation (4) above, and the result compared to the known travel time. Thus, when depth was 1.65 m, mean successful dive duration was 7.03 s, and mean unsuccesful dive duration was 8.25 s. Substituting in equation (4), it is found that the mean time on bottom for an unsuccessful dive would be 2 x (8.25 - 7.03) = 2.44 s. The actual value obtained for mean time on bottom for unsuccessful dives for all animals, was 5.79 s.

It appears that there are a number of problems with Kruuk and Hewson's model, with the result that foraging time on the bottom is underestimated. A major fault appears to be the assumption that duration of successful dives will be half that of unsuccessful dives. This was not found to be the case in this study (see Figs. 3.7, 3.8 for example). Watson (1986) suggested that since prey would be unlikely to be totally passive, then a period of pursuit would occur once prey had been detected. In this study, 'prey' were 'passive', but even so, some time had to be allocated to location of prey. The result was that although mean duration of successful dives was generally shorter than unsuccessful dives, they were never half the duration. It appears that Kruuk and Hewson's model is rather too simplistic, and modifications would be needed before it could be used to give a realistic measure of time on bottom.

From the results of this study, it is felt that some measure of travel time to the bottom would have to be incorporated, based on a knowledge of the water depth in which animals were foraging. An estimate could be obtained of travel time to the bottom at varying depths from a similar type of study to that carried out here. Thus, a laboratory study could be carried out to investigate the speed of travel of otters or mink to varying depths. Since water depth affects the degree of compression of gases in the body, this may affect bouyancy, and as the animal dives deeper, it may become easier to travel still deeper, due to the lowered bouyancy. Thus, it may take a proportionately shorter time to reach the bottom at greater depths, compared to shallow depths. This could easily be investigated in the laboratory.

A second point is that Kruuk and Hewson assume that time to travel up from the bottom at the end of successful and unsuccessful dives would be equal. It is possible that this is not the case, since swimming speed with a prey item, e.g. a large fish, particularly one that is struggling, may not be the same as that without a burden. Further, both otters and mink are relatively streamlined in shape, but having a large object protruding from the mouth may influence drag, and hence again influence speed of travel, and therfore time of travel to the surface. This could be investigated to some extent in the laboratory, by providing, e.g. large, dead fish as prey on the bottom, instead of 5 gm pieces of eel. Using the same recording techniques as were used in this study, it would then be possible to get measures for U and U^1 at varying depths to see if the two really were equal. A similar study using live fish prey would show whether the movement of the fish contributed to the time of travel to the surface. However, there are problems in using live prey, e.g. the predator may not catch the fish at the same depth in successive successful hunting bouts, difficulties of knowing when to start timing particular behaviours etc. Nevertheless, some tests using live prey could also provide valuable information.

The results of this study have shown that F_+ does not equal $1/2F_-$, and it has been suggested (Watson, 1986) that a period of pursuit would be necessary once a prey item is located. Thus, it would be better to restate F_- as :-

$$F_- = F_+ + x \qquad (5)$$

where x = pursuit duration of prey.

This could again be investigated in the laboratory by providing a single fish, of known size, as prey and timing the durations of pursuit, to obtain an estimate of x. It would then be possible to see whether x varied depending on the size of teh prey. Thus, it might be expected that since speed of swimming of fish species varies, and is related to size, large salmon, for example, would require longer pursuit durations than minnows. However, the likelihood of an otter or mink being able to catch a minnow may be much higher that the likelihood of catching a salmon.

Finally, it has been shown previously that for both otter and mink, mean dive durations (particularly of unsuccessful dives, F_-), tend to be much shorter than the theoretical maximum. It is possible that F_- will vary depending on the feeding motivation of the animal. Thus, an animal that had had low hunting success in the previous 24 hours, may have larger F- values than one whose feeding motivation was lower. This could again be investigated in tha laboratory, using the same sort of experimental set-up as was used in this study.

