FORAGING BEHAVIOUR AND FEEDING ECOLOGY OF THE OTTER *LUTRA LUTRA*: A SELECTIVE REVIEW

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ABSTRACT – This paper reviews literature on food, foraging behaviour and feeding ecology of *Lutra lutra* and on the behaviour of their prey species. Otters have a diverse diet, forage in a wide variety of different habitats and have a relatively complex social system. Similarly, their strategies for obtaining food are complex and varied. Three aspects of foraging behaviour (i, ii, iii) and two of feeding ecology (iv, v) are discussed: i) adaptations and ontogeny, ii) energetics and food-limitation, iii) human disturbance, and periods of prey vulnerability, ivj assessing diet, and vj changes in prey vulnerability and selection. The review has three main aims: (a) *to* summarize some recent advances in research, (b) to highlight gaps in current knowledge, and (c) to suggest some areas of future research. The need for such a review arises from a necessity to direct further research effort towards carnivore predator-prey relationships in general, and those of otters in particular, and also to meet demands for conservation management.

Key words: Otters, *Lutra lutra*, feeding ecology, foraging behaviour.

RIASSUNTO – *Foraggiamento ed ecologia alimentare della lontra* Lutra lutra: *un'analisi selettiva della letteratura disponibile* – Questo lavoro prende in esame la letteratura riguardante dieta, foraggiamento ed ecologia alimentare della lontra *Lutra lutra* e il comportamento delle sue prede. La lontra ha una dieta varia, ricerca il cibo in un'ampia gamma di anibienti e ha un'organizzazione sociale relativamente complessa. Similarmente, le sue strategic di ricerca del cibo sono complesse e varie. Tre aspetti del foraggiamento (i, ii, iii) e due di ecologia alimentare (iv, v) sono qui discussi: i) adattamenti e ontogenesi, ii) richiesta energetica e fattori limitanti la disponibilità di cibo, iii) disturbo antropico e periodi di vulnerabilità delle prede, iv) analisi della dieta, e v) cambiamenti nella vulnerabilità delle prede e selezione. Il presente lavoro ha tre principali obiettivi: (a) riassumere alcune recenti acquisizioni scientifiche, (b) sottolineare le attuali lacune conoscitive, e (c) suggerire alcuni temi di ricerca futura. Questo lavoro è dettato dalla necessità di orientare i futuri sforzi di ricerca sulle relazioni preda-predatore, con particolare riferimento alla lontra, e di soddisfare le richieste di gestione conservazionistica di questo mustelide.

Parole chiave: Lontra, *Lutra lutra*, Ecologia alimentare, Foraggiamento.

INTRODUCTION

Otters (subfamily Lutrinae) form one of the two major radiations within the Mustelidae, the most diversified family of carnivores. The recent Lutrinae are divided into three monophyletic groups (Wozencraft, 1989) and although there are different published arrangements within these groups (see Harris, 1968; Ewer, 1973; van Zyll de Jong, 1972 and 1986), the subfamily is generally agreed *to* comprise thirteen species (Wozencraft, 1989). The present review deals primarily with piscivorous otters represented by the *Lutra* otters and the giant river otter (*Pteronura brasiliensis*), and specifically, with the European otter *Lutra lutra*.

Other species (piscivorous and otherwise) will however be mentioned where relevant. Hereafter, *L. lutra* will be referred to as the Otter, other members of the subfamily as otters.

Research into Otter ecology has been largely stimulated by a decline in their populations over wide areas and a perception that it is a 'key species' in the wetland environment (Mason & Macdonald, 1986). Such research has centred mainly on distribution, status and diet, and only relatively recently have more rigorous studies into aspects such as predator-prey relationships and prey selection been undertaken.

The main purposes of this paper are (a) to summarize recent advances in research into the foraging behaviour and feeding ecology of Otters, and relevant studies into the behaviour of their prey, (b) to highlight gaps in current knowledge, and (c) to suggest areas of future research. The need for such a review arises not only from a necessity to direct further research efforts towards an understanding of carnivore predator-prey relationships in general, and those of the Otter in particular, but also to meet a need for knowledge to underpin conservation management. Otter numbers have declined substantially over much of the species' range while in some areas the species is now extinct, most recently in The Netherlands.

