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FRUGIVORY AND SEED DISPERSAL BY CARNIVORES IN THE RHODOPI MOUNTAINS OF NORTHERN GREECE

by

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B.Sc. M.Sc.

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ABSTRACT

The frugivory and seed dispersal by carnivores were studied using a combination of vegetation surveys, fruit production counts and analysis of faeces distribution and content. The study site is situated close to the Greek-Bulgarian border within a protected area. The habitat comprises of a mixed forest of beech, pine, oak and spruce which is occasionally interrupted by patches of fruiting trees. Faecal samples were collected on five permanent transects which were sampled monthly between May and October of 1993 and 1994.

Fruiting plant density was found to be slightly higher in the forest than along forest roads, however the species diversity was much higher on the latter. In some cases, immature fruiting plants were found on transects with no mature plants in the vicinity. Availability of ripe fruit was found to increase steadily between May and September.

There was a significant difference between the numbers of faeces deposited by the carnivores, with fox being the most numerous, followed by marten, bear and wolf. There was spatial and temporal variation in the number of faeces deposited. Nevertheless, there was no variation between different altitudinal zones. Martens were found to defecate more often on stones when compared with the other carnivores.

The analysis of fruit consumption revealed that bears were the most frugivorous carnivores followed by foxes, wolves and martens on the basis of frequency of consumption. The temporal availability of each ripe fruit species coincided with their consumption by the carnivores in most of the cases. A number of seed species were deposited at altitudes where the plants do not normally grow. Foxes dispersed the highest numbers of seeds in the study area and bears were second as they deposited large-size faeces which contained many seeds. Of the dispersed seeds, those of *Rubus* sp., *Rosa* sp. and *Fragaria vesca* were deposited in the highest numbers. Only a small number fraction of seeds were damaged through handling by carnivores.

DECLARATION

I declare that this thesis is original. Any material which is not my own work has been identified as such. The analysis and interpretation of the results are entirely my own unless otherwise stated. No part of it has been submitted previously for a degree at any other university.

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Panayiotis Giannakos
Durham
1997

“.....and the cubs are born at around the time that they (the bears) den.
During this time the bears of both sexes become very fat.”

“Stories about the animals”
Aristotle

To my parents

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CHAPTER ONE

1.0. INTRODUCTION TO SEED DISPERSAL

1.1. Function of seed dispersal

Seed plants are sessile organisms and thus have limited ability for movement. This permanent attachment to the soil poses an interesting challenge when it comes to colonising new habitats. The problem has been overcome by means of dispersal of their seeds and according to Ridley (1930) animals may play a very important role in the dispersal of plants throughout the world, in the following ways:

1) By feeding on the fruits of the plants and passing the seeds, not only unharmed, but actually more fit for germination. In a large number of cases the fruit or seed is especially adapted for this purpose, being developed into drupes or berries, or having a conspicuous edible aril attached. The dispersal of the small seeds of herbaceous plants is effected by the animals, mostly unselective herbivorous mammals, eating the entire foliage of the plant, and with it swallowing the seeds, which are later evacuated unharmed.
2) By the adhesion of fruits or seeds to their fur and feathers, these fruits or seeds being provided with hooks, bristles or spines, or with a viscous or gummy secretion which causes them to adhere. As animals walk through the vegetation, seeds with a multitude of sizes and a diversity of hooks are dislodged from plants and attach to the fur. The dissemination of seeds depends on a number of factors associated with both seed and animal morphology and on animal behaviour (Stiles 1992).
3) By the adhesion of the smaller seeds or fruits to the feet of an animal in mud in which the animal has been trampling.
4) By the adhesion of portions of the plant, or even, in some cases, the whole plant or seedling to the integument of a mammal, bird, or reptile in such a condition that, on being dislodged at a distance, it may continue to grow.

Some of the terms in this thesis might have multiple interpretations hence definitions as to the way in which these terms are used might be helpful. Adaptation is used as a functional property of the organism, evolved by natural selection, which enables it to survive and ultimately reproduce (Howe & Smallwood 1982). Diaspore or propagule is the unit of a plant that is actually dispersed. Dispersal is the departure of a diaspore from the parent plant. Establishment is the process during which a germinated seed takes root, uses up parental provisioning, and assumes independent growth as a seedling. A fruit is the matured gynoecium with or without other floral organs or parts of organs. It is the ripened ovary including the embryo, seed nutrient (endosperm), and other parental tissues. Fruit parts have many anatomical origins. Fleshy fruits eaten by vertebrates are thought to be ancestral in angiosperms, but the pulp has several derivations. The edible portion may be homologous with the seed coat, an outgrowth of the seed coat called an "aril", an outgrowth of the endocarp, or tissue derived from the ovary wall. A herbaceous plant is any species that does not have any woody parts. A shrub is any species of woody plant that branches off at the ground level. A seed predator is an animal that eats and destroys a seed.

There are a number of advantages to local dispersal, as a means either of a) escaping disproportionate seed and seedling mortality near the parent plant (Janzen 1970), b) colonising disturbed areas, or c) locating microhabitats suitable for establishment and growth (Howe and Smallwood 1982). These alternatives are not mutually exclusive, but may differ in importance from one plant population to an other. The "Escape Hypothesis" (a) implies disproportionate success for the seeds that escape the vicinity of the parent, as compared with those that fall nearby. The "Colonisation Hypothesis" (b) assumes that habitats change; dispersal in time and space allows a parent to produce offspring capable of taking advantage of non-competitive environments as they become available. The "Directed Dispersal Hypothesis" (c) assumes that adaptations ensure that diaspores reach localised sites suitable for establishment. The ultimate assumption is that adult distributions closely reflect seed distributions.

Density-dependent mortality of seeds or seedlings near the parent might be due to insect or rodent predation since these animals would concentrate their feeding activities in zones of high seed density near parents, pathogen attack, or seedling competition. Seed predators mainly search for food only in the immediate vicinity of parent plants, ignoring seeds and seedlings only a few meters away (Janzen 1970). Yet, this theory is not universal. Terborgh, Losos, Riley & Bolaños-Riley (1993) studied the pre-germination loss of seeds to mammalian and invertebrate seed predators of five species of Amazonian trees. Only one showed a distance effect. This was a result of higher levels of invertebrate seed predation in the near plot (5 m) than in the more distant (25 m). No distance effect was noted from mammalian seed-predators.

The Colonisation Hypothesis presumes that habitats change in time; the "goal" of the parent is to disseminate seeds so widely that some are likely to encounter a favourable situation, or persist in a viable form in the soil or understorey until a disturbance event such as a treefall, landslide or fire permits seedlings to establish and grow. The hypothesis is testable in a comparative sense by determining whether some diaspores are more likely to colonise new sites than others (Howe and Smallwood 1982).

A somewhat different phenomenon is exhibited by the occupation of special habitats by species requiring unusual edaphic conditions. "Directed Dispersal" has been suggested for nuts cached by birds and mammals, fruits eaten by birds, and diaspores carried to rotten logs by ants (Davidson & Morton 1981). A convincing confirmation must include a demonstration that dispersal agents take seeds to non-random locations that are well-suited for establishment and growth. The best example comes from an Australian saltbush, where two closely related species (*Sclerolaena diacantha* and *Dissocarpus bilflorus*) occupy ant mounds. Davidson & Morton (1981) found that both ant-dispersed and non-ant-dispersed congeners grow well on ant mounds, but the density of the ant-dispersed shrub is much higher on ant mounds. Furthermore, this shrub almost does not exist away from ant mounts. For these and other plants, ant-assisted colonisation of these well-drained and ion-rich soils appears to be obligate.

In the Australian arid zone, a variety of shrubs and small trees produce brightly coloured fleshy fruits or arils that are consumed by birds (Tester, Paton, Reid &

Lance 1987). Many of the shrubs are found in higher densities underneath trees and large shrubs than in the open. Two hypothesis have been proposed to account for this. First, the clumped distribution could reflect the pattern of dissemination by birds, the birds defecating seeds while perched in trees. Alternatively, that the clumping could be due to more favourable growing conditions underneath tree canopies.

Among dispersal hypotheses some supposed advantages have been proved less important than initially believed. Animals may scarify seeds in the gut, thereby enhancing germination. Without such treatment by animals, some seeds fail to break dormancy or summarily rot. Such cases are unusual, most animal-dispersed seeds germinate without handling, or achieve only a slight advantage by handling (Lieberman & Lieberman 1986, Auger 1994). In most cases, scarification is incidental in an attempt to digest the seed, rather than a coevolved means of enhancing germination (Howe and Smallwood 1982).

1.1.1. Coevolution and seed dispersal

Since the early studies on the ecology of seed dispersal, researchers have been concerned about the implications of coevolution between plants and their animal dispersers. Recently it has been widely accepted that exclusive coevolution between one plant species and one vertebrate species could not take place for such a complex interaction as frugivory (Charles-Dominique 1993). The more satisfactory interpretation of 'diffuse coevolution' was proposed by Janzen (1980). This theory considered the selective pressures that govern the mutualistic interactions that link a group of animal species and a group of plant species.

Charles-Dominique (1993) provides a detailed description of the theory of 'step coevolution'. When a plant taxon displays an intense process of speciation, as a result of a particular characteristic that was evolutionary successful, the species within this taxon will become abundant enough to provide a regular food supply to frugivores over long periods. Under these conditions, an assemblage of frugivores can become specialised to feed principally on their fruits. If this frugivore assemblage is comprised of closely related species, the conditions for the initiation of a coevolutionary process are met. This usually leads to specialisations between plants and vertebrates associated with this interaction. At a certain stage of this process, other vertebrates can move into this plant-frugivore system searching for new food resources and can progressively adapt to these fruits which will then be increasingly consumed by a greater number of frugivores. At a certain point, the sum of all interactions will slow down or stop the coevolutionary process. Fruit characteristics will be maintained or evolve according to the evolutionary pressures that will be exerted by this new assemblage of dispersers. This plant group then will probably slow down its evolutionary processes considerably. Therefore existing ecosystems are a combination of coevolved systems, many of which are in a stable phase maintained by dispersers that have not necessarily contributed to their original evolution (Janzen 1980). On the other hand, when intense speciation is in progress then the system could be in a phase of active coevolution.

A similar theory has also been suggested by Fleming, Venable & Herrera (1993). Because the number of frugivorous bird species outnumber the number of mammal frugivores plant adaptations often favour removal by the former. Though, as more and more bird-dispersed plant species migrate or evolve in a habitat, the new-comers will be less likely to attract sufficient numbers of birds because of the competition for dispersers with the “resident” species. This surplus of fruit will attract mammal dispersers and at a certain stage these mammals will be able to remove as many or more of this plant-community seeds and finally all disperser species will be utilised in proportion to their availability.

1.1.2. Fruit adaptations to enhance seed dispersal

Many plants have their seeds dispersed by frugivorous birds and mammals (Ridley 1930, Jordano 1992, Stiles 1992, Willson 1992). Fleshy fruits are eaten by animals, which obtain a reward as a result of digesting the pulp, and take the seeds away from the parent plant to be later discarded in conditions suitable for germination. It seems likely that fleshy-fruited plants have evolved under the pressure of a complex set of selective agents which includes their dispersers, but also invertebrate and vertebrate predators as well as pathogens (Janzen 1982, Augspurger 1984, Debussche & Isenmann 1989).

Among the animal dispersers, there are many species belonging to different classes (birds, mammals, insects, reptiles but also fishes) (McDonell & Stiles 1983, Fialho 1990, Bustamante, Simonetti & Mella 1992, Byrne & Levey 1993, Valido & Nogales 1994, Wallace & Trueman 1995). Each species may interact with others, each one eating the fruits of many plant species. However, most studies focus on dispersers belonging to one class.

Small seed size and morphological design for dispersibility are associated with colonisation potential, while large seed size is associated with competitive ability in saturated habitats (Howe & Smallwood 1982). Characteristics of fruit seem to be a product of selection for seed size. Small size facilitates escape from small mammal predation but on the other hand large size provides the seed with enough food reserves for the first year post germination, which is likely to be in the shade (Smith 1975). Large size often allows for a thick seed coat which enables the seed to withstand destruction during passage through the gastrointestinal tract of the vector and to maintain seed coat dormancy. These selective forces for a large seed size may bring with them selection for altered dispersal devices or may constrain the array of available dispersal agents. Large seeds cannot disperse far by ballistical mechanisms or by adhering to animal exteriors and they need very large wings to be successfully wind-dispersed (Willson 1992). One alternative option is dispersal by vertebrate ingestion but even these have to be of a relatively large size to consume large seeds.

A very good example of adaptations that ensure dispersal and germination is provided by the tropical canopy tree almendro *(Dipterix panamensis)* since it possess characteristics that attract animals as potential dispersers, and characteristics that protect seeds from potential parasites or predators (Bonaccorso, Glanz & Sandford 1980). It produces a large fruit that weights between 18 and 26.3 g. to which attracts animals by providing an edible exocarp, large fruit size, an attracting odour, and large fruit crop. Defensive characteristics of the fruits are: a thick woody endocarp, a large seed that can supply the embryo with adequate nutrition to maintain germinability even when the seed is partially damaged, and an embryo located at one extreme end of the seed where small rodents usually do not attack.

Fleming *et al.* (1993) suggests that seed size is influenced by three factors: the predictability of the establishment site, plant successional status, and plant growth form. Seed size in turn is a critical factor in fruit choice and fruit availability to birds and mammals thus determining its mobility. Whereas large birds and mammals can handle a wide range of fruit sizes with large or small seeds, small animals can usually handle only small fruit that contain small seeds. Therefore a plant selected to maximise its disperser assemblage as a result of its seedling establishment requirements will be constrained to produce fruits containing many small seeds. Fleming *et al.* (1993) suggested that differences in the body sizes of New World and Old World tropical frugivorous birds and mammals appear to have influenced maximum fruit size in several families. A theory that was proved to be true for at least six families of tropical fruit producing plants that are found in both regions (Fleming *et al.* 1993).

McKey (1975) suggested two alternative strategies of dispersal in tropical plants that compete for dispersal agents. In the "low investment model" plants invest little in individual seeds and fruits, using large crops to attract a variety of opportunistic birds willing to use a superabundant, if nutritionally limited, source of food. In the "high investment model" plants limit fruit production to large seeds and rich pulp, and thereby limit dispersal to specialised birds willing and able to seek out rare and bulky, but exceptionally nutritious, food resources.

Herrera (1987) re-examined the theories of Jansen (1970), Snow (1971) and McKey (1975) and combined ideas on the fruit size with the degree of specialisation of the frugivores. He suggested that (i) fruits eaten by specialised frugivores are typically large seeded and have pulp high in fats and protein; (ii) fruits eaten by unspecialised frugivores are small seeded and have less nutritious pericarp; (iii) plants dispersed by specialised frugivores have more extended and constant periods of fruit availability (slower ripening rates) than species dispersed by opportunistic frugivores; (iv) "low investment" plants producing superabundant low-quality fruits should have lower dispersal success than "high-investment" plants producing fewer, high-quality fruits. I believe there to be a problem with simple characterisation such as: “specialised frugivore”. The dependence of these "specialised" frugivores on a particular species of fruit producing plant has yet to be demonstrated. It is to the frugivores benefit to be able to exploit a range of fruit, in order to be able to overcome possible fruit failures from a single fruiting species. Additionally no fruit can fulfil all the nutritional needs of a frugivore as is indicated later on in this chapter. Similarly, it may not be to the plant's benefit to depend on a "specialised" disperser, since this frugivore probably uses a particular kind of habitat for most of its time and hence defecate most of the seeds there, creating a highly directed seed shadow. This habitat may already be saturated and unfavourable (e.g. due to competition) for the germination of the seeds of the fruit-producing plant species. Furthermore, in virtually all cases, it is not known which dispersal agents actually defecate seeds to the most favourable sites (from the plants point of view) because integrated studies of all the factors involved have not taken place yet (Howe 1993). As Dinerstein & Wemmer (1988) summarised the absence of clear dependence of a given fruit on dispersal by a given frugivore may be attributed to: (i) the advantages for the plant to appeal to a wide spectrum of animals, (ii) similar nutritional requirements among the fruit eaters, (iii) opportunistic feeding by frugivores in search of an easy (undefended) meal, (iv) the difficulty of evolving cues to limit detection and palatability for non-target frugivores vs. target species, and (v) the loss of large frugivores over ecological and evolutionary time.

Howe and Estabrook (1977) reason that individual tropical trees should time fruit production to take best advantage of their disperser assemblages. "Low investment trees" should produce superabundant fruits in displays that attract the largest number and variety of visitors possible. Lack of competition among dispersal agents for superabundant fruits promotes diverse frugivore assemblages, dissemination of seeds to a variety of habitats, and freedom from dependence on a limited set of dispersal agents. "High investment plants" extend fruiting seasons to avoid satiating a limited set of specialists, thereby promoting predictable seed removal by efficient foragers.

Herrera (1987) also documented seasonal patterns in fruit quality. On the Iberian Peninsula average lipid content of pulp increases from summer- through winter-ripening species, and water content follows the opposite trend. Protein content of pulp does not vary significantly among species ripening fruit at different times, and average dry-matter yield increases significantly from summer-fruiting to winter-fruiting species. The highest lipid profitabilities are found among autumn-fruiting (*Pistacia terebinthus*) and, principally, winter-fruiting species (*Viburnum tinus, Olea europea, Pistacia lentiscus*), although many autumn- and winter-fruiting species have lipid profitability values as low as those of summer-fruiting ones.

From the frugivore's point of view the profitability from ingesting a fruit is determined by the interaction between fruit characteristics and the physiological and morphological traits of frugivores as proposed by Martínez del Rio and Restrepo (1993). The factors governing diet choice, fruit nutrient composition, and their influence on seed dispersal have proved to be more complicated than the original theory of high (lipid rich) and low (lipid poor) investment plants. The authors stated that relatively subtle differences in the chemical structure of nutrients that have been overlooked by the traditional proximal nutrient analyses until now can have profound implications for frugivores. This analysis quantifies broad nutrient classes but ignores the identity of specific nutrients. The authors claimed that if we focus on the study of specific nutrients, we may find significant patterns of correspondence between groups of animals and groups of plants. For example, the presence of a gall bladder is very variable among fruit eating birds (Martínez del Rio and Restrepo 1993). The gall bladder stores and concentrates bile which functions mainly to emulsify fats prior to digestion and hence, the absence of a gall bladder may prevent the efficient assimilation of lipids. Furthermore, the variation in sugar preferences that have very similar energetic contents among frugivores is still unexplained. Sucrose is a disaccharide that has to be hydrolysed by intestinal enzymes into glucose and fructose to be assimilated. Fruit eating birds appear to be relatively inefficient at assimilating sucrose, but to be very efficient at assimilating glucose and fructose (Martínez del Rio and Restrepo 1993).

Seeds of many species are ingested by birds and mammals, but this does not mean that all such species are dispersed in this manner. The ingestion of intact seed is necessary and requires hard seed coats. These coats must be digested to the extent that premature germination is avoided, dormancy is maintained and yet germination following dormancy is not diminished (Lieberman & Lieberman 1986). Dormancy is an important factor in seed dispersal since it can potentially increase total reproductive success many fold by keeping the embryo alive until favourable conditions arise (Willson 1993b). An additional problem of the dispersal-germination relationship is that apparently enhanced germination may depend on the species of bird ingesting the seed.

In a very interesting study of fruit laxatives, Murray, Russell, Picone, Winnett-Murray, Sherwood & Kuhlmann (1994) demonstrated that plants can, to a certain extent, control the seed retention times by animals. A Costa Rican shrub, *Witheringia solanacea* produces fleshy fruit which are regularly consumed by the Black-faced Solitaire (*Myadestes melanops*). It was found that the presence of the pulp together with the seeds consumed reduced seed retention time by 50%. It was found that 30 minutes of gut retention was the time that birds needed to move the optimal dispersal distance. Dispersal distance increases only slightly thereafter as birds restrict their foraging to well defined home ranges. On the other hand, for seeds that passed through the bird's gut germination success decreased steadily with increased time spent in the gut.

Finally, colour plays an important role in fruit detection for species with colour vision such as birds, primates and squirrels. In addition to their ripe colour, fruits may go through a two-stage colour change (Stiles 1992). It has been suggested that in autumn in the temperate zone some species change leaf colour early providing a long distance signal for migrant frugivores, advertising the potential presence of fruit (Stiles 1992).

1.2. Quality and quantity component of seed dispersal

Schupp (1993) suggested two major components of disperser effectiveness which result from the combined effect of the quantity and quality of seed dispersal (also Fleming & Sosa 1994). The quantity of seed dispersal is affected by the number of visits that the disperser pays to the plant which in turn is influenced by the abundance of the disperser, its diet, and the reliability of its visitations. Species from the same family or even the same genera vary from total frugivory to having fruit as a minor supplement to a diet including a multitude of different feeding items. Fruit choice from the range of species available is governed by disperser size and digestive physiology, fruit presentation, concentrations of nutrients and chemical deterrents (Schupp 1993). Disperser reliability is far from stable. Temporally, a reliable disperser dependably visits plants through the day, the season and the years. Occasionally a frugivore will visit a fruit producing area only during a particular season. Reliability on the annual scale can take several forms. A disperser can be abundant one year and absent the next, or it might be reliably present each year, but unreliably abundant. Quantity is also affected by the number of seed dispersed per visit which is influenced by the number of seeds handled per visit and the probability of dispersing the handled seed.

The quality of seed dispersal is affected by the quality of treatment which is a result of either the destruction or intact passage of the seed through the dispersers gut and in the latter case of any alteration to the percentage of seeds germinating or rate of their germination (Schupp 1993). Different species of animals can have an effect on the germination percentage and can also alter germination rate (Lieberman & Lieberman 1986, Auger 1994). Seed processing in the bill or mouth is often damaging. Seed eating birds and mammalian carnivores feeding on fruit, crush variable numbers of seeds while swallowing the rest undamaged. Frugivorous birds rarely damage seeds during passage through the gut. On the other hand, seed-eating birds destroy the majority of seeds in the grinding gizzard, but pass some in viable condition.

Quality is also affected by the quality of deposition which is a complicated factor influenced by the movement patterns of the disperser such as the habitat and microsite selection and the length and directionality of movement (Schupp 1993). The sites on which the seeds are deposited are not simply suitable or unsuitable, they vary continuously with respect to seed survival, germination, seedling growth and survival. Wheelwright & Orians (in Schupp 1993) suggested that species of dispersers differ relatively little in quality because sites for dispersal are unpredictable in space and time, and seeds have a low probability of surviving to maturity. This is true to a certain extent but there are sites that can be completely unsuitable for germination. If a disperser habitually deposits seeds on such a site, the quality of dispersal is clearly diminished. This factor is further influenced by the rate and pattern of deposition and the mixing of seeds in the diet. The probability of a particular seed being deposited in a faecal clump with another species differs with disperser species.

1.3. Comparison of avian versus mammalian seed dispersers

Tables 1.1. and 1.2. give an indication of the number of studies that have focused on the families of seed dispersing birds and mammals. The search was based on a data base which contains articles published during the years 1981-1997. Furthermore, not all the biological periodicals are reviewed in this database and therefore the numbers given below serve only to give comparison between the families of frugivores. There is a peak of studies of mammals in the neotropics; in the main these investigate frugivory by primates and bats (Table 1.1.). The Cebidae are a family of neotropical primates which are reported to be legitimate seed dispersers of a number of plants. The Phyllostomatidae are a large family of fruit bats with an important role in the dispersal of plant seeds in the same region. Frugivory by mammals has also been very well studied in North America. The Sciuridae (squirrels) are a rodent family that has attracted a lot of attention in order to define for which seed species they act as seed predators as opposed to seed dispersers. A large number of studies have been carried out in the Australasian region where there is also a high diversity of species that feed on fruit. Most of the studies were carried out on the family Bovidae mainly in the Palearctic and Ethiopian zones because of the importance of these animals to humans as livestock.

MAMMALS		**Faunal zone**						
Order	**Family**	**Pal**	**Nea**	**Neo**	**Eth**	**Ori**	**Aus**	**Total**
	Canidae	-	3	4	-	-	-	**7**
	Felidae	1	-	-	-	-	-	**1**
CARNIVORA	Mustelidae	5	1	-	-	-	-	**6**
	Procyonidae	-	3	1	-	-	-	**4**
	Ursidae	-	1	-	-	-	-	**1**
	Viverridae	2	-	-	1	2	-	**5**
	Callitrichidae	-	-	2	-	-	-	**2**
	Cebidae	-	-	15	-	-	-	**15**
PRIMATES	Cercopithecidae	-	-	-	6	2	-	**8**
	Hominidae	4	1	-	-	-	-	**5**
	Pongidae	-	-	-	3	1	-	**4**
	Equidae	-	-	1	-	-	-	**1**
PERISSODACTYLA	Rhinocerotidae	-	-	-	-	1	-	**1**
	Tapiridae	-	-	3	-	-	-	**3**
	Bovidae	4	3	2	5	2	-	**16**
	Cervidae	3	1	2	-	-	-	**6**
ARTIODACTYLA	Giraffidae	-	-	-	1	-	-	**1**
	Suidae	-	-	-	-	1	-	**1**
	Tayassuidae	-	-	2	-	-	-	**2**
	Mystacinidae	-	-	-	-	-	2	**2**
CHIROPTERA	Phyllostomatidae	-	-	8	-	-	-	**8**
	Pteropodidae	1	-	-	-	2	-	**3**
	Dasyproctidae	-	-	4	-	-	-	**4**
	Echimyidae	-	-	1	-	-	-	**1**
RODENTIA	Geomyidae	-	1	-	-	-	-	**1**
	Heteromyidae	-	3	-	-	-	-	**3**
	Muridae	3	3	-	-	-	-	**6**
	Sciuridae	3	10	-	-	-	-	**13**
LAGOMORPHA	Leporidae	2	1	-	1	-	-	**4**
PROBOSCIDEA	Elephantidae	-	-	-	3	-	-	**3**
TUBULIDENTATA	Orycteropodidae	-	-	-	1	-	-	**1**
MARSUPALIA	Phalangeridae	-	-	-	-	-	2	**2**
	Total	**28**	**31**	**45**	**21**	**11**	**4**	**140**

Table 1.1. Families of mammals that have been reported to consume fruits in the published literature between 1981 and 1997. The data were retrieved from BIDS online database. Pal=Palearctic, Nea=Nearctic, Neo=Neotropical, Eth=Ethiopian, Ori=Oriental, Aus=Australasian.

The main purpose of this table however, is to stress the fact that out of the 140 cases of mammalian seed dispersal only 24 focused on carnivores and the vast majority of these was published in the last four years. The Canidae (wolves and foxes) have attracted most of the attention among the carnivores. All the studies were carried out in either north or south America. This is probably one of the most widespread families of carnivores in the world and their frugivory in most of the habitats in which they exist still remains to be studied. Seed dispersal by Mustelidae (weasels and martens) has been well studied in Europe but not in the rest of the world. The family expands over all the faunal zones apart from Australasia and many of its species have been reported to consume seeds (Hargis and McCullough 1984, Clevenger 1993a, Lucherini and Crema 1993). Little is known of the frugivory of members of this family in the Neotropical, Ethiopian and Oriental zones. A small number of studies have focused on procyonids (racoons) in the Nearctic and Neotropical zones. I did not manage to find any studies on seed dispersal by the red panda (*Ailurus fulgens*) although it is known to consume fruits (Macdonald 1984). The only study on the Ursidae (bears) comes from the Nearctic, yet they are well known for their frugivory. They exist in the Palearctic, Neotropical and Oriental zones but have been little studied there. Reports on seed dispersal by Viverridae have come from all the three regions that the family is found. There was only one report on Felidae in the Palearctic although this a very widespread family too. In this case though, it is probably not surprising since cats are rarely reported to consume fruit.

Seed dispersal by birds (Table 1.2.) has been studied very well in the Australasian zone, followed by the Neotropic and Palearctic. A surprisingly small number of studies comes from the Ethiopian region and studies from the Oriental zone were non-existent. The best studied family by far, are the Muscicapidae. Many well known frugivorous birds belong to this family (thrushes, warblers) and reports come from four regions. Corvids were very well studied in the Nearctic and less extensively so in Palearctic. Finally a large number of studies were carried out on Meliphagidae (honeyeaters) in the Australasian region.

Around the world the percentage of woody plants that have evolved mechanisms for the animal dispersal strategy is very high and as Jordano (1992) suggested the frequency of endozoochorus seed dispersal is associated with the forest type. In Neotropical, Australian and African rainforests dispersal by vertebrates is very common (70-94% of the species) among woody plants. In Mediterranean scrubland this usually ranges between 50% and 70% and temperate coniferous and in broad-leaved forests may vary between 30-40% of animal dispersed woody species.

	BIRDS		**Faunal**	**Zone**			
Order	**Family**	**Pal**	**Nea**	**Neo**	**Eth**	**Aus**	**Total**
PASSERIFORMES	Corvidae	4	14	-	-	-	**18**
	Cotingidae	-	-	3	-	-	**3**
	Dicaeidae	-	-	-	-	2	**2**
	Emberizidae	-	-	3	-	-	**3**
	Fringillidae	1	-	-	-	-	**1**
	Furnariidae	-	-	1	-	-	**1**
	Meliphagidae	-	-	-	-	10	**10**
	Mimidae	-	1	2	-	-	**3**
	Muscicapidae	18	7	3	-	8	**36**
	Paradisaeidae	-	-	-	-	1	**1**
	Paridae	2	-	-	-	-	**2**
	Pipridae	-	-	1	-	-	**1**
	Ptilogonatidae	-	4	-	-	-	**4**
	Ptilonorhynchidae					1	**1**
	Pycnonotidae	2	-	-	2	-	**4**
	Rhinocryptidae	-	-	1	-	-	**1**
	Sittidae	1	-	-	-	-	**1**
	Sturnidae	-	1	-	-	1	**2**
	Tyrannidae	-	-	1	-	-	**1**
	Vireonidae	-	-	1	-	-	**1**
	Zosteropidae	-	-	-	-	6	**6**
ANSERIFORMES	Anatidae	-	-	1	-	-	**1**
CASUARIIFORMES	Casuariidae	-	-	-	-	3	**3**
COLUMBIFORMES	Columbidae	1	-	1	-	6	**8**
GALLIFORMES	Cracidae	-	-	2	-	-	**2**
	Phasianidae	-	1	-	-	1	**2**
CUCULIFORMES	Cuculidae	-	-	-	-	1	**1**
CORACIADIFORMES	Motmotidae	-	-	1	-	-	**1**
GRUIFORMES	Otididae	-	-	-	1	-	**1**
PICIFORMES	Picidae	1	1	-	-	-	**2**
	Ramphastidae	-	-	5	-	-	**5**
PSITTACIFORMES	Psittacidae	-	-	3	-	1	**4**
STRUTHIONIFORMES	Struthionidae	-	-	-	1	-	**1**
APODIFORMES	Trochilidae	-	-	1	-	-	**1**
TROGONIFORMES	Trogonidae	-	-	2	-	-	**2**
	Total	**30**	**29**	**32**	**4**	**41**	**136**

Table 1.2. Families of birds that have been reported to consume fruits in the published literature between 1981 and 1997. The data were retrieved from BIDS online database. Pal=Palearctic, Nea=Nearctic, Neo=Neotropical, Eth=Ethiopian, Aus=Australasian.

Debussche and Isenmann (1989) mentioned that 46% of the plants in Montpellier, southern France, dispersed by frugivores are dispersed by one or several mammals.

Furthermore, frugivory is common in a few species, especially the red fox (*Vulpes vulpes*) and the stone marten (*Martes foina*), which disperse a great number of seeds when the crop size is large e.g. blackberry (*Rubus ulmifolius),* dog rose *(Rosa canina),* and Mediterranean juniper *(Juniperus oxycedrus*). Generally mammals perform long distance dispersal, spreading seeds from several hundred metres to some kilometres. This is due to the rather long intestinal transit time (e.g. 5-10 hours for the red fox) and their large home range size. It has been suggested that in temperate regions, mammals play a significant role as selective forces in the evolution of some fleshy fruit features (Debussche & Isenmann 1989). On the other hand the retention times of frugivorous birds are quite often between 10 and 30 minutes (Murray *et al.* 1994) and as a result many seeds are defecated directly under the parent tree (Pratt & Stiles 1983). However, Willson (1991) claimed that frugivorous birds are much more important than mammals as seed dispersers simply because their numbers are much higher and therefore the quantities of seeds transported are much greater.

McKey (1975) proposed that entirely frugivorous birds perform high quality dispersal: (i) by not harming the seeds, (ii) by removing the seeds from the vicinity of the parent tree, (iii) by delivering the seeds to habitats suitable for germination and growth, and (iv) by visiting the tree on a regular basis. Pratt and Stiles (1983) have criticised these proposals on a theoretical basis. The former study did not consider or at best underestimated, the potential for frugivores to linger in a tree before or after feeding or between feeding bouts. Such behaviour could lower the value of dispersal performed by a frugivore because time spent in a tree after feeding increases the possibility that the frugivore will regurgitate or defecate seeds beneath the tree from which the seeds originated. There is an alternative situation for frugivores visiting a fruiting tree where there is some likelihood of predation. These birds should not take their fill of fruit, but instead retreat to adjacent trees to wait between short feeding bouts. Under this system lengthy visits would be out of the question for smaller, vulnerable species, but larger, reputedly more secure frugivores could take their time feeding. Many reasons have been sought to explain why a bird should leave a fruiting plant after feeding. The bird could be induced to leave by depletion of food in the plant relative to food available in other plants, the need for other foods (e.g. insects, other types of fruits, or water), evasion of predators or more aggressive competitors, flocking behaviour, or nesting duties (Pratt and Stiles 1983). If these factors are not present in a given situation, it might be to the birds advantage to stay longer. For example, if a bird decides to feed twice or more in succession at a particular plant, it may be energetically inefficient to perform some other activity between feeding bouts, or there may be insufficient time to do so. Or, if the bird has consumed a large quantity of fruit, it may be more efficient to digest its bulky meal before setting out on some energetically demanding activity. Or, when an aggressive frugivore is faced with competition from subordinate individuals, it may be reluctant to defend a part or all of a fruiting plant.

As Gautier-Hion, Duplantier, Quris, Feer, Sourd, Decoux, Dubost, Emmons, Erard, Hecketsweiler, Moungazi, Roussilhan & Thiolay (1985) suggested birds choose fruits by colour, weight, and outer protection, as well as by type of flesh. Colour alone doubtless has an essential role in fruit discrimination by birds, as these diurnal frugivores have good colour vision. The choice by birds of purple-black and/or red seems universal and correlates with their good discrimination of near-red wavelengths (Morden-Moore & Willson 1982). Nevertheless, what really governs the choice of fruits by birds is the dispersers weight and gape size (Herrera 1984a, Jordano 1992). Gape size of the dispersers determines the maximum, but not minimum fruit volume. The fleshy fruit-eating animal system does not work exactly like the classical predator-prey system in which there is a correlation between the size of the predator and the minimum size of prey consumed. Small fruits are conspicuous and often clumped in a manner totally different from animal prey, and are probably as easy to detect and then to swallow as the bigger ones. The "bird fruits"-"mammal fruits" gradient in relation to fruit size is weakened because large-sized dispersers also disperse small-sized fruits and because certain large soft fruits with small seeds are partially eaten by small birds which swallow some seeds along with a piece of pulp. This latter case is well illustrated by dispersal of strawberry tree (*Arbutus unedo)* and fig (*Ficus carica)* by the European robin (*Erithacus rubecula*) and sylviid warblers, birds that are morphologically unable to swallow these fruits whole (Herrera 1984a). The number of seeds and their placement in fruits should be selected by the main handling techniques of dispersers such as birds and mammals. The percentage of fruit crop removed by birds declines significantly with increasing fruit diameter. Small variations in fruit width thus lead to measurable interspecific differences in dispersal success even among those plants having fruits below the upper size limit acceptable to dispersers in function of gape width. As a rule, mammals can probably ingest much larger fruits than the majority of birds as they are not so limited by a small gape size, with the possible exception of small rodents (Willson 1991).