Thus, from the above discussion, it is possible to suggest modofications to Kruuk and Hewson's formula which might then allow a better calculation of the time on bottom available for foraging. Thus:-

$$S_- = D + F_- + U \qquad (1)$$

$$S_+ = D + F_+ + U^1 \qquad (2)$$

But, now $$U^1 = U + y \qquad (6)$$

where y = effect of carrying a large prey item back to the surface.

and from above $F_- = F_+ + x$ (5)

Both x anfd y may vary depending on the size of the prey. Thus:-

$$S_+ = D + (F_- - x) + (U + y) \qquad (7)$$

Therefore $$F_- = S_+ - D + x - U - y \qquad (8)$$

this would give a measure of time on bottom available for foraging. This model is by no means perfect, as the values used for D, x, U and y would all be mean estimates based on laboratory studies, but it is possible that this would provide a better estimate than the minimum time available for foraging provided by Kruuk and Hewson's present model.

When foraging underwater, the main problem that the mink faces is that it must return to the surface in order to breathe. When foraging for mobile prey, this may mean that sensory contact with the prey is lost, and the mink would then have to initiate a new sequence of detecting prey, pursuing it, and ultimately capturing it. Obviously, it would be beneficial if mink could control their breathing activities such that loss of contact with a potential prey item would be minimized. A similar problem has been investigated for the smooth newt (*Triturus vulgaris*). Here, courtship is carried out underwater. The male newt has to balance his need for oxygen against the possibility of interrupting his courting behaviour at a crucial point, e.g. prior to transfer of a spermatophore (Halliday and Sweatman, 1976). Newt sexual behaviour consists of a complex series of interactions between male and female behaviour patterns (Halliday, 1974a, b), which can be divided into a number of clear sequences. Halliday (1976) found that breathing excursions by a male newt engaged in courtship were not randomly distributed throughout these courting sequences. The majority of breathing ascents occurred at a late stage in the courtship, and particularly after the male had completed his sexual behaviour. Halliday (1976) also noted that for individual newts, the breathing ascents occurred when they would cause least disruption to the whole sexual cycle. Further, a sequence was rarely interrupted once started, and the spermatophore transfer sequence was never observed to be interrupted by a breathing ascent.

Halliday and Sweatman (1976) carried out a more detailed investigation into the relationship between courtship behaviour and breathing in the male smooth newt. The amount of time that a male could devote to sexual behaviour will obviously be limited by how long he could sustain himself without a fresh supply of oxygen. Further, the newt's chances of relocating the same female after a breathing ascent would be small in the natural situation. This is analagous to the mink's problem of relocating a potential prey item. Halliday and Sweatman (1976) found that the relationship between breathing rate and sexual activity was very complex. Their general conclusions however, were that the timing of the male's behaviour depended on the female's behaviour, and his own internal state, i.e. whether he was highly aroused or not. Thus, the male newt, in the absence of a positive response from the female, persists in his courtship display until he is forced to breathe. Thus, the two behaviours are in competition. If the female leaves the male, he takes the opportunity of breathing (disinhibition, i.e. when the causal factors for the first-in-priority activity (sexual behaviour) undergo a decrease, the second-in-priority behaviour (breathing) is carried out) (from McFarland, 1969). However, once the female begins to respond positively, the pattern of the male's behaviour comes more under his own control, and his sexual activity suppresses breathing until a convenient stage in the courtship sequence is reached. That is, sexual behaviour disinhibits breathing. Thus, once the newt has control over the timing of breathing ascents, breathing is totally suppressed unless disinhibited at the most optimal moment (Halliday and Sweatman, 1976).