For the purposes of this review, foraging behaviour is defined as that which is required to stalk, catch, manipulate and eat prey. It will be influenced by age-related factors, habitat type, and predator-avoidance strategies of the prey. Feeding ecology is defined as the processes which determine general diet. and will include various factors such as prey selection. Such definitions are, by necessity, arbitrary as the processes covered by each term are not mutually exclusive and there are considerable areas of overlap.

In order to discuss some aspects of Otter foraging behaviour and feeding ecology it is important to begin with a brief description of their general diet, foraging habitats and social organization. Earlier summaries are given by Chanin (1985) and Mason and Macdonald (1986).

GENERAL DIET

Otters feed on a whole range of prey but mainly fish (Webb, 1975; Jenkins et al., 1979; Wise et al., 1981) while in a few areas crayfish (*Austropotamobius pallipes*) or frogs (*Rana temporaria*) may predominate (Erlinge, 1967; McFadden & Fairley, 1984). These, together with waterfowl, are more usually seasonal in the diet and are generally regarded as being of 'secondary importance'. Mammals are taken rarely, rabbit (*Oryctolagus cuniculus*) and water vole (*Arvicola terrestris*) more than other species (Jenkins et al., 1979; Wise et al., 1981). Aquatic insects are occasionally recorded as eaten deliberately, rather than ingested with other prey, and on the coast crustaceans are again thought to be of secondary importance (Webb, 1975; Mason & Macdonald, 1980).

Proportions of different fishes in the diet are assumed to depend on their swimming speed as well as abundance; slower moving species being apparently favoured (Erlinge, 1968a). Coastal otters feed mainly on inter-tidal or benthic species (e.g. Watson, 1978; Kruuk & Moorhouse, 1990). The size of fish taken is

also dependent on availability; small individuals usually predominate (Mason & Macdonald, 1986). Seasonal variation in diet is thought to be affected by prey activity as well as abundance (Webb, 1975; Wise et al., 1981; Chanin, 1981).

FORAGING HABITAT

Otters catch food in a wide variety of habitats. They forage in lakes, rivers, streams and marshes and are capable of making overland journeys often well away from watercourses and sometimes moving between watersheds (pers. obs.). They also inhabit coastal areas, particularly those of western Ireland, western and northern Scotland, Portugal and Norway (Mason & Macdonald, 1986). Here they may alternate between marine and freshwater habitats or live almost entirely on the coast (e.g. Kruuk et al., 1987).

SOCIAL ORGANIZATION

The majority of carnivores, including otters, are primarily solitary. That is they never cooperate with conspecifics except when mating (Sandell, 1989). Most however, interact regularly (Gorman & Trowbridge, 1986) and so 'solitary' is not contrary to 'social' (see Leyhausen, 1965). Erlinge (1968b) and Green et al. (1984) came to essentially similar conclusions about the social organization of Otters. Adult females appeared to have overlapping home ranges 'with a degree of mutual exploitation of resources' (Green et al., 1984) while males had a more rigid system with dominant animals maintaining relatively exclusive territories and sub-dominants in sub-optimal habitat. More recently Kruuk and Moorhouse (1991) postulated that female Otters lived solitarily in group ranges, each individual using the whole range, but with a core area where the individual spent more than half its time. Core areas were exclusive of each other. Male ranges overlapped those of females and they were also used by several males at the same time.

Otters thus have a diverse diet, forage in a wide variety of different habitats and have a relatively complex social system. Similarly, their strategies for obtaining food are complex and varied, there is a considerable amount of literature, and this review is therefore, by necessity, selective. It takes as its theme five aspects of foraging behaviour and feeding ecology and draws on a number of widely differing studies, involving both wild and captive otters, and a number of their prey species.

FORAGING BEHAVIOUR

(i) Adaptations and ontogeny

Carnivore adaptations for aquatic living have recently been extensively reviewed by Estes (1989), whilst both Chanin (1985) and Mason & Macdonald (1986) discuss otter hunting and feeding behaviour in some detail. Species of the Lutrinae have evolved two distinct, though not mutually exclusive, foraging specializations: piscivory and invertebrate feeding. The former is the otters' primitive foraging mode and has apparently twice given rise to the latter (Berta & Morgan, 1986). Related to this dichotomy of foraging modes are differences in brain structure, dentition, search and handling strategies (Estes, 1989). Piscivorous otters capture most prey with their mouths and the areas of the brain associated with

facial sensitivity are expanded (Randinsky, 1968), they also have carnassial molars and premolars for shearing the soft flesh of fish. They search for and locate prey after submergence (Erlinge, 1968a) using vision in clear water, supplemented by their vibrissae in murky water (Green, 1977).