Dispersal by primates is endozoochorous for small seeded fruits and they are among the best studied seed dispersers (Estrada & Coatesestrada 1991; Defigueiredo 1993; Gautier-Hion, Gautier & Maisels 1993; Guillotin, Dubost & Sabatier 1994). For others the dispersal mode depends on the degree of attachment of the flesh to the seed. The more strongly attached, the more probable that the monkey will swallow both flesh and seed. When the soft flesh is free from the seed, the latter is often spat out. This usually happens at some distance from the parent tree because monkeys fill their cheek-pouches and move to another place to eat the contents. When the seed is very easily separated from the fruit, it may be spat out under the parent tree. Finally, depending on the relative sizes of monkey and fruit species, the seed may or may not be swallowed with the aril. Like birds, monkeys are attracted by the red and multicoloured displays and are important consumers of arils and effective dispersers of plant species with arilate seeds. They are also attracted by orange and yellow fruit which characterise mainly the succulent fleshy fruit (Gautier-Hion *et al.* 1985).

Fruits consumed by mammals should contain many small seeds which escape mastication, or seeds with a hard tooth-resistant coat (Debussche and Isenmann 1989). These adaptations are well-illustrated on the one hand by *Ficus carica* (1000-2000 seeds/fruit, 1-2 mm in diameter) and *Rubus* sp. (30-50 seeds/fruit; 2-3 mm in diameter), with their numerous small seeds, and on the other hand by cherry plum (*Prunus cocomilia)* and Cornelian cherry (*Cornus mas*), with only one stone (8 and 10 mm long). When the seed volume remains low relative to fruit volume, however, medium sized (6 to 8 mm) and even not very resistant seeds occurring in low numbers can be swallowed without harm by mammals (Debussche and Isenmann 1989).

According to Schupp (1993) frugivorous birds can be categorised as ‘swallowers’, ‘mashers’ or ‘biters’. Swallowers generally swallow fruits and included seeds whole so they have a high probability of dispersing handled seeds. The number of fruits handled per visit roughly increases with disperser size. Mashers manipulate the fruit in the mouth and swallow the pulp together with a number of seeds which mainly depends on the size of the seeds with small seeds having a higher probability of dispersal. Biters remove bits of pulp by pecking a fruit that is either still attached or held against the brunch. Seeds are not usually swallowed and are only dispersed when the bird carries the fruit to another tree for feeding.

In certain cases when the germination potential of the dry seed is destroyed, during ingestion and passage through the animals' digestive system, then the animal is acting as a predator. These seed predators feed on either pulp or seeds alone, and when eating pulp and seeds together damage the latter either in the gut or prior to swallowing (Krefting & Roe 1949, Gautier-Hion *et al.* 1985). Although a sharp distinction generally exists between seed dispersers and seed predators, a few species are dispersers of some plants and fruit predators of others. This is particularly the case for squirrels and small rodents, which are chiefly granivores that eat only the flesh of a few fleshy fruits with many tiny seeds (e.g., *Ficus* spp.) (Benkman 1995; Steele, Hadjchikh & Hazeltine 1996) . For small seeds they are dispersers (as are almost all consumers), but for the most part they tear off and spit out the fibrous flesh that surrounds nuts and eat only the seeds . The small bite size of small rodents prevents them from eating very large fruits unless the husk has been first removed by another agent, such as a ruminant, or has rotted off (Gautier-Hion *et al.* 1985).

Howe & Smallwood (1982) mention that small "fearful frugivores" process fruits in the cover of surrounding underbrush, rather than expose themselves to predators in open feeding trees. The predators complicate the effect of bird visitation on fruiting phenology because bird activity is only loosely tied to fruit abundance. Gautier-Hion *et al.* (1985) suggest that a feeding tree is the focal point for predators and thus in most cases frugivores transport fruits to safer places for ingestion. Hornbills

(Bucerotidae), feeding on *Pycnanthus angolensis* (Myristicaceae) tree rapidly gather several fruits in their beaks and immediately fly to a neighbouring tree with dense foliage. Likewise, monkeys usually fill their cheek pouches before retiring to an area of dense foliage in order to eat. Risk of predation by birds of prey is reduced in dense vegetation. Large fruiting trees may also serve as focal points for terrestrial predators: remnants of brush-tailed porcupines (*Atherurus* sp.) captured by leopards have been found several times under large fruiting *Drypetes gowweileri*, under which porcupines congregate to feed (Gautier-Hion *et al.* 1985). On the other hand frugivorous carnivores and particularly the larger ones e.g., brown bears (*Ursus arctos*) and red foxes do not have pressure from predators to drive them away from the feeding trees where they consume fruits. They can therefore take their fill of fruits and ingest maximum numbers of seeds. In some extreme cases though, when the carnivore feeds and subsequently rests under the fruiting tree, there is a possibility that the seeds consumed will be defecated under the parent plant.

Pratt and Stiles (1983) suggested that high metabolic rates of passerines were probably due to their high levels of activity and did not allow sufficient time for the birds to move to another site before defecating the seeds that have been eaten on the fruiting tree and thus many seeds end up under the parent tree. Evidence for rapid passage through the gut comes from Murray *et al.* (1994) who found in their study of the black-faced solitaire that as many as 20% of the seeds were voided in the first 10 minutes after ingestion and after only 20 minutes up to 65% of the seeds had been defecated. In case the birds stay in the vicinity of the fruit-producing tree, there is little advantage for dispersal to the fruiting plants.

Sorensen (1984) proposed that seed passage rates play an important role in determining preference, particularly if nutritional and other properties of fruit species are similar. Calculations show that birds obtain a high rate of energy gain by consuming fruits whose seeds are then regurgitated (also Stiles 1992). This is because gut volume may place a constraint on fruit uptake. Seed regurgitation results in a rapid elimination of non-nutritional seed "ballast" and creates space in the gut for additional food. Fruit species containing seeds which are defecated have lower rates of energy gain because the seeds remain in the gut for much longer periods of time. Models of food selection by herbivores have predicted that food processing rates in the gut are more limiting to food consumption than food intake rates (Sorensen 1984). Experiments on non-frugivorous animals have indicated that food passage rates have an important influence on preference for this reason.

Although with some species of birds, due to their high passage rates, there is a possibility for the seeds to be defecated under the parent plant, with mammals this seems rather unlikely considering that their gut passage time which may amount to several hours in duration. Dinerstein & Wemmer (1988) mention that in a feeding trial with a rhinoceros (*Rhinoceros unicornis*) 114 fruits of *Trewia* sp. were ingested in 10 minutes. The first seeds emerged in the dung 46 hours after ingestion, peak passage occurred 64-88 hours, and the last intact seeds were passed 172 hours (7 days and 4 hours) after ingestion. They estimated seed mortality ranging between 26.7 and 47.7%. Passage though the gut and manuring hastened germination and had a significant positive effect on aboveground dry mass and on dry leaf mass.

1.3.1. Mammalian legitimate dispersers

Fruit eating bats have been well studied in the tropics (Engrizer 1995; Izhaki, Korine & Arad 1995; Kalko, Herre & Handley 1996) but temperate bats are almost exclusively insectivorous (Willson 1991) and therefore do not have a potential for seed dispersal. Fleming & Sosa (1994) after having undertaken considerable work on *Carollia* species in Costa Rica, concluded that these bats are excellent at finding ripe fruit and removing high proportions of these fruits on the first night that they are available. Although ingestion does not have an effect on germination most of the seeds are deposited beneath dark, heavily vegetated night roosts where they have low germination rates. Nevertheless, due to the thousands of seeds that each individual ingests some land on potential germination sites and therefore the bats can be considered as effective dispersal agents.

Ruminants normally eat entire fruits: husk, flesh and seed are destroyed by chewing (Gautier-Hion *et al.* 1985). Nonetheless, a few observations in the field and experiments in captivity show that for a few medium-sized fruits with hard nuts, the ruminant may spit out seeds during rumination. This always occurs away from the fruit source. When the fruits have seeds that are too large, the role of ruminants is neutral, and the husk is chewed off and the nuts are left where found. It is thus likely that the size of seeds dispersed increases with the size of the ruminant consumer: the larger the animal, the greater the number of seed species it disperses (Middleton & Mason 1992; Mandujano, Gallina & Bullock 1994).

African elephants (*Loxodonta africana*) are certainly one of the major terrestrial seed dispersers and some plant species may primarily depend on them for dispersal (Feer 1995). Piles of old elephant dung are commonly covered with vigorous seedlings that have sprouted from seeds that have passed through the animal, complete with fertiliser (Short 1981). Some huge fruits for which African elephants would seem the only dispersers could conceivably also be eaten by the largest primates (apes and possibly mandrills-*Papio sphinx*). The fruit species most commonly eaten show adaptations to dispersal by elephants. Fruits are inconspicuously coloured when ripe (yellow or green) and possessed a strong smell. Probably these features have developed in response to the keen sense of smell and lack of colour vision of elephants. Similarly the large size of many of these fruits may be an adaptation to make them attractive to elephants which require a large food intake. An African elephant's diet can vary considerably between different areas, ranging from almost completely frugivorous to heavy dependence on the bark of the trees (Short 1981).

Dinerstein and Wemmer (1988) studied the dispersal of *Trewia nudiflora* (Euphorbiaceae) by rhinoceros in lowland Nepal. They found for the seeds which had passed through the rhinoceros' digestive system that the heavy manure loads were significant because the seeds defecated into latrines received a substantial boost from the manure in which they germinate, and that seeds defecated in grassland latrines can grow to robust saplings after only two monsoon seasons. Considering this information they suggested that the extinct tropical megafauna once played a major role in the dispersal of the woody flora. Furthermore, the long coexistence between Neotropical plants and large frugivores could have influenced the evolution of fruit and seed traits of some plants for consumption and dispersal by large mammals. Although rhinoceros figure prominently in the dispersal of *Trewia* and probably strongly contributed towards the evolution of fruit traits, it is unrealistic to expect that *Trewia* should disappear in the absence of rhinoceros.

Thorough studies on the significance of carnivores in seed dispersal have just recently started to appear in the literature (Herrera 1989, Debussche & Isenmann 1989, Willson 1993a, Hernández 1993, Chavez-Ramirez & Slack 1993). Most temperate carnivores have large home ranges, nocturnal habits and have suffered many centuries of persecution by humans. Hence any study of them is difficult. As a result most of the information gathered on their importance as seed dispersers comes from the analysis of stomach contents and the collection of faecal material. However the consumption of fleshy fruit is very widely documented for the carnivores investigated during this study as it will be demonstrated in Chapter 4. There are some generalisations that can be made about the seed dispersal potential of carnivores. The widespread utilisation of fruit and the large numbers of seeds in faeces suggests that carnivores may be important dispersal agents for the species of plants whose seeds they consume. Furthermore, seeds emerge intact after mastication and digestion process (Rogers & Applegate 1983, Herrera 1989, Chavez-Ramirez & Slack 1993). Finally, they have the potential to disperse seeds great distances from parent trees because of their long distance movements and extended gut retention times.

Studies on the seed dispersal by carnivores other than those investigated in this study have been conducted on coatis (*Nasua narica*), kinkajous (*Potos flavus*) and tayras (*Eira barbara*) which have been observed to eat the exocarp of the fruiting tree *Dipteryx panamensis* in Panama. The first two animal species were often observed to consume these fruits and may act as seed dispersal agents when they carry the fruits short distances away from the parent tree (Bonaccorso, Glanz & Sandford 1980). During an extensive review of the literature Willson (1993a) gave a list of all the fruit species that have been reported to be eaten by North American carnivores such as: black bears (*Ursus americanus*), polar bears (*Thalarctos maritimus*), racoons (*Procyon* sp.), ringtails (*Bassariscus astutus*), coyotes (*Canis latrans*) and skunks (*Spilogale* sp., *Mephitis* sp., *Conepatus* sp.)

Hernández (1993) studied the fruit consumption of *Rhamnus alpinus* by western polecats (*Mustela putorius*) and other vertebrates. He found that the majority of seeds passed through the gut of the polecats intact. Polecats also consumed rowan berries (*Sorbus aucuparia)* and blueberry (*Vaccinium myrtillus).*

Pendje (1994) studied the African civets (*Civettictis civetta*) in a disturbed rain forest of the Mayombe district, in Zaire. Nine species of forest-tree fruits were regularly eaten and civets selected dens close to fruit-bearing trees. They dispersed these seeds to an average minimum dispersal distance of about 40 m from the parent tree. The most common dispersal areas were their dens, in which they buried whole mature fruits and deposited undigested seeds and faeces. When these dens were deserted, many seeds germinated, forming clumps of seedlings. The germination rates of the dispersed seeds, as well as the mortality rates of the seedlings, varied widely according to the species.

Castro, Silva, Meserve Gutierrez, Contreras & Jaksic (1994) monitored fruit consumption by culpeo foxes (*Pseudalopex culpaeus*) and studied their role as potential seed dispersers in Fray Jorge National Park in Chile. The foxes ate a very low diversity of fruits in relation to field availability, thus suggesting a selective consumption. The greatest levels of frugivory were found when the density of their major prey item (small mammals) decreased below 10 individuals/ha. With regard to seed dispersal, their results showed that the passage of seeds through the fox's gut increases their probability of germination in lab trials and that foxes defecate seeds in microsites where successful establishment of seedlings is possible. Leonlobos and Kalinarroyo (1994) studied the effect of the passage of the seeds of three native species through the gut of same animal in the Chilean Matorral. They found that seeds recovered from fox scats germinated in general in a lower proportion than seeds collected directly from the plants. They suggested that the passage through the fox's gut could have a delaying effect on seed germination and a laxative effect on the animal. Bustamante, Simonetti & Mella (1992) also studied seed dispersal by culpeo foxes in Chile. They conducted laboratory tests which showed that defecated seeds were viable and germinated in higher proportion than the controls. In the field, germination varied with the habitat type. Seeds that were located underneath shrub canopies germinated better whether or not they had passed through the digestive tract of a fox. Foxes deposited seeds more often in unprotected habitats than under shrubs, an indication that they are legitimate but inefficient seed dispersers.

Novaro, Walker & Suarez (1995) studied the food habits of the grey fox (*Urocyon cinereoargenteus*) in north-western Belize. They found that the most common food item were the fruits present in 96% of the faeces and suggested that foxes can potentially play an important role in the dispersal of the fruiting species. Mottajunior, Talamoni, Lombardi & Simokomaki (1996) studied the diet of the maned wolf (*Chrysocyon brachyurus*) in central Brazil and found that fruits formed a considerable amount of the animals diet.

Clevenger (1996) studied the effect of genets (*Genetta genetta*) in the Balearic Islands, Spain. He found that on most islands seeds from cultivated fruit were more common in the scats than wild fruits. Microhabitat characteristics at most genet latrine sites did not appear favourable for seed survival and germination and that makes them poor quality seed dispersers.

Nogales, Medina & Valido (1996) studied the indirect and direct seed dispersal by the introduced feral cat (*Felis catus*) in the Canary Islands. Seeds from two plant species were significantly matched with lizard prey indicating that these seeds were the stomach contents of the lizards that the cats preyed upon. Three more species were directly consumed by the cats. The passage through the gut of the lizards and the cat did not damage the seeds. However, the number of seeds dispersed indirectly was not high and therefore it does not seem to have a great quantitative importance in the natural regeneration of the plants.

1.4. Aims of the study and structure of the thesis

The phenomenon of dispersal of plant propagules by carnivores was almost completely overlooked by ecologists until ten years ago. Although zoologists who studied the diets of these animals reported their fruit eating habits from early this century, ecologists were slow to investigate the subject, mainly focusing their attention on birds, bats and herbivores. It was probably the reputation of the strict meat eater from which the carnivores took their name that delayed the investigation of this important ecological interaction until recently.

Carnivores with their bigger body size, compared to birds and bats, can ingest many more seeds during each feeding bout. Additionally the need for higher food intake makes the mixing of different species of seeds in the gut more likely. Furthermore they have never been reported to act as seed predators. Their longer gut-passage rates make the dissemination of seeds under the parent plant unlikely. Their digestive systems lack the adaptations needed to digest cellulose and therefore they cannot digest seeds, unlike herbivores which very often do so. The only time that seeds are likely to get damaged is during mastication, but even this rarely affects a substantial proportion of the ingested seeds (Herrera 1989). Recent literature reviews on animal seed dispersal have focused on either a single plant-animal species interaction, or a half assemblage: a single plant species and numerous dispersers, or a single animal and numerous plant species (Lieberman & Lieberman 1986). The present study finds its niche in ecology by investigating for the first time the dispersal of seeds of particular fruiting species by a community of carnivores comprising brown bears, red foxes, grey wolves and stone martens in a way that allows comparisons to be made between the dispersers and their preferences from the fruit that were available to them. Furthermore, it looks at the spatial and temporal patterns that emerge from this interaction. I will refer to the four species of carnivore in my study area as bear, fox, marten and wolf. In the following chapters I refer to a large number of animal and plant species. Whenever a species is mentioned for the first time, both the common English name and the scientific name are given and only one of these thereafter. If the need to relate a common name to the scientific one arises, the reader may refer to the Appendix section at the end of this thesis.

The aim of this investigation is to examine the following hypothesis:

1) Is fruit important in the diet of the carnivores? Which factors affect the number of fruits removed from the plants? This was investigated by carrying out monthly faecal collections. The results are presented in Chapter 4.
2) Do carnivores display a temporal reliability in their function as seed dispersers? The monthly faecal collections will provide an answer to this question. The presence of each species in the study area over the year together with the variation between years in carnivore activity is presented in Chapter 3.
3) Does fruit choice or preference by the disperser affect the number of seeds that are dispersed? A comparison of the dietary composition of fruit with the species availability in the habitat was undertaken in order to elucidate fruit preferences of these carnivores species. In order to achieve this, extensive vegetation surveys were carried out in the study area along with fruit counts and phenology observations. The results appear in Chapter 2 and they demonstrate what was available to the carnivores.
4) How many species of seeds were contained in each carnivore faeces? Do carnivores damage seeds during ingestion? Is damage related to the carnivore that consumes the seed or to the species of the seed? In order to answer these questions the number of seed species found in carnivore scats was recorded. The number of damaged seeds was monitored in every faeces analysed. This was to provide an insight into the extent to which seeds passed through the gut intact. The results are presented in Chapter 4.
5) Are seeds consumed by the carnivores deposited in the vicinity of the parent plant? Do carnivores deposit seeds homogeneously on all the available locations? An attempt to answer the first question was made by combining the results of the vegetation survey and the dietary analysis as discussed in Chapter 5. The habitat in which the scat was deposited was recorded together with the nature of the substrate. An analysis of these factors is presented in Chapter 3.
6) Did all the fruiting plants have the same level of success with dispersing their seeds throughout the habitat? The number of seeds dispersed by the carnivores in each habitat was counted to provide an answer to the above hypothesis. An evaluation of these data can be found in Chapter 4.

CHAPTER TWO

THE STUDY AREA AND ITS VEGETATION

2.1. INTRODUCTION

2.1.1. General description of the Rhodope massif and the research area.

The Macedonian-Thracian Massif (Rhodope block), is the major exposure of crystalline rocks in eastern Europe. It stretches from the Black Sea (Istranca Mountains) to the mountains of east Yugoslavia. In Greece it stretches to the east coast with the mountains of Olympus, Ossa, Pilion and Euboea. High mountain ranges such as the Rhodope Mountains, Rila, Pirin and Olympus have probably been created by Tertiary upheavals. These isolated high mountain areas have acted as refuges for certain ancient Tertiary plant species (Polunin 1980).

The plant-life of the Balkans is richer than any area in Europe of comparable size (Polunin 1980). It has been estimated (Turrill 1929) that in the Balkan area, excluding the eastern Aegean islands, there are at least 6530 species of native seed plants, 1754 of which are endemic. This diversity of the flora is a result of the following factors: i) it is an old flora with many Tertiary species that have survived the Quaternary Ice Age; ii) the changes in the level and the area covered by the Mediterranean sea isolated land masses and mountain ranges. This in turn had an effect on the flora and resulted in the fragmentation, isolation, and migration of species; iii) many species migrated from the adjacent central European, Asia Minor, and Pontic regions surrounding the Black sea floras. The migration took place across the land bridge of Thrace and across the land masses that existed in the central and southern Aegean region before the final flooding of the eastern Mediterranean sea; iv) the many centuries of human influence such as the destruction and modification of the natural vegetation and introduction of new ornamental and cultivated species from other parts of the world.

The Rhodope is one of the longest mountain ranges of south-eastern Europe and forms the natural frontier between Greece and Bulgaria. The western Rhodope includes the highest peaks of the range (Deliboska 1953 m, Gyftokastro 1827 m) and it is the most interesting ecologically (Tsipiras 1992). It is the southmost dispersal area for Norway spruce and silver birch. It is a suitable habitat for many rare and endangered animal species of Greece and Europe like brown bear, chamois, and capercaillie.

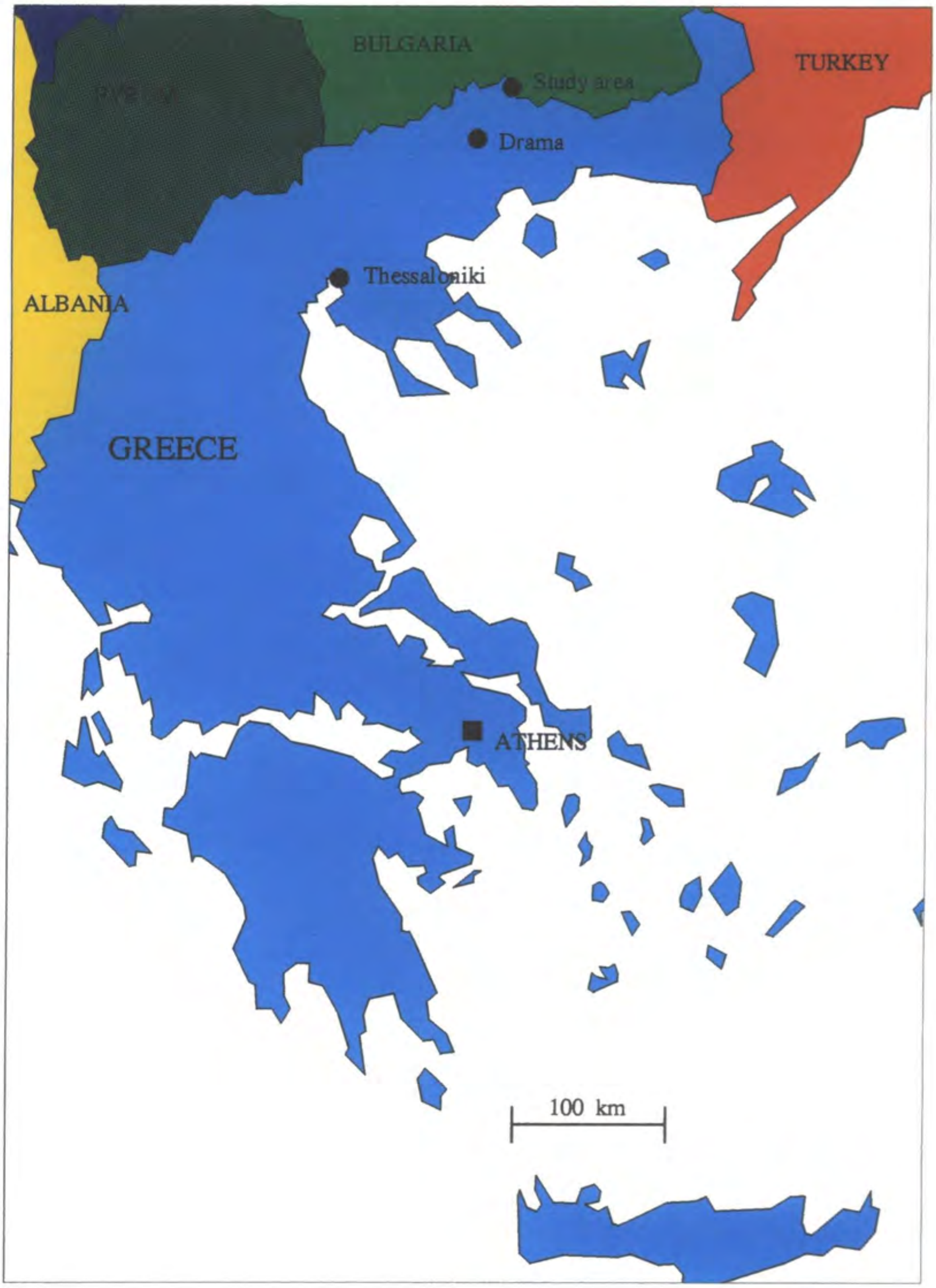
The Rhodope Massif forms the core of the Balkans, mainly consisting of ancient igneous and metamorphic rock including much crystalline limestone (Polunin 1980). It shows little evidence of having ever been submerged. The altitudes are relatively low in Turkish Thrace, but builds up to nearly 3000 m to the highest peaks of the Rila and Pirin mountains in south-west Bulgaria. From there it runs northwards to end south of Belgrade gradually becoming lower in altitude. The mountains that form the Greek-Bulgarian border are very old formations with rounded summits which rise wave upon wave and rarely exceed 2000 m. Deep river valleys cut into these heavily forested mountains and form gorges and shady ravines. The humidity is high during most of the year due to autumn and winter rains and water from melting snows. The short summers are often hot and dry. Often an exposed cliff or rock wall towers above the steep forested slopes (Polunin 1980). The dense forests comprise species such as: *Fagus sylvatica,* hornbeam *(Carpinus betulus), Ostrya carpinifolia*, and oak (*Quercus dalechampii)* which cover the cooler and north-facing slopes and deep ravines which at higher altitudes are replaced by *Pinus nigra* and *Abies borisii regis.* A more sub-Mediterranean vegetation can be found on warmer slopes with species such as: *Quercus pubescens,* eastern hornbeam *(Carpinus orientalis),* manna ash *(Fraxinus ornus), Juniperus oxycedrus,* and *Cotinus coggygria.* Shrubs in the forests include: cotoneaster (*Cotoneaster integerrimus),* alpine spindle tree *(Euonymus verrucosus),* rock buckthorn *(Rhamnus saxatilis),* lilac *(Syringa vulgaris),* fly honeysuckle *(Lonicera xylosteum)*, and amelanchier (*Amelanchier ovalis).*

The tree line on the Balkan mountains usually lies between 1700 and 2500 m. Higher up there is often a shrub zone and the most common species are: common juniper

(*Juniperus communis* ssp. *nana)*, wild rose (*Rosa* spp.), Dyer's greenweed (*Genista tinctoria)*, and daphne (*Daphne oleoides)* (Arabatzis 1986). Human activities such as grazing of domestic animals, cutting, and burning of the upper forests have created many sub-alpine and alpine meadows which may descend as low as 1600-1700 m.

The temperature of the area is affected not only by latitude and altitude, but also by the topography of the land and its distance from the sea. The winter temperatures occurring in the Balkans are characterised from extreme cold in the interior and high mountains with the area being below freezing for several months. In Rhodope the rain falls throughout the year with maxima in May, June, and October. At higher altitudes the snow mainly falls in winter and continues to lie till early summer (Polunin 1980). Above 1000 m, snow may lie from mid-December to early March, while above 2000 m continuous snow may lie mid-May.

The research area was selected for this study because of the natural vegetation which has not been altered much by humans. There is little disturbance apart from wood cropping and a short grazing period. The fauna is among the richest in Europe and many of the large predators still survive in the area. It is situated in the north-eastern part of Drama county and approximately 95 km to the north of the city of Drama, in the vicinity of the virgin forest of Paranesti and in Frakto, near the border with Bulgaria (Map 2.1.). The area is situated between longitude 23° 29' 00" and 23° 31' 00" East and between latitude 41° 29' 00" and 41° 33' 00" North. The protected area occupies 589.25 ha and was declared a virgin forest on the 19/12/1979 by Greek law and since then it is fully protected from human activities. An adjoining area of 483 ha was also protected in 1981 (Mentis 1993). The patches of the protected area cover a total area of 1072.25 ha (Map 2.2.). The forest is considered virgin since the area has remained unaffected by humans and the regeneration and composition of the vegetation depend exclusively on natural factors (Map 2.3). The virgin forest is at the shelterwood stage of succession and consists of small, same-aged patches and large different-aged patches. The large patches can be in different successional stages



Map 2.1. Map of Greece showing the location of the study area. Scale 1:4,630,000.

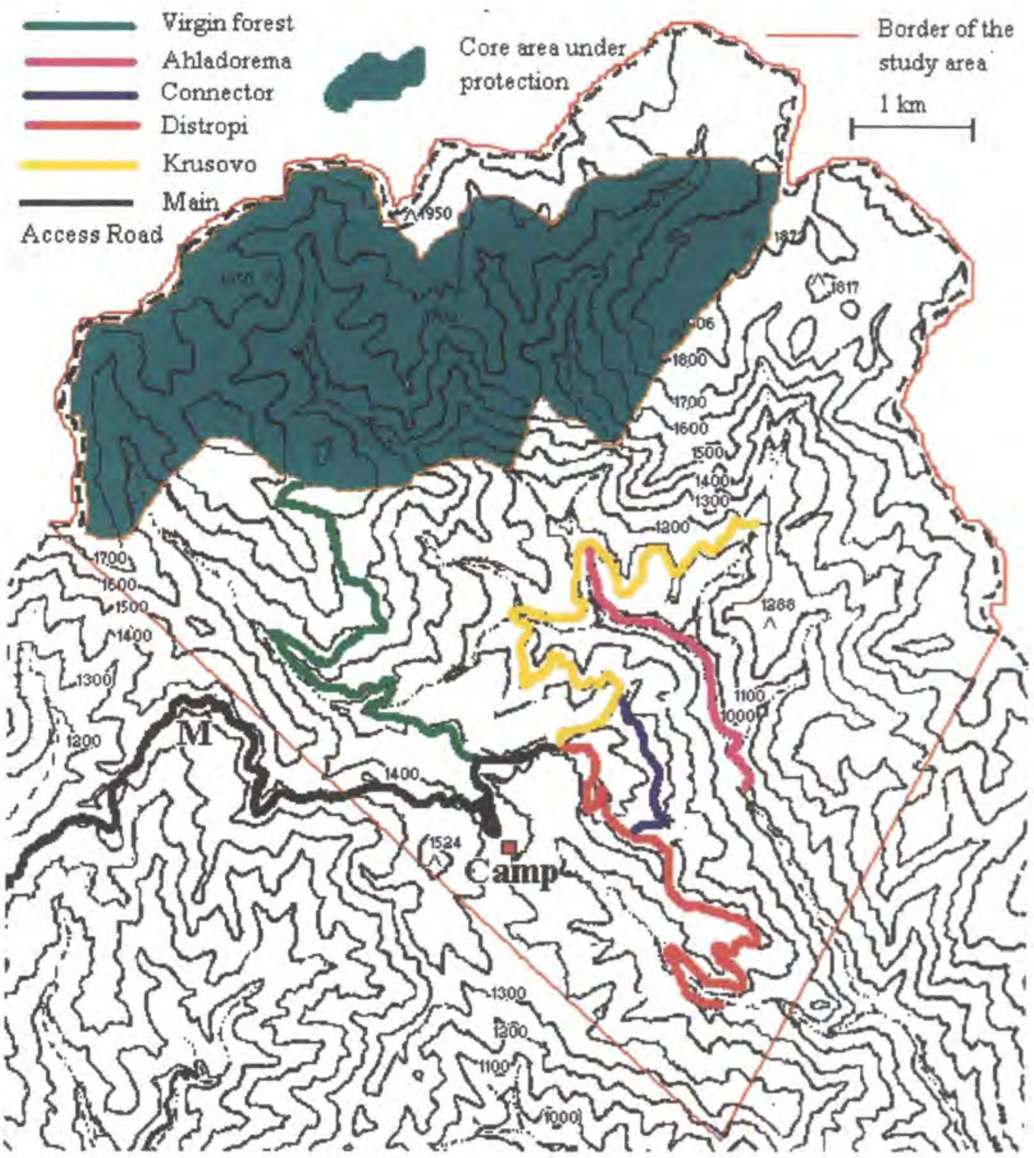
such as: regeneration, young stage, optimum, old-aged, breaking-off, and shelterwood. The number of trees per ha is between 586 and 1071 and the number of seedlings is 4-8/m^2. The proportion of dead trees on the forest floor is 10% of those standing (Mentis 1993). Limited light reaches the forest floor due to the dense and multi-layered canopy. The vegetation zones found in the area are the Fagetum and Abietum according to Mayr or Fagetalia and Vaccinio-Picetalia according to Braun-Blanquet (Arabatzis 1986). This forest has a considerable potential for botanical and ecological studies. The flora of the forest is particularly diverse and includes many species which are rare or unique to Greece. Some particularly rare herbaceous species include: Rhodope lily *(Lilium rhodopeum),* heartsease *(Viola tricolor),* Rhodope violet *(Viola rhodopea),* crocus *(Crocus sativus), Geum coccineum, Geum rhodopeum,* dog's tooth violet *(Erythronium dens-canis),* burnt orchid *(Orchis ustulata),* Austrian leopardsbane *(Doronicum austriacum), Maricaria trichophylla,* wood ragwort *(Senecio nemorensis)* and wood anemone *(Anemone nemeorosa).*

The virgin forest of Paranesti falls under the authority of the Drama forestry service, which has developed the following objectives for the area: *Core area*: Total protection from human activities other than scientific research (1072.25 ha). *Adjacent areas*: Limited protection together with the development of wood production and controlled forest recreation (41753.50 ha) (Mentis 1993). In the Frakto area there is intense wood-cropping activity during summer and autumn. Heavy trucks are also used for the transportation of the timber. All these heavy machines produce a lot of noise that can be heard a few kilometres away due to the topography of the area. It is likely that this affects the normal routines of the animals to a certain extent. A number of dirt roads are opened every year in order to assist the transportation of timber and to give access to fire engines in the incident of forest fires. At the beginning of the century there were a few human settlements in the area, mainly nomads who were moving in the area with their livestock during spring and moving out in late autumn. They also planted a number of fruiting trees in the area. The wild descendants of these trees are part of the rich flora of fruiting trees that still grow in the area. The nearest village is now around 50 km away to the south and the only way to get into the area is by a dirt road in poor condition. The only humans living in the area are people working for the Forestry service. They move to the area in May and usually leave at the beginning of November. A herd of free ranging cattle moves into the area in July and remains there until late September. The whole the area has been declared a wild animal sanctuary and hunting is forbidden all year round, as is also any handling of the animals. What the situation is during winter is uncertain, since the area is left unguarded soon after the first heavy snowfall (photographs in Appendix III) since supplying a guard becomes extremely difficult due to the bad condition of the roads in the area.

The large mammals of the area are: the chamois (*Rupicapra rupicapra*), the red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), the grey wolf, the brown bear, the red fox, the wild cat (*Felis sylvestris*), the golden jackal (*Canis aureus*) in the lowlands, the stone marten, the wild boar (*Sus scrofa*), and the brown hare (*Lepus capensis*). The common small mammals found in the area (Tsachalidis pers. communication) are the snow vole (*Microtus nivalis*), the bank vole (*Clethrionomys glareolus*), wood mouse (*Apodemus sylvaticus*), fat dormouse (*Glis glis*), forest dormouse (*Dryomys nitedula*), dormouse (*Muscardinus avellanarius*), pipistrelle (*Pipistrellus pipistrellus*), Kuhl's pipistrelle (*Pipistrellus kuhli*), Savi's pipistrelle (*Pipistrellus savii*), hedgehog (*Erinaceus concolor*), the weasel (*Mustela nivalis*), and red squirrel (*Sciurus vulgaris*).

The avifauna consists of 120 reproducing species, 25% of which are included in the E.U. list of protected species (Mentis 1993). Apart from the common birds of the mountainous regions of south-east Europe, the avifauna also includes the regionally rare: Capercaillie (*Tetrao urogallus*), hazel grouse (*Tetrastes bonesia*), lesser spotted eagle (*Aquila pomarina*), the booted eagle (*Hieraaetus penatus*), golden eagle (*Aquila chrysaetos*), honey buzzard (*Pernis apivorous*), short-toed eagle (*Circaetus gallicus*), Tengmalm's owl (*Aegolius funereus*), black woodpecker (*Dryocopus martius*), grey-headed woodpecker (*Picus canus*), green woodpecker (*Picus viridis*), middle spotted woodpecker (*Dendrocopus medius*), white-backed woodpecker (*Dendrocopus leucotos*), three-toed woodpecker (*Picoides tridactylus*), red-backed shrike (*Lanius collurio*), and lesser grey shrike (*Lanius minor*) (Mentis 1993).