Although there are analogies between the behaviour of newts and mink foraging underwater, the two are not directly comparable, since mammals and amphibians have different respiratory requirements etc. However, the evidence of Stephenson et al. (1988) that mink may be able to trigger a bradycardia which would enhance their breath hold capability, does suggest that there may be an element of disinhibition between breathing and foraging. From McFarland's (1969) model, disinhibition occurs when the causal factors for the 'first-in-priority' activity undergo a sudden decrease. In the mink's case, if it had successfully captured a prey item, there is no requirement to continue foraging, and animals would surface to breathe. It was found that duration of successful dives were shorter than unsuccessful dives in all experiments. However, when the foraging bout underwater is not successful, it might be expected that breathing and foraging are in competition. In this case, other factors such as prey density might be expected to influence the mink's behaviour. Thus, if prey density were high, breathing should be suppressed. Thus, mink would be expected to have longer foraging dives to enhance the chances of successfully locating a prey item. When the results for mean dive duration of unsuccessful dives (Fig. 5.7), in the density experiment, are studied, it is found, however, that this does not seem to be the case. However, in the other experiments, e.g. the effect of depth, there was a significant increase in mean dive duration of unsuccessful dives with depth (Fig. 3.7). This was not related to an increase in travel time with depth, but appeared to be a response by the mink to the increased costs of travel to the pool bottom. Thus, breathing was suppressed in order to maximise the time on bottom available for foraging.

Thus, the final conclusions of this study are that in general the mink appear to be able to efficiently exploit what, at first sight, would appear to be a difficult resource, i.e. food in the aquatic habitat. It seems that mink may employ a number of physiological and behavioural strategies to both prolong the time available for foraging underwater, and to make the most efficient use of this time.

SUMMARY

(1) The effects of changes in four environmental parameters on the underwater foraging behaviour of the American mink were investigated. The parameters were: Water Depth, Current Flow, Prey Density and Habitat Complexity. All experiments were conducted in an indoor pool.

(2) The water depths tested were 0.3 m, 0.6 m, 0.75 m, 1.0 m, 1.05 m, 1.2 m, 1.45 m and 1.65 m. It was found that as depth increased, dive rate, (i.e. the number of dives per min) decreased sharply, as did the number of hide visit dives per min, but the mean number of successful dives per min declined very slowly with depth.

(3) Analysis of Variance tests showed that foraging success was an important influence on changes in foraging behaviour, thus, for the most part, data for unsuccessful dives were examined. Mean unsucessful dive duration increased with depth, but it was not due simply to increased travel time, rather animals were increasing the amount of time on the pool bottom as depth increased.

(4) It was found that this increased amount of time available for foraging was, in fact, used to locate hides underwater, since as depth increased, animals became progressively less able to locate hides aerially as is their normal habit.

(5) The effect of current flow was examined using a deep current of maximum speed 0.86 m s^{-1}, and a surface current whose speed was negligible, but which caused a surface disruption.

(6) It was found that, in general, the deep current was not sufficiently powerful to influence the behaviour of the animals. The main effect of the surface current seemed to be due to the surface disruption generated. Animals performed more dives per min when surface current was operating, but, generally, successful dive rate and hide visit dive rate were not significantly different between the two experimental situations, or between experimental conditions and control.

(7) Measures of foraging efficiency such as the proportion of successful hide visits to total hide visits also showed no significant effects of current flow.

(8) Finally, the effects of prey density and habitat complexity were investigated. Four prey densities were tested: 25%, 50%, 75% and 100%. In addition, for each density, hides were arranged either randomly, regularly or in clumps, in an attempt to alter the complexity of the foraging environment. The results of these two parameters were considered separately.

(9) It was found that, generally, mean dive rate declined with density, while mean successful dive rate showed a tendency to increase. Further, the proportion of dives visiting a hide and the proportion of successful hide visits, tended to increase with density. None of these findings were surprising, since as prey density increases, the probability of a hide containing prey increases, and this would be expected to encourage hide visiting with a consequent rise in success rate.

(10) Parallel with the above, dive duration for successful and unsuccessful dives showed a tendency to decrease with density, as did time on bottom. This could generally be accounted for by a decrease in the number of hides visited per dive as density increased, again reflecting the fact that as prey density increased, the probability of the first hide visit yielding a prey item also increased.