Age-related differences in feeding performance have been shown for a variety of vertebrates, including piscivores. Much of the literature refers to fish-eating birds including grey heron (*Ardea cinerea*; Draulans, 1987), brown pelican (*Pelecanus occidentafis;* Orians, 1969), olivaceous cormorant (*Phalacrocorax olivaceous;* Morrison et al., 1978) and shag (*P. aristotelis*; Carss, 1993). There are obviously aspects of the capture and manipulation of fish prey which need to be learned by birds, and presumably this is also true for mammals.

Compared to the large number of studies on birds, age-related foraging differences in mammals have received little attention. In the Lutrinae, Sandegren et al. (1973) stated that dive duration and the ratio of successful to unsuccessful dives by juvenile sea otters (*Enhydra lutris*) increased with age but presented no data. Payne and Jameson (1984) described the ontogeny of prey-handling and tool-use behaviour in the same species leading to self-sufficiency for prey capture by 24 weeks of age. More recently, Polotti et al. (in this volume) and Watt (1993) have studied the ontogeny of hunting behaviour in the Otter in captivity and in the wild, respectively. Watt's (1993) study was in a marine environment on Mull, an island off the Scottish west coast, where animals were individually recognisable and foraged diurnally (see iii). Cubs began to capture a small proportion of their own food by five months of age and this proportion increased with age, the remaining food was provided by the mother. Only after 13 months were all the cubs self-sufficient foragers. They also had shorter dive duration than adults, resulting in a lower dive: pause ratio.

It may not always be possible to differentiate between increasing foraging success as a result of learning, and that arising from development acting independently of experience. However, Watt (1993) made observations which indicate that learning may be important in the development of foraging behaviour. Cubs were sometimes observed repeatedly dropping fish, provisioned by their mother, in shallow water and recapturing it. This behaviour seemed deliberate and may have been a type of 'prey capture play' (Rasa, 1973). Similar observations have been made by Kruuk in Shetland (reported in Watt, 1993); females dropped live fish into rockpools in front of cubs which then recaptured them. Such play may be useful in developing the skills and co-ordination required for successful prey capture (Bekoff & Beyes, 1985).

Watt (1993) suggested that observational learning may occur during the close association of cubs and females, particularly when foraging. Such close contact could permit the transmission of information on likely prey locations, prey suitability and perhaps capture techniques. Kruuk et al. (1990) interpreted their data on Otter dive success as indicating that the animals fished in areas where they would have a given probability of success. **As** many of the fishes preyed on by Otters in a variety of habitats are territorial, or always associated with particular habitat features (e.g. 'home stones'), it is quite possible that there will be a number of specific sites which normally hold prey. Moreover, Kruuk et al. (1988) demonstrated that fish removed from such sites were replaced by others within 24 h.

A 'mental map' of likely prey locations would certainly have to be learned, as would an ability to recognise such locations when seen for the first time.

There may also be dietary differences between juvenile and adult Otters. Watt (1993) recorded that the diet of cubs and sub-adults comprised a significantly greater proportion of crustaceans, mainly shore crab (*Carcinus maenas*), and less fish than that of adults; there was a negative correlation between age and the proportion of crustaceans in the diet. Shore crabs are relatively unprofitable prey for Otters as they provide little meat and require a lengthy handling time (Watt, 1991). The low proportions of crabs in the diets of more successful adult Otters probably indicates a preference for fish, which were demonstrably more profitable. This age-related shift towards more profitable prey suggests that as animals grow up they learn to take prey which they can exploit more efficiently (Hinde, 1959). The extended period of relatively low foraging efficiency in young otters observed by Watt (1993) may, in part at least, explain the relatively long period of parental care in the species and provides support for the hypothesis that age at independence for carnivores is related to hunting efficiency (Gittleman, 1986).

(ii) Energetics, and food-limitation

Water is over twenty times more thermo-conductive than is air (Schmidt-Nielson, 1983) and for herbivorous aquatic animals such as the muskrat (*Ondatra zibethicus*) and beaver *(Castor canadensis)*, water temperature has been shown to affect body temperature as well as the duration of swimming bouts (MacArthur, 1979 and 1984; MacArthur & Dyck, 1990). Water temperature may have similar effects on Otters, and indeed it has been shown to have a large effect on the metabolism and behaviour of captive animals, with activity increasing as water temperature decreases (Kruuk et al. a, in prep).