2.1.2. Choice of transects

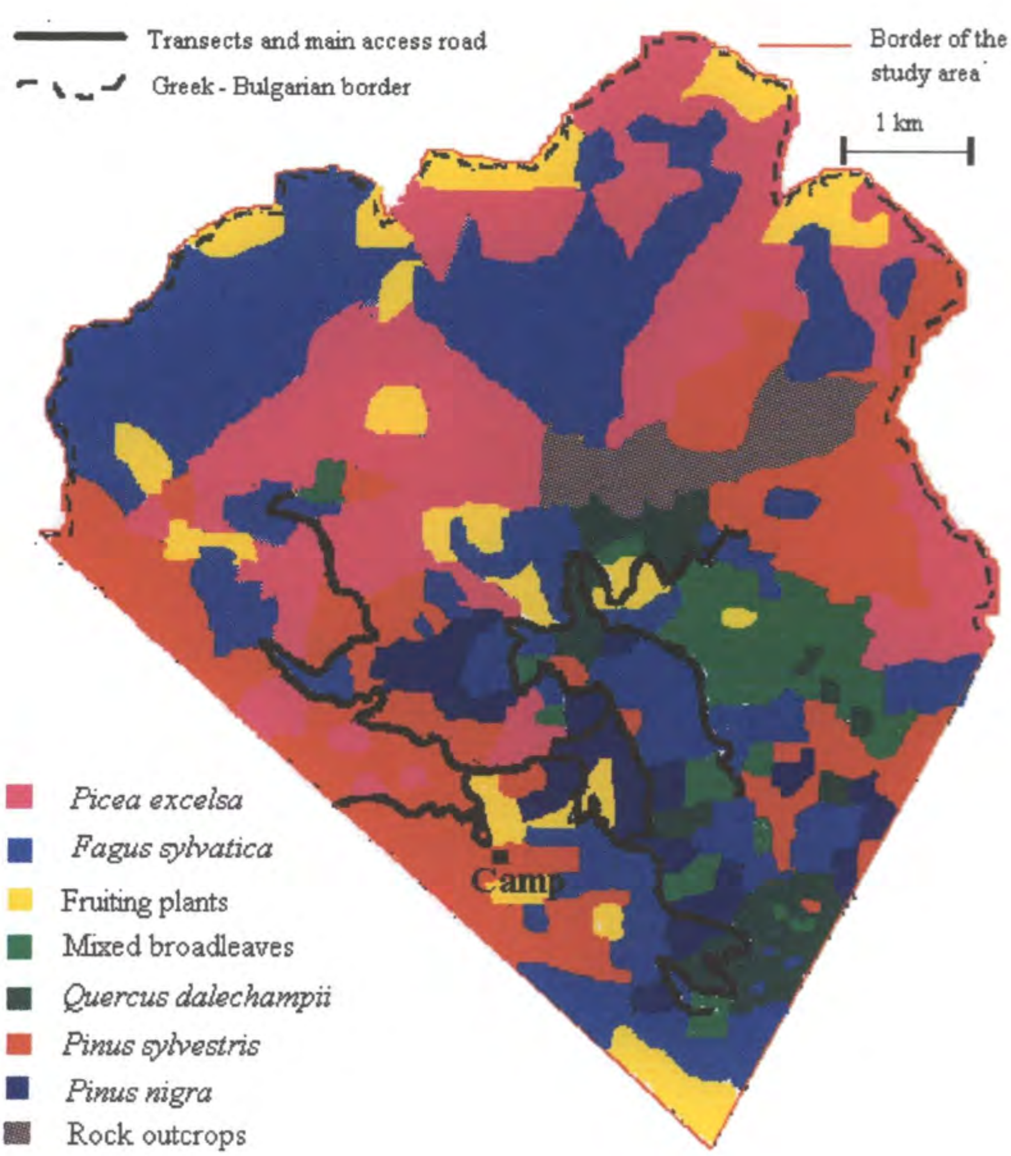


- - - - - - - - Greek-Bulgarian border

.... Rivers-Creeks

^ Highest points in the area

Map 2.2. Map of the study area. The transects are in colour. The core area which is under full protection is highlighted. Longitude :23° 29' 00" - 23° 31' 00" East, Latitude: 41° 29' 00" - 41° 33' 00" North. Contour interval 100 m. Scale approximately 1:60,000. Original map provided by the Drama Forestry Service.



Map 2.3. The dominant tree species in the study area. Scale approx. 1:60,000. The area displayed is the same as in Map 2.2. Original map provided by Drama Forestry Service.

The choice of transects resulted from a consideration of the needs of the project, the harshness of the environment and the limits of walking distances from the camp of Frakto. The transects are not randomly distributed through the forest, but they follow the existing forest roads that encompass the Frakto area. The transects were established after considering the following factors:

1) *The steepness of the slopes.* The slopes range between 20% to more than 100% (45 degrees). Vertical limestone cliffs are also common in the area.

2) *The density of the vegetation.* Conifer forests in the locality have a very dense undergrowth and the forest ground is often covered with broken branches and dead trees which makes walking through them difficult for long distances.

3) *Ease of sampling.* As research was carried out on foot, the remotest sampling points were 10 to 11 km away from the camp of Frakto (Map2.2.). It had to be possible to walk to the beginning of the transect, do the sampling and walk back within one day.

4) *Altitudinal sampling.* There was an effort to sample all the altitudinal zones in the research area.

The use of dirt roads for the collection of faeces is widespread among mammalogists (Chavez-Ramirez & Slack 1993, Cavallini 1994, Clevenger 1994b). Adamakopoulos (1991) also reports from the Pindus mountain range, central Greece, that most of the 112 brown bear faeces that he collected in a year were found along forest roads. In a previous project (Giannakos, Vidakis & Vafidis 1991) concerning the brown bears' diet, I found brown bear faeces along these transects and this fact gave an indication that faeces would be found during this study as well.

The intention was to sample all the altitudinal zones from 900 to 1700 m so that every transect covered a part of this altitudinal range. Table 2.1. presents the length of each transect within every altitudinal zone.

Transects	ALTITUDE (m) **900-1099**	**1100-1299**	**1300-1499**	**1500-1700**	**Total**	**Type of transect**	**Distur-bance**
Ahladorema	2.8	0.0	0.0	0.0	2.8	FR-FP	very low
Distropi	0.5	3.5	1.0	0.0	5.0	FR-blocked	very low
Virgin forest	0.0	0.0	3.3	3.7	7.0	FR	very high
Connector	0.0	2.3	0.0	0.0	2.3	FR-partial. blocked	average
Krusovo	1.0	5.5	0.3	0.0	6.8	FR	very high

Table 2.1. The length of each transect within the range of the altitudinal zones (Numbers indicate distances in km). FR = forest road FP = foot path (a short part of the road was destroyed due to landslide).

2.2. METHODS AND MATERIALS

Two vegetation sampling methods were used during this study in order to collect plant sociological data. During the first year of the study the Point-Centred Quarter Method (PCQM) was used which is a plotless sampling method that provides detailed quantitative descriptions of the structure and the composition of the dominant canopy (Shimwell 1971). It provides both total tree density and basal area estimates and relative frequency, density and basal area estimates for each constituent species of the canopy. Along the five established transects a point was selected approximately every 500 m and well away from the transect so that any effects from the road were minimal or non existent. The length of the transect largely determined the number of points. Care was taken so that the point did not correspond with the position of an individual tree. Additionally, one more survey was carried out on this point covering the shrubs and trees that were less 10 cm in girth. A 10 × 10 m quadrat was established and all the shrubs within it were identified and counted. Finally, from the same point, a ground vegetation survey was carried out within a 4 × 4 m quadrant where I recorded all the readily-identifiable seedlings, graminoids, grasses and broad-leafed annuals.

The second sampling method consisted of 100 × 4 m linear samples along the five established transects. The transects were walked and measured with the help of a hand-held road-length measuring device. The accuracy of the device was ± 1 cm/km. One linear sample was surveyed for both sides of the road every 500 m of transect. The first 100 m of the transect were sampled and then 400 m were walked before the next sampling started again. All the fleshy fruit- and nut-producing trees and shrubs were counted and distinguished as mature or immature plants. The density of each species was then calculated as the number of trees or shrubs per hectare.

The phenology of all the fruit- and nut-producing species in the area was followed month-by-month in order to investigate the temporal availability of fruit in the area. The fruit production of five individuals of each of the main fleshy fruited species was counted over two years in order to estimate the amount of fruit that was available. The individuals were chosen on the basis of being separated from other plants so their branches would not intermingle. This was important in order to undertake reliable fruit counts. These individuals were not on the same transect if the could be found on more than one and an effort was made to locate them near fruiting tree patches so the fruit counts would reflect similar conditions to the ones at the main fruit producing areas. All the selected trees were mature individuals. The fruit counts were undertaken by counting the number of fruits produced by one branch and then multiplied by an estimated number to make up for the total volume of the crown of the individual. In the cases of small trees and shrubs the total number of fruits produced was counted directly using a hand-tally.

2.3. RESULTS

2.3.1. Vegetation surveys

One of the objectives of the study was to examine the factors that affect the abundance of the fruiting plants along the transects as this would directly influence the number of fruits that were available to carnivores. Analysis of variance of the effects of Plant species and Transect on the logarithm of the number of fleshy fruited trees from the 100 m samples along transects found that these effects were significant (Table 2.2.). The most abundant species were *Rosa* sp., *Juniperus communis* and common hawthorn (*Crataegus monogyna)*, the rarest were wild cherry (*Prunus avium)*, *Sorbus torminalis, Sorbus aucuparia* and crab apple (*Malus sylvestris)* (Table 2.3.). The order of transects in decreasing fruiting tree density was: Distropi, Krusovo, Virgin forest, Ahladorema, and Connector (Table 2.3.). The number of species varied from 8 on Ahladorema to only 3 on Virgin forest.

Source of Variation	**Sum of Squares**	**DF**	**Mean Square**	**F**	**Significance**
Plant species (Ps)	3.743	10	0.374	11.685	$p<0.001$
Transect (Tr)	0.370	4	0.093	2.890	$p<0.050$
Ps-Tr	4.134	40	0.103	3.226	$p<0.001$
Residual	32.323	1009	0.032		
Total	42.605	1063	0.040		

Table 2.2. Results of ANOVA analysing the effect of Plant species and Transect on the logarithm of fruiting trees found on the 100 m samples along the transects.

The two way interaction between the effects of Plant species and Transect was also significant. *Rosa* sp. was nine times more abundant on Distropi than on Ahladorema and *Cornus mas* was abundant on Ahladorema but absent from all other transects (Table 2.3.). Some species were only found on a single transect (*Cornus mas, Sorbus aucuparia*).

Table 2.4. displays the same parameters but this time the data were collected inside the canopy with two methods: the PCQM and 10 × 10 square sampling units. The average density of fruiting shrubs found by this method was a little higher. These figures also include young fruiting trees (<10 cm in diameter). It is interesting that the differences between the transect with the highest density and the one with the lowest are much more pronounced by this method. Some species like *Prunus avium, Crataegus monogyna, Juniperus communis* and *Sorbus torminalis* were much more abundant inside the canopy, particularly if the plants that also exist in a tree form are included. Furthermore there were cases where a species was found in the canopy near the transect but not along this transect such as *Cornus mas* in Distropi and *Crataegus monogyna* in Virgin forest. On the other hand there are species such as: *Malus sylvestris*, elder (*Sambucus nigra),* alpine elder *(Sambucus racemosa) and Sorbus aucuparia* that were never found inside the canopy.

Plant species	**Ah (12)**	**Di (20)**	**Vf (28)**	**Co (10)**	**Kr (28)**	**Transect mean**
Prunus avium	6.25	-	-	-	3.57	1.96
Prunus cocomilia	2.08	-	-	-	14.29	3.27
Rosa sp.	10.42	95.00	41.97	22.50	36.61	41.30
Crataegus monogyna	-	2.50	-	-	39.00	8.30
Cornus mas	60.42	-	-	-	-	12.08
Malus sylvestris	-	5.00	-	-	3.57	1.71
Sambucus nigra	6.25	12.50	-	2.50	9.82	6.21
S. racemosa	4.17	-	18.75	-	-	4.58
Sorbus torminalis	6.25	-	-	2.50	-	1.75
Sorbus aucuparia	8.33	-	-	-	-	1.67
Juniperus communis	-	77.50	40.18	2.50	9.82	25.98
Rubus sp. *	1000.00	250.00	607.14	700.00	357.14	582.86
Total **	104.16	192.50	100.90	30.00	116.68	108.81
Number of species	9	6	4	5	8	6.40

Table 2.3. Density (number of trees/ha) of the fruit-producing plants along transects using 100x4 m sampling units. Numbers of sampling units in parenthesis. The transect mean was calculated from the number of sampling units. Transects: Ah = Ahladorema, Di = Distropi, Vf = Virgin forest, Co = Connector, Kr = Krusovo.
* The density of *Rubus* sp. is given as the area that the plants cover per hectare (m^2/ha) due to the growth form of the species.
** Excluding Rubus sp.

Table 2.4. shows the density of all the common tree species in the study area as revealed by the Point-Centred Quarter Method. The most abundant species revealed by this method were: *Fagus sylvatica, Pinus nigra, Pinus sylvestris, Carpinus*

betulus, aspen *(Populus tremula)* and *Picea excelsa.* Fruiting species which can take a tree form such as *Prunus avium, Prunus cocomilia* and *Juniperus communis* are among the least abundant with the exception of *Crataegus monogyna.*

Shrub species	**Ah**	**Di**	**Vf**	**Co**	**Kr**	**Mean**
Prunus avium	-	-	-	-	37.50	8.70
Prunus cocomilia	-	-	-	-	6.25	1.45
Rosa sp.	9.09	146.67	40.00	57.14	56.25	63.77
Crataegus monogyna	-	-	5.00	-	18.75	5.80
Cornus mas	18.18	20.00	-	-	-	7.25
Malus sylvestris	-	-	-	-	-	-
Sambucus nigra	-	-	-	-	-	-
S. racemosa	-	-	-	-	-	-
Sorbus torminalis	27.27	-	-	-	-	4.35
Sorbus aucuparia	-	-	-	-	-	-
Juniperus communis	-	220.00	55.00	-	62.50	78.26
*Rubus sp.**	-	-	525.00	-	-	152.17
Total**	54.55	386.67	100.00	57.14	181.25	169.65
Number of species	3	3	4	1	5	2.2
Tree species						
Fagus sylvatica	293.52	125.98	177.03	304.90	212.40	222.77
Carpinus betulus	139.29	33.76	-	-	99.81	54.57
Carpinus orientalis	77.46	-	-	-	-	15.49
Ostrya carpinifolia	15.63	-	-	-	12.78	5.68
Acer pseudoplatanus	77.46	-	-	-	-	15.49
Quercus dalechampii	30.58	75.59	-	30.75	-	27.38
Populus tremula	46.20	16.63	-	60.64	50.30	34.75
Pinus nigra	-	210.14	-	366.40	75.06	130.32
Pinus sylvestris	-	25.20	325.79	-	50.30	80.26
Juniperus communis	-	8.57	9.67	-	-	3.65
Crataegus monogyna	-	8.57	18.60	-	99.81	25.40
Betula pendula	-	-	18.60	32.46	37.53	17.72
Picea excelsa	-	-	167.36	-	-	33.47
Prunus avium	-	-	-	-	37.53	7.51
Juglans regia	-	-	-	-	12.78	2.56
Prunus cocomilia	-	-	-	-	12.78	2.56
Corylus avellana	-	-	-	-	62.28	12.46
Abies borisii regis	-	-	22.31	-	-	4.46
Canopy density	680.14	504.44	739.36	795.15	763.36	696.49

Table 2.4. The upper half of the table displays the density (number of trees/ha) of the fleshy-fruit producing shrubs within the canopy. These data were collected from 10 × 10 m square sampling units. The mean in the upper half was calculated from the number of sampling units. The lower part of the table displays a vegetation description of all tree species in the habitat surrounding transects. Numbers indicate the density of the most common tree species in the study area as revealed by the PCQM. The species in bold indicate that they were found in both shrub and tree form. Transects: Ah = Ahladorema, Di = Distropi, Vf = Virgin forest, Co = Connector, Kr = Krusovo.

* The density of the *Rubus* sp. is given as the area that the plants cover per hectare (m^2/ha) due to the growth form of the species. ** Excluding *Rubus* sp.

The data on the density of fruiting plants were also grouped in altitude categories (Table 2.5.). The altitudinal zone between 900-1099 m was the richest as far as fruiting plants were concerned. In the next higher zone (1100-1299 m) there was a sudden drop in the density of the fruiting plants. This density was much smaller than the two higher zones (1300-1499 m and 1500-1700 m) but on the other hand, the diversity of species was much greater. Although the density followed an irregular pattern, the diversity of fruiting plants clearly declines as altitude increases. The irregularity of this pattern can be largely attributed to the considerable increase in the density of *Rosa* sp. and *Juniperus communis* as the altitude increases and the decreasing density of the other species.

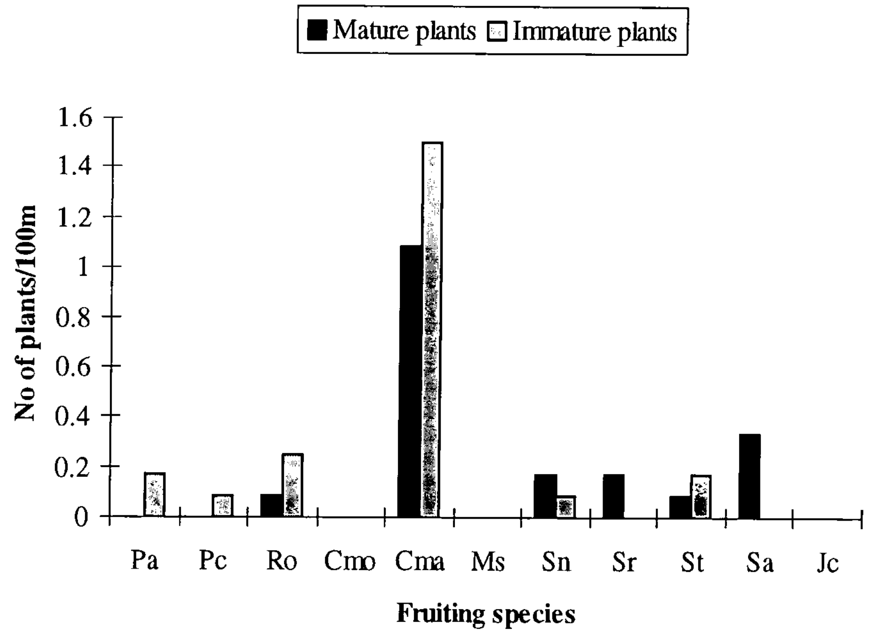
Figure 2.1. illustrates the number of mature and immature fruiting plants growing along the five transects. These data were taken from the linear samples along transects. The five transects had dissimilar ratios of young to mature trees. These ratios were as follows: Ahladorema 1.17, Distropi 0.08, Virgin forest 0.36, Connector 1.33, Krusovo 0.14.

	Altitude (m)				
Plant species	**900-1099 (20)**	**1100-1299 (50)**	**1300-1499 (20)**	**1500-1700 (8)**	**Zone average**
Prunus avium	8.75	8.00	0	0	4.19
Prunus cocomilia	18.75	1.00	0	0	4.94
Rosa sp.	47.50	27.50	90.00	128.33	73.33
Crataegus monogyna	75.00	1.00	2.50	0	19.63
Cornus mas	37.50	0	0	0	9.38
Malus sylvestris	3.75	1.50	0	0	1.31
Sambucus nigra	11.25	8.50	0	0	4.94
S. racemosa	2.50	2.50	30.00	0	8.75
Sorbus torminalis	3.75	0.50	0	0	1.06
Sorbus aucuparia	0	1.50	0	0	0.38
Juniperus communis	15.00	20.00	76.25	150.24	65.37
*Rubus sp.**	600.0	460.0	600.0	375.6	508.9
Total **	223.75	72.00	198.75	178.57	193.27

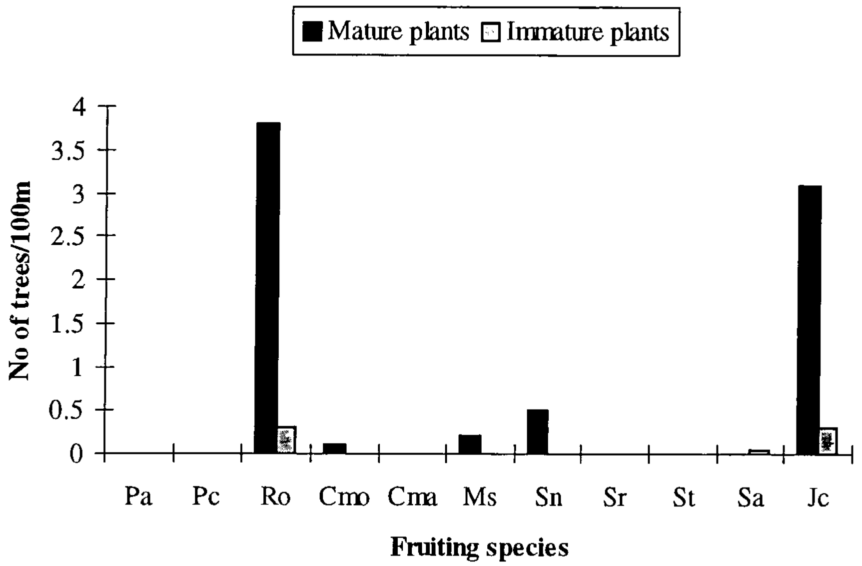
Table 2.5. Density (number of trees/ha) of the mature and immature fruit-producing trees in the altitudinal zones of the study area using 100 x 4 m sampling units along transects. Numbers of sampling units in parenthesis.
* The density of the *Rubus* sp. is given as the area that the plants cover per hectare (m^2/ha) due to the growth form of the species.
** Excluding *Rubus* sp.

Ahladorema had the richest regeneration of fruiting trees. Young *Prunus avium* and *Prunus cocomilia* were establishing themselves although no mature trees were found along the transect. *Sambucus racemosa* and *Sorbus aucuparia* on the other hand were not reproducing at all. Distropi had very low levels of regeneration. Only young trees of *Rosa* sp., *Juniperus communis* and *Sorbus aucuparia* could be found and even these in very small numbers. The latter were growing there without any mature trees being present.

All the shrub species were producing seedlings in Virgin forest. Immature trees of *Sorbus aucuparia* were found on this transect although the sampling did not detect any mature ones. The regeneration in Connector indicated that changes were happening in the fruiting plant community there: a large number of immature *Prunus avium* trees was found although there were no mature specimens. On the contrary, species such as *Sambucus nigra, Sorbus torminalis* and *Juniperus communis* which were present in very low populations were not reproducing at any level that could be detected by the survey. Krusovo has probably the most diverse fruiting plant community of all the transects. The numbers of immature trees were quite lower than the mature ones but nevertheless it seemed that an adequate level of regeneration was maintained.

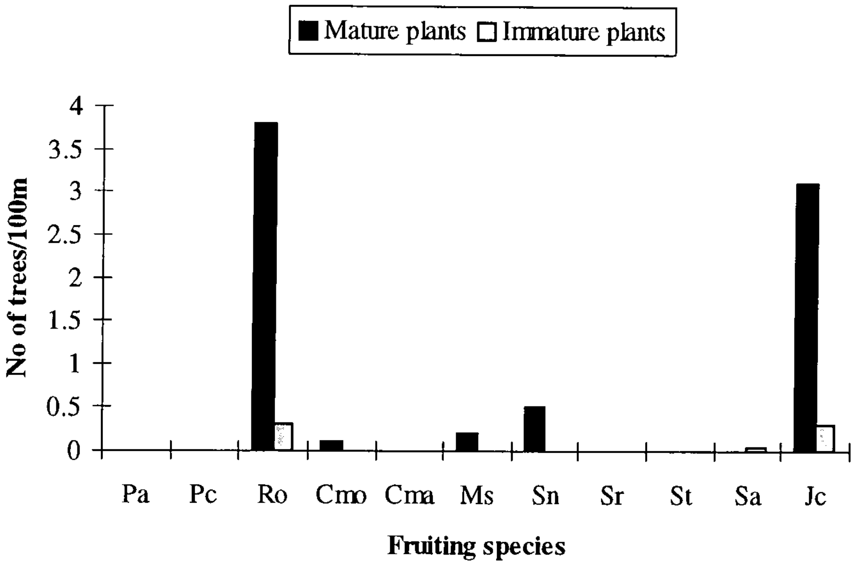


(a) Ahladorema

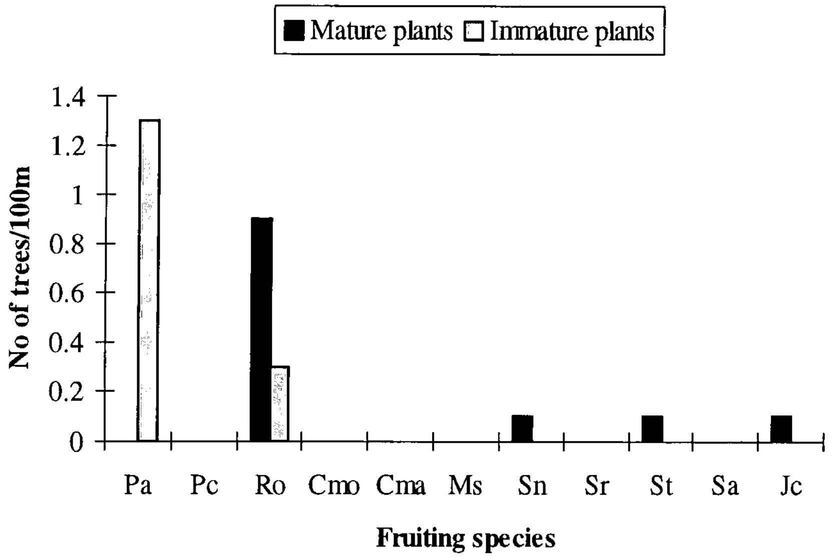


(b) Distropi

Fig 2.1.(a), (b). Number of mature and immature fruiting plants per 100 m length of road as revealed by the linear samples along transects. *Pa=Prunus avium, Pc=Prunus cocomilia, Ro=Rosa* sp., *Cmo=Crataegus monogyna, Cma=Cornus mas, Ms=Malus sylvestris, Sn=Sambucus nigra, Sr=Sambucus racemosa, St=Sorbus torminalis, Sa=Sorbus aucuparia, Jc=Juniperus communis.*

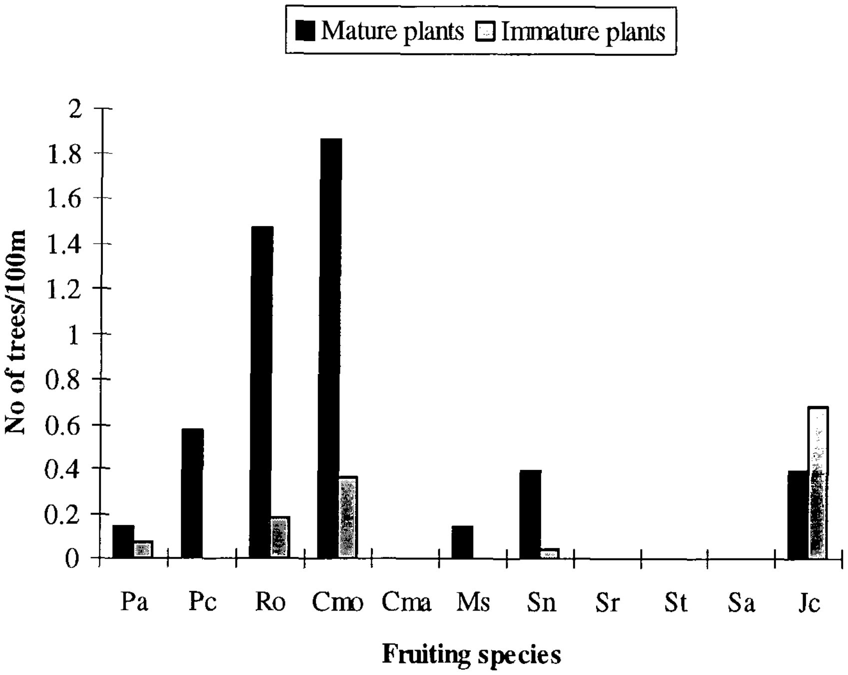


(c) Virgin forest



(d) Connector

Fig 2.1.(c), (d). Number of mature and immature fruiting plants per 100 m length of road as revealed by the linear samples along transects. *Pa=Prunus avium, Pc=Prunus cocomilia, Ro=Rosa* sp., *Cmo=Crataegus monogyna, Cma=Cornus mas, Ms=Malus sylvestris, Sn=Sambucus nigra, Sr=Sambucus racemosa, St=Sorbus torminalis, Sa=Sorbus aucuparia, Jc=Juniperus communis.*



(e) Krusovo

Fig 2.1.(e). Number of mature and immature fruiting plants per 100 m length of road as revealed by the linear samples along transects. *Pa=Prunus avium, Pc=Prunus cocomilia, Ro=Rosa* sp., *Cmo=Crataegus monogyna, Cma=Cornus mas, Ms=Malus sylvestris, Sn=Sambucus nigra, Sr=Sambucus racemosa, St=Sorbus torminalis, Sa=Sorbus aucuparia, Jc=Juniperus communis*

2.3.2. Fruit production

An estimate of the availability of fruit to the carnivores during each month sampled was important in order to make comparisons with what was actually consumed. For this purpose the phenology of the fruit production was followed. Table 2.6. shows the timing of the flowering and presence of unripe and ripe fruit. It is clear that the availability of fruit increases between May (no ripe fruit species) and September (10 ripe fruit species). The longevity of the ripe fruit display varies greatly between species. *Prunus avium* bears ripe fruit during July only, whilst blueberry (*Vaccinium myrtilus)* and *Sorbus aucuparia* have fruit displays that last at least four months. The lengthiest display of all, *Rosa* sp. unfortunately remains undetected by this survey as the observations did not extend into the winter. However, fruit from the previous season remained on branches stripped of their leaves and were frequently detected during spring surveys and sometimes as late as the next flowering period. The time that the fruits take to ripen also varies. There are cases such as *Prunus avium,* *Sambucus nigra* and *Rubus* sp. where ripe fruits appear within a month after the end of flowering. Some other species such as: *Rosa* spp., *Malus sylvestris, Juniperus communis* and eastern hawthorn (*Crataegus orientalis)* can take between three and four months to ripen.

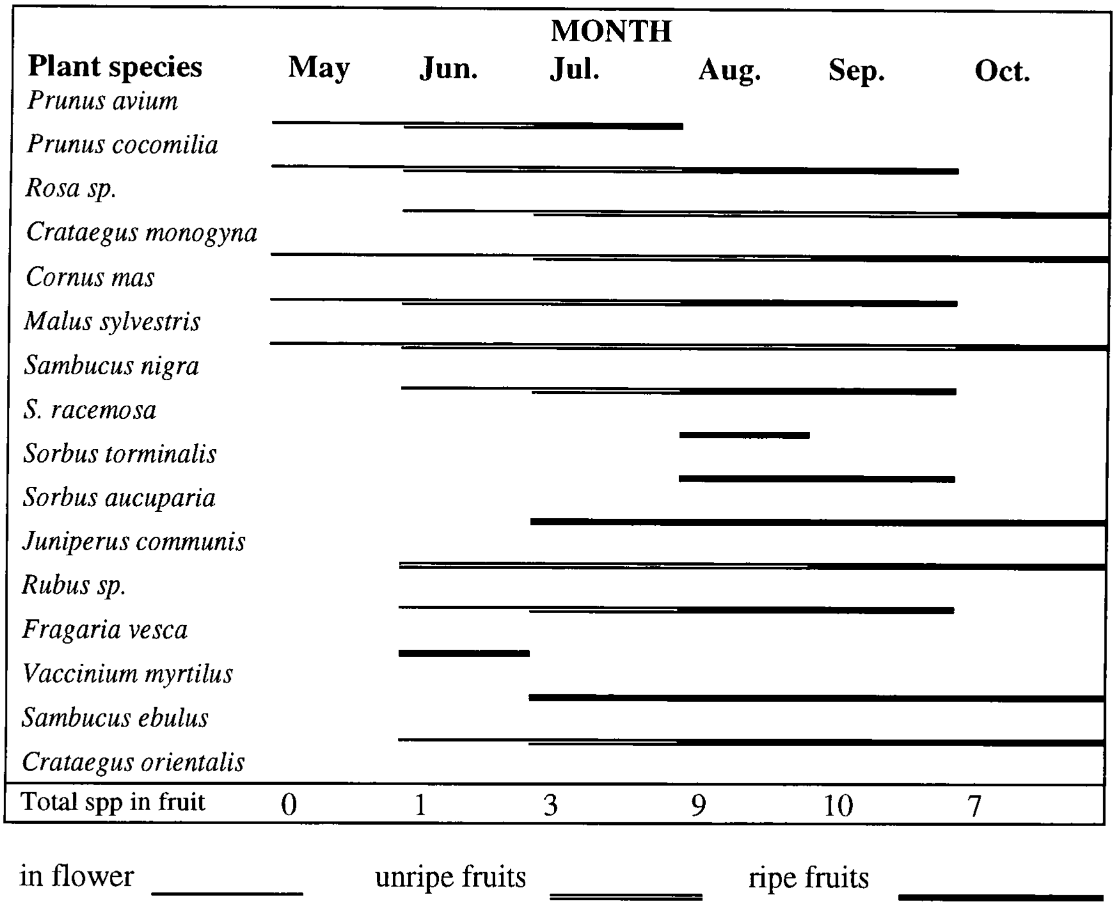


Table 2.6. Phenology of flowering, presence of unripe fruit and presence of ripe fruit of the most common fruiting plants in the study area

Table 2.7. combines information on the fruit production of the individual trees together with the number of the individuals of this species on the transects. The ANOVA therefore, analyses the effects of Plant species and Transect on the logarithm of the number of fruits produced. The mean number of fruits produced by five individual trees from each species was taken into account in order to calculate this production. This number was then multiplied by the number of individuals present in the linear samples. The effect of the Plant species was significant and therefore every species produced a different total amount of fruits as indicated in Table 2.8.

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig of F
Plant species (Ps)	7.676	5	1.535	12.717	p<0.001
Transect (Tr)	0.546	4	0.137	1.131	not sig.
Residual	7.485	62	0.121		
Total	16.191	71	0.228		

Table 2.7. Results of ANOVA analysing the effects of Plant species and Transect on the logarithm of fruit produced on the 100m samples along the transects.

Plant species		Ah (12)	Di (20)	Vf (28)	Co (10)	Kr (28)	Transect mean
Prunus avium	Mean	-	-	-	-	6144	1228
	SE	-	-	-	-	4667	
Prunus cocomilia	Mean	-	-	-	-	26494	5299
	SE					5949	
Rosa sp.	Mean	1821	41515	18341	9833	15999	17319
	SE	594	2836	1888	1380	1763	
Crataegus monogyna	Mean	-	5575	-	-	86970	18509
	SE		3844			14508	
Cornus mas	Mean	42353	-	-	-	-	8471
	SE	5976					
Malus sylvestris	Mean	-	2005	-	-	1432	687
	SE		930			785	
Rubus sp.	Mean	249000	62250	151178	174300	889280	145131
	SE	4807	2403	3745	4021	9083	
Total		292262	111345	169519	184133	225967	196645

Table 2.8. Fleshy fruit production (number of fruits/ha) in the study area calculated from the mean number of mature trees along transects using 100 × 4 m sampling units. The mean number of fruits produced by each species was calculated from averaging the fruit counts of five individual trees. Transects: Ah = Ahladorema, Di = Distropi, Vf = Virgin forest, Co = Connector, Kr = Krusovo.

After calculating the mean numbers of fruit produced in the study area I found that the order of diminishing fruit production was as follows: *Rubus* spp., *Crataegus monogyna, Rosa* spp., *Cornus mas, Prunus cocomilia, Prunus avium,* and *Malus sylvestris.* The effect of transect was not significant as the total fruit production did not vary very much among transects. Unfortunately the size of the dataset did not allow the examination of any higher order interactions but from Table 2.8. we find that a few species had different production on each transect. *Crataegus monogyna,* for example, produced no fruit in Ahladorema, Connector and Virgin forest but in Krusovo it totalled around 87,000 fruits per hectare.