(11) Analysis of the amount of revisiting of hides, showed that at lower densities, animals tended to visit new hides, but at higher densities, encounter rate was so high, and so few hides were visited per trial, that it was not possible to see if animals were using any systematic foraging strategy. There was some indication that hide arrangement played an important role in this.

(12) The effects of hide arrangement were investigated only for prey density 50%, so that results could be compared with those of other experiments.

(13) It was hypothesized that the regular arrangement would be the least complex, followed by clumped then random, and a number of other predictions concerning foraging behaviour with regard to dive rate, number of hides visited per dive etc., could then be made.

(14) Actual results indicated that more dives per min were performed when hides were arranged in clumps. The proportion of dives visiting a hide was least when hides were arranged regularly (less than 40%), which was the reverse to what had been predicted if the regular arrangement was the least complex.

(15) For other parameters such as number of successful hide visits, there were no significant differences between any of the hide arrangement conditions.

(16) Overall, the results indicated that animals appeared to be foraging more efficiently when hides were randomly arranged and not when regular as expected. There were also indications that individual females were adopting different foraging strategies to those of males.

(17) A brief review of individual differences in foraging strategies, in terms of mean unsuccessful dive duration, mean number of hides visited per dive and mean dive rate, was carried out. It was found that individuals had consistently different foraging strategies, and that these could not be related to differences in body weight.

(18) Finally, a review of known information regarding the habits and swimming speeds of fish species known to be preyed on by mink, was carried out. The results were compared to published results of swimming speed of mink, and to the results obtained in this study. It was concluded that mink may not be such a harmful addition to the native fauna as has been suggested, since the available evidence suggests that most fish prey are sedentary bottom dwellers, and where fish of commercial importance, e.g. salmon, are taken, mink may well be removing spent or diseased specimens.

APPENDIX I

Table I.1: Details of animals used in the various experiments.

Experiment	Animal	Mean Weight ± S.D. in g.	Eye Colour	Coat Colour	Sex
Depth	Dexa	669 ± 89	Normal	Standard	Female
	Inka	917 ± 91	Normal	Standard	Female
	Raja	1195 ± 141	Normal	Pastel	Male
	Titan	977 ± 78	Normal	Pastel	Female
Current	Amber	1103 ± 129	Normal	Pastel	Male
	Boris	1210 ± 101	Normal	Pastel Cross	Male
	Dexa*	654 ± 81	Normal	Standard	Female
	Flash	841 ± 98	Normal	Pastel	Female
	Inka	882 ± 66	Normal	Standard	Female
	Jaspa *	1276 ± 88	Normal	Standard	Male
	Karla D	577 ± 75	Normal	Pastel	Female
	Titan	881 ± 66	Normal	Pastel	Female
Prey Density	Amber	1385 ± 96	Normal	Pastel	Male
	Bill	1456 ± 106	Normal	Standard	Male
	Boris	1344 ± 105	Normal	Pastel Cross	Male
	Flash	799 ± 44	Normal	Pastel	Female
	Inka	860 ± 62	Normal	Standard	Female
	Titan	870 ± 48	Normal	Pastel	Female

* indicates animal died after experiment terminated.

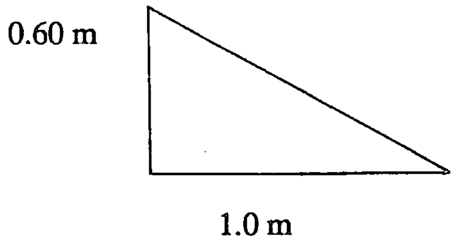
D indicates animal died during the experiment.

APPENDIX II

Calculation of distance travelled underwater during depth experiment.