In a companion study, Kruuk and colleagues (b, in prep.) measured the core body temperatures of free-living Otters foraging over a range of water temperatures. They did so by using intraperitoneally implanted temperature-sensitive radio transmitters. Body temperature rose significantly at the beginning of a swimming bout but fell at a rate independent of water temperature during the bout. Intervals between dives were longer in colder water but this was not thought to be temperature dependent. Water temperature appeared not to have a significant effect on either body temperature or the length of a swimming bout. Kruuk et al. (b) suggest that Otters in cold water maintained their body temperature at a considerable cost, increasing it before they enter the water and begin to cool. Animals either leave the water on reaching a minimal threshold body temperature, or they maintain a higher body temperature by varying their activity and leave the water at a time determined by other environmental variables. Thus water temperature does not appear to affect otter dive duration as it does for herbivorous mammals which merely swim to travel and do not forage by diving.

As a result of their studies, **Kruuk** et al. produced a tentative model of the relationship between prey capture rates and the average length of time an Otter has to spend fishing in order to maintain its metabolic requirements. This allows the 'viability' of Otter populations to be predicted from observed prey capture rates at known water temperatures. For instance, observed prey consumption by coastal

Otters in Shetland averaged 0.39 kg per hour for water temperatures of 6-12°C (Nolet & Kruuk, 1989) and the daily requirements of such animals could be met by fishing for 2-3 hours per day. However coastal Otters on Mull caught only 0.25 kg per hour in waters of 14°C in summer (Watt, 1991) and it was concluded that a reduction in the effective intake rate by 50% could make this Otter population 'non-viable' during periods of low water temperature.

In practice this may mean that Otters are food limited under certain circumstances and that they are vulnerable to fluctuations in prey abundance (= availability). Thus certain foraging areas or habitats may become untenable during periods of low prey availability or low water temperature. At these times Otters may have to increase their range size, forage in different habitats, and possibly take different prey. Such changes have been observed in other piscivores, particularly in cold weather. For instance, Marquiss et al. (1983) recorded young grey herons wandering farther afield during severe cold, while Draulans and van Vessem (1985) and Carss (1993) found that the birds regularly visited fish farms during the winter and preyed on stocked fish. Similarly Bodner (in this volume) reported increased Otter predation at Austrian carp (*Cyprinus carpio*) ponds in winter.

Other predictions from a food-limitation hypothesis, that both the consumption of 'sub-optimal' food and natural mortality would be highest during times when natural fish biomass (= availability) were lowest, appear to be supported by the limited number of field studies both in coastal habitats (Kruuk & Conroy, 1991) and freshwaters (Kruuk et al., 1993).

(iii) Human Disturbance, and periods of prey vulnerability

As discussed previously, otter foraging behaviour may be influenced by age-related differences in efficiency, and energetic limitations which may be related to water temperature and/or prey abundance (= availability). However, it is usually suggested that over most of their geographical range, Otter activity is ultimately limited by disturbance and persecution from humans and that animals respond by being largely nocturnal (e.g., Mason & Macdonald, 1986). An alternative explanation, and one which is becoming increasingly credible in the light of studies from a wide range of ecological disciplines, is that Otter feeding behaviour is primarily related to the availability of prey (e.g., Kruuk & Moorhouse, 1990; Carss et al., 1990).

The basic diel cycle of rising and setting of the sun imposes a dramatic and overriding set of predictable constraints on both the behaviour and activity of fishes, the effects of which have been reviewed by Helfman (1986). Although much of the available data relate to coral reefs, temperate lakes and temperate marine assemblages, they are also relevant to fishes in other systems. One basic theme common to several studies in all three habitat types discussed by Helfman is the risk of predation during twilight. The 'quiet period' (Hobson, 1972), when neither diurnal nor nocturnal fishes are truly active is a time of major activity for predatory fishes such as groupers (Serranidae), jacks (Carangidae) and snappers (Lutjanidae) (Hobson, 1968; Major, 1977). The changing levels of light during twilight, and the increased activity of predators at that time, suggests a direct link between vision and predation during crepuscular periods. Both diurnal and nocturnal fishes have eyes

better matched to prevailing wavelengths during twilight than to night-time conditions. Apparently both sacrifice some nocturnal abilities in favour of better vision during twilight. Helfman (1986) concluded that the selective force driving this twilight match appeared to be crepuscular predation. Furthermore, twilight-active piscivorous fishes possess intermediate eyes which function poorly, relative to the visual capabilities of potential prey, during the day or night but may function better than either a diurnal (photopic) eye or a nocturnal (scotopic) eye during twilight.