An ANOVA analysing the effect of Year and Plant species did not find the effect of Year significant ($F_{(1, 38)} = 1.694$, not sig.) and therefore the production of fruit was similar in 1993 and 1994. The interaction of the effects was not significant either ($F_{(5, 38)} = 1.789$, not sig.). Thus, the fruiting species did not alter their production significantly between the two years.

2.4. DISCUSSION

A large part of the discussion that follows is based on the analysis of the data collected from the 100 × 4 m samples along the five transects. By sampling along these narrow strips of land it is certain that I created a biased picture of the density of the fruiting trees as far as the habitat as a whole is concerned. I tried to compensate for this by making comparisons with the vegetation survey within the canopy (PCQM and 10 × 10 m quadrats). Furthermore, we have to keep in mind that these strips of land which run parallel to the forest roads are among the main fruiting zones of the study area.

The vegetation surveys along the roads revealed that the composition and the numbers of the fruiting plants varied extensively among transects. *Prunus cocomilia* for example had a high density in Krusovo but was almost non-existent in the other transects. *Cornus mas* was only found in Ahladorema where it was very abundant there. The exposure, altitude and soil parameters are most probably the factors that determine the abundance of these species in relation to their ecological needs. Undoubtedly though, the ability of each species to disperse seeds in adequate numbers over the different habitats that are present in the adjacent areas of the transects plays an important role as well. The transects also differ in their plant diversity. Ahladorema is the most diverse and Virgin forest is the least. It happens that Ahladorema is at the lowest altitude and Virgin forest is the highest (Map 2.2.).

One would probably expect to find a greater number of fruiting trees and shrubs in the openings created by road building than inside the canopy because of the improved light conditions and less competition from tall trees. However, if we compare Table 2.3. and Table 2.4. we find that the average density of fruiting trees is higher inside the canopy. This is largely due to the increased abundance of *Rosa* spp. and *Juniperus communis* which grow happily inside the canopy. The most abundant species in the area, *Rubus* spp., is not included in the transect's average density because of its growth form that makes calculating the number of plants per hectare difficult. This species is present at reduced density inside the canopy (25% of that along road openings). Nonetheless, a completely different pattern emerges if we look at species diversity. Inside the canopy most of the transects have less than half the number of species growing on them than along the road openings. Furthermore, although I did not collect quantitative data it was apparent from the fruit counts that the fruiting trees/shrubs inside the canopy were producing considerably lower numbers of fruit than the ones along the transects. Blake & Hoppes (1986), during their study in Illinois (U.S.A.), also found that abundance of fruit was significantly greater in openings than in forest understorey (also Thompson & Willson 1978) during autumn. They explain this fact as a result of the amount of light, highest daily temperatures and amount of precipitation reaching the ground are higher in openings than in the adjacent forest canopy. They also found that this fruit abundance in openings attracted a large number of frugivores. Fruit removal by frugivores was complete inside the canopy after the first week in October, but some openings retained fruit into December.

When the data collected from the 100 × 4 m samples along the transects were grouped into five altitude categories there was no clear relationship between fruiting plant density and altitude. However, the number of species found is inversely related to altitude. Reducing from 11 species to 5 and finally 3. The influence of altitude is almost certainly due to the severe winter conditions that are more pronounced in higher altitudes. This imposes limitations on the distribution of species probably caused by the number of days of frost that can affect fleshy fruited species (Debussche *et al.* 1987).

Table 2.4. indicates that the forest covering the study area is a mixed forest of conifers and broad-leaved trees. Fortunately it has escaped the monoculture strategies that were applied in other European countries in order to increase wood production. No species accounts for more than 32% of the total tree density. This diversity creates suitable micro-habitats for a variety of animal species. It is interesting to note that in this case of climax species, Krusovo transect is again the most diverse one. A possible explanation for this could be that the rolling hills of the area provide a multitude of exposures and micro-climates which are suitable for different species. Furthermore,

there are the ruins of an old village in this area. It is almost sure that some of these species were planted by the inhabitants for their fruit production or for shade from the summer sun.

The number of immature plants along the transect provides some information on how well the species is reproducing in a particular area. In Ahladorema young *Prunus avium* and *Prunus cocomilia* were present although no mature trees were found on the transect. This could result from inefficiency of the sampling method used to detect the mature individuals that were further away and inside the canopy, but I have to stress the fact that these species were not detected by either the PCQM or by the 10 × 10 m sampling technique within the canopy. On the other hand, the areas sampled were small relative to the adjacent area of the transects and these trees could have been growing further away. Nonetheless, it is very possible that these plants grew from seeds that were carried there by animal vectors. In contrast *Sambucus racemosa* and *Sorbus aucuparia* mature trees were not reproducing very well. This could that be because these species were not dispersed by carnivores and were therefore losing the competition for space? This hypothesis will be investigated in Chapter 4.

Very low regeneration rates were found in Distropi. There might be several reasons for this, e.g. more competitive species (such as beech and oak) moving into the openings resulting in the fruiting trees and shrubs are being slowly excluded from the transect. In Virgin forest there were good levels of regeneration. Small numbers of *Sorbus aucuparia* were found but not mature trees. Connector was another case where a large number of young plants of *Prunus avium* were detected but not any mature trees (see also Chapters 4 & 5).

The available species of ripe fruits increased from one in June to three species in July, nine in August and in September it reached a peak of 10 species bearing ripe fruits. In October numbers started to decline again. These data agree extensively with Jordano (1992) who, in a review of the published literature, indicated that for woody fruit producing species in temperate forests, the lowest production is in June, followed by a sharp increase during the following months with a peak in September and October. Blake and Hoppes (1986) found that in Illinois the abundance of ripe fruits was highest in early September and declined thereafter. Plants are faced with a trade-off when timing their fruit production. Snow (1971) suggested that "the succession of ripe fruits in Europe seems to be adapted to the seasonal shifts of the bird populations, and the more nutrient fruits tend to have a more southerly distribution and so ripen later than the more succulent fruits". In Northern America, Thompson and Willson (1979) described three phenological strategies found in plants which appear "to have been selected primarily by the seasonal patterns of avian frugivore and the probability of destruction of ripe fruit before dispersal." Thompson (1981) concluded that "availability of frugivores provides a strong selective pressure on the seasonal timing of fruit maturation in plants with dispersed seeds." Debussche, Cortez & Rimbault (1987) suggested that fruit characteristics and the ripening season are results of various selective pressures and among these, climate plays an important role. The Mediterranean climate operates mainly by summer drought and also, in certain areas, winter frost; this latter component is important, with the cool to cold winters found to the southern Europe areas. The unpredictability of the intensity and length of the drought period acts on the evolutionary response of plant species under this climatic type; frost periods are certainly important too.

The scarce summer rainfall of the Mediterranean climate results in a gradual diminishment, starting in summer, of soil water resources. Debussche *et al.* (1987) concluded that for a Mediterranean region of southern France the most favourable period for the enlargement stages of high water content fruits takes place from May to July and the least favourable from August to September. Ripening follows a few weeks afterwards in summer and autumn, respectively. During and after November the success of a high water investment is very limited by frost damage.

Ripening periods are much more aggregated than flowering seasons, and most species tend to mature their fruits in late summer and autumn, regardless of the flowering time (Herrera 1984a, Willson 1991, Willson 1993b). As a consequence, flowering and fruiting overlap in most species that flower in late summer and autumn. Ripening periods of individual species in the shrublands are, on average, longer (mean=2.2 and 3.5 months) than in northern temperate forests (0.6-1.3 months) and shorter than in tropical forests (4.3-5.8 months). Length of ripening period of individual species has been related to seed dispersal strategy in relation to disperser abundance and the risk of fruit damage. Without denying the importance of these factors, other aspects unrelated to the dispersal process seem more important to explain variation across communities in the length of ripening seasons. There is a strong relationship between length of ripening season and average temperature of the coldest month of the year. As the potential ripening vegetative period increases, more time may be allocated by plants to each of their primary functions, and progressively longer ripening seasons will be incorporated into the plant community (Herrera 1984a).

The frequent frosts of November undoubtedly limit the number of fleshy fruit available after this month (see Herrera 1984a) and I suspect that there is a steady decline after the first indication of it in October as it was also documented by Debussche *et al.* (1987). Fruit production per hectare was highest in the two lowest transects, Krusovo and Ahladorema (Table 2.8.). Herrera (1984a) found that the average fruiting density in Mediterranean shrublands in southern Spain ranged from 0.4 (April) to 20.1 ripe fruits/m^2 (November). If the fruit production of *Prunus avium,* which mainly fruits in July is excluded, the rest of the fruiting plants produced the maximum number of fruits in September which was when the fruit counts took place. The average fruit density along the transects was 19.5 fruits/ m^2. However, I believe it is not safe to make direct comparisons between the two areas, as different sampling techniques were used.

Smith (1975) suggests that seeds passing through the digestive tract of animals benefit from fruiting at different times through the year. In Lemont, Illinois (U.S.A.) early fruiting by *Prunus* and later fruiting by wild grape (*Vitis* sp.) and *Cornus* may enable these species to take advantage of the same bird populations at different times and thus relieve competition for seed dispersal vectors. Simultaneous fruiting by *Vitis* and *Cornus* produces a competition for dispersal which may be partially countered by utilisation of different bird species. Information on small-seeded species shows similar relationships: a fruiting time displacement between *Rubus* species enables them to exploit the same bird populations of shrub-feeding birds, mainly blue jays and brown thrashers. Herrera (1984b) suggests that it is reasonable to assume that fruiting phenology is under genetic control in *Rosa* since its seed dispersal pattern depends partly on the simultaneous availability of its fruits and those of *Crataegus*. Natural selection might be responsible for fruiting synchronisation with *Crataegus*. Infrequent, yet consistent, consumption of *Rosa* fruits by birds that rely mostly on *Crataegus* fruits may result from the need for adequate amounts of some important nutrients which are required in small amounts, scarce in *Crataegus*, and readily obtainable from *Rosa* (e.g., carotenoids and vitamin C). The production of these nutrients is probably a heritable trait and might therefore been selected for, leading to the simultaneous dispersal of both species (Herrera 1984b).

CHAPTER THREE

TEMPORAL AND SPATIAL DISTRIBUTION OF SEED DEPOSITION BY CARNIVORES

3.1. INTRODUCTION

An investigation of the spatial distribution of the potential carnivore dispersers is of great importance to a study of seed dispersal because it can provide us with a measure of where and how far away from the parent plant seeds are likely to be dispersed. This chapter investigates the way in which the carnivores used the study area together with how this utilisation changed over the year. The carnivores studied were brown bears, red foxes, stone martens and grey wolves. The initial plan was to include weasels in the study, but the data obtained for them were limited. In the introduction, I review the published literature on home ranges, territoriality, movements and habitat requirements of these carnivores since this influences their spatial and temporal distribution.

3.1.1. Carnivores

3.1.1.1. Home ranges and territoriality

The concept of home range is an important one in the interpretation of the behaviour of mammals as it relates to the restricted area within which individuals or groups live and the manner in which they use space (Jewell 1966). As early as 1910 Seton (in Jewell 1966) described the "home regions" or "home ground" utilised by mammals. Burt (1943) was the first to distinguish the concepts of home range and territoriality and establish separate uses for these terms. He also gave two different definitions of home range: a) "that area traversed by the individual in its normal activities of food gathering, mating and caring for young" and b) "the area, usually around a home site, over which the animal normally travels in search of food". He also noted that an animal can shift its home range but that "occasional sallies outside the area, perhaps exploratory in nature, should not be considered as part of the home range", hence excluding in this way the dispersal movements of young animals.

Carnivores display a range of social organisation from solitary individuals to complex societies. These do not relate to phylogenetic division as in some instances the simplest and the most advanced are found in the same genus, e.g. *Felis, Canis* (Delaney 1982). Solitary carnivores typically feed on prey items smaller than themselves, but association into groups makes possible the consumption of appreciably larger animals. As a result of their feeding habits on widely dispersed prey, the home ranges of carnivores are relatively large (Hazumi & Maruyama 1987; Keenan 1981; Trewhalla, Harris & Mcallister 1988; Huber & Roth 1993). Furthermore, the home ranges of large carnivores are disproportionately bigger than those of smaller carnivores when compared with differences in range sizes of large and small herbivores (Harestad & Bunnell 1979; Lindstedt, Miller & Buskirk 1986; Macdonald 1995). This is because the prey of large carnivores tends to be especially rare. All else being equal, the diminishing relative costs of running larger bodies should lead to an increase in home range size with body weight but this would be less marked in larger species. However, in nature different species quite often have access to more habitats than others. Additionally, accessible and acceptable food stuffs decrease with increasing body weight probably due to patchiness of resources in the environment (Harestad and Bunnell 1979).

The spacing pattern within a local population is the result of the tactics chosen by individual animals in their attempts to survive and maximise reproductive success. It is often stated (e.g. Sandell 1989) that female spacing patterns and therefore their home ranges are determined by the abundance and dispersion of food, whereas male spatial organisation, at least during the mating season, is determined by the distribution of females. The females' reproductive success is closely correlated with the amount of energy they can allocate to reproduction. This mainly depends on the food resources available during the rearing period. Thus for solitary females, food is the most important resource, hence females should follow a strategy that maximises their chances of securing sufficient food resources for reproduction and survival (Sandell 1989).

Male spatial organisation is influenced by two resources (Sandell 1989): food outside the mating season and receptive females during the mating period. It is understood that during a substantial part of the year, male and female spacing patterns are determined by different factors, and home range size in males should be a function not only of food requirements, but also of female distribution. Since feeding ranges tend to be minimised whereas mating ranges are expected to be maximised, it follows that male ranges should be larger than expected by energy requirements. Males may adopt one or two alternative ways to achieve matings; either they stay within their territory and try to monopolise a number of females, or they roam and compete for access to each single female that comes into heat (Clevenger, Purroy & de Buruaga 1992b). Since receptive females and available food in almost all cases have different characteristics, a change in tactics is expected to exploit the different resources. Thus the spatial organisation of males will differ between the mating and non-mating seasons. When mating ranges are exclusive, competition over access to high female density will probably go on for most of the year, since it is easier to maintain an exclusive area than to establish a new one. Hence for species that have restricted mating season, it can be predicted that if male ranges overlap there is a change in range between mating and non-mating season, with mating ranges being the largest (Sandell 1989).

One important factor for the spacing of a carnivore population is the extent of range overlap between individuals. For ranges to be exclusive, the food resource must be sufficiently evenly distributed and stable so that an area just large enough to support the animal during the critical period contains adequate food throughout the year (Macdonald 1995). If the food resource varies in space and time, the range must be large enough to provide for the animal at all times. This larger area may contain surplus food for most of the year; thus several animals may utilise the same area and a system of overlapping ranges develops.

Many carnivores invest considerable amounts of energy into excluding conspecifics from resources such as food and mates. They do so by either being territorial or by gaining high status within a social group. Defending a territory is very expensive, it not only requires a huge investment in the initial struggle for supremacy, but also represents a long term commitment to patrol and defence (Macdonald 1995). Mammals and other animals opt for a territorial system when the resources are distributed in such way that the costs of defending them are outweighed by the benefits of doing so. The costs of territoriality determine the size of plot defended. The occupant should defend a territory to provide the necessary resources. Territory holders are constantly under the threat of invasion by the non-territory holders. Any territory owner whose ambitions lead it to try to monopolise more territory than it needs will be incurring unnecessary costs in defending resources it cannot use. Territory holders probably opt for a size of territory that maximise the returns on the investment they make in property, e.g. maximise their daily rate of food intake or minimise the risk of starving (Macdonald 1995).

Maintenance of an exclusive territory without an overlap zone is possible in highly mobile species (e.g. birds) with which neighbouring residents may maintain direct contact. However, the lesser mobility of carnivores would make this kind of defence very costly, especially for carnivores whose home ranges have to be large relative to their body size (Jewell 1966). In such species communication between neighbours is indirect, usually through the exchange of scent signals. Overlapping of individual ranges is tolerated, but neighbours are aware of and avoid each other, i.e. there is a spatial as well as a temporal separation (King 1975). The overlap zone is a necessary part of each range, in which scent marking "posts" are visited by neighbouring residents to obtain and deposit information. Almost all carnivore territories are scent marked. Individuals, are generally reluctant to enter occupied areas after having detected the signals, so fights over possession of territory are rare (Gorman and Trowbridge 1989). When the intruder and the resident meet, the result is usually withdrawal of the intruder without escalation to fighting. Nevertheless, animals do on occasion trespass into the territories of others. When they do, carnivores often cease to scent mark, indicating that they are well aware that they are outside their own territory (also in Hoskinson and Mech 1976).

Gosling (1982) argues the individuals resident in a territory have more to gain from retaining the territory than do intruders from taking it over. This is because the residents have invested a lot of time and energy into getting to know their areas and resources and they may possibly have dependent young. Since a resident has more to lose, it will defend the territory vigorously. Therefore if an intruder meets an individual whose odour matches that of the majority of the scent marks in the area, it would do well to withdraw as rapidly as possible as his opponent is likely to be the resident.

Territory size in social carnivores is governed by different factors than that of solitary species. Kruuk and Macdonald (1985) argued that territory size ultimately sets limits upon group size, so in species where several individuals may occupy a range, a territory owner follows one of two alternative strategies which will determine the size of its range and the number of its cohabitants: a) an "expansionist" tends to increase the size of its territory in excess of minimal requirements for breeding. Expansionists would therefore increase their territory sizes up to a species-specific or habitat-specific optimum. Therefore, all else being equal, the territory owners with the strongest or largest group will occupy the largest range. b) A "contractor" will maintain the smallest economically defensible area which will encompass sufficient resources for reproduction. This does not require that group size for contractors be restricted to a single animal or a breeding pair. In habitats where resources are patchy in availability, a "contractor's" territory may support additional residents. These will be tolerated as resources allow and balance the costs and benefits of their presence against the expense of expelling them.

A number of studies have tried to relate the body size of an animal and the size of its home range by means of allometric equations (McNab 1963, Harestad and Bunnell 1979, Lindstedt *et al.* 1986, Gautestad & Mysterud 1995). These analyses have taken into account a wide range of factors such as the energetic requirements of the animal, its trophic status (herbivore, carnivore, omnivore), productivity of the habitat (related to latitude and precipitation), and season. Nevertheless, allometric equations are not precise predictive laws and this is because social interaction and behaviour, habitat productivity and investigative methods are complicating factors in determining home-range size. For instance, observed sexual differences in home range size often exceed that predicted by size dimorphism alone. A male carnivore's home range may include those of several females. Yet, since the young depend on their mother during and after lactation, the females of some species may have higher energy requirements. Additionally the age class and the status of an animal may affect the size of its home range. Subadults may disperse and be forced to live as transients until they can establish themselves socially (Lindstedt *et al.* 1986). They may be forced to live in suboptimal habitat because dominant individuals exclude them from preferred areas.

Furthermore, subadults may need more nutrients for growth, yet lack food-gathering skills. These factors appear to favour larger home ranges. There is no doubt that the parameters mentioned above influence the sizes of home ranges of these animals and therefore, dictate the maximum distance that carnivores can transport seeds.

3.1.1.2. Movements

After reviewing an extensive range of papers published on the families Canidae, Felidae and Mustelidae, Goszczynski (1986a) presented average figures for the home ranges and the daily movements of several species of these carnivores. He found that distances travelled daily by different species of carnivores were correlated with body mass. Although canids are thought to range widely, they actually move over shorter distances than mustelids with the same body mass. His findings, relative to the species of my study are given below:

Carnivore	**Mean Body mass (Kg)**	**Daily movements (km/day)**	**Home range (km^2)**
Mustela nivalis	0.075	1.1	0.07
Martes martes	1.142	7.2	13.5
Martes foina	1.462	6.4	5.2
Vulpes vulpes	6.100	9.1	9.7
Canis lupus	37.000	25.7	217.0

3.1.1.3. The role of faeces in territorial marking by carnivores

Biologists are usually faced with a problem when they have to distinguish faeces deposited as means of excretion or communication, as both urine and faeces are used as scent marks (Gorman and Trowbridge 1989). Quite often, small token amounts of faeces are used for signalling (Macdonald 1985; Vila, Urios & Castroviejo 1994). These faeces are usually placed on prominent, often elevated objects called signal posts. Such token marking is common in most carnivore families. In many species, large quantities of faeces can accumulate at discrete sites, known as latrines.

Social odours are a limited resource, whether they be faeces, urine, or glandular secretions (Gorman and Trowbridge 1989). Scent marking usually involves a significant investment in terms of time and energy. It is predictable therefore, that scent marks should be distributed in a way that maximises their chance of being discovered by potential intruders to the territory. This seems to be the case since scent marks are not placed at random within the territory, but instead at visually and olfactory conspicuous and traditionally used landmarks.

3.1.2. Brown bear (*Ursus arctos*)

3.1.2.1. Habitat requirements and preferences

All brown bear habitat is characterised by extensive timber cover as well as open grasslands and meadows (Ball 1980, Knight 1980, Schneegas & Frounfelker 1980, Banner 1985, Hamilton & Archibald 1985, Martinka & Kendall 1985). Brown bear populations can thrive in open areas, as they do in the less settled portions of Alaska and Canada (Banfield 1958). Roth (1983) mentions that in the Italian Alps one main factor determining the shape of the ranges seems to be the distribution of good cover. Most brown bears' movements could be made without leaving dense forests. Bears usually used a different daybed each day. Most daybeds used by brown bears are found in timber stands, even in areas where bears are commonly observed foraging in the open. Although the species apparently has no real need for extensive timber cover, populations living relatively close to settled areas may require such refuges (Clevenger, Purroy & Pelton 1992c). Although areas occupied by European brown bear populations may contain large clearings, few bears are observed in them at any one time.

3.1.2.2. Home ranges and territoriality

Bears are large, generally omnivorous, solitary carnivores. This indicates large home ranges. Within any area, numerous brown bears may conduct daily and seasonal activities without any major intraspecific conflict (Craighead 1976). Territorial defence of seasonal or home ranges has not been mentioned, and all behaviour indicates that defence activities are largely non-existent. Range peripheries are definitely not defended, feeding areas are sometimes temporarily defended, and den sites are not defended against mature members of the same sex. Occasionally there may be a show of dominance at refuse dumps or around carcasses which is used to temporarily delay communal feeding. For most of their lives, brown bears are not territorial and their individual ranges overlap. Many brown bears congregate at food sources such as refuse dumps, carrion, berry patches, pine nut stands and clover fields. Their daytime beds are made nearby in dense timber, and numerous brown bears regularly use the same timbered retreats simultaneously (Craighead & Craighead 1972; Craighead 1976; Craighead, Craighead & Craighead 1985).

Long term movements of some brown bears indicate that a large proportion of the available habitat might be covered in a lifetime. Some mature males may have life-time home ranges of 2,600 km^2 or more. Knight (1980) reports from U.S.A. that even a female with cubs-of-the-year may have an annual home range exceeding 518 km^2. However, seasonal ranges are localised and not excessively large. The availability of food during spring, summer and autumn tends to limit seasonal range size more than any other factor.

Roth (1983) fitted four brown bears with radio collars in the Italian Alps and in Pritvice National Park, Yugoslavia (former). He found home ranges between 57 km^2 and 74 km^2 in summer-autumn whereas in November the ranges were between 4 and 12 km^2. The bears made "excursions" lasting 3-15 days which took them more than 5 km beyond the boundary of their core areas on an average of 36 day intervals. Judd and Knight (1980) reported minimum home ranges were between 26 and 741 km^2 in Yellowstone National Park (USA) . The largest home range was occupied by an adult female accompanied by a cub-of-the-year.

Some authors (Berns, Atwell & Boone 1980, Knight 1980, Knight & Eberhardt 1984) suggest that the large variation in brown bear home ranges found by different researchers can probably be explained by wide differences in habitats and the availability of alternative food resources. Some major foods fluctuate between extremes of abundance, and brown bears must substitute for scarce items. A particularly favoured site under periods of average or greater food supply may attract and serve several bears. During periods of food scarcity, bears probably take longer foraging journeys that carry them beyond their "average" home ranges.

3.1.2.3. Movements

Craighead (1976) provides extensive information on daily movements within Yellowstone. One female habitually made a 5 km trip to a refuse dump, taking 1.5 hours. Brown bears often made trips of 16 km of straight line distance in a 12-hour period and one covered 25.6 km. Movements of 14 km in a single afternoon were also recorded. Other authors have reported regular movements ranging between 14.5 and 80 km in 2-3 days (Berns *et al.* 1980, Knight 1980).

Several authors (Miller and Ballard 1982, Judd and Knight 1980) report movements of brown bears that have been transplanted up to 258 km away from the site of capture. Extreme movements were recorded such as one male which was transplanted 215 km away from where he returned to his original locality in 13 days. These movements exhibit the potential mobility of brown bears but they were undoubtedly unnatural and took place after the bear's homing instinct was triggered by the relocation.

Weber (1987) reports that Romanian brown bears in Hargita mountains travelled through their home ranges on clearly developed trail systems. Brown bear trails generally were the shortest distance between feeding and resting areas, apparently offering security and ease of travel. Undisturbed bears regularly used these trails for most of their travel. Parts of trails, especially near preferred feeding sites, were frequently used by several bears concurrently. Up to 12 bears were observed on a single trail during one afternoon. Bears used trails with a certain punctuality. The first bears that appeared on a path, beginning in the afternoon, were young animals. They moved cautiously, stopping frequently to examine their surroundings. After a bear travelled the route, others moved more confidently, hesitating less than the first one. Before a bear walked into an exposed area, it often paused for more than 20 minutes to evaluate the situation from cover.

Weber (1987) also found that brown bears defecate throughout their home range, with scats concentrated in areas where they linger, e.g. feeding and resting sites, and along the border of thickets where they hesitate before entering exposed areas. In the later situation, defecation appears to be spontaneous, perhaps a nervous response, and certainly not as a result of examining existing scats. He also noticed that bears defecate while fleeing, particularly at the beginning of flight, with excrement being spread over 1.5 m. Bears often passed the fresh scats of other bears without reaction, indicating that scats are of little if any social importance on these occasions.

3.1.3. Red fox (Vulpes vulpes)

3.1.3.1. Habitat requirements and preferences

Red foxes have the most extensive geographical distribution of any wild carnivore and are extremely varied in habitat requirements (Macdonald 1987, Artois 1990). Their natural habitat is dry, mixed landscape, with abundant scrub and woodland. They are found throughout almost all of the northern hemisphere, as well as in Australia where they were introduced. In North America their range covers the continent from the Aleutian Islands to Newfoundland. In the Palearctic region they stretch from Ireland to the Bering Sea. In North America on Ellesmere Island at 76° N, red foxes are well within the Arctic Circle. In the south they almost reach the tropics where they extend to the Caribbean coast of Texas. Individuals of the same species that are abundant in the English landscape are just as much at home in the deserts of the Middle East or Spanish Sahara with scarcely 80 mm of annual rainfall, or in Arctic tundra, or on Alpine passes at over 4,000 metres, or in the concrete jungles of Central London. In many habitats, they appear to be closely associated with man.

3.1.3.2. Home ranges and territoriality

Red foxes hold the record for variation in territory size ranging from 0.1 km^2 to more than 20 km^2 (Kruuk and Macdonald 1985). They are found in a wide variety of habitats, in some of which they live as pairs and in others they form groups of one male and up to five females (Macdonald 1981). Although overlap between neighbouring home ranges varies, most populations appear to be territorial. Variation between group and range sizes is most probably influenced by differences in the resource dispersion within the habitat and mortality. In a study area where the food was patchily distributed, there was no correlation between group and territory size (Macdonald 1981).

Meia and Weber (1995) reported that red fox home ranges in Swiss Jura mountains were small, ranging between 0.48 and 3.06 km^2 although a nomadic adult used a significantly larger area (12.71-25.90 km^2). Blanco (1986) reported home ranges of 1.13 km^2 from Sierra de Guadarrama (Spain). The former authors did not note any differences in home range size between subadults and adults, and attributed this to the similarity in body mass and hence energy requirements. Although small home range size could be possibly explained by a high food density during previous years, they mention that during their study, northern water voles (the main food for red foxes in the area) became extremely scarce and although foxes obtained food from other sources, overall food supply was poor. In such a situation one would expect home range size to increase to compensate for the loss of food. Such a strategy has a great disadvantage: to expand its territory each individual must fight against neighbouring conspecifics (Meia and Weber 1995). Sargeant (1972) discussed the spatial characteristics of red fox family territories and concluded: "The findings of this study and other studies suggested that red foxes have an innate minimum and maximum spatial requirement that was manifested in their territoriality. Within these limits, territory size was a reflection of population density, which in turn was dependent on overall environmental conditions. As densities of red fox populations diminished, the size of the territory of the remaining animals increased." Kruuk and Macdonald (1985) on the other hand, have expressed the idea that red foxes choose a minimum territory size for periods of food scarcity and share it with conspecifics when food is plentiful. Allen and Sargeant (1993) mention that red fox populations contain family groups that occupy well-defined, largely non-overlapping territories.

3.1.3.3. Movements

Red foxes typically move in a zig-zag fashion (Blanco 1986). Meia and Weber (1995) noticed that the travel route was different every night, allowing complete occupation of the home range after a few days. Oriented and non-oriented movements correspond to two ways of resolving the main problems affecting movements of red foxes. Foxes need to feed in favourable patches yet to be present, for territorial reasons, in other parts of the home range. This is achieved mainly by non-oriented journeys and this results in foxes not spending the greater part of the night in only one or two favourable patches but also moving extensively throughout their home range. Blanco (1986) reported daily movements of between 3.4 and 6.3 km. The larger the home range, the longer the distance travelled daily. This relationship is, however, characterised by an upper limit, which is set by the physical characteristics of red foxes (Goszczynski 1986a).

Allen and Sargeant (1993) reported that of 854 red foxes tagged in North Dakota (USA) 9.9% of males and 8.5% of females were recovered 80 km from the release sites. Three foxes were recovered more than 200 km from the release sites. It is obvious that red foxes have the potential to range very far over the habitat that they inhabit or possibly through several types of habitat during their life span.

3.1.4. Grey wolf (*Canis lupus*)

3.1.4.1. Habitat requirements and preferences

The grey wolf was originally the world's most widely distributed mammal, living throughout the northern hemisphere north of 15° N latitude (Mech 1990). Present distributions are much restricted; wolves occur primarily in wilderness and remote areas. In North America they are found throughout Canada and Alaska. In the rest of the United States, Minnesota has a viable population together with smaller populations in Michigan and Wisconsin. In Europe, there are small isolated populations in Sweden, Norway, Italy, Portugal and Spain where the species is endangered or threatened. Larger populations survive in the Balkan countries such as:

Greece, Albania, Bulgaria, former Yugoslavia, Romania and also in Poland, former Czechoslovakia and the former European USSR. Wolves occur throughout continental Asia apart from southern India and Indochina, with a status ranging from fully viable (USSR) to highly endangered (Lebanon) (Mech 1990).

Mladenoff, Sickley, Haight &Wydeven (1995) report that in northern Wisconsin and upper Michigan (USA), grey wolf pack territories have significantly greater proportions of mixed-hardwood forest and forested wetlands than areas not occupied by wolves. Mixed forest is the most prevalent of all cover types in wolf pack areas. Agriculture was the least common habitat type in areas used by wolf packs although it comprises 28% of the total area. Mean road density is much lower in pack territories than in the region overall. This reflects human avoidance strategies as human-caused mortality usually takes the form of hunting or deliberate, illegal killing of wolves and unintentional killing such as vehicle collisions (see also Blanco, Reig, de la Cuesta 1992, Okarma 1993).

3.1.4.2. Home ranges and territoriality

Wolves are a very interesting species as far as their spatial requirements are concerned as their social structure results in large-scale territorial behaviour. Grey wolf packs comprising an extended family and breeding unit occupy consistent territories. These packs are the subpopulation units that can move or become locally extinct, occupying habitat patches within the larger population area (Mladenoff *et al.* 1995). It has been suggested that grey wolf territories resemble elastic discs that are shaped primarily by population pressures and environmental resources. It is likely that such territories are entirely discrete only when minimum territory size is approached, probably due to increased efficiency when patrolling small territories (Ballenberghe, Erickson & Byman 1975). Mech (1977) reports from north-eastern Minnesota (USA) that grey wolf packs inhabit a mosaic of adjoining territories covering areas between 125 and 310 km^2, although Ballenberghe *et al.* (1975) estimated home ranges of 49 to 135 km^2 in the same area. Interestingly, between each territory lies a strip about 2 km wide, the "buffer zone", in which the pack on either side can be found but in which neither probably spends much time (Rogers, Mech, Dawson, Peek & Korb 1980, Lewis and Murray 1993). The main reason suggested for this is that wolves will try to kill members of neighbouring packs when they meet, and the maximum chance of an encounter is in the buffer zone. The rate of scent-marking by each pack in the buffer zone is about twice that in the core area, which suggests higher stress near the territory edge. Only when wolves become desperate for food do packs begin to trespass widely into neighbouring territories and only then begin killing deer in the buffer zone. Mech (1977) observed that packs occupied territories for at least 9 years. Furthermore, the spatial organisations of wolf populations would tend to keep boundaries stable because of the constant territorial pressure of adjacent packs. Hoskinson and Mech (1976) reported that when a pack began trespassing far into neighbouring territories preying on moose, they produced fewer pups, and slept much more. On the other hand, Thurber and Peterson (1993) observed on Isle Royale National Park that small groups (less than four) and solitary wolves roamed large areas of the island (300 to 540 km^2), frequently moving through territories of established packs (see also Ballenberghe *et al.* 1975). This did not happen with total impunity. One radio-collared female was killed by a pack near a moose she had killed in their territory. Some lone wolves were harassed, but not killed, by residents. One solitary male was observed on several occasions near kills that either he or they had made. On at least two occasions he was chased by the resident pack, but he either evaded them or was allowed to escape. A solitary female also seemed to be tolerated as close as 50 m to a pack. A second lone female was chased and caught by this pack and released later.

3.1.4.3. Movements

Ballenberghe *et al.* (1975) mention that radio-tagged wolves did not use their home ranges uniformly, but appeared to frequent certain specific sites while avoiding others. Individual adult wolves ranged widely during hunting forays, but returned regularly to resting sites frequented by their pups. The adult wolves were frequently absent from pack rendezvous sites during daylight hours and were found to range up to 13 km from the site, even pups ranged as far as 6.9 km, but the mean distance they ventured was less than that of the adults. Burkholder (1959) has demonstrated that grey wolf packs are capable of moving 56 to 72 km in a 24-hour period and may occupy territories of up to 12,950 km^2.

3.1.5. Stone marten (*Martes martes*)

3.1.5.1. Habitat requirements and preferences

Habitats used by the stone martens (*Martes foina*) differ from those used by martens that inhabit boreal forests (Buskirk & Powell in Herrmann 1994, Herrmann 1994). Stone martens are in many cases synanthropic, living even in the centres of European cities (Clevenger 1994, Powell 1994). Consequently, a wide variety of urban, rural, and forest habitat is available to stone martens. In Herrmann's (1994) study area in south-western Germany, high ranking habitats were most abundant in villages, whereas low ranking habitats were most abundant in farmland and forest. He also found that warm, dry resting sites were important to stone martens, particularly during winter. In villages, stone martens sleep in straw, hay, and roof insulation during winter. Resting sites in farmland and woodland, such as holes in the earth and trees were not as good. Cover and vertical structures provide protection against predators and facilitate foraging. The best cover was available in or near buildings, in gardens, along riverbanks, in hedges and thickets, and in semi-natural forest.