Results on distance travelled were obtained from the Behpath data which, for this experiment, were produced using the light pen system (see 2.4). as described, the light pen was used to track the movements of an animal. The co-ordinate position of the light pen was recorded every 0.5 s, and these data were then used to calculate distance travelled in arbitrary units. The first problem was that the computer screen was obviously two-dimensional, whereas the animals were hunting in a three-dimensional environment. Further, as soon as an animal dived below the water surface, recording of its movements was begun, i.e. in this experiment data for distance travelled underwater included travel to and from the pool bottom, as well as the actual distance travelled on the bottom. At the end of a dive, animals generally swam vertically up to the water surface, and the light pen would record this as zero distance travelled. Since it is the distance travelled while foraging on the pool bottom that is of interest, no correction was made for distance travelled from the pool bottom to the water surface at the end of a dive. There were some problems with this, because occasionally, animals did ascend at an angle to the pool bottom and here the distance recorded would be an underestimate, but since the occurrence of such behaviour was rare, it was not considered further. Thus, the obvious problem is that the distance travelled to the pool bottom would vary with depth, but this would not be correctly recorded by the system used. Further, the angle at which animals dived to the pool bottom varied with each dive, occasionally animals would dive in vertically from the rostrum to the pool floor, but, generally, the angle of descent was closer to 45°. Thus, some form of correction factor had to be introduced. This was calculated using simple geometry as follows. For each depth, a variety of 'dive lengths' were chosen, i.e. it was assumed that if an animal dived at an acute angle from the rostrum, it might reach the bottom 0.5 m, 1.0 m, 1.5 m etc. from the rostrum. In each csae the light pen would have recorded a distance travelled of 0.5 m, 1.0 m or 1.5 m as the csae may be. However, since the animal would also be travelling through a certain depth of water, the actual distance travelled could be obtained using Pythagorean geometry.

Thus, if it is assumed that the dive angle is 60°, the actual distance travelled is the hypotenuse of a triangle. Thus:-



In this case the distance travelled recorded by the light pen system would be 1.0m, but the 'real' distance travelled would be 1.17m. To obtain the 'depth correction factor', similar calculations were carried out for dive lengths of 0.5 m, 1.0 m and 1.5 m. (Most dives had reached the pool bottom by a distance of 1.5 m from the rostrum.) The difference between each 'real' distance (i.e. the hypotenuse) and each 'recorded' depth, (i.e. the dive length) was recorded. The final figure for the 'depth correction factor' was obtained by taking the mean value of these differences at each depth. (see Table II.1.) The reason for taking the mean was that it was not known precisely how many dives were vertical, (i.e. where the recorded distance for that section of the dive would be zero, but where the real distance was equivalent to the water depth), and how many had 'dive lengths' of 0.5 m, 1.0 m, 1.5 m or any figure in between. It was thus felt that a mean value of the differences

Table II.1: Table of data for calculation of 'depth correction factor'.

Water Depth in m.	Real distance travelled for various dive lengths. (difference between real and measured distances)			Correction Factor in m.
	0.5 m	1.0 m	1.5 m	
0.30	0.59 (0.09)	1.05 (0.05)	1.53 (0.03)	0.06
0.65	0.81 (0.31)	1.19 (0.19)	1.63 (0.13)	0.20
0.75	0.90 (0.40)	1.25 (0.25)	1.68 (0.18)	0.28
1.00	1.12 (0.62)	1.41 (0.41)	1.80 (0.30)	0.44
1.05	1.18 (0.68)	1.46 (0.46)	1.84 (0.34)	0.49
1.20	1.30 (0.80)	1.56 (0.56)	1.92 (0.42)	0.59
1.45	1.53 (1.03)	1.76 (0.76)	2.09 (0.59)	0.79
1.65	1.72 (1.22)	1.93 (0.93)	2.23 (0.73)	0.96

calculated from Pythagoras' Theorem would at least approximate to the correction to be applied to distance measured for each dive at a given depth.

As can be easily seen from Table II.1, as depth increases so the possible margin of error increases. Thus, any discussion of the effect of depth on distance travelled must, of necessity, involve a considerable degree of uncertainty.