Although there are few comparable data on mammalian piscivores, Estes (1989) suggested that sea otter foraging activity and their efficiency in catching fish may be greater near dawn and dusk than at other times. He also reported (Estes et al., 1982) that all observed fish captures by sea otters occurred in the morning and evening. By dilating their pupils, mammalian piscivores accommodate rapidly to changes in light levels and so, at dawn and dusk, may have an advantage over fishes which are visually impaired by the transformation between photopic and scotopic vision (Munz & McFarland, 1973).

Studies of otters in temperate freshwaters have shown that they are indeed largely nocturnal or crepuscular (e.g. Green et al., 1984; Carss et al., 1990). The former authors recording that the longest periods of night activity began at sunset and lasted three to five hours. As the period of danger for fish prey during twilight apparently increases in relation to the length of twilight (Helfman, 1986), in temperate regions where twilight periods are longer, the period of vulnerability, and presumably predator activity, will also be longer. The precise nature of a fish's vulnerability to predation during twilight will depend on whether it is diurnal and seeking cover at night, or nocturnal and emerging. For instance Carss et al. (1990) concluded that spawning adult Atlantic salmon (*Salmo salar*) were most vulnerable to Otter predation after dark as fish became active and left the cover of holding pools. On the other hand juvenile salmonids often become inactive at night and are presumed to be more vulnerable to predation then (see discussion in Kruuk & Moorhouse, 1990).

For certain prey species activity may also change seasonally. In summer brown trout (*Salmo trutta*) and Atlantic salmon are known to be active both during the day and at night, but with decreasing water temperatures they appear to seek shelter in the substrate by day (Gardiner, 1984). Daytime observations of both species have confirmed that they remain concealed in the substrate during the day (Cunjak, 1988b; Heggenes & Saltveit, 1990). However, Hegennes et al. (1993) have recently observed that brown trout, at least, become nocturnal during the winter remaining active above the substrate. Such changing patterns of prey activity and inactivity are predictable and may well influence the timing of Otter foraging activity. This could be investigated during long-term radio-tracking studies of animals in salmonid-dominated habitats. Such studies should include regular 24-hour tracking sessions, as it cannot be assumed that focal animals have been inactive all day if they are merely followed to a daytime rest site and picked-up again in the evening. Periods of daytime activity may be short and so continual monitoring is required, but this is labour intensive. However an automatic receiver placed close to the rest site could be used to record the frequency and duration of any activity periods. Concurrent spraint collection and analysis would allow the proportions of trout and salmon in

the diet to be assessed seasonally to determine whether any change in otter activity was associated with a change in diet.

In coastal habitats Otters forage during the day either frequently (e.g., Watson, 1978) or almost exclusively (e.g., Kruuk et al., 1987; Kruuk & Moorhouse, 1990) and so increased prey vulnerability at twilight cannot be the only factor influencing the timing of Otter foraging activity. Other explanations may be related to the cover-seeking of diurnal fishes, the emergence of nocturnal ones, and the overall influence of water temperature.

The diet of Otters in coastal studies by Kruuk et al. (1987) and Kruuk & Moorhouse (1990) consisted mostly of eelpout (*Zoarces viviparus*) and rockling (*Ciliata* spp.), which are nocturnal species most active at night (Kruuk et al., 1988). During the day these fishes spend their inactive phase under stones or weeds and Kruuk and Moorhouse (1990) concluded that they were most vulnerable to Otter predation whilst inactive in cover. Conversely some night-active fishes such as eels (*Anguilla anguilla*) (Tesch, 1977), which are commonly taken by Otters in freshwaters (Mason & Macdonald, 1986), are presumably more vulnerable to predation when they leave their day-time refuges and become active.