Stone martens, and more extensively so, pine martens (*Martes martes*) and American martens (*Martes americana*) are often associated with old forests (Power 1984, Slough 1989, Clevenger 1994a, Thompson and Harestad 1994). It is sometimes speculated that managed forests do not provide the same habitat quality as the former. The structural characteristics associated with old virgin forests (woody debris, large old trees with cavities, abundant shrub layer, diverse vertical structure) may be less abundant in managed forests (Brainerd, Helldin, Lindström & Rolstad 1994). On the other hand, forestry practices often create an abundance of dead and rotting trunks, branches and stumps in younger forests. Brainerd *et al.* (1994) found that pine martens preferred old forests during winter in two areas near the southern limit of the boreal zone in Norway and Sweden, but there was no such indication for spring and summer. If pine martens depend on old forests, they should exhibit a strong preference for such forests when they are scarce within their home ranges and prefer them less as availability increases; this was not the case. Large scale clear cutting may adversely affect marten populations (Thompson and Harestad 1994). The rather broad use of all the forest age classes indicated that pine martens were able to meet their requirements in forests altered by modern forestry practices. Additionally large trees and trunks with cavities excavated by black woodpeckers, were important to martens as natal dens, and found in a variety of forest types and ages in commercial forests. Martens have many predators (Pulliainen 1981, Hargis and McCullough 1984) including red foxes, golden eagles, eagle owls (*Bubo bubo*) and great grey owls (*Strix nebulosa).* Canopy cover probably influences habitat selection. Thompson and Harestad (1994), reviewing information on the effects of habitat change caused by commercial logging on American martens, found that coarse woody debris and large-diameter trees characteristic of old forests were needed for winter resting, maternal denning and to provide access beneath the snow surface to hunt small mammals in winter. This feature is characteristic of old conifer-dominated forest, as winter canopy in deciduous forest is thin and likely to provide less protection from avian predators than do conifer dominated stands. Furthermore, deciduous monocultures lack the structural diversity of older mixed forest. They also suggest that American martens generally avoid recent clear fells and will neither cross large areas with little canopy cover nor use direct-line travel between uncut edges. Regenerating successional forest (<45 years after clear fell) supported 0-33% of marten population levels compared with nearby uncut forest, depending on type of regeneration and amount of original forest removed. Thompson and Harestad (1994) speculated that timber harvesting may have long term effects on American martens when: a) the second-growth forest type is not favoured by martens even at the mature stage, and b) logging proceeds at an unsustainable rate so that insufficient habitat is available over a sufficiently long time to support martens. This could result in a local extinction. A usual case is the conversion of mature and old forest to short rotation plantation or pre-commercially thinned forest.

Buskirk, Forrest, Raphael & Harlow (1989) studied the winter resting site ecology of American martens in the central Rocky mountains (USA) and found that the most important winter home sites were in subnivean locations partially or entirely surrounded by coarse wood debris (CWD). This was probably because of the warm subnivean environment. The use of subnivean sites associated with CWD is probably due to the ability of these sites to trap small air spaces and to the low thermal conductivity of CWD relative to soil and rock. This characteristic of CWD prohibits the snow from melting around the animal as it would have done because of the radiated heat from the body surface.

3.1.5.2. Home ranges and territoriality

Herrmann (1994) reports from Southwest Germany that he found stone marten home ranges varying from 12 to 211 ha and concluded that four factors influenced their size:

a) *Habitat quality*. The higher habitat quality in villages was correlated with significantly smaller home range sizes.

b) *Sex*. Male home ranges were significantly larger than these of the females.

c) *Season*. The home range sizes of the stone martens appeared to vary seasonally. Home ranges of adults in particular were largest during summer and smallest during winter.

d) *Age and social status*. Size of home range and seasonal variation in size appeared related to an animal's age. The home ranges of adults were larger than those of juveniles or subadults, especially during the mating season.

Power, (1994) in a review of the published literature on spatial use by various *Martes* spp., reports ranges varying between 0.1 and 3.0 km^2 for stone martens and 0.4 to 58 km^2 for pine martens. Slough (1989) reports from Yukon Territory (Canada), male American marten home ranges between 6.0 and 7.3 km^2 and a mean of 1.9 km^2 for females.

Herrmann (1994) also observed that two males were never caught on the same site. Stability of home ranges and aggressive interactions observed near territory borders support the idea of exclusive male territories. Furthermore male home ranges were on average 1.8 times larger than female home ranges and larger than predicted on the basis of energetic requirements (see also Powell 1994). The major factor causing the disproportionate home ranges of males seemed to be related to mating; the largest home ranges were found during the mating season and not in winter when resources should be scarcest. Powell (1994) argues that although the total home range used by males and females is not proportional to their body size, the actual area used is. By maintaining territories as large as they can defend, male martens increase their chances that their territory will overlap with more than one female territory. Females increased their territories during the period that they were rearing their young. That probably compensated for the increased energy needs during this period and additionally it is possible for the young to stay longer with the mother giving them time to learn.

Buskirk and McDonald (1989) after reviewing 26 studies of the home range of the American martens found that mean male home-range sizes were 1.93 times larger than those of females although male body weights were only 1.5 times heavier. Mean home-range size showed no obvious geographic pattern. Mean annual temperature, latitude and longitude were not significantly correlated with home-range size.

3.1.5.3. Movements

Hargis and McCullough (1984) found that American martens travelled in all major habitat types, without any detectable habitat preferences. Pauses occurred only in forests, and on frozen streams. Martens travelled across <50 m wide meadows but did not rest or hunt in them. Meadows >50 m were crossed using the cover of scattered trees. The longest open distance crossed was 135 m. They avoided areas lacking cover and preferred areas with 100% cover, especially when pausing. Martens selected cover by travelling in a zig-zag pattern from one tree to the next. As a result, two-thirds of the travel points occurred less than 2 m from a tree.

3.1.6. Summary

From the studies reviewed earlier, two carnivores emerged as the ones with the largest home ranges: the brown bears and the grey wolves. Large areas are covered routinely by both carnivores but the most extreme value has been reported for a wolf pack that occupied a home range of 12.950 km^2 (Burkholder 1959). The area covered for the needs of this study could be only a fraction of an individual's or a family group's home range. The daily movements reported were those ranging from 5 to 25.5 km for brown bears and from 13 to 72 km for grey wolves, which were the most mobile carnivores.

Foxes travel a different route every night, thus allowing complete occupation of their home range after a few days (Meia & Weber 1995). Bears seem to have favourite trails that they use to travel through their home ranges (Weber 1987). These trails are generally the shortest distances between feeding and resting sites.

Martens are the only carnivores that are not entirely habitat generalists. Nevertheless, the only habitat requirement that martens have is sufficient tree cover. This provides them with protection from avian predators and additionally, cavities in tree trunks are often used as maternal dens and resting sites.

The habitat preference studies were reviewed in order to investigate whether the carnivores utilise particular types of habitat disproportionally to their availability. Such behaviour would have a direct effect on the deposition of faeces, creating accumulations in the preferred areas. However, as it was mentioned earlier the carnivores were habitat generalists to a large extent. Territorial animals clearly limit the number of conspecifics and sometimes heterospecifics that can utilise one area and therefore exclude them from feeding on the fruit in this area. The size of home ranges which are directly related to the mobility of the animal are of great importance for a study on seed dispersal, since they govern the maximum dispersal distances that a seed can be moved away from the parent plant. This will be described in the following chapters. The hypothesis that I am going to tast in this chapter is that all the carnivores have the same temporal and spatial distribution and that they use homogeniously all the altitudinal zones, substrates and habitats for the deposition of their faeces.

3.2 METHODS AND MATERIALS

Although some ideas have been put forward about how to use faeces counts as an index of red fox abundance (Cavallini 1994), it must be considered that while the distribution of faeces along the transects may be near-random, the preference of foxes for certain tracks may make the overall distribution biased. Additionally, differential defecation rates, influenced by food habits, digestibility of various food items, and physiological variations among and between individuals may confuse the estimation of absolute numbers. Furthermore, the amount of rainfall during the days before the collection of faeces also has an influence on their numbers (Cavallini 1994). In the following chapter, whenever the word "density" is mentioned, this refers always to faeces density and not to animal density.

To avoid bias arising from differential visibility of faeces due to different types of roads, transects were located along forest roads of similar width. The transects were the same with ones used for the vegetation surveys. Survey routes were walked by the author after sunrise and before dusk. Walking speed was equal for all routes. As all transects were wider than 2 m, they were divided in half and both laterals were covered, one side out and one back down. Some uncontrollable, often seasonal biases (weather, new tall grass, dead leaf cover, etc.) along the transects may have influenced the results. Each transect was searched at monthly intervals. Sampling started in May 1993 until October of the same year. Sampling was interrupted by snowfall in November, was resumed in May 1994 and went on until November 1994 when it was interrupted once again due to adverse weather conditions. Three transects were searched during November 1994, but for reasons of data consistency I excluded the samples for this month from the analysis. Data collected during May of the two years of the study were also excluded from the analysis as it is possible that these faeces had accumulated during late winter and early spring and were preserved under ice and snow. Faeces were also collected outside the transects for purposes of comparison but they are not included in the present analysis. Carnivore faeces were identified on the basis of their size and shape. Wolf faeces almost always contained hair and had a conical shape. The cone was up to 4 cm in diameter at its wider point. Fox faeces were much smaller very often containing only seeds and sometimes hair. They were more tubular than wolf faeces and had a maximum diameter of 2 cm; they often became white and chalky on weathering. Marten faeces were even smaller than those of fox, maximum diameter was 1.5 cm. They had a more conical shape than fox faeces and very often they were twisted. Feathers were present in the contents more often than the other carnivores. Bear faeces were the most distinctive, they had a flatened irregular ellipsoid shape with a maximum diameter of up to 30 cm and were almost always full of seeds (Photographs in Appendix III). There are a small number of stray dogs in the area which deposit faeces that can sometimes look similar to fox or wolf scats. These faeces were classified as "canid" or "unidentified" faeces and amounted to 12.2% of the total they were later excluded from the statistical analysis. They were analysed in the laboratory for identification of feeding items however.

3.2.1. Data recorded

Each carnivore faecal sample was stored in a plastic bag and numbered. All data were entered on a data sheet especially prepared for the sampling. Information collected about the faecal characteristics was concerned with faeces type and condition. An effort was made to estimate the age of the scat, but factors such as exposure to sun and rain complicated the estimations. The position of the scat along a particular transect was recorded using a GPS (MAGELLAN-NAV 5000 D, accuracy 10-100 m). The altitude was recorded using a barometric altimeter which was calibrated before every collection at a point of known altitude. The substrate on which the faeces was deposited was noted, as was the plant community, with the dominant tree and shrub species growing near the spot where the scat was collected.

3.3 RESULTS

3.3.1. The temporal distribution of faeces along the five transects

During the examination of the distribution of carnivores I was mainly concerned with whether each of the carnivores species used the transects in a different way. In order to analyse the effect of carnivore, transect and month on the frequency of faeces in the study area, I used analysis of variance (ANOVA) on the number of faeces collected per km (log-transformed) (Table 3.1). The ANOVA gave highly significant results for all main effects and their interactions. There was a significant difference ($p<0.001$) among the number of faeces collected from each carnivore with numbers declining in the following order: fox, marten, bear and wolf (see also Table 3.2). The number of faeces collected from each transect varied significantly ($p<0.001$). The higher frequency of faeces was found in Ahladorema, followed by Connector, Distropi, Krusovo and the Virgin forest which had the lowest frequency of faeces (Table 3.2). The effect of month was also highly significant ($p<0.001$) indicating a clear seasonality on the numbers of faeces collected. As the season progressed there was a steady increase in the numbers of faeces collected. Numbers collected increased in the following order: June, July, August, September, October (Fig. 3.1).

A significant interaction between transect and carnivore was found ($p<0.001$, Table 3.1) indicating that different numbers of faeces were collected for each carnivore on the five transects. This is also displayed in more detail in Table 3.2. Bear and fox faeces were found at the highest frequency on Ahladorema transect and with the lowest on Virgin forest. Marten scats were more numerous on Ahladorema also, but this time the lowest was Krusovo. Wolf scats were mainly found on Distropi but never found on Connector. The interaction of carnivore and month was also highly significant ($p<0.001$), as different numbers of scats were found for each carnivore as the year progressed. This is clearly demonstrated in Figures 3.1(a)-(d).

Source of Variation	Sum of Squares	DF	Mean Square	F	Significance
Carnivore (Ca)	234.96	3	78.32	137.93	$p<0.001$
Transect (Tr)	96.29	4	24.07	42.40	$p<0.001$
Month (Mo)	12.41	4	3.10	5.46	$p<0.001$
Ca-Tr	131.02	12	10.92	19.23	$p<0.001$
Ca-Mo	37.96	12	3.16	5.57	$p<0.001$
Tr-Mo	24.10	16	1.51	2.65	$p<0.010$
Ca-Tr-Mo	95.13	48	1.98	3.49	$p<0.001$
Residual	56.78	100	0.57		
Total	688.64	199	3.46		

Table 3.1. Results of ANOVA on the effects of Carnivore, Transect and Month on the logarithm of the frequency of faeces (faeces/km).

Transect		Bear	Fox	Marten	Wolf
Ahladorema	**Mean**	0.18	5.64	2.39	0.04
	SE	0.11	1.25	0.33	0.04
Distropi	**Mean**	0.10	2.36	0.84	0.22
	SE	0.06	0.36	0.20	0.13
Virgin forest	**Mean**	0.01	0.61	0.27	0.03
	SE	0.00	0.12	0.12	0.02
Connector	**Mean**	0.17	4.35	1.13	0.00
	SE	0.07	0.65	0.40	0.00
Krusovo	**Mean**	0.13	0.77	0.22	0.03
	SE	0.05	0.16	0.10	0.03
Average	**Mean**	0.12	2.75	0.97	0.06
	SE	0.03	0.40	0.16	0.03

Table 3.2. Mean frequency of faeces (faeces per km) and standard error (SE) collected on each transect.

Bear faeces were present in the area from August until October, with the highest numbers collected in September. In 1994 one faecal sample was found in each of June and July respectively, but this was exceptional. The peak value for fox faeces was in October and their presence was continuous throughout the study period. Martens displayed an irregular seasonality, with the highest numbers of faeces being collected in July with a second lower peak in October. Wolf faeces were mainly found in the area during 1993. Their distribution was very irregular and faeces were found very sporadically. The peak was found in October and it was much higher than any other month. In 1994 only one wolf scat was collected and that was also in October.

The interaction between transect and month was significant ($p<0.01$) as different numbers of faeces were collected on each transect each month. The Ahladorema transect usually had the highest frequency of faeces during the study period. This changed only in July when Connector was greater. Apart from this case, Connector usually averaged second each month with Distropi third. Krusovo and Virgin forest transects alternate between them for the fourth and fifth.

The significant effect of the three way interaction ($p<0.001$) can be more easily comprehended by comparing Figures 3.1(a)-(d) which demonstrate this combined effect. Bear faeces were found only on Ahladorema in June and only on Krusovo in July. The only time that they were found in Virgin forest was September. The frequency of fox faeces steadily increased from June to October. Ahladorema yielded a constant high frequency of fox faeces that increased to a maximum of 11.25 faeces/km in October, more than twice the values of the second ranking transect, Connector. Connector peaked in June and July but that was before forestry work started there. Distropi peaked in August, whereas Krusovo and Virgin forest had constantly low values, reflecting their disturbance by vehicles and logging activities. Martens were present in the area throughout the sample period with a peak in July. Ahladorema had the highest average frequency of marten faeces throughout summer and autumn. Connector and Distropi ranked next with similar frequency values. The faeces of wolves were present at the lowest frequency of faeces found in the study area. The peak of their occurrences came in October and apart from that there is no clear pattern of increase or decrease as the season progressed. The frequency was higher on Distropi transect, probably because it was the corridor to the lower areas where livestock were kept. The mean frequency of faeces ranged from 2.75 faeces per km for fox to 0.06 faeces per km for wolf (Table 3.2). The highest values for the frequency of faeces are those of fox on Ahladorema transect and the lowest from wolf on Connector transect.

Summarising, the highest frequencies of faeces were found on Ahladorema transect for all the carnivores apart from wolf where the highest frequency was on Distropi. Bear and fox faecal frequencies increase during the year, peaking in autumn. Martens and wolves had a more irregular seasonality with the latter appearing in the area only temporarily.

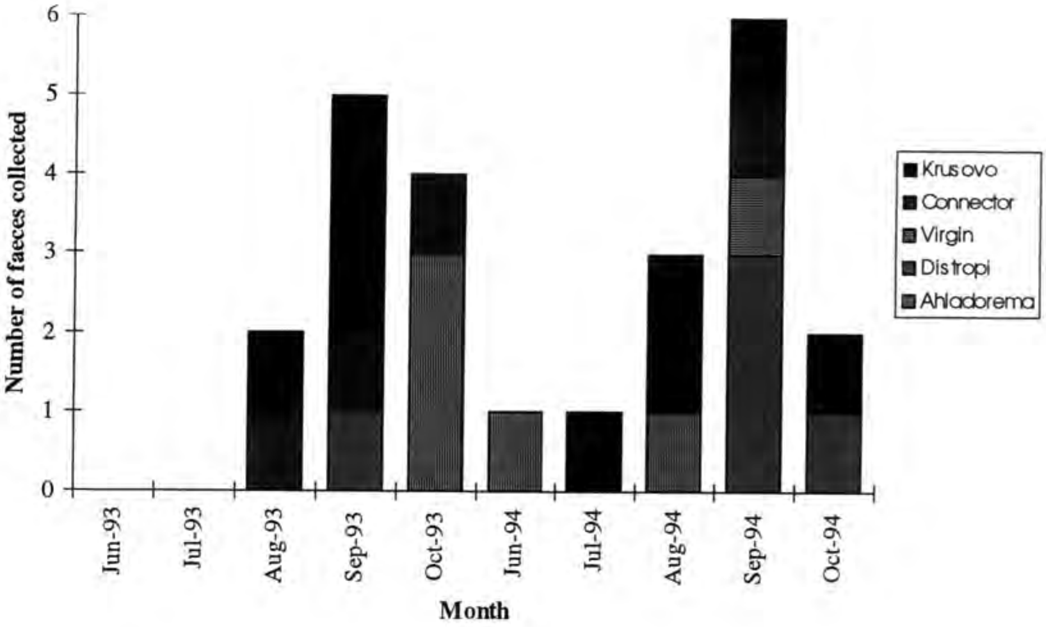


Fig. 3.1(a). The total number of bear faeces collected on the transects during the study period.

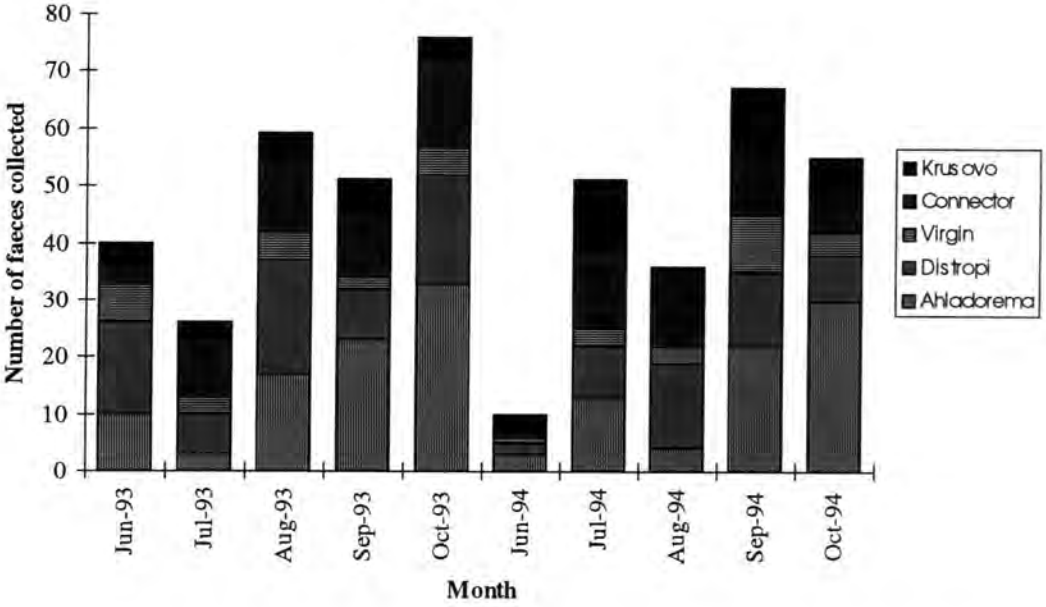


Fig. 3.1(b). The total number of fox faeces collected on the transects during the study period.

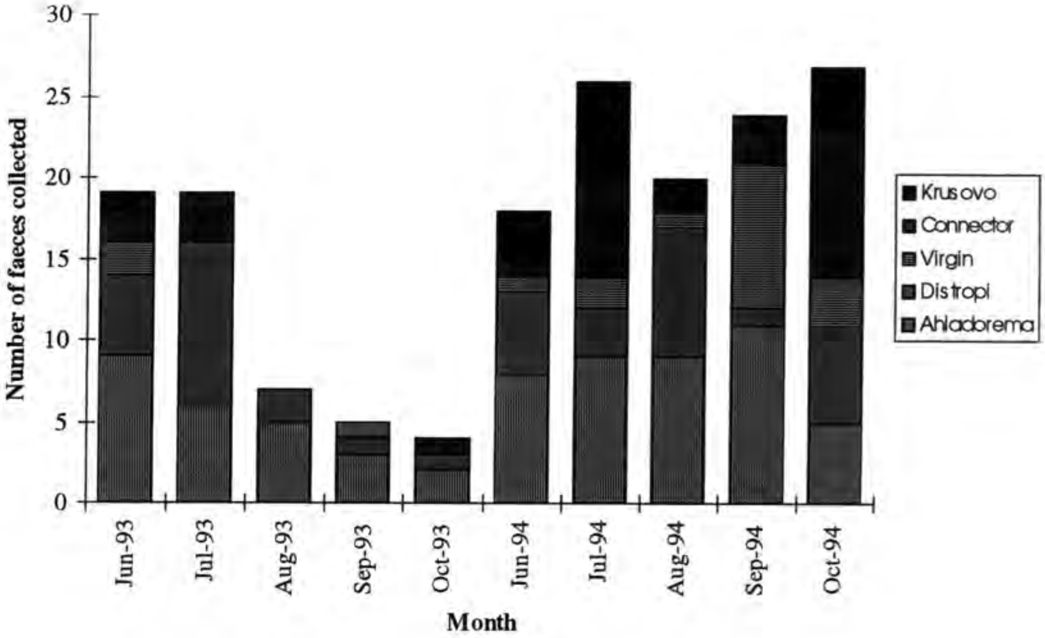


Fig. 3.1(c). The total number of marten faeces collected on the transects during the study period

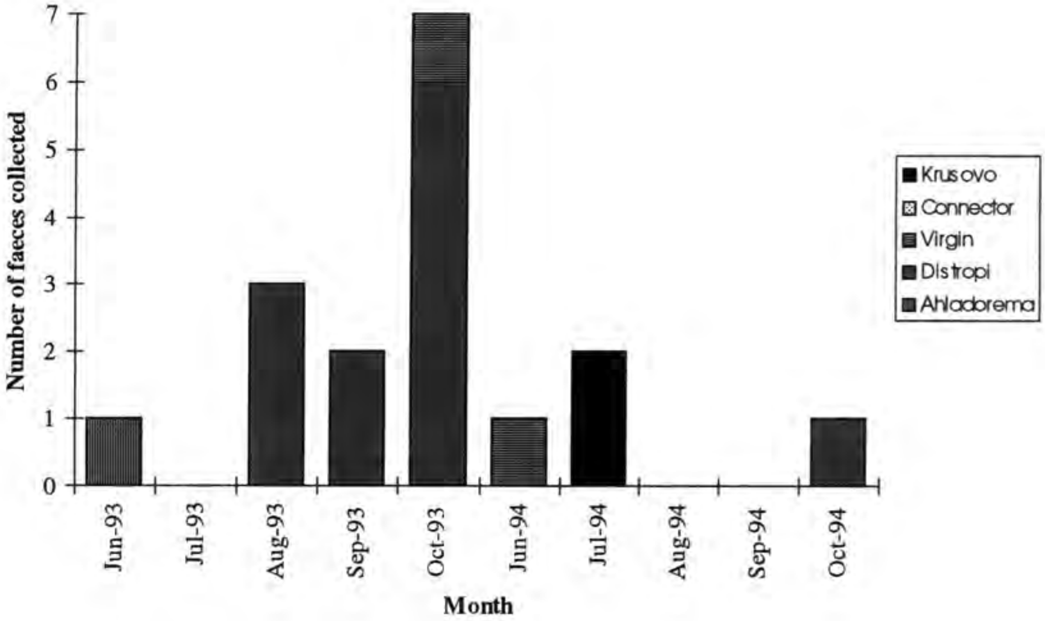


Fig. 3.1(d). The total number of wolf faeces collected on the transects during the study period

3.3.2. The distribution of faeces in relation to altitude

A contingency table was used to examine the extent to which each carnivore species utilised the altitudinal zones available in the study area. Wolves were excluded from the analysis because of their small sample size.

The distribution of the carnivores was homogeneous along all the altitudinal zones in the study area (Table 3.3.). Overall the contingency table was not significant ($\chi^2 = 4.898$, 6 d.f., $p>0.05$) but bears used the 1100-1300 m zone more and the 1500-1700 m zone less than the other carnivores. An equivalent usage of all zones was shown by foxes and martens.

ALTITUDE									
	900-1100 m		**1100-1300 m**		**1300-1500 m**		**1500-1700 m**		
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Total
Bear	9	11.03	17	12.76	3	3.90	0	3.70	29
Fox	209	212.99	248	246.31	75	75.34	28	36.97	560
Marten	76	69.98	75	80.93	26	24.76	7	8.33	184
Total	294		340		104		35		773

Table 3.3. Contingency table testing the null hypothesis that faeces have a homogeneous distribution along the altitudinal zones in the study area (wolf faeces not included due to small sample size) ($\chi^2 = 4.898$, 6 d.f., not sig.).

3.3.3 Deposition of faeces on different substrates

A contingency table was used to investigate whether some carnivores deposited their faeces on a particular substrate more often than others. Again, wolves were excluded from the analysis because of the small sample size.

There is evidence that in most of the cases the carnivores deposited their scats on different substrates ($\chi^2=23.47$, 6 d.f., $p<0.001$, Table 3.4.). Bears used stones as defecation substrates less than foxes and martens. Foxes deposited scats on stones proportionally less often than the other carnivores, but evenly defecated on all other substrates. Martens, on the other hand, deposited faeces on stone proportionally more frequently than the other carnivores. Gravel was used less by martens than was expected by chance.

	SUBSTRATE								
	Soil		**Stone**		**Gravel**		**Grass**		**Total**
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	
Bear	12	12.23	0	3.54	9	6.28	2	0.95	23
Fox	222	218.10	51	63.02	121	111.88	16	16.99	410
Marten	74	77.66	38	22.44	28	39.84	6	6.05	146
Total	308		89		158		24		579

Table 3.4. Contingency table testing the null hypothesis that carnivores use all substrates equally to deposit faeces on (wolves faeces were not included due to small sample size) (χ^2=23.47, 6 d.f., p<0.001).

3.3.4 Deposition of faeces within the plant communities of the study area

The available habitats within study area were grouped into five categories according to the dominant tree species present in each. From the contingency table it can be concluded that there was no disproportional use evident by any of the carnivores for any habitat (χ^2=2.31, 8 d.f., p>0.05, Table 3.5.). Therefore the plant community surrounding the transect did not seem to influence the utilisation of the transect by the carnivores.

Habitat		**Bear**	**Fox**	**Marten**	**Total**
Fagus sylvatica	**Obs.**	5	111	32	148
	Exp.	4.87	107.90	35.24	
Pinus sp.	**Obs.**	6	108	30	144
	Exp.	4.73	104.98	34.29	
Mixed broadleaves	**Obs.**	11	262	89	362
	Exp.	11.90	263.91	86.19	
Picea & Abies	**Obs.**	1	36	13	50
	Exp.	11.90	36.45	11.90	
Pinus & Fagus	**Obs.**	6	126	46	178
	Exp.	5.85	129.77	42.38	
Total		29	643	210	882

Table 3.5. Contingency table testing the null hypothesis that carnivores use equally all available forest habitats (wolf faeces not included due to small sample size) (χ^2 =2.31, 8 d.f., not sig.).

3.4 DISCUSSION

3.4.1. The distribution of the faeces along the five transects

The usage of each transects was not uniform even within the same season. Some carnivore faeces were found more often on particular transects whereas others had a more equal distribution. All the findings are based on the number of faeces collected on the established transects. As a result, I made the assumption that the faeces collected on the transects were representative of the faeces deposited outside the transects and within the rest of the habitat. However, there is a possibility that these transects had a higher concentration of faeces than the rest of the habitat if they were used as corridors for the movements of carnivores. Furthermore, we have to be aware of the possibility that the abundance of faeces is influenced by the proportion of plant material in the diet, as plant consumption may induce the deposition of a higher number of faeces, although Cavallini (1994) reported that there is a weak correlation between the two factors in his study of red foxes. He also suggested that the number of faeces found is strongly related to the amount of rainfall in the area during the days before the collection of scats took place, as heavy rain washes them away and light rain breaks them down. The driest months in my study area are July and August. In September and October the rainfall increases considerably. The highest number of faeces was collected in the study area during these two months. If Cavallini's observations were correct, it means that in September and October there were even more faeces deposited than the ones that I collected, but that they were destroyed by rain. Finally, the collected faeces were used only as an indication of the distribution of carnivores in the knowledge that accurate results on this matter can only be obtained by radio tracking, chemical markers and direct observations. Unfortunately, these facilities were well beyond the funding limits and man-power of this study.

The general outcome of the analysis of the distribution data is that Ahladorema transect had the highest faecal frequency for most of the study period, apart from July when Connector was greater with Distropi third, Krusovo averaged fourth place, and Virgin was usually the lowest. The importance of Ahladorema is easily explained when we consider that it was not used for forestry activities, had no vehicle traffic and even hikers rarely used it. Moreover, after an initial cropping the foresters do not return to the same stand until a decade has passed. As a result, no logging activities had taken place near the transect for at least five years. Therefore most of the secondary roads, opened to assist the removal of logs from the stand, were overgrown by vegetation or washed away by creeks. The plant community is very diverse, as the topography of the area protects it from exposure to severe weather conditions. The dominant tree species along the transect form a dense canopy providing cover to carnivores' activities. Furthermore the transect runs next to a creek which provides the animals with easy access to water so as to reduce the stress caused from the heat during summer and early autumn.

Connector transect runs through very steep slopes and is situated on the top of Ahladorema gorge. Landslides are common in the area around the transect. I suggest that it is easier for the carnivores which move in the area to follow the forest road to get to the food sources. The transect was not used for forest activities during the first year, and only partially during the second, which most possibly affected the number of faeces collected on this transect. It is relatively free of ground vegetation and therefore faeces are readily detectable. It is likely to be used by bears as a corridor between the lower altitude feeding areas towards the Virgin forest and Krusovo feeding grounds. This is supported by the number of bear tracks found along the transect.

Distropi is an undisturbed transect, but a part of it is overgrown by ground vegetation which makes the detection of faeces very difficult. Furthermore, it has the lowest fruit production among the transects (Table 2.8). It runs through a variety of habitats including pine stands, open shrubland, beech, oak and mixed stands. Brown bear tracks are often found on this transect, mainly because there are patches of mud where tracks are easily identifiable, in contrast with the stony or dry surface of the other transects. It also forms a continuum with Connector transect (see Map 2.2.) to the lowland shrubland outside the research area which has high fruit production.

The last third of the Krusovo transect lies within a tree-shrub habitat with high fruit production. Although this should attract many frugivores, the intense usage of the transect for forestry purposes probably disturbs the animals. This road carries a lot of traffic which, apart from the disturbance, destroys some of the faeces deposited on it. Furthermore, during August and September a nomadic herd of cattle grazes in the area with shepherds and dogs that make it less attractive to carnivores with the possible exception of wolves.

Virgin forest was heavily used for forestry activities during the two years of the study. There was an almost constant noise heard on the transect during daytime, mainly from chain saws and log-transporting vehicles. A relatively high number of cars were using the transect (5-10 per day) which, as far as bears are concerned, may be more disruptive than constant traffic, to which animals can become habituated more easily (Servheen, personal communication). Apart from the traffic, other forestry activities such as the removal of the bark from the trees that had been cut down and loading of the logs on trucks were also taking place on the transect. The surrounding vegetation mainly comprises spruce, beech and pine. Thus the availability of food is low for most of the year, apart from August-September when raspberries come into fruit.

Clevenger *et al.* (1992c) reported from Spain in his study of bears that the shortest distance between feeding sites or daybeds and a little used forestry road was about 800 m, which seems to agree with Servheen (personal communication) who claims that there is a strip of 500 m on either side of forest roads where animals can sense the cars and therefore avoid them (see also Weber 1987). Wolves also avoid roads and prefer habitats where road density is low (Mladenoff *et al.* 1995). The presence of foxes and stone martens even in the middle of cities (Macdonald 1987, Clevenger 1994a) indicates that those particular populations of these adaptable carnivores are not negatively affected by the presence of roads in their habitat.

Brown bear tracks were found on the transects Distropi and Connector from time to time, indicating that these transects were used as corridors between feeding areas or that the areas surrounding the transects were carrying more bear activity. Fox and marten tracks were found on all transects with fox tracks being much more numerous. The lower number of marten tracks might reflect the arboreal life style of the animals or lower population densities than foxes. Foxes are known to occasionally be predators of martens when on the ground (Pulliainen 1981). This could also be a result of their overlapping diets as reported by Serafini & Lovari (1993). Thus where foxes are numerous martens might be forced to minimise the time that they spend on the ground. A number of large-sized dogs were present in the area and, as a result, I was never very sure whether the tracks were left by dogs or wolves.

If the frequency of faeces on a transect is an indication of carnivore activity, then there is little doubt that Ahladorema transect is the centre of activity in the study area. The only time that this changes is in July when Connector has more carnivore activity. The first two halves of Ahladorema and Connector are within 2 km of each other (straight line distance). It is therefore possible that the two transects could fall within the home ranges of the same carnivores (Goszczynski 1986a). Thus the shift in faecal frequency could be a spatial shift in the carnivores' activity from one side of the home range to the other. This could be triggered by disturbance avoidance or as an effort to take advantage of favourable conditions. The second half of Connector is close to part of the Distropi transect, so a spatial shift between these two is also a possibility.

Spatial shifts of home range can only be considered for martens and foxes as bears and wolves could routinely traverse the entire study area. It is possible for these large carnivores that the faeces collected were from the same individuals on all the transects.

3.4.1.1. Estimated numbers of carnivores

During this chapter I have often referred to the number of faeces collected and to their distribution. This raises the question of how many animals were depositing these faeces. Was this just one individual, or was there a large population? I will try to estimate this by comparing the size of my study area (53.122 km^2) with the size of home ranges that have been reported for carnivores. Because of the large variation between the area covered by the home ranges that have been reported for each carnivore, the range of estimated numbers is very broad.

Bear ranges were reported to be from 12-2600 km^2. As a result, up to five bears could be inhabiting the area but the most possible situation is that the study area was just a part of one individual's home range. Wolf ranges have been reported to be from 49 to 12950 km^2. Therefore one or two packs could be patrolling the area, with 3-15 animals using the area temporarily. Fox home ranges cover an area from 0.1 to 25.6 km^2, hence the number of animals that the area could support is 2-531. Stone martens have the smallest home ranges among the carnivores studied, ranging from 0.1 to 3 km^2. Thus their estimated population is 18-531 animals.

3.4.2. The distribution of faeces and the seasonal changes

It can be seen from the analyses of the deposition of bear faeces that there was a strong seasonality. Numbers reached their peak in September, but nevertheless, there was no evidence of a spatial shift as numbers increased simultaneously over all five transects. The only surprising fact was the complete absence of bear faeces from Ahladorema transect during this month. The mating period of bears extends from May to mid July with the peak in June (Ewer 1973; Pearson 1975; Herrero & Hammer 1977; Clevenger *et al.* 1992b), low numbers of faeces collected in the early season coincided with the period of oestrus and mating which possibly take place away from the study area. They may also coincide with post-den-emergence hypophagia (Mattson, Blanchard & Knight 1991). An explanation for the peak of activity in late summer-autumn period would be that it coincides with the hyperphagia-the period during which they accumulate fat before the winter, and when they need to consume as much food as possible (As is discussed further in Chapter 4).

The frequency of fox faeces increased steadily from June to October. Ahladorema has a constantly high concentration of faeces which increased to a maximum of 11.25 faeces/km in October, more than two times greater than the value of the second transect (Connector) at that time. Connector's values peaked in June and July which was before forest activities started on it. Distropi values peaked in August. Krusovo and Virgin forest had constantly low values, which I believe reflected their use by traffic. Cavallini (1994) reports that the highest frequency of faeces (>1.5 samples per km) in spring (March to May) and summer (July and August), and the lowest (<1 sample per km) in autumn (October to December). The mating period of foxes extends from the beginning of January to February and therefore any changes in the animals' behaviour would not affect my data as this is outside the study period. I believe that for foxes, as well as with the bears, the high faeces' frequency in October reflects an effort to store energy for the winter.