Finally, it must be noted that the measurements of distance travelled were initially recorded in arbitrary units, and a conversion factor had to be applied so that results could be expressed in m. This conversion factor was calculated by using the light pen to record the distance across the video image of the pool and obtaining this distance in units. Since the real distance across the pool could be measured in m, it was possible to calculate the conversion factor. This procedure was repeated several times to ensure accuracy. It was thus calculated that all distance unit measurements had to be multiplied by a conversion factor of 0.03 to obtain distance travelled in m. Analysis of mean distance travelled was carried out on the mainframe computer using SPSS. The raw data were input to the computer (i.e. distance travelled in units), and the computer was then programmed to convert the data to distance in m and add the appropriate correction factor.

APPENDIX III

S.E. of Slope and Intercept for results of linear regression analysis in the depth experiment.

Fig. No.	Parameter Tested	Animal	S.E. of Slope	S.E. of Intercept
3.2	Dive rate	ALL	0.0444	0.1338
		Inka	0.0703	0.2129
		Dexa	0.0776	0.2369
		Raja	0.0573	0.1694
		Titan	0.0779	0.2336
	Successful Dive rate	ALL	0.0110	0.0331
		Inka	0.0167	0.0505
		Dexa	0.0139	0.3795
		Raja	0.0222	0.0657
3.3	Hide Visit Dive rate	ALL	0.0308	0.0929
		Inka	0.0376	0.1137
		Dexa	0.0424	0.1296
		Raja	0.0744	0.2201
		Titan	0.0553	0.1658
3.7	Unsuccessful Dive Duration	ALL	0.1991	0.1948
		Inka	0.5422	0.4887
		Dexa	0.3960	0.3917
		Raja	0.4616	0.4260
		Titan	0.2808	0.2937
3.8	Successful Dive duration	ALL	0.2949	0.3051
		Inka	0.5969	0.5879
		Dexa	0.6647	0.6825
		Raja	0.5680	0.5807
		Titan	0.4042	0.4132
3.10	Mean No. of hides visited	ALL	0.0390	0.0382
		Dexa	0.0880	0.0882
3.14	Mean distance travelled	ALL	1.0193	0.9983
		Inka	3.0301	2.7355
		Dexa	1.9755	1.9799
		Raja	2.2087	2.0153
		Titan	1.4818	1.5503

APPENDIX IV

S.E. of slope and intercept for linear regression analysis, and S.E. of intercept and coefficients for curvilinear analysis of the Density experiment.

Fig. No.	Animal/ Condition	S.E. of Density	S.E. of Density^2	S.E. of Density^3	S.E. of Intercept
5.2	Boris:Random	0.0577	0.00101	0.000005	0.9517
	Flash:Random	0.0019	-	-	0.1307
	Inka:Random	0.0016	-	-	0.1037
	Titan:Random	0.1152	0.00206	0.00001	1.8632
	Boris:Regular	0.0900	0.00157	0.000008	1.5218
	Bill:Regular	0.0180	0.00014	-	0.5090
	Flash:Regular	0.0020	-	-	0.1456
	Inka:Regular	0.0080	0.00006	-	0.2290
	Titan:Regular	0.1408	0.00250	0.00001	2.2794
	ALL:Clumped	0.0623	0.00110	0.000006	1.0112
	Flash:Clumped	0.0423	0.00074	0.000004	0.6855
	Inka:Clumped	0.0532	0.00095	0.000005	0.8625
	Titan:Clumped	0.1067	0.00190	0.000010	1.7578
5.3	Boris:Random	0.0589	0.00103	0.000005	0.9720
	Flash:Random	0.0097	0.00008	-	0.2459
	Inka:Random	0.0081	0.00007	-	0.2137
	Titan:Random	0.1033	0.00185	0.000010	1.6700
	Amber:Regular	0.0127	0.00010	-	0.3750
	Flash:Regular	0.0346	0.00060	0.000003	0.5662
	Inka Regular	0.0073	0.00006	-	0.2111
	Boris:Clumped	0.0196	0.00016	-	0.5050
	Flash:Clumped	0.0533	0.00093	0.000005	0.8630
	Titan:Clumped	0.0792	0.00139	0.000007	1.3047
5.4	ALL:Random	0.0199	0.00035	0.000002	0.3231
	Amber:Random	0.0107	0.00008	-	0.2935
	Boris:Random	0.0083	0.00007	-	0.2301
	Flash:Random	0.0320	0.00056	0.000003	0.5111