The swimming performance of trout and other fishes is considerably reduced at low water temperatures (see discussion in Hegennes et al., 1993). Furthermore, Hegennes and Borgstrom (1988) concluded that salmonid populations were more vulnerable to predation from endothermic predators such as mink (*Mustela vison)* during cold weather and the same may be true for otters. Mason and Macdonald (1986) reported studies which showed a decline in the proportion of eel in the diet during winter and concluded that as eels become torpid at this time they may be difficult to find, Otters then turning to other prey. Such evidence is however circumstantial and an experimental study would be required to demonstrate a temperature-related shift in diet.

FEEDING ECOLOGY

(iv) Assessing diet

In order to investigate feeding ecology it is essential to have an assessment of diet. There are three main methods of assessing otter diet: a) prey remains found in the field, b) analysis of stomach contents and c) analysis of the undigested prey remains in faeces ('spraints'). Otter spraints are not merely the result of the elimination of waste material and undigested hard parts, they also serve as scent markers (Trowbridge, 1983). In many vertebrates, including carnivores, scent marking plays an important part in social organisation (see review in Gorman & Trowbridge, 1986). Jenkins and Burrows (1980) found that half of the spraints which they marked in the field had disappeared within two weeks while Mason and Macdonald (1986) found in another area that a similar proportion had disappeared in just over three weeks, with 90% gone in eight weeks and some, in sheltered places, persisting for up to a year. More recently Kruuk (1992) found that more than 30% of the spraints deposited by otters on the coast of Shetland were below the high tide mark and were washed away within hours. Furthermore, many, if not most, spraints may be deposited in the water whilst otters are swimming. Spraints are thus

relatively ephemeral and those collected from within a relatively small study area over a short period of time can only give an incomplete 'snapshot' of Otter diet.

"Frequency of occurrence" of prey remains is the most easily applied spraint analysis method and has been used in numerous studies (see summary in Mason & Macdonald, 1986, and more recently Adrian and Delibes, 1987; Carss et **al.,** 1990; Kemenes & Nechay, 1990; Beja, 1991). Results are presented as either 'percent frequency', the proportion of spraints containing a particular item, or 'relative frequency', the number of occurrences of a particular item as a percentage of all identifiable items recorded. As frequency of occurrence relies on the presence of undigested hard parts in spraints, any food which has a large proportion of soft material will be underestimated. Moreover, as prey items are scored on a presence or absence basis, the occurrence of both a single item, and a number of similar items, is weighted similarly. Thus minor items are overestimated and major ones underestimated. Although many authors acknowledge these limitations, most argue that the method is simple and gives a reasonable indication of the diet, citing feeding trials conducted by Erlinge (1968a) and Rowe-Rowe (1977).

Unfortunately, confidence limits were not presented in either of these studies. Erlinge (1968a) concluded that analysis of Otter spraints 'calculated by frequency, gave a reasonably true picture of the relative importance of the different food categories' but data were not tested statistically. Rowe-Rowe (1977) conducted trials with captive clawless otter (*Aonyx capensis*) and concluded that relative frequency of occurrence gave 'the truest reflection of food actually consumed' but presented no supporting data to show how 'true' it was.

Very few, if any, studies of otter diet have attempted to calculate confidence limits for various prey categories and this is probably acceptable in those which merely record diet in one area at one time of year. However, for comparative studies which attempt to investigate diet in different habitats and seasons, the unknown accuracy of estimates may be a severe restriction. If studies of otter feeding ecology are to become more than mere lists of prey items there is an urgent need to quantify current spraint analysis techniques and their associated errors more rigorously than in the past, using feeding studies with captive animals.

Problems also arise when the statistical independence of spraints, and the remains within them, are considered. There appears to be no consistent method of interpreting results; for instance, López-Nieves and Hernando Casal (1984) considered that the remains of a prey item in a spraint represented a single specimen, whilst Kozena et al. (1992) concluded that a spraint invariably contained only part of a prey item and that an individual fish may be recorded several times in different faecal samples. Feeding trials with captive animals are needed to resolve such inconsistencies. Moreover, independence will also be affected if the spraints collected from an area over a short period of time are produced by only a few individuals, a situation which is probably fairly common. For example Carss et al. (1990) concluded from the proportions of spraints labelled with a radionuclide, that the otter they were radio-tracking was probably the only one living on a tributary of the River Dee, north-east Scotland, during at least part of their study. Samples of spraints from the same individual are obviously open to biases caused by individual variation in foraging behaviour and diet. Such feeding differences have not been extensively investigated in otters (but see Kruuk & Moorhouse, 1991). However,

they are known to exist for a number of other animals including sea otters (see summary in Riedman & Estes, 1990). Within any particular area there is substantial variation among individual Californian sea otters with respect to diet and individuals specialise in particular foods or foraging strategies regardless of age, sex, or body morphology. Although individual patterns seem to persist for periods of several years there is evidence that the diet and foraging strategies of some females varied with their reproductive status. Observations of both the tagged pups and juveniles of tagged females indicate that mothers and their offspring may in fact feed on the same types of prey and use similar foraging techniques. Such observations may be further evidence that juvenile otters are taught at least some foraging techniques by their mothers (see i).