Marten faeces were found to be present in the area constantly (see Fig. 3.1(c)) with a peak production of faeces in July. Ahladorema had the highest average frequency throughout summer and autumn. Connector and Distropi came next, with similar frequency values. Clevenger (1994b) reports that in Minorca (Spain) the highest frequency of pine marten scats occurred during July-August and the lowest during September to December. The peak in July coincides with the peak of the mating season of martens (Ewer 1973, Herrmann 1994) when males are maximising the size of their home range. As martens are territorial and maintain exclusive home ranges, they probably increase their activity by patrolling their home range in search of intruders and receptive females resulting in an increase of their energy requirements and consumption of food. By that time females are still looking after cubs and therefore have increased energy requirements as well (Pellew 1984).

Wolf scats were the least common in the study area. The peak of their occurrence came in October and, apart from that, there is no clear pattern of increase or decrease as the season progresses. The activity was higher on Distropi transect, probably because it is the corridor to the lower areas where livestock are kept. Wolves mate between January and April (Ewer 1973, Mech 1990) and therefore any changes in the activity patterns of these animals during this period would not affect my results. Additionally, the sample size of wolf faeces was too small to draw any effective conclusions.

It is possible to detect some general trends in the way that the carnivores' faecal frequency is related with seasonality. For bears, foxes and wolves, I found the highest faecal frequency during early autumn, although the sample of wolf faeces was small. This was probably an effort by the carnivores to consume more food and build up their fat reserves for the winter. Marten-faeces numbers peaked in July and this coincided with the peak of the mating period. I suspect that this was a result of higher food consumption in order to compensate for the increased energy expenditure that mating demanded. This is generally more pronounced for the males.

Another explanation of the higher faecal frequency could be the increased use of transects as a result of reduced human disturbance. However, this hypothesis can be rejected straight away, as early autumn was one of the busiest times of the year as far as forestry operations were concerned. I do not believe that foxes and martens living outside the study area would move in to take advantage of the increased food supply because the relatively small size of their home ranges would not allow movements of such a scale. The situation with wolves was probably that the study area was part of the family groups home range (considering the size of the home ranges) that was moving into the area in autumn following a nomadic herd of cattle. The higher occurrence of wolf faeces that coincided with the arrival of the heard and herdsmen reports of attacks to the cattle come to support this theory. Wolves' territoriality would not allow any conspecifics to enter their territory, even during periods of food abundance. Bears are probably the only carnivores which could migrate into the area from elsewhere just to congregate where food was abundant without much conflict (Pearson 1975, Craighead 1976).

3.4.3. The distribution of the faeces in relation to the altitude

Analysis of the frequency of faecal samples collected over the altitudinal range revealed an homogenous distribution. Martens and foxes used all the altitudinal zones almost equally. These carnivores regularly prey on small mammals and supplement their food with fruit, therefore they do not have to restrict themselves in the altitudes where fruit production is higher. Additionally, there is no indication in the literature that they prefer particular altitudinal zones. Moreover, they are not as sensitive to human disturbance as are bears and wolves. The avoidance of the 1500-1700 m zone within the Virgin Forest transect by bears should be attributed to the human disturbance. This is supported by the evidence of bears where Virgin forest transect ended, and in the strictly protected area where human activities are not allowed. Although the altitude is approximately the same or even higher in this area, bear and fox faeces were frequently found there. The concentration of bear activity in the lower altitudes agree with Clevenger *et al.* (1992c) who found that brown bears in the Cantabrian Mountains (Spain) selected areas much lower in elevation than expected. Though it appeared that the bears might utilise lowland areas, they were situated far above the average elevation of the 28 villages in their study area, which is another indication of human avoidance. Subalpine and alpine habitats formed approximately one-third of their study area; however they were generally limited in food for bears and were highly exposed. The most productive habitat offering a wide variety of foods and also protection, was a multi-community complex of deciduous forest, shrubland and grassland situated in the montane zone, located between 1100 and 1400 m. Clevenger *et al.* (1992c) concluded that: "Within this narrow band are fragmented stands of native beech and oak forests that are critical in maintaining this remnant brown bear population."

3.4.4. Deposition of faeces on different substrates

An analysis of the deposition of faeces on different substrates showed some interesting features. Bears were defecating proportionally less frequently on stones than other carnivores. Stones do not seem to have the importance that they have for martens when presumably brown bears are not territorial (Craighead 1976). It seems that the lack of territoriality of brown bears does not force them to make an effort in order to make their faeces conspicuous. Observations by Weber (1987) in Romania suggest that faeces do not play an important role as markers or signals and Ursidae do not have any external scent glands (Macdonald 1985) suggesting that scent marking is probably minimal.

Johnson (1973) documented that in mustelids, scats serve a communication function and are often deposited in conspicuous sites, hence they have a tendency to be non-randomly distributed. Martens, in the present study, deposited faeces on stones more often than the other carnivores, probably serving their territory marking needs in this way. Many territorial carnivores leave token faeces on stones as they elevate faeces to nose level and therefore make them easily detectable (Gorman and Trowbridge 1989). Similar observations were made by Hargis and McCullough (1984) where American martens scent-marked small, snow-free rocks and urinated on top of rocks covered by snow. Foxes did not go to great length in order to select a particular substrate and deposited faeces on the substrates according to their availability.

3.4.5. Deposition of faeces within the plant communities of the study area

No significant trends were apparent from analysis of the distribution of the carnivore faeces within distinct plant communities. Probably all the forested areas were equally good for providing cover and hunting grounds. Bears, foxes and wolves have not been reported to be habitat specialists (Knight 1980, Macdonald 1987, Artois 1990, Mech 1990, Clevenger *et al.* 1992c).

Clevenger (1994a) also found that pine martens "...showed no preference for any of the available habitat types, as they used them all in proportion to their availability." He also claims that the foraging habitat of the pine marten is distinctly shrubland and open areas although Hargis and McCullough (1984) suggest that martens avoid open areas and prefer those with good cover to minimise the risks of predation from eagles and owls. The potential avian predators e.g. golden eagles (*Aquila chrysaetos*), eagle owls (*Bubo bubo*) and great grey owls (*Strix nebulosa*) are absent from the Balearic Islands, therefore overhead cover would not be expected to be an important factor affecting pine marten habitat choice there (Clevenger 1994a).

Mladenoff *et al.* (1995) found that in northern Wisconsin and upper Michigan, wolves use some habitats more often than others, but they concluded that because the grey wolf is a top carnivore, they are not habitat-specific to a vegetation structure or ecosystem type. Clevenger *et al.* (1992c) found that brown bears showed a strong preference for forested habitats in the Cantabrian Mountains (Spain), using the beech and durmast/Pyrenean oak vegetation types more frequently than in proportion to their availability. Surprisingly, the pine plantation class, which constituted only about 1% of their study area, was also used more frequently than expected. The remaining vegetation types, heath-broom, montane grassland, subalpine shrub-grassland and rock outcrop, were all under-used by bears. Bears also selected areas at a greater distance from villages and further from roadways than expected by chance.

To summarise, the Ahladorema transect had the highest faecal frequency with Connector, Distropi, Krusovo and Virgin forest following in diminishing order. The main factor that limited the utilisation of transects by carnivores was most probably human activity. The numbers of fox and bear scats increased in the autumn probably because of higher food intake in an effort to accumulate fat for the winter. Marten scat numbers peaked in July and this most probably reflects a higher food intake to compensate for the high energy expenditure during mating and rearing of the cubs (Corbet & Ovenden 1980). All carnivores used all altitudinal zones homogeneously, apart from bears who showed a higher usage of the 1100-1300 m zone in comparison with the other carnivores. Martens were the only carnivores showing a higher usage of stones as faecal deposition substrates, but there was a similar use of all habitats available by all the carnivores.

CHAPTER FOUR

THE IMPORTANCE OF FRUGIVORY IN THE DIET OF THE CARNIVORES

4.1. INTRODUCTION

The carnivore's life is full of decisions, and wrong ones are often costly and sometimes fatal. Even in the unsophisticated business of finding food, mammals face a plethora of choices of when, where, how much and how often to eat. The problem of deciding what to eat is worst for species with omnivorous or generalists diets, because the more varied their menu, the more choices they face. The omnivore must not only eat enough quantity to provide energy, but also select the right quality to provide a balanced diet (Macdonald 1995).

The main aim of this chapter is to investigate the factors affecting the frugivorous habits of carnivores. This will provide us with an insight on the importance of carnivores in assisting fruiting plants to colonise new habitats. I will test the following hypothesis:

- Do carnivores consume the same species of fruit throughout the year?
- Do carnivores consume fruit homogeniously from all the fruit producing species?
- In a given short time-period do carnivores restrict their feeding to one species of fruit?
- Do carnivores cause similar levels of damage to all the species of seeds?

For the rest of the introduction to this chapter I present a literature review on the importance of frugivory in the diet of the four carnivores of interest. In most of the studies reviewed in the following chapter, the frequency of occurrence of various items was the most common method of presenting the results of diet analysis (Table 4.1.). Hence the results of this study were presented in the same manner, whenever

Carn.	Publication	Area	%	Species
Brown bear	Servheen 1983	Montana, USA	-	*Crataegus sp., Malus sp., Prunus sp., Pyrus sp.*
	Slobodyan 1976	Carpathians, Romania	-	*Fragaria sp., Rubus sp., Vaccinium sp., Malus sylvestris, Rosa canina*
	Pearson 1975	Yukon, Canada	-	*Vaccinium sp.*
	Mattson *et al.* 1991	Yellowstone, USA	4.3	*Vaccinium scoparium, V. globulare*
	Elgmork & Kaasa 1992	south Norway	-	*Vaccinium sp.*
	Cicnjak *et al.* 1987	Plitvice Lakes, Yugoslavia	64	*Prunus sp., Pyrus sp., Malus sylvestris*
	Clevenger et al. 1992d	Cantabrian mountains, Spain	27.2	*Vaccinium myrtilus, Malus sylvestris, Rubus fruticosa, Rosa canina, Crataegus monogyna, Sorbus sp.*
	Frackowiak &Gula 1992	Bieszczady mt., Poland	30.4	*Pyrus communis, Vaccinium myrtilus, Rosa canina*
	Berducu *et al.* 1983	Pyrenees, France	39	*Vaccinium myrtilus, Rubus idaeus, Sorbus aucuparia, S. aria,*
	Giannakos *et al.* 1991	Rhodope, Greece		*Prunus avium, Prunus cocomilia, Rubus idaeus, Cornus mas, Rosa canina*
	Adamakopoulos 1991	Pindus mts, Greece		*Vitis sp., Rubus idaeus*
Red fox	Hernández 1993	Cantabrian mts	> 50	*Rhamnus alpinus, Rubus sp., Prunus avium, Arctostaphylos uva-ursi, Vaccinium myrtilus*
	Papageorgiou *et al.* 1988	northern Greece		*Vitis vinifera, Pyrus communis, Malus sylvestris, Pyrus amygdaliformis, P. pyraster, Prunus pseudoarmeniaca, Prunus persica, Prunus armeniaca, Morus alba, Ficus carica, Cornus sp.*
	Macdonald 1981	Oxford, UK	16-25.5	*Rubus ulmifolius, Malus sylvestris*
Red fox	Cook & Hamilton 1944	New York,	73	*Fragaria vesca, Rubus sp., Malus*

		USA		*sylvestris, Prunus sp., Vaccinium sp., Amelanchier sp., Crataegus sp., Vitis sylvestris, Viburnum sp.*
	Goszczynski 1986b, 1992	Central & West Poland	6.5	
	Jedrzejewski 1988	Bialowieza, Poland		*Malus sp., Pyrus sp., Rosa canina*
Grey wolf	Ballenberghe *et al.* 1991	Minnesota, USA	6.6	*Rubus sp., Vaccinium sp., Prunus virginiana, Amelanchier sp.*
	Meriggi *et al.* 1991	Apennines, Italy	26	*Rosa canina, Malus sylvestris, Pyrus sp., Prunus sp., Sorbus sp., Rubus sp.*
Pine marten	Goszczynski 1986	Central Poland	37	*Prunus avium, Rubus idaeus, Pyrus communis, Malus sylvestris, Prunus sp.*
Pine marten	Clevenger 1993a	Minorca, Spain		*Rubus ulmifolius, Ficus carica, Vitis vinifera, Malus domestica, Prunus sp., Juniperus phoenicea*
Pine marten	Clevenger 1993b	Minorca, Spain	80.6	*Rubus ulmifolius, Arbutus unedo, Sorbus aucuparia, Crataegus monogyna, Prunus sp., Rubus sp., Rhamnus sp.*
Pine marten	Lockie 1961	Ross-shire, UK	56*	*Sorbus aucuparia, Vaccinium vitis-idaea*
Stone marten	Lucherini & Crema 1993	Torino, Italy	53.7	*Rosa sp.*
Amer. Marten	Hargis & McCullough 1984	Yosemite, USA	14	*Juniperus sp.*
Stone marten	Hernández 1993	Cantabrian mountains	100	*Arctostaphylos uva-ursi*
Amer. Marten	Buskirk & MacDonald 1984	S-Cent. Alaska, USA	20.5	*Vaccinium uliginosum, Vaccinium vitis-idaea, Rubus idaeus, Rosa acicularis*

Table 4.1. Studies which refer to carnivores consuming fleshy fruit. Percentages indicate the frequency of appearance of the fleshy fruit in the diet of the carnivore studied.
* Percentage of weight.

results were given in more than one way, the frequency of occurrence was selected for inclusion here. Cook and Hamilton (1944) suggest that this method is one of the best among the ones used to represent the findings from faecal analysis but this view is not universal since it underestimates or overestimates particular food items.

4.1.1. Brown bear

One of the first aspects of brown bear natural history usually investigated by research workers is their food habits. Information has been published on bear diets in the Smoky Mountains (Beeman & Pelton 1977), Karluk Lake, Kodiak Island Alaska (Berns *et al.* 1980), California (Assembly Interim Committee Reports 1954), Yellowstone (Cole 1972), Montana (Mace & Bissell 1985), Baikal region (Ustinov 1976), the Carpathians (Slobodyan 1976), the Southern Urals (Sharafutdinov and Korotkov 1976), Hokkaido, Japan (Ohdachi & Aoi 1987), Pindus mountain range (Adamakopoulos 1991), the Pyrenees (Berducou, Faliu & Barrat 1983; Camara 1983), Abruzzo National Park, Italy (Zunino and Herrero 1972, Zunino 1981), Norway (Mysterud 1980, Elgmork 1982), Cantabrian mountains, Spain (Clevenger, Purroy & Pelton 1992d), and Plitvice Lakes National Park, Yugoslavia (Cicnjak, Huber, Roth, Ruff & Vinovrsky 1987).

Most researchers have reported that brown bears feed heavily on vegetable matter immediately after emergence from the den in the early spring. Adamakopoulos (1991) reports that brown bears fed on herbs in the spring and on cereal grains. During summer they preferred insects, *Prunus avium* and other fruit. Later in autumn they increased their activity to accumulate fat reserves for the winter, and fed on grapes (*Vitis vinifera*), wild fruits, *Rubus idaeus*, acorns and mushrooms.

For the Rhodope Range of Northern Greece it was found (Giannakos *et al.* 1991) from scat analysis' that during summer brown bears depended heavily on *Prunus avium* and *Prunus cocomilia* for their subsistence. During this part of the year the animals caused extensive damages to fruit trees. Ants and carrion also appeared occasionally. In autumn, soon after *Rubus idaeus* ripened, they were heavily utilised by the bears. Later in the season bears fed on the berries of *Cornus mas* and *Rosa canina.*

In the Carpathian mountains of Romania, Slobodyan (1976) reported that brown bears apparently fasted in early spring when they leave their dens and do not find sufficient food available. They frequently preyed on wild animals, particularly ungulates, occasionally wild boar but there have also been cases of livestock being attacked by bears. They were also feeding on carrion, often in an advanced state of decomposition. Bilberries, green aspen shoots, willow, birch (*Betula* sp.), various herbs, forest fungi and other green vegetation was also consumed, later in the season. The diet of bears in the summer consisted of stems and leaves of forest herbs, thistles, French willow and others. They also scratched the trunks of spruce and firs, striped off adjacent pieces of bark, licked the sap and gnawed the exposed bark with their teeth. Later in the summer they fed on whortleberries (*Vaccinium scoparium*), strawberries (*Fragaria vesca*), bilberries and raspberries (*Rubus idaeus*) as these became available. Autumn was the most important period for bears since it is at this time that they complete the build-up of their reserves then they ate mature *Rubus* sp., *Sorbus aucuparia* berries, the apples of *Malus sylvestris* and common pears (*Pyrus communis.*), clachthorn and *Rosa* spp.

In Finland the percentages of ungulate protein, ants, and other insects were conspicuously high from May through July (Pulliainen 1985). During this period, berries, roots and other plant matter were of minor importance. Once the berries had ripened in August, they became important diet items. In south Norway, berries were very important (Elgmork and Kaasa 1992), particularly *Vaccinium* spp. and *Empetrum* spp. were the main items found in brown bear faeces which were collected on or in close proximity to caching sites where the bear had killed or eaten sheep. Bears ate relatively large quantities of berries, even when ample amounts of fresh meat were available (found also by Pearson 1975).

Cicnjak *et al.* (1987) found in Plitvice Lakes National Park, Yugoslavia, that herbaceous plants, mostly grasses, lords and ladies (*Arum maculatum*), and ferns were the most important components of the brown bear diet from March to May and represent the only major foods available. Lords and ladies occurred in 67% of the spring scats, whereas young grasses and ferns occurred in 78%. In summer, the green plants of spring were replaced in the bear diet by cultivated oats and summer fruits (*Prunus avium, Rubus fruticosus*). Oat consumption peaked in August and early September. Bears consumed large amounts of oat seeds (12% of total scat volume, present in 70% of summer scats). The autumn diet was composed primarily of fruits, particularly *Prunus cerasifera, Pyrus communis* and *Malus sylvestris* (53% of volume), and nuts (33% of autumn scat volume). Fruits occurred in 64% and nuts in 38% of the scats. During that period, they observed claw marks of bears that climbed hazel (*Corylus avellana*) trees and plum trees to feed on the fruit before the fruits dropped. During the pre-dening period, bears depended heavily on beechnuts (*Fagus sylvatica*). Irregular annual production of beechnuts may result in nutritional deficiency in bears in years when availability of these nuts is low. This study also shows that insects were the most frequently eaten animal food (22% of scats) but comprised only 1% of diet volume. Underground nests of wasps (Vespidae) and ants (Formicidae) were excavated by bears during summer and autumn; larvae and adults were consumed. Intensive digging for small mammals occurred in autumn, and parts of mammals were found in 3% of the scats. Evidence of bears preying on cattle and sheep was also documented during the study.

Clevenger *et al.* (1992d) reported from the Cantabrian mountains in Spain, that herbaceous plants (grasses and broad-leaved annuals) were consumed most frequently in spring and comprised the largest seasonal contribution of any food category (83.7% mean-total volume, 86.9% frequency of occurrence). Newly-sprouted grasses, particularly wavy-hair grass (*Deschampsia flexuosa),* appeared to be eaten most. In summer, lesser proportions of herbaceous material occurred (40.9%), but it was still the dominant food item. Fleshy fruits were heavily utilised (22.2% of mean volume) such as blueberries and alpine buckthorn (*Rhamnus alpinus*) when they ripened during August. In autumn, hard mast (nuts and acorns) peaked in mean volume (61.5%). It was strongly selected during both seasons and was found in 80.7% of the autumn faeces. Acorns (*Quercus* sp.) were eaten in greater quantities than beechnuts (34.0 and 24.4%, respectively). Hazelnuts were rarely consumed, appearing in only 3.4% of the scats. To the fleshy fruits (27.2% of faeces) there was a third addition, *Malus sylvestris*, maturing at the end of the season. Also present, though in small proportions were the fruit of *Rubus fruticosa, Rosa canina, Crataegus monogyna, Ilex aquifolium* and *Sorbus* sp. In winter, herbaceous material occurred in 32.1% of the faeces. Hard mast was found in 60.9% of the faeces. Soft mast (98% *Malus sylvestris*) consisted 12% of the mean volume. The proportion of ungulates in the diet was small, but consistent among seasons and it was the second most important food category during spring, accounting for 9.6% of the total volume. Most were taken in summer (13.2%) with the predominance of sheep and cattle. In autumn, ungulates formed 11.1% of the volume of faeces analysed and livestock was the predominant food type. Brown bears rarely fed on ungulates in winter when they contributed only 5.6% of the total volume of faeces and appeared in 7.1% of the sample, again, livestock were mainly consumed. Insects were encountered in the remains of faeces only during spring and summer. They were eaten mostly during summer (19.5% mean volume) and bees and ants in roughly equal proportions. Attacks on beehives occurred mostly in summer.

Frackowiak and Gula (1992) reported from the Bieszczady mountains of Poland that beech nuts, pears, oats and maize comprised the largest dry weight fraction in autumn samples. In spring, beechnuts and maize alone amounted to over 10% dry weight of faeces. In fact, beechnuts seemed to be a key element in the pre-hibernation diet, so much so that they believe that a drop in beechnut production, which occurs every few years may negatively influence the build up of fat reserves as well as the bears nutritional status in the difficult post-hibernation period. Pears also appeared to be an important component in the autumn diet (present in 30.4% of the faeces). In their study area numerous abandoned orchards were an abundant source of these fruits. Furthermore, hazel nuts and blueberry were present in 13% of the autumn diet and in spring *Rosa canina* appeared in 4.3% of the scats which were presumably fruits from the previous year.

Berducu *et al.* (1983) found that in the Pyrenees the diet of brown bears consisted up to 39% of berries, mainly blueberries with a frequency of occurrence of 22.3% in the faeces analysed, *Rubus idaeus* (6.6%), *Sorbus aucuparia* and *S. aria* (3.8%), and *Rhamnus alpina* (1.4%). They also found small quantities of acorns, beechnuts and hazelnuts. Other important items were graminoids, domestic mammals and ants. They also suggested that the variety found in the animals' diet proves that at any time they can utilise a large number of very different sources of energy and matter, almost independently from the seasonal changes in resources availability.

In the Yukon Territory, Canada, Pearson (1975) reported that in spring the favourite food were the roots of alpine sainfoin (*Hedysarum alpinum).* Other green vegetation particularly grasses and willow catkins (*Salix* spp) were also consumed. In two cases bears were observed feeding on moose (*Alces alces gigas*) carrion that had been killed in spring snowslides. During summer brown bears were eating willow catkins, dry bearberries (*Arctostaphylos uva-ursi*) and as soapberries (*Sepherdia canadensis*) ripened, grizzlies were commonly observed browsing on the large patches of these growing in the scrub zone. A small part of the diet also consisted of the roots of *Hedysarum* sp. grasses, remains of wasps and carrion. In autumn bears were feeding on occasional concentrations of crowberry (*Empetrum nigrum*), blueberry and bearberry in alpine regions. In late September and October they were traversing large areas digging for ground squirrels (*Spermophilus undulatus*). The period of increase of brown bear body weight corresponds to the ripening and utilisation of the soapberries. When the soapberry crop failed in 1965 in Yukon Territory, the bears turned to digging roots instead. Decreased body weight indicated that this source supplied insufficient energy, and the condition of the animals deteriorated. However, no over-winter mortality was detected, so bears can obviously extract sufficient energy from roots alone to survive over winter. However there is no information on whether this condition affected their breeding success during the following year.

In the Mission mountains of Montana, Servheen (1983) observed that perennial graminoids and forbs such as dandelian (*Taraxacum* spp.) together with mammal carrion and birds comprised the bulk of spring foods. Beaver (*Castor canadensis*) and grouse remains were also occasionally identified in faeces. In spring grizzly bears obtained insects by excavating rotting wood from tree stumps and logs. In the beginning of summer succulent forbs such as hogweed (*Heracleum lanatum)* and other Apiaceae attained sufficient growth to become food sources. Later on, forbs with starchy, tuberous roots, such as *Erythronium gradiflorum, Lomatium* spp and *Hedysarum* were excavated. Horsetails were eaten until shrub fruits, such as *Vaccinium* spp, *Shepherdia canadensis, Amelanchier alnifolia,* and *Crataegus* spp. began to ripen. Domestic tree fruits (apples, plums and pears) were the major autumn food resource used on the west slope of the Mission Mountains. Occasionally, dead domestic livestock were consumed in autumn, together with small rodents such as Columbian ground squirrels (*Spermophilus columbianus*) and deer mice (*Peromyscus maniculatus*).

Mattson *et al.* (1991) in a very interesting study of the Yellowstone brown bears that extended over 11 years, found that the relative volume of the major diet items were Whitebark pine seeds 25.7%, graminoids 23.8%, forbs 22.8%, mammals 8.3%, insects 5.8% and fleshy fruits 4.3%. The volume of fleshy fruits constituted a substantial portion of total scats only during August when most of the shrubs came in fruit. The majority of the fleshy fruits found in scats were: whortleberry, huckleberry (*Vaccinium globulare*), and soapberry. The leaves of the first two species were also eaten. The diet of the brown bears in the Yellowstone area differed from those of virtually all other bear populations by the paucity of fleshy fruits in their diet which was a result of the area's chronically poor production, limited abundance of productive plants, and low efficiencies associated with use of the widespread but small fruited whortleberry (Mattson *et al.* 1991). Bears compensated for this with a high consumption of pine seeds, which is a high quality food but available for a shorter period.

From the studies mentioned above we can conclude that the brown bear although displaying obvious characteristics of an omnivore, functions as a herbivore for most of the year. The importance of plant material in the diet may help to explain the often solitary foraging behaviour of brown bears, since there appears to be very few food resources which individual brown bears can better exploit co-operatively. However, occasionally, food items may occur in such an abundance that many conspecifics will congregate together to feed (Bledsoe 1975, Egbert & Stokes 1976).

Food is sometimes in short supply because of environmental variability. A basic understanding of food habits is therefore essential to understand the ecology and behaviour of the species. Brown bears are omnivorous, which does not mean that they will eat anything, but that they have relatively unspecialised digestive systems essentially a carnivore's digestive system which has been lengthened, probably to allow for better digestion and absorption of vegetable matter (Herrero 1978, Pritchard & Robins 1990). They have no ceacum and their stomachs are too acidic to support the microflora and microfauna needed for the digestion of cellulose. Therefore they cannot, or can only very poorly, digest the structural components of plants. They are not ruminants, but the species can survive on plant diets of 95% or more. They do this by maximising the quality of the food items ingested; for example, choosing items which can be digested by their relatively simple guts. Starch, sugar from berries and other fruits, animal and plant protein, as well as most animal and plant storage fats, are all digested. The proportions of each in the diet vary greatly from area to area and seasonally. Plant protein from succulent herbs appeared to be about 43% digestible compared with about 78% digestibility for animal protein and fat sources. Starch is about 79% digestible, sugar from berries and other fruits is assumed to be highly digestible (Herrero 1978).

Although in most of the studies above the brown bear behaves largely as a herbivore there are areas such as north-western USSR (Vereschagin 1976, Davilov 1983) where during certain seasons it behaves as an active predator, attacking wild ungulates.

4.1.2. Red fox

Studies of the diet of the red fox in Greece are very limited. Papageorgiou, Sfougaris, Christopoulou, Vlachos & Petamidis (1988) analysed 190 red fox stomachs mainly collected in northern Greece. They found that mammals occurred in 73.9% of the stomachs with small rodents and sheep *(Ovis aries)* remains being the most common, birds in 43.6%, cold-blooded vertebrates comprised 11.5% mainly lizards, invertebrates in 49.7% of which the most commonly occurring were Coleoptera and Orthoptera and plant material in 62.4%. The most frequently appearing plant material were graminoids (27.2%). The remains of fleshy fruits of several species were found most frequently during summer and autumn such as: *Vitis vinifera* in 7.2% of the scats, *Pyrus communis* in 9%, *Pyrus malus* in 11.5%, *Pyrus amygdaliformis* in 7.8% and many others consisting less than 3% such as: *Pyrus pyraster, Prunus pseudoarmeniaca, Prunus persica, Prunus armeniaca,* white mulberry *(Morus alba), Ficus carica,* walnut *(Juglans regia), Cornus* sp. and the nuts of *Corylus* sp.. They concluded that the wide range of feeding items found in the fox's diet in relation to the seasonal variation suggests that the fox is an opportunistic feeder utilising foods which were abundant and easily obtainable at any given time.

Southern and Watson (1941) analysed scats and stomachs from Oxford, Wales and Scotland and they found sheep 18.9% (frequency of occurrence), rabbit (*Oryctolagus cuninculus*) 55%, short tailed vole 8.6% poultry 10.3%, large birds 8.6%, small birds 15.5% and vegetable matter 25.8%. The vegetable matter was mainly grass and pine needles and the authors speculated that it was probably accidentally taken with animal food or from stomach contents of prey.

The diet of red foxes was also investigated in central and western Poland by Goszczynski (1986b) and Goszczynski & Wasilewski (1992). The food of foxes comprised about equal proportions (by weight) of three prey items: small mammals (33.3%), hares (25.9%) and birds (25.5%). Fruits and carrion comprised most of the remaining diet. Among small mammals the common vole (*Microtus arvalis*) dominated as did domestic hens among the birds. Fruits accounted for 6.5% of the diet and they were mainly found during summer and autumn. Traces of fruits were also found in winter. The author suggests that predation of foxes on hares is negatively correlated with the abundance of voles in his study area and foxes usually compensate for the lack of rodents by increased hare (*Lepus capensis*) consumption.

In an earlier study by the same author (Goszczynski 1974) in the Koscian district, Poland there was no mention of plant material eaten. Small rodents constituted 65.1% of the weight of the faeces, hares 26%, birds 5.5%, roe deer 3% and insectivores 0.4%.

Another study in Poland was carried out in Bialowieza National Park by Reig and Jedrzejewski (1988). It was a comparative study of the five main predators of the region which are the lynx (*Felis lynx*), the grey wolf, the red fox, the racoon dog (*Nyctereutes procyonoides*) and the pine marten. There was a certain amount of diet overlap but there were some well pronounced differences as well, mainly reflecting the differences in habitat utilisation by the five species. Foxes were mainly hunting at the edges of the forest expanding their ranges to the adjacent open areas. Important items in the diet of foxes were remains of Cervidae (21% frequency of occurrence), wild boar (15.7%), *Microtus* sp., *Apodemus* sp., *Sorex* sp. and other small mammals were present in 85.8% of the faeces, birds in 18.3% and plant material only in 3.9%. The remains from the large mammals were consumed as a result of scavanging activities which were well established in Bialowieza forest in contrast to other areas were large predators were absent. Foxes fed on wolf and lynx kills, but also utilised the carcasses of ungulates that had died from severe winter conditions. They explained the restricted use of fruits in their area by the presence of very deep snow that covered the edible fruits during the whole winter and the sporadic occurrence in their study area of trees and shrubs such as: *Malus* sp., *Pyrus* sp. and *Rosa canina.*

Macdonald (1981) during his studies of red foxes on the outskirts of Oxford found that while foxes ate many prey, the bulk of their diet comprised scavenged scraps and earthworms, with fruit like *Rubus ulmifolius* and apples being seasonally important. There were significant differences in the overall diet, even between neighbouring groups which reflected the abundance of different foods in each territory. The frequency of occurrence of fruit in the faeces collected from the different territories ranged between 16 and 25.5%.

Hernández (1993) in his study of the seed dispersal ecology of *Rhamnus alpinus* in the Cantabrian mountains (Spain) reported that red foxes were the most important carnivore dispersers of this species considering the total number of seeds. Seeds of this species were found in 50% of the faeces and furthermore 99.68% of the seeds were intact after dispersal. They also consumed *Rubus* spp. and *Prunus avium,* bearberry and blueberry.

Errington (1937) compared the food habits of red fox in Iowa (USA) between two years: 1933 which was a normal year as far as weather conditions were concerned and 1934 which was a year of a very severe drought. He compared data extracted from food remains outside dens, faeces and stomachs and intestines. There were considerable differences between the results extracted from the different sources but there are some food items which were consistently found. Mice were very readily taken both years. Cottontail rabbits (*Sylvilagus* sp.), ground squirrels, ring-necked pheasants (*Phasianus colchicus*) and insects were all important parts of the diet. During the drought year there was an increase in predation on muskrats (*Ondatra* sp.), pocket gophers (Geomyidae), domestic chickens, partridges (*Alectoris* sp.) and insects. The fact that is really interesting though is the complete absence of any plant material from the diet.

Cook and Hamilton (1944) collected 537 red fox scats over six years in Rensselaer County, New York (USA). Based on the yearly consumption they found that mammals had a frequency of occurrence of 68%, fruits 73%, insects 18% and birds 7% of the total. *Fragaria* sp. were found during June and July and in 4.5% of the scats, *Rubus* sp. were mainly found August and September (11.5%), *Malus sylvestris* were the most frequently found fruits (29.5%) and their peak was during October and November. *Prunus* sp. were mainly found in August, September and October (17.7%) and *Vaccinium* sp. predominantly during July and August. Species such as: *Amelanchier* sp., *Crataegus* sp., wild grape (*Vitis* spp.), wild sarsaparilla and *Viburnum* sp. were also found but infrequently. Furthermore, this study is one of the very few that gives information on the availability of these fruits in the study area. *Fragaria* sp. were abundant in the more fertile grassland types and all the edible fruit is produced in the open. They were among the first to ripen and were eagerly eaten during their short season in June and early July. *Rubus idaeus* produced a scant fruit crop which ripened in June and July. The blackberry was abundant along roadsides, banks and the edges of clearings. This plant produced rich crops of large berries which ripened later than raspberries, from July to mid-September. Fallen fruits were available for sometime subsequently. Foxes ate these fruits in quantity as long as they were present. Apple trees were found around the site of every old house, along roads and in overgrown pastures. The earliest varieties ripened in August, while the last apples did not drop from the late varieties before spring. The crop was always good and they were readily eaten by foxes. *Amelanchier* sp. trees were quite frequently found in the area and they had a long fruiting period starting in June and ending in September. They also persist on the ground for sometime after they drop and they were greedily eaten until as late as November. *Crataegus* sp. shrubs were uncommon and their fruit were consumed rarely. Chokecherry and wild black cherry were fruits much relished by foxes. They produce a heavy crop of fruits which ripened in September and persisted on the ground until they were covered by snow. Wild grapes were also present in the area but they were seldom consumed. *Vaccinium* sp. was abundant almost everywhere. Ripe fruit were present from late June until September and they were very frequently found in faeces. *Viburnum* sp. were common in the plant communities of the area but their fruits were very seldom consumed. Cook and Hamilton (1944) also commented that June brought great changes in the diet of foxes and until far into autumn they depend heavily upon fruit. At the height of the fruiting season each of the fruits that were consumed had an occurrence approximating 50%. They often found scats crammed with the seeds of berries and others that were aggregations of *Prunus avium* stones.

4.1.3. Grey wolf

The only published study found me on the diet of grey wolves in Greece was undertaken by Papagergiou, Vlachos, Sfougaris & Tsachalidis (1994). Remains of goats and sheep were found in 25.0% and 14.3% respectively of the stomachs they examined. Wild mammals like mice (10.7%), and interestingly badger (7.1%) and pine marten (7.1%) were also found in the diet. Fleshy fruit such as pears (14.3%), plums (7.1%) and figs (7.1%) together with beech nuts (7.1%) were part of the wolves' diet when they were abundant.

Meriggi, Rosa, Brangi & Matteucci (1991) investigated the diet of the grey wolves in the northern Apennines (Italy) and found that Rosaceae fruits (*Rosa canina, Malus* sp., *Pyrus* sp., *Prunus* sp., *Sorbus* sp., *Rubus* sp.) comprised 26% mean volume and with livestock (26% mean volume) were the dominant food items. Other important items by volume were wild ungulates (13%) and small rodents (5%). The analysis of faeces revealed that the presence of wild boar and hares in the diet increased in winter. Nevertheless, the main food was Rosaceae fruits (mainly *Rosa canina*) that are very common in the bushy areas of their study. In spring Rosaceae fruits were again forming the bulk of the diet. Livestock was the main food for grey wolves in summer. In autumn grasshoppers, livestock, Rosaceae fruits and wild boar were the feeding items that wolves were depending upon.