	Inka:Random	0.0012	-	-	0.0803
	Titan:Random	0.0015	-	-	0.1015
	ALL:Regular	0.0036	0.00003	-	0.1035
	Amber:Regular	0.0077	0.00006	-	0.2282
	Boris:Regular	0.0067	0.00005	-	0.1953
	Bill:Regular	0.0011	-	-	0.0778
	Flash:Regular	0.0239	0.00041	0.000002	0.3956
	Inka:Regular	0.0058	0.00004	-	0.1684
	Titan:Regular	0.0468	0.00083	0.000004	0.7569
	ALL:Clumped	0.0007	-	-	0.0482
	Boris:Clumped	0.0083	0.00007	-	0.2136
	Bill:Clumped	0.0012	-	-	0.0789
	Flash:Clumped	0.0257	0.00045	0.000002	0.4169
	Inka:Clumped	0.0009	-	-	0.0613
	Titan:Clumped	0.0018	-	-	0.1259
5.5	ALL:Random	0.0190	0.00034	0.000002	0.3099
	Boris:Random	0.0063	0.00005	-	0.1751
	Bill:Random	0.0037	0.00003	-	0.1056
	Flash:Random	0.0107	0.00009	-	0.2704
	Titan:Random	0.0334	0.00050	0.000003	0.5402
	ALL:Regular	0.0047	0.00004	-	0.1333
	Boris:Regular	0.0272	0.00048	0.000003	0.4602
	Bill:Regular	0.0104	0.00008	-	0.2978
	Flash:Regular	0.0347	0.00060	0.000003	0.5675
	Inka Regular	0.0083	0.00006	-	0.2404
	Titan:Regular	0.0437	0.00078	0.000004	0.7078
	ALL:Clumped	0.0168	0.00030	0.000002	0.2729
	Amber:Clumped	0.0055	0.00004	-	0.1472
	Boris:Clumped	0.0013	-	-	0.0841
	Bill:Clumped	0.0049	0.00004	-	0.1338
	Flash:Clumped	0.0362	0.00063	0.000003	0.5859
	Inka:Clumped	0.0011	-	-	0.0750
	Titan:Clumped	0.0181	0.00032	0.000002	0.2979
5.6	ALL:Random	0.0170	0.00030	0.000002	0.2766
	Amber:Random	0.0224	0.00040	0.000002	0.3656
	Boris:Random	0.0010	-	-	0.0716
	Bill:Random	0.0183	0.00032	0.000002	0.3050