Further research on foraging differences between individual Otters could be investigated in study areas where several animals have been injected with different radionuclides simultaneously (see Crabtree et al., 1989 for techniques). The recent development of DNA molecular methods has provided new tools which may complement some conventional field techniques and the potential to develop 'molecular tags' which can identify individuals from tissue fragments such as fur, feathers and faeces is now becoming a possibility. These techniques would involve the amplification of short microsatellite sequences of DNA from the gut cells of otters expelled in their faeces, and would allow individuals to be recognised from such samples. The ability to identify individuals from their faeces would allow individual variation in diet to be determined as well as an estimate of the relatedness within, and between, populations and possibly even range size or an index of range use without the need for capture. The development of cheap and repeatable methods for such molecular tags could provide the basis for a large advance in the understanding of animal populations, helping to integrate concepts from population genetics, population dynamics and behavioural ecology. It would also provide crucial data on concepts such as effective population size and minimum viable population size, which are currently only speculated about for many animals, including Otters and other carnivores.

(v) Changes in prey vulnerability and selection

Predation risk as a cost of reproduction in animals has recently received increased empirical and theoretical attention (e.g. Magnhagen, 1991). For instance, rock greenling (*Hexagrammos lagocephalus*) in the Aleutian Islands are most vulnerable to sea otter predation during the summer breeding season, when they spawn and defend their eggs (Van Blaricom & Estes, 1988). Moreover, studies of otter feeding ecology in both freshwater and marine habitats have shown that intra-sexual differences in fish behaviour during or after mating may make one sex more vulnerable to predation than the other (Carss et al., 1990). The spawning behaviour of male Atlantic salmon, which are resident in small tributaries for considerable periods and which frequently cross shallow riffles, exposed them to higher otter predation than females. Similarly, male lumpsuckers (*Cyclopterus lumpus*) on the coast were probably more vulnerable to Otter predation, as after spawning they alone guard the egg mass in shallow or inter-tidal waters.

As breeding is usually seasonal, there will be changes in the vulnerability of prey animals throughout the year. Furthermore, as most animals have special

habitat requirements for such things as foraging, breeding or hibernation sites, and as these are usually distributed in patches, there may also be spatial differences in prey vulnerability. An interesting example of this is the relationship between otters and amphibians in north-east Scotland. Weber (1990) found that the consumption of amphibians by otters increased in late winter and spring, when frogs and toads were hibernating or spawning. Such predation was also associated with particular habitats.

Despite the limitations of spraint analysis (see iv), several workers have attempted to relate diet to some measure of prey availability by investigating food selection, often in terms of prey size, species or sex. Where otters are day-active, for instance on the coast (e.g. Kruuk & Moorhouse, 1990), it is possible to study food selection by observing foraging animals and comparing their prey with intensive fish sampling in the same areas (e.g. Kruuk et al., 1988). The requirement for rigorous data on fish populations is obviously essential in such studies, but a review of fishing techniques, and their associated biases, is outside the scope of the present paper. It is likely however that a variety of fishing methods should be used, and unlikely that true 'availability' will be quantified. Such studies are therefore comparisons between what otters are thought to eat and what is demonstrated to be present by various fishing techniques. In the majority of studies otter prey cannot be observed directly and diet is assessed indirectly from spraints.