Thurber and Peterson (1993) in their study of a grey wolf population on Isle Royale National Park report that the mean percent biomass of the most important food items during their research (1975-1991) were as follows: adult moose (63%), yearling moose (22%), beaver (14%) and snowshoe hare (*Lepus americanus*) (1%) but they did not detect any plant material. Small and large packs did not differ very much in their patterns of winter feeding, but lone wolves tended to have a more variable diet.

Ballenberghe *et al.* (1975) conducted an extensive study of the ecology of the grey wolf in north-eastern Minnesota. They collected 637 scats and found that the principal food items of wolves in the study area were deer (56.9% percentage occurrence), moose (13.6%), and beaver (9.4%). Deer was the single most important food item. The analysis of scats collected from mid-May to September revealed the seasonal importance of deer fawns to wolves. They became a significant food item immediately following the peak fawning period. Five genera of small rodents appeared occasionally. Remains of vegetation and mainly the fruit and seeds of *Rubus* spp., *Vaccinium* spp., *Amelanchier* spp. and *Prunus virginiana* appeared in 6.6% of the scats. Another set of faeces were collected from frequently used “rendezvous sites” where family groups used to meet after their hunting and patrolling sorties during August and September. Vegetation, consisting mainly of fruit remains, constituted significant percentages of the total food items identified. Deer and beaver were again important items but moose were seldom utilised. Adult wolves and their pups apparently frequently used the fruiting shrubs common at all the “rendezvous sites”. Many adult grey wolf scats contained entirely *Rubus idaeus* remains when found near these meeting points.

4.1.4. Stone marten

Clevenger (1994b) conducted an extensive review of 14 studies of the diet of the stone martens in Europe. He found that the most common vegetation items found in faeces were wild and cultivated fruits. In southern France, Cheylan and Bayle (in Clevenger 1994b) found that more than 80% of stone marten faeces consisted of varieties of fruits, mostly *Juniperus* sp. berries. *Sorbus aucuparia* were found to be important seasonal foods for martens in Switzerland and central Italy (Marchesi *et al.*, Serafini *et al.*, cited in Clevenger 1994b). A wide variety of foods were reported in these 14 studies including passerines and Columbiformes. Invertebrates, primarily insects, were important in all studies. Reptiles such as: *Malpolon monspesulanum* and grass snake (*Natrix* sp.) were rarely eaten. Stone martens living in or near cities and villages often consume human refuse. In the same review Clevenger (1994b) compared the diets of the pine and the stone marten and suggests that they are opportunistic feeders with generalised diets. The diets of the two martens overlap considerably, but mammals were the most important prey of pine martens. On the other hand, vegetation was the most important food category in the stone marten diet. Living in and around villages, stone martens encounter a more stable and diverse food supply that of the pine martens which occupy the nearby woodland habitats (Herrmann 1994).

Reig and Jedrzejewski (1988) in their combined study of the carnivores of Bialowieza National Park in eastern Poland found that rodents were the dominant food in the diet of pine martens. They clearly selected forest-living rodents, i.e. *Clethrionomys glareolus* and *Apodemus* sp., reflecting their habitat preferences. Martens were feeding more on medium sized mammals e.g. brown hare, red squirrel and hedgehog, during the winter but that changed in spring when they switched to preying on rodents. Plant material appeared only in 4.8% of the faeces and this lower occurrence was attributed to the severe climatic conditions and the relative scarcity of fruit producing shrubs and trees.

Another study, in central Poland, found that the most important food items were fruits which formed 37% by weight of the diet, small mammals (29%), birds (19%) and hares (8%) (Goszczynski 1986). The highest proportion of common vole in the diet was found in autumn, when agricultural practices, such as ploughing, forced these animals in the forest. The bank vole was intensively exploited during most of the year. The highest proportion of birds occurred in winter and spring. Fruits dominated the diet of the martens during summer with fruits like sweet cherry (*Prunus* sp.), bird cherry (*Prunus avium*), sour cherry (*Prunus* sp.) and raspberry (*Rubus idaeus*) appearing in the scats and later in the autumn pears, apples and garden plum were frequently found. This extensive frugivory coincided with a drop of the proportion of animal food below 50%. A comparison of the diet of martens and foxes that were also investigated during this study revealed that the diet of these two predators was more similar during winter and spring than in summer and autumn.

The food habits and habitat use of the pine marten on the Balearic Island of Minorca were studied from March to August by Clevenger (1993a). During March to April, small mammals were the dominant food found in the faeces (74.2% frequency of occurrence), followed by birds (31.2%). From May to June, birds were the principal food (53.4%), then small mammals (34.8%). Plant material (67.1%) and insects (67.7%) were the most important foods in July-August. The most frequently found fruits were blackberry (*Rubus ulmifolius*), fig (*Ficus carica*) and wild grape (*Vitis vinifera*). Other less common fruits in the diet were domestic apple *(Malus domestica), Prunus* sp. and Phoenician juniper (*Juniperus phoenicea)* and the fruits of the carob tree (*Ceratonia siliqua)* The same author conducted a comparative study of the diet of the pine marten throughout a year on Minorca and in the Cantabrian mountains of northern Spain. In Minorca, mammals and plant material were the predominant foods. Mammals were most important during spring (68.6% frequency of occurrence) and winter (56.7%) while plant material was most frequently found in faeces in autumn (80.6%). During summer martens had a balanced diet comprising four food categories. The total occurrence of insects was the highest among all food categories (44.1%) whereas reptiles appeared in low quantities throughout the year. Fleshy fruits were the main food component during July-August (65.7%), September-October (80.6%) and November-December (81.9%). *Rubus* sp. and *Ficus carica* were dominant during the first period and carob fruit during the second and third when it composed nearly half of the diet. *Arbutus unedo* fruit also appeared frequently. In the Cantabrian mountains mammals were the main food item during spring (97.6% frequency of occurrence) and summer (80.7%). As found with the island population, plant material was most important in autumn and was found in 78.1% of the faeces primarily due to the nearly exclusive consumption of *Sorbus aucuparia* berries. Other fruits eaten by pine martens were: *Crataegus monogyna, Rubus ulmifolius, Rhamnus alpinus, Prunus* sp. and *Rosa* sp. Insects were common food items during summer appearing in 36.5% of the faeces. Reptiles and birds were rarely taken during the three seasons of the study.

Hernández (1993) reported from the Cantabrian mountains that martens were the second most important seed disperser of *Rhamnus alpinus* after the red fox and the seeds of the plant were found in all the marten faeces examined and 99.8% of the seeds consumed passed intact through the gut of the animal. However, his sample size was very small (4 faeces). They were also found to consume the fruits of bearberry.

Lockie (1961) reported from west Ross-shire that the food eaten by the pine martens varied among seasons and in the size of the individual items which ranged from the violet ground beetle (*Carabus violaceus)* to large birds such as wood pigeons (*Columba palumbus*). Small rodents formed a considerable part of the diet in all seasons and were supplemented by small birds, insectivores, insects and carrion. Young rabbits (*Oryctolagus cuninculus*) or mountain hares (*Lepus timidus*), Lepidoptera and berries, were consumed in large quantities as they became available. Between July and October in one year of the study berries formed as much as 56% (estimated weight) of the diet. Berries eaten in large quantities included rowan-berries and blaeberries (*Vaccinium vitis-idaea*).

Lucherini and Crema (1993) studied the diet of urban stone martens by collecting faeces in the attic of a nunnery in Pregaleto, province of Torino, Italy. They found that the most frequent prey remains were those of birds which were present in 87.8% of the faeces. Small mammals occurred a little less frequently than birds (63.4%). *Rosa* sp. fruits were present in 53.7% of the faeces, but formed a small proportion of the total volume (7%). Insect remains, mainly Hymenoptera, were found frequently, but always in small quantities. Reptiles were uncommon in the scats but formed a considerable proportion of the volume when present. The frequency of human waste products was negligible.

Hargis and McCullough (1984) investigated the food habits of the American marten over two winters in Yosemite National Park, California. White tailed jack rabbits (*Lepus townsendii*) and voles (*Microtus* spp.) were the dominant food items. *Juniperus* sp. berries were found in the diet and they were present in 14% of the faeces collected during the second winter. Nuts and seeds were also found (16-23%) but the authors believe that these may have been acquired from squirrel caches. Human food was obtained from rubbish dumps and food scraps left by skiers were found and bait from live traps was also taken.

The seasonal food habits of American marten in south-central Alaska were studied by Buskirk and MacDonald (1984) between autumn 1980 and autumn 1981. Microtine rodents were the dominant food item in the diet appearing in 88% of the digestive tracts and faeces of martens, sciurids were important (7.2%) and birds (9.7%) as well as fruits (20.5%). There were some interesting fluctuations in the percentage volume that some items occupied when present: ungulates constituted 30% of volume during the first autumn of the study but were completely absent during the second autumn. The same happened with fruit that contributed 13.3% to the total volume in autumn

1980 but was absent in the same season of 1981. The low value for the latter season reflected an area-wide crop failure. Fruit consumption progressively decreased over winter probably reflecting lower fruit accessibility as snow depths increased. Berries of five species were found: boy whortleberry (*Vaccinium uliginosum),* blaeberry, crowberry and raspberry (*Rubus idaeus)* and Rosa sp. which collectively made up 5.7% of the total volume, although the frequency of occurrence was 20.5%. The authors suggest that the difference between frequency of occurrence and percent volume is either a result of the high digestibility of berries, or indicates that marten eat only a few fruits at a time, or both.

The winter diet of American martens was also investigated on Vancouver Island by Nagorsen, Morrison and Forsberg (1989). Plant material was present in 43.1% of the digestive tracts investigated, fish in 21.8%, ungulates in 20%, small mammals 28.8% and birds in 29.7%. The majority of plant material was conifer needles, moss fragments and ferns. This material was probably ingested accidentally with prey. Seeds were found only in three digestive tracts, partly digested apples were recovered from the stomachs of four martens. Interestingly martens on Vancouver Island demonstrate minor sexual variation in winter diet. Males consume less small mammals than females overall. Furthermore total avian prey taken by the sexes is similar but females consume more small birds.

Martin (1994) reviewed 22 studies on the American marten and drew some interesting conclusions about their feeding ecology. Vegetation seemed to provide an important food resource for the species but probably is secondary to mammals in dietary importance. Birds were found to be significant items in almost half of the studies reviewed but it is possible that they are over-represented in contents of faeces (Martin 1994). This is because feathers are more easily observed in faeces than hairs and birds also have larger volumes of indigestible materials per unit weight than do similarly sized mammals. Hence, more scats per kilogram of food of avian prey than for mammalian prey will be produced. The percent occurrence of insects may be a misleading indicator of the true importance of this food category, as the proportion of insects by volume of the sample was usually low in the studies reviewed (Martin

1994). Furthermore, martens may have consumed insects accidentally by eating the stomach contents of birds.

During the same review some other dietary patterns were revealed in relation to some environmental factors such as latitude. The diet of martens in subarctic habitats had the lowest diversity. This can be probably attributed to the fact that high latitude ecosystems are less complex in terms of community structure than temperate zone ecosystems. Also, diets in these habitats are dominated by larger prey such as the snowshoe hares and red squirrels which would provide more meals per carcass, necessitating fewer kills per time unit and ultimately resulting in a less diverse diet. Martin (1994) concludes that diversity in the diet will be influenced by what foods are available to the animal, a reflection of ecosystem richness, and by the food gathering abilities of the animal. On the other hand, habitat preferences may be a consequence of the availability of food, which is a function of both prey density and "catchability".

4.1.5. Summary

Some general conclusions can be drawn from the studies reviewed earlier. In no area where the brown bear has been studied does the species feed exclusively on one particular item throughout the annual cycle. Food items important in the early spring are often insignificant later in the season. The brown bear can utilise a wide selection of foods ranging from an almost complete herbivorous diet to a heavy dependence on animal matter. Thus the diet varies greatly from one geographical area to another and within areas, depending upon the season and the abundance of various food items. Brown bears were the carnivores with the most widely reported frugivorous diet. Red foxes were the extremists among the carnivores reviewed. They ranged from largely frugivorous to true carnivores with zero quantities of plant material in their diet. The diet of red foxes varies following the seasons of the year as was the case with bears. The reports on grey wolves feeding on fruits were very limited. They were the true predators among the carnivores studied. They took prey ranging in size from small rodents to polar bear cubs (Ramsey and Stirling 1984). In none of the studies did they depend on fruits and they seemed to supplement their diet where fruits are readily available and near their usual patrolling routes (Ballenberghe *et al.* 1975). Martens displayed a truly omnivorous diet and they were often characterised as opportunists by the authors studying them. They would switch to any food which was in good supply and easy to catch.

4.1.6. Aims

In the rest of this chapter, the results section starts with an investigation of the frequency with which fruit material occurs in the diet of the carnivores. Afterwards, there is an effort to discriminate between the influence of the different factors studied on the presence of every fruiting species in the faeces. The factors taken into account were the month of collection, the transect on which the faeces was found, the species of seed(s) that were found in the faeces and the carnivore that deposited the faeces. Subsequently, I compared the number of seed species found inside the faeces of each carnivore in order to investigate whether some of them were more polyphagous than others. Following that, there is an attempt to find any associations between the seed species which were found together in faeces.

The second part of the results section is concerned with the factors affecting the number of seeds found in the scats. The number of the seeds dispersed is important as the plant which manages to spread the most seeds around the habitat stands a better chance of some of the seeds finding favourable conditions for germination, escape the predators and survive to maturity. The main factors studied were the seed species and the carnivore that deposited the faeces. Other factors such as the year and month were also examined. Finally at the end of this section I investigated the factors that influenced the survival of the seeds after the passage through the carnivores' digestive system.

4.2. METHODS AND MATERIALS

Soon after their collection the faeces were placed in plastic bags in order to prevent any excessive moisture loss that would kill the seed embryos and therefore jeopardise the germination trials. Faeces were then stored at room temperature for up to two weeks as there were no refrigerators available in the research area. They were then taken to the T.E.I. of Drama (see Chapter 2) where they were refrigerated (+4° C) until required for the germination trials, when seeds were extracted. A discription of these trials can be found in Appendix II. Afterwards the faeces were oven dried at 60° C to constant weight whereupon they were stored in paper envelopes at room temperature.

Due to the large number of faeces collected during the field it was necessary to sub-sample by randomly selecting five faeces per carnivore, per transect, per month. If less than six collected, all were analysed. The selection was undertaken with the help of a random number generator. The paper envelopes that were used fir the storage of faeces were reopened for the identification of the seeds that were contained in the faeces. The analyses were carried out on the dried faeces simply by spreading them on a petri-dish and removing all the seeds found using a microscope (× 10 magnification). The seeds were counted and statistical analysis of the results was carried out. The seeds were thoroughly inspected for signs of mechanical damage.

Bear faeces were subsampled at 1/10 of their dry weight when they contained small sized seeds e.g. *Rubus* sp., and the total number of seeds that they contained was estimated by multiplying up from the subsampling procedure. All the seeds extracted from the faeces were weighed to an accuracy of at least 1 mg. A small proportion of faeces were very compact and impossible to analyse when dry. These were left to soak in water in petri dishes and then analysed. Seeds extracted from such faeces were left to dry at room temperature and were then weighed.

In order to assist identification of the seeds extracted from faeces a reference seed collection was prepared. These seeds were collected directly from the identified fleshy fruited plants. Personal observations (also Arabatzis pers. communication) reveal that there are a number of *Rosa* sp. growing in the study area such as: *R. pendulina, R. canina* and *R. pimpinellifolia* and a number of *Rubus* sp. such as *Rubus canescens* and *Rubus idaeus*. As it proved impossible to differentiate between the seeds of the three species of *Rosa* and the two of *Rubus* with any amount of certainty, these species are referred to as *Rosa* sp. and *Rubus* sp. Particular care was taken to detect any remain of seed coat that would indicate the presence of destroyed seeds. When remains of seeds where present, I estimated the number of entire seeds that would best account for them. Separate records were kept for intact, damaged and destroyed seeds. The total number of faeces analysed was 287 fox, 24 bear, 160 marten, and 12 wolf faeces.

In the rest of this chapter I refer to fruit consumption by these carnivores. This information was derived from the seeds that were found in the faeces which I believe gives a measure of the fruit-eating habits of the carnivores. It is therefore not a direct measure, since fruit fragments were not included in the count of fruits consumed by the carnivores.

4.3. RESULTS

4.3.1. Species of seed found in faeces

4.3.1.1. Factors affecting the frugivory index

For each carnivore species a frugivory index (FI) was calculated each month by finding the percentage of faeces collected on each transect which contained seeds of fleshy fruit. Analysis of variance of the frugivory index (arc sine transformed) identified significant main effects for month, carnivore and year (Table 4.2.). The months in order of increasing frugivory were June, July, August, October and September. As was expected the carnivores differed in the frequency of fruit consumption. (see also Fig. 4.1, 4.2, 4.3, 4.4). Bears appeared to be the most frugivorous carnivores since all their faeces contained seeds, followed by fox (FI = 68.5%), wolf (FI = 50.0%) and marten (FI = 43.0%). The interesting result was the effect of year, with frugivory index 22% higher in 1994 compared to 1993. This was mainly because of the considerable increase in the frugivory in martens in 1994. As far as the frugivory index is concerned there were not any significant differences between the transects.

Source of Variation	Sum of Squares	DF	Mean Square	F	Significance
Month (Mo)	39509.95	4	9877.49	18.64	p<0.001
Transect (Tr)	3577.34	4	894.34	1.69	not sig.
Carnivore (Ca)	19072.48	3	6357.49	12.00	p<0.001
Year (Yr)	9394.45	1	9394.45	17.73	p<0.001
Residual	51921.34	98	529.81		
Total	134290.98	110	1220.83		

Table 4.2. Results of ANOVA analysing the effects of Month, Transect, Carnivore and Year on the frugivory index (arc-sine, square root transformed).

Higher order interactions could only be analysed for data on fox and marten, since insufficient data was available for bear and wolf. Only one higher order interaction was significant, between year and month and only for fox ($F_{(1)} = 4.73$, $p<0.01$) This was because June 1993 had a relatively high frugivory index and July was the minimum for this year, whereas in 1994 June was very low and July had one of the highest values of the year.

4.3.1.2. Factors affecting the presence of seed species in faeces

Analysis of variance was used to examine the influence of seed species (found in the faeces) as well as carnivore and month on the number of faeces collected each month (log transformed). All the effects were highly significant (Table 4.3.). The species found at the highest frequency in faeces were: *Rubus* sp., *Rosa* sp., and *Malus sylvestris* whereas *Crataegus orientalis, Fragaria vesca,* and *Vitis sylvestris* were rarely found. The different number of faeces collected each month for the species of carnivores have been discussed in the previous chapter. All the two-way interactions were significant also, indicating that:

a) some carnivores consume particular seed species more frequently than others. b) different numbers of faeces were collected from each carnivore during each month of collection as it was previously discussed (Chapter three) and c) each month different numbers of faeces were found containing various seed species. In June the most frequently found seed species in the faeces of all carnivores was *Rosa* sp. and in July *Prunus avium* appeared most frequently. In August and September *Rubus* sp. was found in many more faeces than any other seed species. Whilst, in October, *Malus sylvestris* dominated the diet of the carnivores.

The three way interaction was also significant. During the following section I shall attempt to interpret this three way interaction of the effects of Carnivore, Seed species and Month. Figures 4.1(a, b) present the percentage of faeces that contained one or more species of the fruiting plant seeds. In June foxes were the most polyphagous carnivore feeding on *Rubus* sp., *Rosa* sp. and *Malus sylvestris* while martens and bears were having a restricted diet of *Rosa* sp. No wolf faeces containing seeds were found in June.

Source of Variation	**Sum of Squares**	**DF**	**Mean Square**	**F**	**Signifi-cance**
Carnivore (Ca)	2.57	3	0.86	32.44	$p<0.001$
Seed species (Ss)	4.07	8	0.51	19.31	$p<0.001$
Month (Mo)	1.32	4	0.33	12.56	$p<0.001$
Ca-Ss	2.14	24	0.09	3.38	$p<0.001$
Ca-Mo	0.70	12	0.06	2.23	$p<0.050$
Ss-Mo	5.07	32	0.16	6.01	$p<0.001$
Ca-Ss-Mo	5.08	96	0.05	2.01	$p<0.001$
Residual	4.75	180	0.02		
Total	26.33	399	0.07		

Table 4.3. Results of ANOVA analysing the effects of Carnivore, Seed species and Month on the logarithm of the number of faeces.

In July martens became much more polyphagous consuming the same number of seed species (5) as did foxes. Both carnivores consumed seed species such as *Rubus* sp., *Rosa* sp. and *Prunus avium.* Bears consumed *Prunus cocomilia* and *Prunus avium* with the latter being the most frequently found seed in the carnivores' diet during this month.

In August foxes and martens consume three species of fruit both including *Rubus* sp. and *Prunus avium* in their diets. Bears have the same fruit diet as in July. It is interesting that *Prunus avium* is the only fruit commonly eaten by the three carnivores this month as was the case in July. Wolves appear to consume fruit for the first time this month and they focused their feeding on *Rubus* sp. which is the fruit species that forms the bulk of the fruit component of the diet of foxes, martens and wolves.

Frugivory increases in September for foxes, martens and bears when they all consumed 5 or 6 species of fruit. *Rosa* sp. and *Cornus mas* were commonly consumed. The species eaten by all the carnivores were *Rubus* sp. and *Prunus cocomilia.* Once again this month *Rubus* sp. was the most frequently found in the diet of the carnivores.

October is the month in which all the carnivores consume several fruit species with *Rubus* sp., *Rosa* sp. and *Malus sylvestris* being the species commonly consumed. *Prunus cocomilia* was also eaten by all but foxes. *Malus sylvestris* was the species most frequently found in the diet of all carnivores during this month.

Analysis of variance of this data set was used to investigate the occurrence of seed species (in faeces) along the transects (Table 4.4.). The results indicated that the abundance of different seed species in the faeces differed significantly as it was discussed earlier. The effect of transect was also found to be significant indicating that different numbers of faeces containing seed were analysed from each transect. Most faeces were analysed from Ahladorema and the diminishing order of the other transects was: Distropi, Krusovo, Connector and Virgin forest. This reflects the original abundance of the faeces on the transects together with the effects of subsampling (see Methods and Materials). The interaction of these two effects is not significant, suggesting that the fruit composition of faeces was similar on all the transects ($F_{(32, 135)} = 0.56$, $p>0.05$).

Source of Variation	**Sum of Squares**	**DF**	**Mean Square**	**F**	**Significance**
Seed species (Ss)	6.04	8	0.76	7.32	p<0.001
Transect (Tr)	1.08	4	0.27	2.62	p<0.050
Ss-Tr	1.84	32	0.06	0.56	not sig.
Residual	13.92	135	0.10		
Total	22.88	179	0.13		

Table 4.4. Results of ANOVA analysing the effect of Seed species and Transect on the logarithm of the number of faeces. Only these faeces containing seeds were used in the analysis.

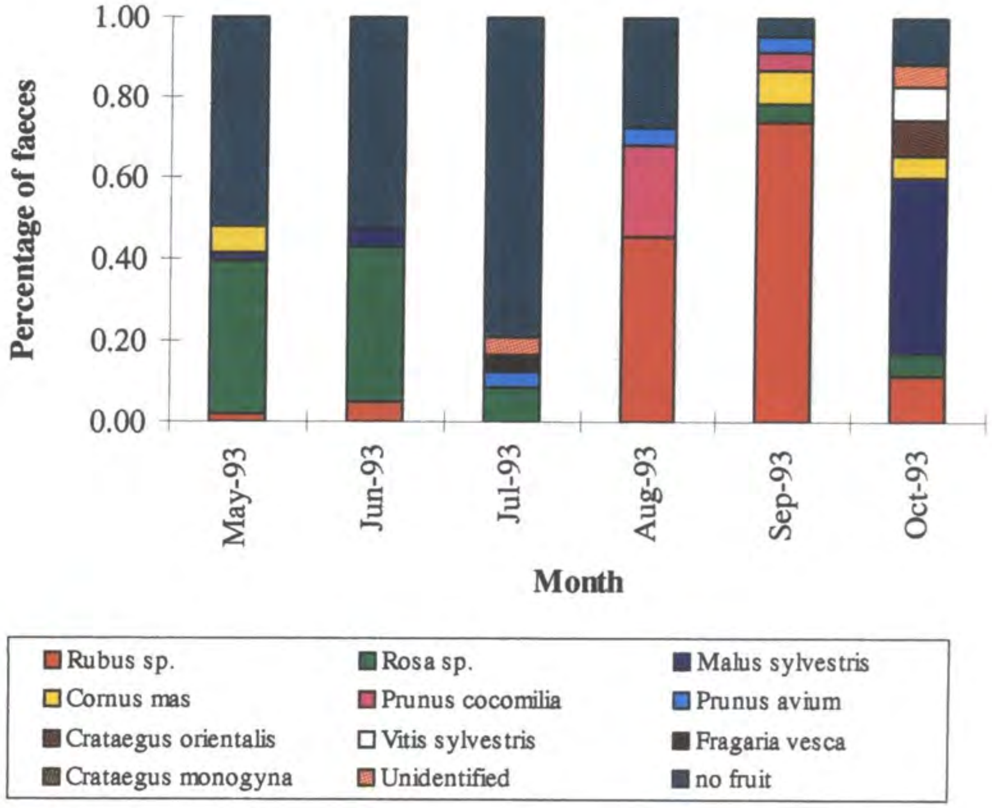


Fig. 4.1(a). Proportion of fox faeces collected in 1993 containing each species of fruit

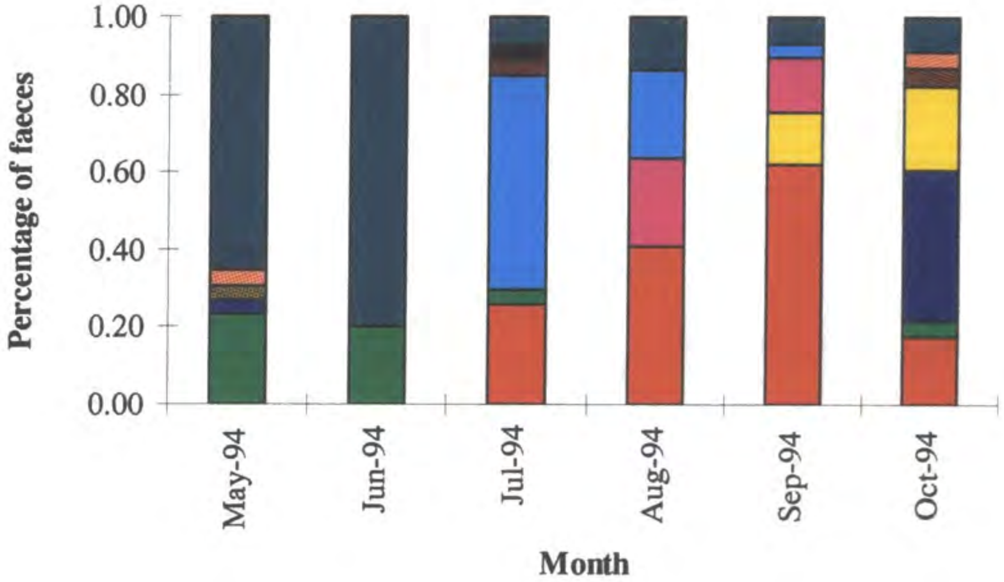


Fig. 4.1(b). Proportion of fox faeces collected in 1994 containing each species of fruit

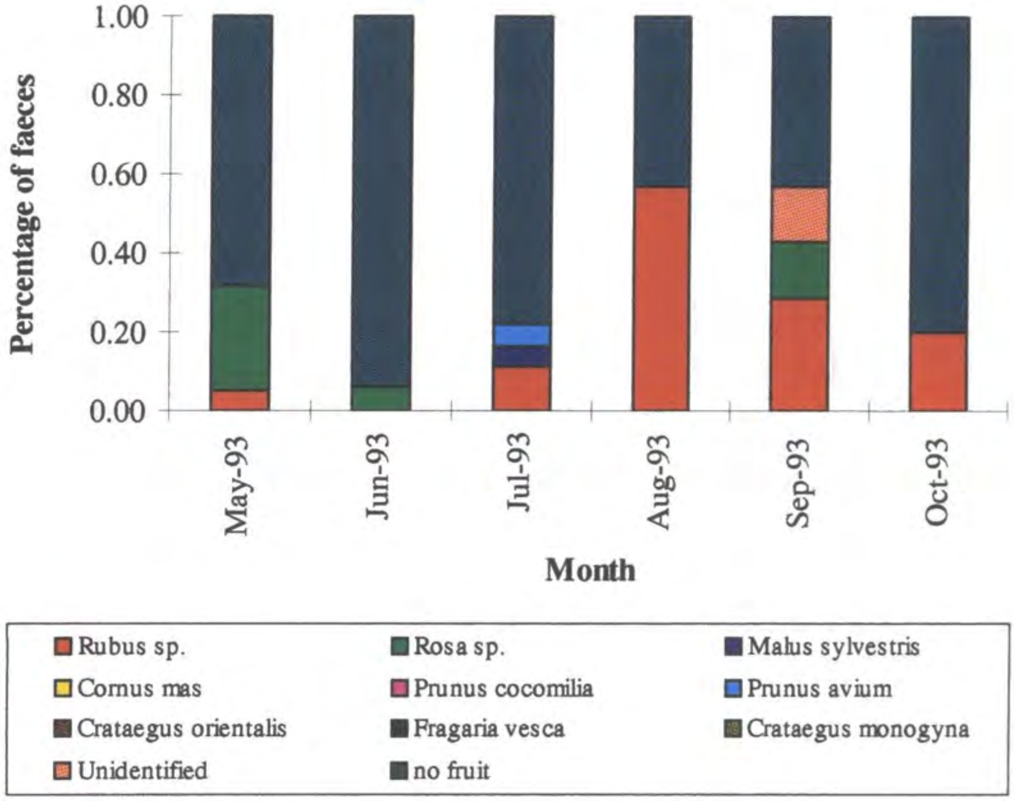


Fig. 4.2(a). Proportion of marten faeces collected in 1993 containing each species of fruit

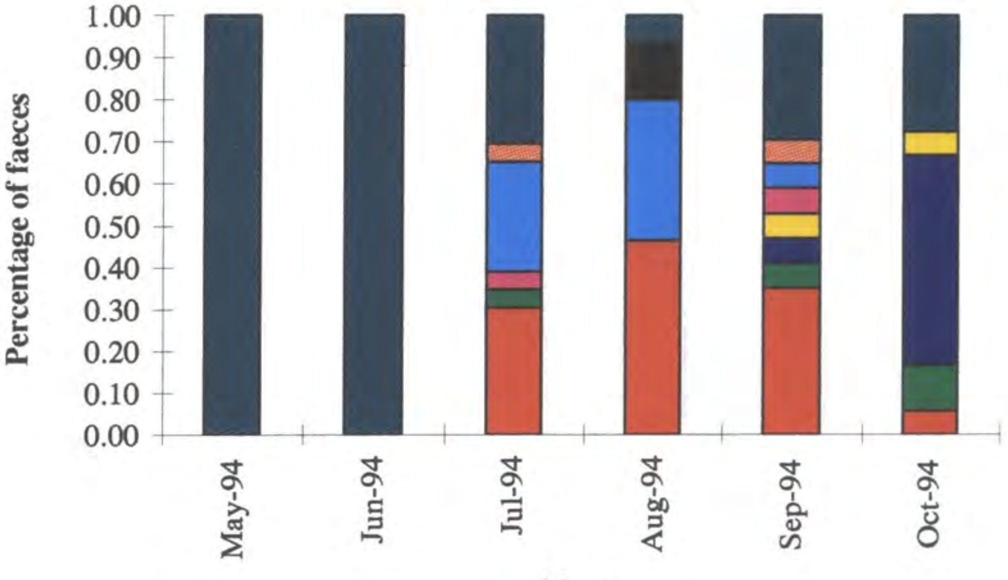


Fig. 4.2(b). Proportion of marten faeces collected in 1994 containing each species of fruit.

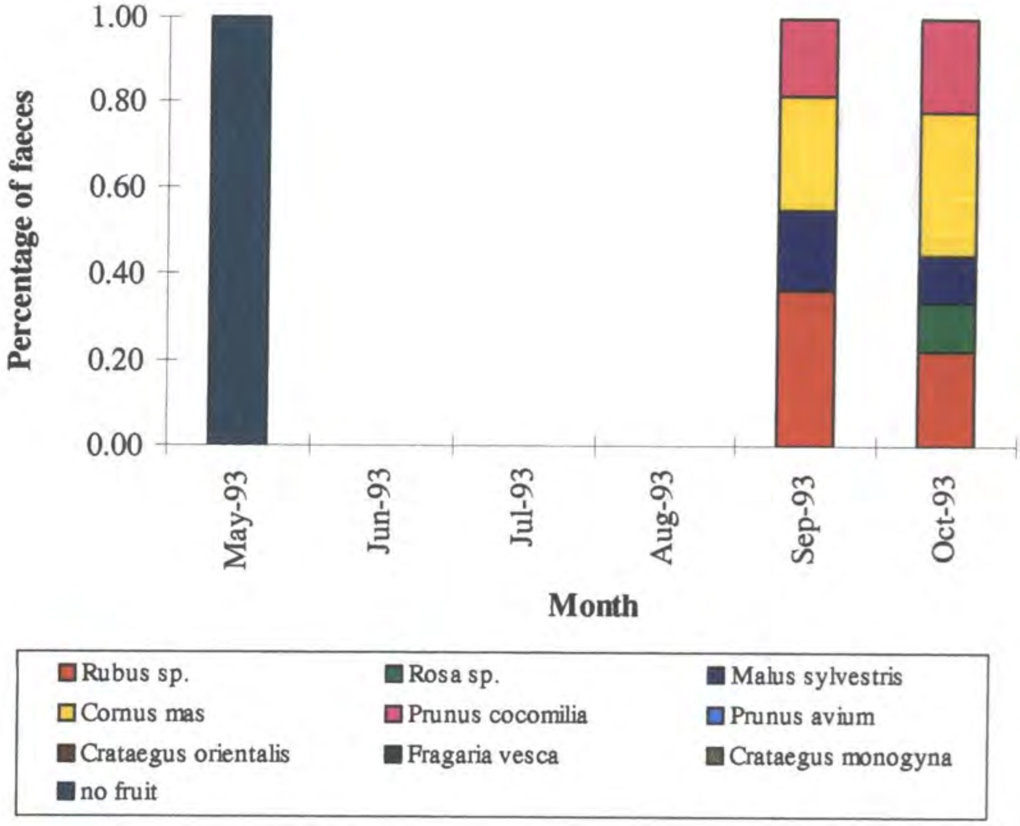


Fig. 4.3(a). Proportion of bear faeces collected in 1993 containing each species of fruit.

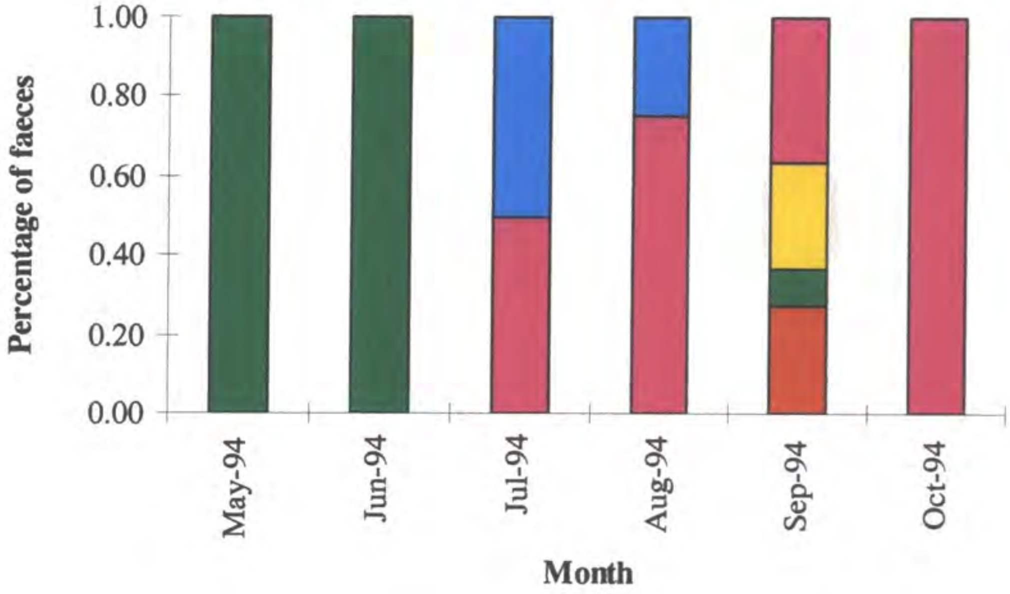


Fig. 4.3(b). Proportion of bear faeces collected in 1994 containing each species of fruit.