	Flash:Random	0.0408	0.00072	0.000004	0.6520
	Titan:Random	0.0366	0.00065	0.000004	0.5913
	ALL:Regular	0.0192	0.00034	0.000002	0.3189
	Amber:Regular	0.0015	-	-	0.1136
	Bill:Regular	0.0011	-	-	0.0746
	Flash:Regular	0.0016	-	-	0.1150
	Inka:Regular	0.0019	-	-	0.1370
	Titan:Regular	0.0399	0.00071	0.000004	0.6458
	ALL:Clumped	0.0177	0.00031	0.000002	0.2866
	Amber:Clumped	0.0211	0.00037	0.000002	0.3395
	Boris:Clumped	0.0005	-	-	0.0316
	Bill:Clumped	0.0185	0.00033	0.000002	0.3030
	Flash:Clumped	0.0015	-	-	0.1104
	Inka:Clumped	0.0053	0.00004	-	0.1440
	Titan:Clumped	0.0233	0.00041	0.000002	0.3835
5.7	ALL:Random	0.1443	0.00253	0.000010	2.3466
	Amber:RAndom	0.2803	0.00489	0.000030	4.5337
	Boris:Random	0.2075	0.00368	0.000020	3.3815
	Bill:Random	0.2776	0.00484	0.000030	4.5497
	ALL:Regular	0.0060	-	-	0.4006
	Boris:Regular	0.2550	0.00447	0.000020	4.1852
	ALL:Clumped	0.1497	0.00267	0.000010	2.3832
	Amber:Clumped	0.0087	-	-	0.5191
	Boris:Clumped	0.1877	0.00337	0.000020	3.0556
	Bill:Clumped	0.0077	-	-	0.5017
	Flash:Clumped	0.0190	-	-	1.0671
5.8	ALL:Regular	0.0046	-	-	0.3506
	Amber:Regular	0.0072	-	-	0.5476
	Bill:Regular	0.0737	0.00056	-	2.0677
	Flash:Regular	0.4730	0.00780	0.000040	8.8506
	Inka:Regular	0.0742	0.00057	-	1.9912
	Titan:Regular	0.0086	-	-	0.6482
	ALL:Clumped	0.0051	-	-	0.3961
	Boris:Clumped	0.2399	0.00410	0.000020	4.1171
	Flash:Clumped	0.0115	-	-	0.8922
	Titan:Clumped	0.2672	0.00450	0.000023	4.5673
5.9	ALL:Random	0.1415	0.00248	0.000013	2.3013

	Amber:Random	0.2739	0.00478	0.000025	4.4295
	Boris:Random	0.2042	0.00363	0.000019	3.3280
	Bill:Random	0.2834	0.00494	0.000026	4.6449
	Boris:Regular	0.0089	-	-	0.6248
	ALL:Clumped	0.0048	-	-	0.2952
	Amber:Clumped	0.0084	-	-	0.5041
	Boris:Clumped	0.1803	0.00324	0.000017	2.9357
	Bill:Clumped	0.0074	-	-	0.4868
	Flash:Clumped	0.0179	-	-	1.0022
5.10	ALL:Random	0.0076	0.00006	-	0.1990
	Amber:Random	0.0218	0.00018	-	0.5596
	Boris:Random	0.0138	0.00011	-	0.3721
	Bill:Random	0.0151	0.00012	-	0.4127
	Inka:Random	0.0199	0.00016	-	0.5160
	Titan:Random	0.0774	0.00136	0.000007	1.2372
	ALL:Regular	0.0095	0.00008	-	0.2550
	Amber:Regular	0.0263	0.00021	-	0.7074
	Boris:Regular	0.0163	0.00013	-	0.4516
	Bill:Regular	0.0148	0.00011	-	0.4260
	Inka:Regular	0.0315	0.00026	-	0.7479
	Titan:Regular	0.0051	-	-	0.2963
	Amber:Clumped	0.0144	0.00012	-	0.3553
	Boris:Clumped	0.0412	0.00074	0.0000004	0.6715
	Flash:Clumped	0.0827	0.00150	0.0000080	1.3107
? 2	Inka:Clumped	0.0028	-	-	0.1789
5.1~~3~~	ALL:Random	0.0072	0.00013	0.0000007	0.1177
	Boris:Random	0.0124	0.00022	0.0000012	0.2019
	Bill:Random	0.0034	0.00003	-	0.0921
	Inka:Random	0.0027	0.00002	-	0.0699
	ALL:Regular	0.0016	0.00001	-	0.0425
	Boris:Regular	0.0030	0.00002	-	0.0815
	Bill:Regular	0.0160	0.00276	0.0000014	0.2673
	Inka:Regular	0.0038	0.00003	-	0.0906
	ALL:Clumped	0.0015	0.00001	-	0.0381
	Amber:Clumped	0.0045	0.00004	-	0.1095

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