Wise et al. (1981) used spraint analysis to study the diet of otters in a small, shallow lake in Devon, south east England, and compared their dietary data with those from concurrent studies of fish populations which involved seine and gill netting, trapping and electrofishing. They found no evidence of selection in respect of prey-size for four fishes, roach (*Rutilus rutilus*), pike (*Esox lucius*), perch (*Perca fluviatilis*), and eel. Similarly, Libois and Rosoux (1989) found no evidence of size-selection by Otters preying on eels in a study area in western France. Such apparent lack of size-selection could be because there was none, or because it could not be detected with the available data. Current spraint analysis techniques may not allow the proportions of fish of various sizes to be estimated accurately, as it is not always possible to determine whether bones in a spraint originate from the same, or different, individuals. Wise (1980) concluded that 'if the vertebrae are clearly of different sizes and if the maximum estimate of fork length for the smaller fish does not overlap with the minimum estimate for the larger fish, then it can be considered probable that the two bones are from different fish, but when vertebrae are of similar size then it appears safer to assume that they are the remains of a single fish'. Unfortunately this method breaks down if a spraint contains the remains of more than two different fish, which is not uncommon (Carss & Parkinson, unpublished data). Furthermore, the assumption that similarly-sized vertebrae are from the same individual results in the under-recording of a number of similarly-sized fish.

Recently, Feltham and Marquiss (1989) developed a method of accurately separating, and estimating the size of, brown trout and Atlantic salmon from a single bone, the atlas vertebra. Moreover, because of its prolonged resistance to digestion, the bone produced the highest minimal numbers estimate of salmonids consumed by red-breasted mergansers (*Mergus serrator*). If the same were true for atlases in Otter spraints, the use of this bone would overcome both limitations of the

current methodology described above. Kruuk et al. (1993) used this bone when investigating Otter numbers and fish productivity in two rivers in north-east Scotland and concluded that two species of salmonids were not taken in proportion to their 'availability' as determined by electrofishing. These authors also concluded that, overall, Otters appeared to take more young salmon than trout compared with proportions in the electrofishing catches; 18% of atlases in spraints were from salmon compared with 6% of electrofishing catches. However, they also highlighted problems with this comparison as there were likely to be seasonal differences in vulnerability between the fishes (see iii) which had yet to be investigated fully.

CONCLUSIONS

Otters have a diverse diet, forage in a wide variety of different habitats and have a relatively complex social system. Factors affecting Otter foraging behaviour and feeding ecology are complex and often inter-related. Both influence, and can be influenced by, habitat utilisation and social organisation. There is a need to study such relationships but Otters are commonly perceived as being shy, elusive and hard to study. However, this should not be used as an excuse for less than rigorous scientific research. Previous research has centred mainly on status, distribution and diet and only recently have more rigorous studies been undertaken.

The ontogeny of foraging behaviour has been investigated in both wild and captive animals, and age-related differences in both foraging performance and diet are apparent. This is taken as evidence that aspects of some foraging techniques need to be learned, and may help to explain the relatively long period of parental care in the Otter. The effect of water temperature on otter foraging has been investigated and tentative models produced to investigate the relationships between water temperatures, prey capture rates and length of foraging bout. Otters may be food-limited under certain circumstances, for instance low prey abundance or low water temperatures. Predictions from a food-limitation hypothesis that both the consumption of 'sub-optimal' food and natural mortality would be highest when natural food abundance was lowest appear to be supported by the limited number of studies undertaken. Under most circumstances human disturbance is not likely to be the main factor influencing Otter activity, and the availability of prey appears to be more important. Specific, predictable periods of prey vulnerability in relation to time of day, tidal cycle, and season probably allow Otters a wide spectrum of foraging strategies.

Spraint analysis is the commonest method of assessing the food of Otters, although it can only provide a 'snapshot' of diet. Moreover, its true accuracy is unknown as current methods do not provide confidence limits. The inter-dependence of both spraints, and the items within them, is also unknown as is any influence caused by individual variations in foraging behaviour and diet. Prey remains collected in the field may show differences in vulnerability between sections of the prey population, but do not indicate selection. Some studies have attempted to investigate selection by comparing an index of availability, derived from a variety of fishing techniques, and spraint analysis. However, in many cases, current spraint analysis techniques are probably not sufficiently rigorous to accurately assess the diet of Otters.

Many aspects of Otter foraging behaviour and feeding ecology are currently unresolved and there is an urgent requirement for standardisation in a number of techniques, but particularly in spraint analysis. Further long-term studies of Otter ecology are needed, and where necessary these should be supplemented by work with captive animals. Recent advances in molecular biology may allow significant progress to be made in areas which were previously only open to speculation. Refined techniques should allow for more rigorous studies of Otter ecology which will be invaluable in formulating conservation plans, not only for Otters, but also for wetland habitat mosaics in general.

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