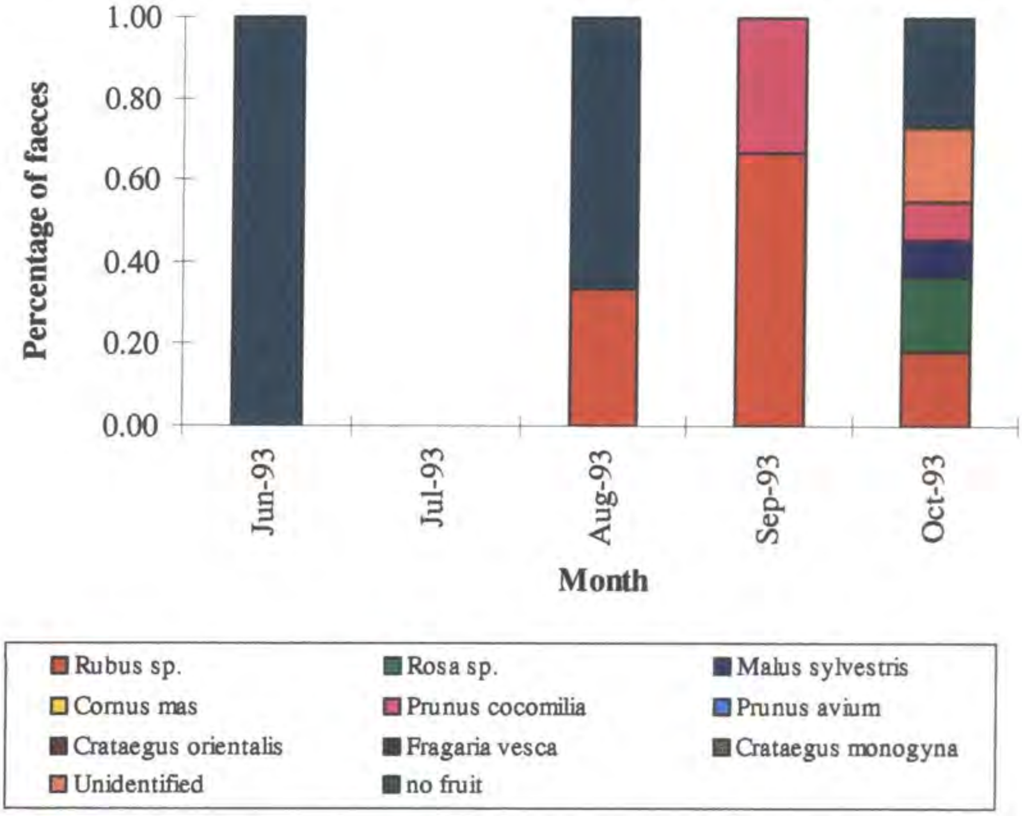


Fig. 4.4. Proportion of wolf faeces collected in 1993 containing each species of fruit.

4.3.1.3. Frequency of occurrence of the different seed species in faeces

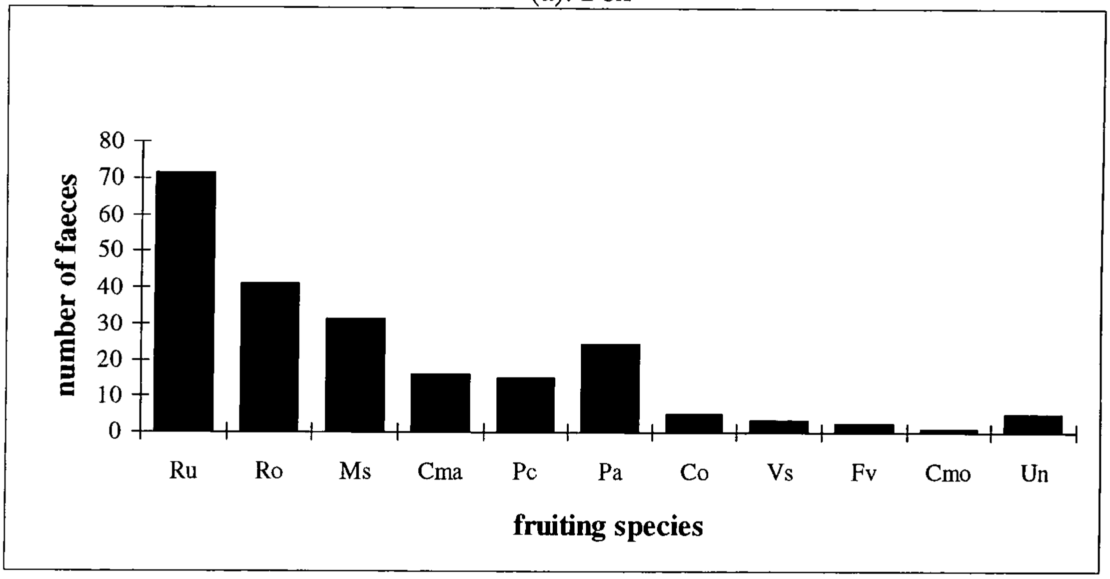
A chi-square table was used to analyse the frequency of the different species of fruit in the faeces of the carnivores in order to investigate whether each carnivore was consuming the seed species proportionally more or less than the others. The frequency of the seed species was significantly different in the carnivores' faeces (χ^2= 42.92, 10 df, $p<0.001$) with bears contributing the most to the variation (Fig. 4.5.a-d, Table 4.5.). Bears were consuming *Prunus cocomilia* and *Cornus mas* seeds proportionally more than other carnivores. However, the consumption of *Rubus* sp. and *Prunus avium* was lower than for the other carnivores. Martens consumed many fewer *Prunus cocomilia* seeds and more *Prunus avium* seeds than the other carnivores.

BEAR						
	TRANSECTS					
Fruit species	**Di**	**Vf**	**Kr**	**Co**	**Ah**	**Total**
Rubus sp.	4	0	3	1	2	**10**
Rosa sp.	1	0	0	0	2	**3**
Malus sylvestris	0	0	2	0	1	**3**
Cornus mas	3	0	4	0	3	**10**
Prunus cocomilia	3	1	6	1	3	**14**
Prunus avium	0	0	1	0	1	**2**
Total	**11**	**1**	**16**	**2**	**12**	**42**
FOX						
Rubus sp.	16	16	4	20	14	**70**
Rosa sp.	7	2	1	0	7	**17**
Malus sylvestris	7	1	0	7	15	**30**
Cornus mas	1	0	8	2	2	**13**
Prunus cocomilia	3	0	2	6	3	**14**
Prunus avium	8	3	5	4	4	**24**
Crataegus orientalis	1	1	2	1	0	**5**
Vitis sylvestris	0	3	0	0	0	**3**
Fragaria vesca	1	1	0	0	0	**2**
Crataegus monogyna	0	0	0	0	0	**0**
Unidentified	2	3	0	1	1	**7**
no seeds	9	14	17	10	8	**58**
Total	**55**	**44**	**39**	**51**	**54**	**243**
MARTEN						
Fruit species	**Di**	**Vf**	**Kr**	**Co**	**Ah**	**Total**
Rubus sp.	5	4	3	6	12	**30**
Rosa sp.	0	0	0	1	5	**6**
Malus sylvestris	3	3	1	7	1	**15**
Cornus mas	0	0	1	0	1	**2**
Prunus cocomilia	1	0	1	0	0	**2**
Prunus avium	4	0	4	1	4	**13**
Fragaria vesca	1	1	0	0	0	**2**
Unidentified	1	0	1	0	1	**3**
no seeds	22	8	7	10	26	**73**
Total	**37**	**16**	**18**	**25**	**50**	**146**
WOLF						
Rubus sp.	5	0	0	0	0	**5**
Rosa sp.	2	0	0	0	0	**2**
Malus sylvestris	1	0	0	0	0	**1**
Prunus cocomilia	2	0	0	0	0	**2**
Unidentified	2	0	0	0	0	**2**
no seeds	5	1	0	0	1	**7**
Total	**17**	**1**	**0**	**0**	**1**	**19**

Table 4.5. Number of faeces containing seeds that were deposited on the transects during the study period. These numbers exclude the faeces collected during May 1993 and May 1994. Transects: Ah = Ahladorema, Co = Connector, Di = Distropi, Kr = Krusovo, Vf = Virgin forest.

It is clear from figures 4.5.(a-d) and Table 4.5. which display the numbers of faeces found containing particular seed species, that some carnivores were taking particular seed species more readily than others. *Rubus* sp. and *Rosa* sp. were readily eaten by all the carnivores, *Malus sylvestris* was consumed less frequently by bears. Foxes were also consuming *Crataegus orientalis, Vitis sylvestris, Fragaria vesca,* and *Crataegus monogyna,* but these cases were rare. They were frequently consuming *Cornus mas* seeds, as were martens, and bears even more extensively so. Martens were the only other carnivore consuming *Fragaria vesca.* All four carnivores consumed *Rubus* sp., *Rosa* sp., *Malus sylvestris* and *Prunus cocomilia.* Some other seed species like *Crataegus orientalis, Crataegus monogyna* and *Vitis sylvestris* were only eaten by foxes. Overall foxes consumed 9 identified seed species during the two years of the study, martens consumed 7, bears 6 and wolves 4.

(a). Fox



(b) Marten

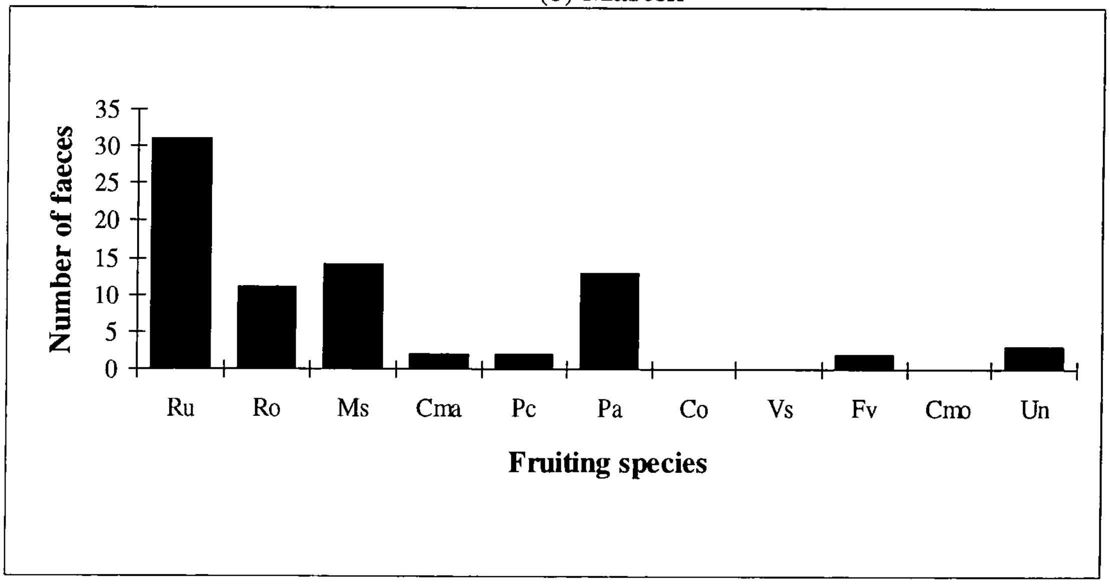
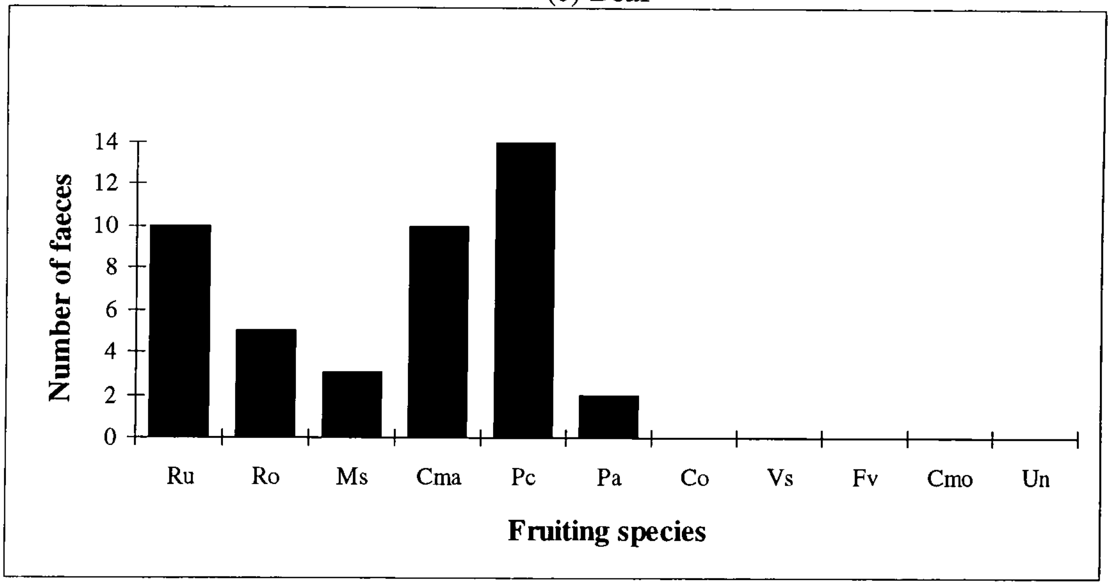


Fig. 4.5. Number of carnivore faeces containing seeds of the fruiting species.
Ru = *Rubus* sp., Ro = *Rosa* sp., Ms = *Malus sylvestris*, Cma = *Cornus mas*, Pc = *Prunus cocomilia*, Pa = *Prunus avium*, Co = *Crataegus orientalis*, Vs = *Vitis sylvestris*, Fv = *Fragaria vesca*, Cmo = *Crataegus monogyna*, Un = unidentified seeds.

(c) **Bear**



(d) **Wolf**

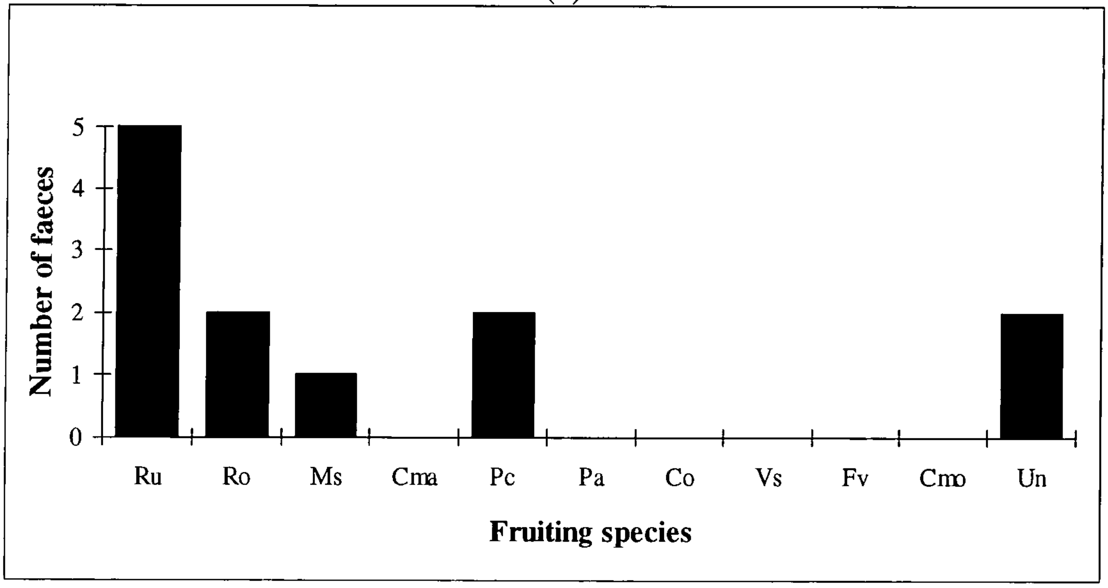


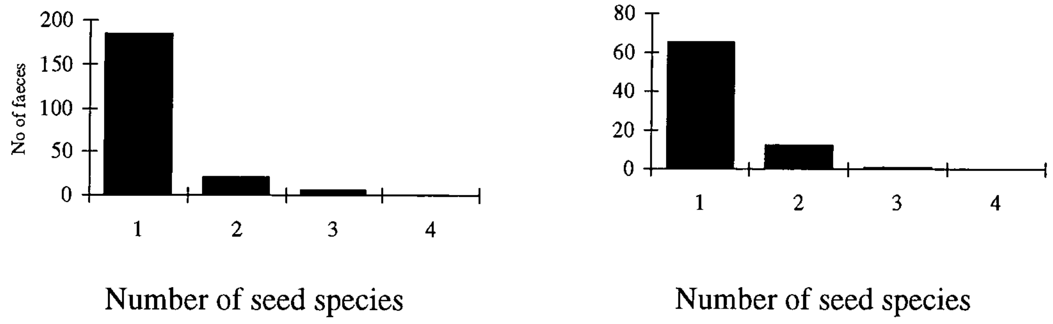
Fig. 4.5. Number of carnivore faeces containing seeds of the fruiting species
Ru = *Rubus* sp., Ro = *Rosa* sp., Ms = *Malus sylvestris*, Cma = *Cornus mas*, Pc = *Prunus cocomilia*, Pa = *Prunus avium*, Co = *Crataegus orientalis*, Vs = *Vitis sylvestris*, Fv = *Fragaria vesca*, Cmo = *Crataegus monogyna*, Un = unidentified seeds.

4.3.1.4. Number of seed species found in faecal samples

In the following section the number of species of seed found in each scat are analysed. There was a significant difference between the numbers of faeces containing one species of seeds and those which contained more than one (χ^2 = 18.36, 3 d.f., p<0.001). More fox faeces were found to contain more than one species of seed than other carnivores (Fig. 4.6.). Bear faeces usually contained more seed species than any others. This figure was much higher for bears' faeces in relation to the total number of their faeces when compared to the figure of the other carnivores. Bears and wolves were the only carnivores which occasionally had four species of seeds found in a single faecal sample. No more than four species of seeds were found in any faeces.

(a) fox

(b) marten



(c) bear

(d) wolf

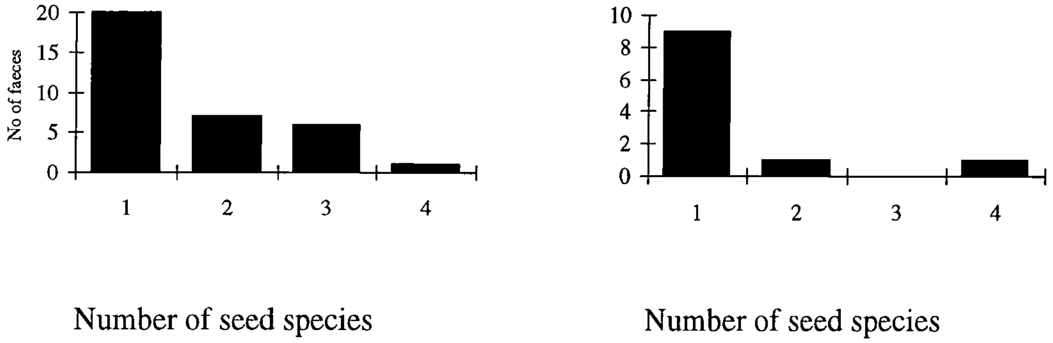


Fig. 4.6. Number of faeces containing 1, 2, 3 or 4 species of seeds. The vertical axis indicates the number of faeces examined.

4.3.1.5. Combinations of seed species found in faeces

After testing the statistical significance of the seed species found together in carnivore scats by using thirty eight 2×2 contingency tables which investigated all the combinations found, I obtained the following pairs of significant negative and positive associations. For the tables that contained expected values below five, a Fisher Exact test was used to investigate the significance level. There were not enough data on wolf to carry out the same test.

	Fox	**Marten**	**Bear**
Positive Associations	*Malus sylvestris-C. monogyna* *Cornus mas-C. orientalis*	*P. cocomilia-P. avium*	*Rubus sp.-P. cocomilia* *C. mas-P. cocomilia* *P. avium-P. cocomilia* *C. mas-M. sylvestris* *Rubus sp.-C. mas*
Negative Associations	*Rubus sp.-Rosa sp.* *Malus sylvestris-Rosa sp.*	*Malus sylvestris-Rubus sp.* *Rosa sp.-Rubus sp.*	

Table 4.6. Positively and negatively-associated seed species found in carnivore scats

There was a positive correlation between *Malus sylvestris-Crataegus monogyna* and *Cornus mas-Crataegus orientalis* in the faeces of foxes. The negative correlations came from the pairs *Rubus* sp.-*Rosa* sp. and *Malus sylvestris-Rosa* sp. which mainly reflect the fact that foxes were consuming these fruit at different times of the year. Martens consumed *Prunus avium* and *Prunus cocomilia* during the same period. The negative correlations came from the pairs *Malus sylvestris -Rubus* sp. and *Rosa* sp.-*Rubus* sp., again possibly reflecting different plant phenologies. The pairs of fruit positively correlated from bear scats reflect the animals' tendency to consume 2 or 3 species of fruit during the same period. As a result they had the highest number of positive correlations. There were no negative correlations.

4.3.1.6. Occurrence of seed species in the altitudinal zones

Table 4.7. indicates the frequency that each seed species (in faeces) was found in each of the altitudinal zones. The number is corrected for the length of transects in each zone. The total frequency of occurrence of seed species clearly declines with increasing altitude and does not seem to follow the trend of the density of the fruit-producing plants in the altitudinal zones (Table 2.5). The frequency in which each species was found steadily declines with increasing altitude as well. The only exceptions were rarely found species such as: *Vitis sylvestris, Fragaria vesca*, and *Crataegus orientalis*. The species diversity displays no clear trend (Table 4.7.).

	Altitude (m)				
Seed species	**900-1099**	**1100-1299**	**1300-1499**	**1500-1700**	**Average**
Rubus spp.	9.47	6.53	4.35	1.89	5.56
Rosa spp.	7.89	2.03	1.96	0.54	3.11
Malus sylvestris	5.53	2.37	0.43	0.54	2.22
Cornus mas	3.68	1.27	0.43	-	1.35
Prunus cocomilia	3.16	2.12	0.43	0.27	1.50
Prunus avium	5.00	2.88	1.74	0.27	2.47
Crataegus orientalis	-	0.25	0.43	-	0.17
Vitis sylvestris	-	-	0.65	-	0.16
Fragaria vesca	-	0.17	0.65	-	0.33
Crataegus monogyna	0.26	-	-	-	0.07
Total	34.99	17.63	11.09	3.51	16.81
No of species	7	8	9	5	7.25

Table 4.7. Mean number of times that each species (in faeces) was found per km.

4.3.2. Numbers of seeds found in faeces

4.3.2.1. Factors affecting the number of seeds found in faeces

As an indication of the quantity of seeds that are being dispersed by the carnivores I calculated the mean number of seeds per scat, is 801 for bears, 121 for foxes, 84 for wolves and 38 for martens. An analysis of variance was carried out to examine the effects of seed species and carnivore on the number of seeds found in faeces. The number of seeds found in faeces was significantly different for each carnivore (Table 4.8.). If we consider the total number of seeds dispersed on the transects we find that foxes dispersed the most

Source of Variation	Sum of Squares	DF	Mean Square	F	Significance
Seed species (Ss)	31.07	8	3.88	10.58	p<0.001
Carnivore (Ca)	15.60	3	5.20	14.17	p<0.001
Ss-Ca	8.87	14	0.63	1.73	not sign.
Residual	96.19	262	0.37		
Total	200.31	287	0.70		

Table 4.8. Results of ANOVA analysing the effects of Seed species and Carnivore on the logarithm of the number of seeds found in faeces.

seeds followed by bears and then martens and wolves with much lower figures (Table 4.9). Undoubtedly this reflects the high number of fox faeces deposited in the habitat (see previous chapter) as well as the large volume of bear scats. If we look at the average number of seeds dispersed every time each carnivore consuming a particular seed species, then bears were dispersing three times as many as foxes which came second with wolves following and then martens.

The seed species had a significant effect on the numbers of seeds to be found in every faeces (Table 4.8.). Either some of the fruits have more seeds as is the case with *Rosa* sp., *Rubus* sp. *Malus sylvestris* and *Fragaria vesca* and/or more fruits of some species were consumed by carnivores and their seeds were dispersed in greater numbers in the habitat. This obviously increased the chances that the seeds would be transported to favourable sites for germination. The order of number of seeds dispersed decreased from *Rubus* sp., *Rosa* sp., *Fragaria vesca, Prunus cocomilia, Malus sylvestris, Prunus avium, Cornus mas, Crataegus orientalis* to *Vitis sylvestris*. The two-way interaction of the two effects was not significant and therefore all carnivores were consuming proportionally equivalent numbers of seeds from each species.

Unfortunately the scarcity of some species of seed in the diet of the carnivores made the examination of the effects of month and year impossible. Nevertheless, some important points should be noted from Figures 4.7, 4.8, 4.9 and 4.10 which show the percentage of seeds of every fruiting plant found in each carnivore's scats as a proportion of the total number of seeds dispersed by carnivores during that month.

BEAR						
	TRANSECTS					
Fruit species	**Di**	**Vf**	**Kr**	**Co**	**Ah**	**Total**
Rubus sp.	12430	0	3112	32	447	**16021**
Rosa sp.	4890	0	0	0	2120	**7010**
Malus sylvestris	0	0	132	0	11	**143**
Cornus mas	10	0	234	0	167	**411**
Prunus cocomilia	280	32	71	3	702	**1088**
Prunus avium	0	0	128	0	100	**228**
Total	**17610**	**32**	**3677**	**35**	**3547**	**24901**
FOX						
Rubus sp.	8074	6629	904	6693	7737	**30037**
Rosa sp.	321	64	65	1	244	**695**
Malus sylvestris	150	?	0	174	441	**765**
Cornus mas	5	0	78	2	7	**92**
Prunus cocomilia	15	0	6	47	26	**94**
Prunus avium	136	52	134	131	109	**562**
Crataegus orientalis	11	80	67	10	0	**168**
Vitis sylvestris	0	40	0	0	0	**40**
Fragaria vesca	483	735	0	0	0	**1218**
Unidentified	110	17	0	0	?	**127**
Total	**9305**	**7617**	**1254**	**7058**	**8564**	**33798**
MARTEN						
Rubus sp.	1702	772	289	474	1443	**4680**
Rosa sp.	0	0	0	4	143	**147**
Malus sylvestris	?	29	18	65	?	**112**
Cornus mas	0	0	5	0	1	**6**
Prunus cocomilia	1	0	1	0	0	**2**
Prunus avium	45	0	13	2	26	**86**
Fragaria vesca	30	1120	0	0	0	**1150**
Unidentified	45	0	?	0	?	**45**
Total	**1823**	**1921**	**326**	**545**	**1613**	**6228**
WOLF						
Rubus sp.	1772	0	0	0	0	**1772**
Rosa sp.	167	0	0	0	0	**167**
Malus sylvestris	2	0	0	0	0	**2**
Prunus cocomilia	27	0	0	0	0	**27**
Unidentified	3	0	0	0	0	**3**
Total	**1971**	**0**	**0**	**0**	**0**	**1971**

Table 4.9. Number of seeds found in faeces that were deposited on the transects during the study period. . These numbers exclude the faeces collected during May 1993 and May 1994. Transects: Ah = Ahladorema, Co = Connector, Di = Distropi, Kr = Krusovo, Vf = Virgin forest.

In 1993 all carnivores were surprisingly similar in the species of seed found in the scats. They all readily consumed *Rubus* sp. fruit, the seeds of which were found in the highest numbers in scats. *Rosa* sp. seeds were the next most frequent for all carnivores species. Other species found in large numbers were *Malus sylvestris and Fragaria vesca* for fox, *Prunus cocomilia* and *Cornus mas* for bear and *Prunus cocomilia* for wolf.

In 1994 this similarities in the number of seeds deposited in the faeces of carnivores ceased to exist. Foxes consumed high numbers of *Rubus* sp. and *Rosa* sp. seeds as in the previous year and *Fragaria vesca* was the third most numerous. For martens *Rubus* sp. was the most commonly occurring with *Fragaria vesca* second and *Malus sylvestris* third. Bears increased their consumption of *Rosa* sp. seeds by approximately 12 times comparing to the previous year. *Rubus* sp. and *Prunus cocomilia* were also found in large numbers. One striking difference between the two years is the remarkable increase in the numbers of *Prunus avium* seeds found in scats in 1994. Foxes increased their consumption of this species by 42 times and martens by 21 times. It was also found to be the fourth highest in bear faeces although none was found in 1993. In 1994 I found no seeds in wolf faeces during which time all other carnivores increased considerably the mean number of seeds that they consumed.

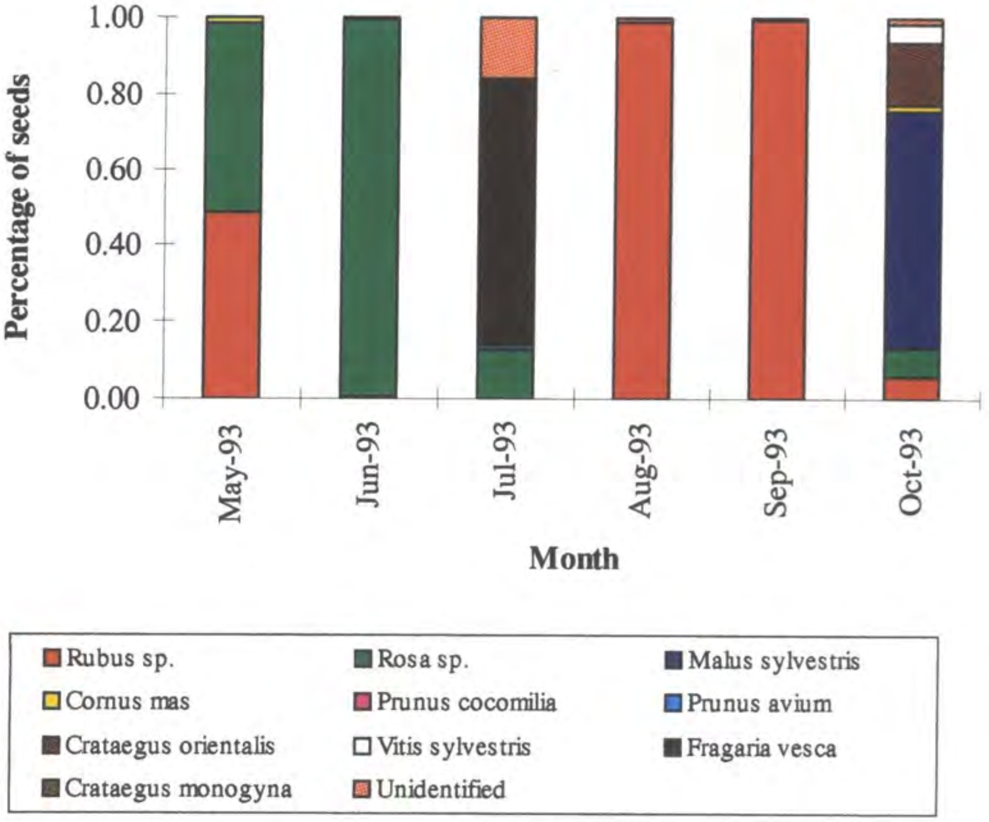


Fig 4.7(a). Proportion of seeds from the fruiting plants in the diet of foxes during 1993.

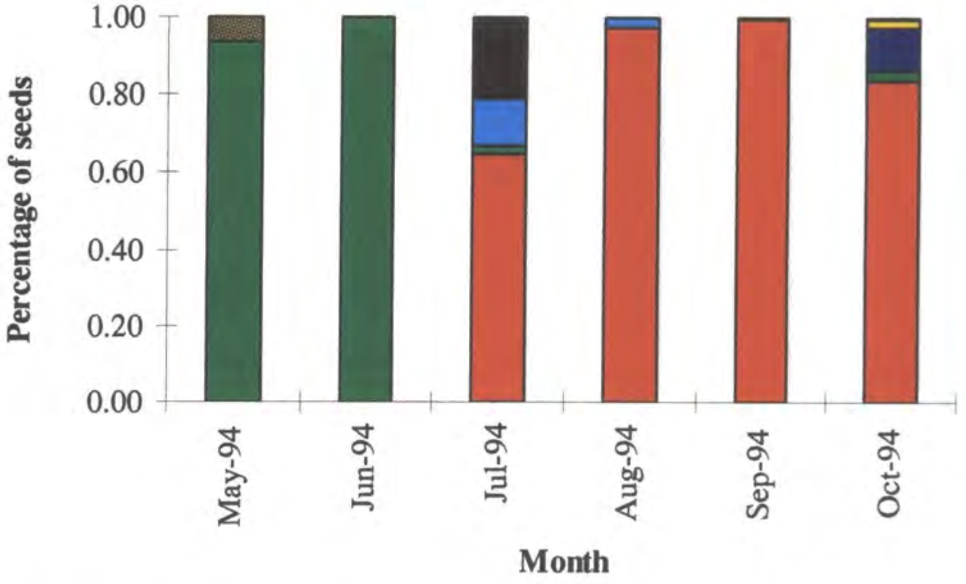


Fig 4.7(b). Proportion of seeds from the fruiting plants in the diet of foxes during 1994.

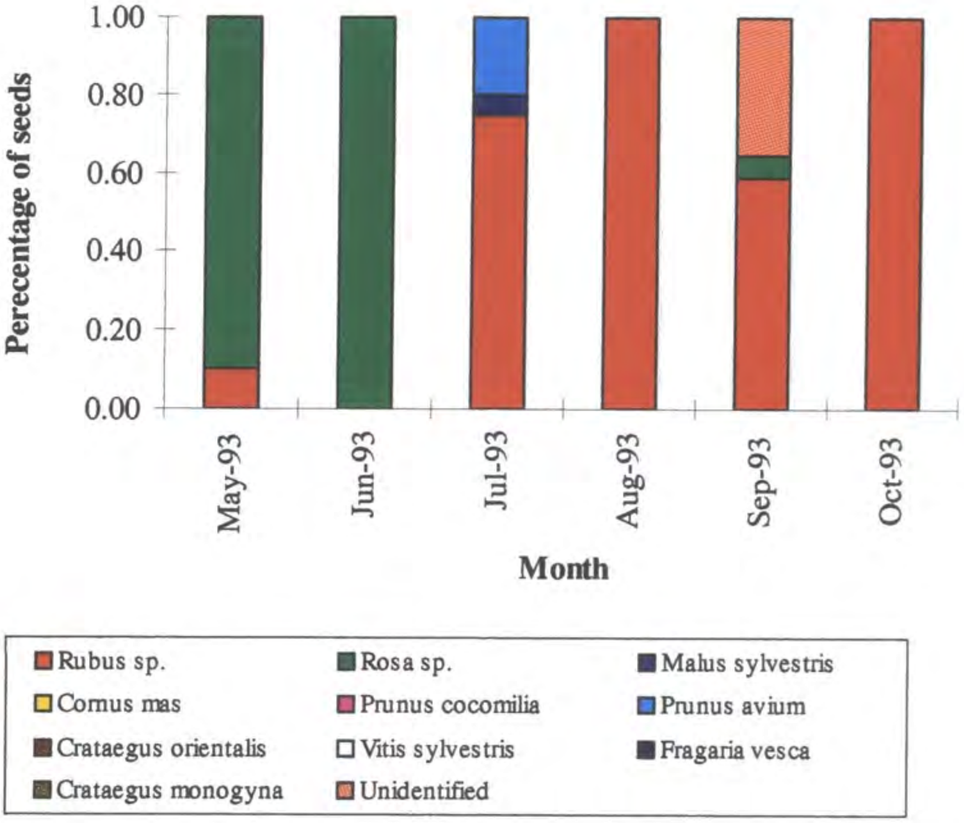


Fig 4.8(a). Proportion of seeds from the fruiting plants in the diet of martens during 1993.

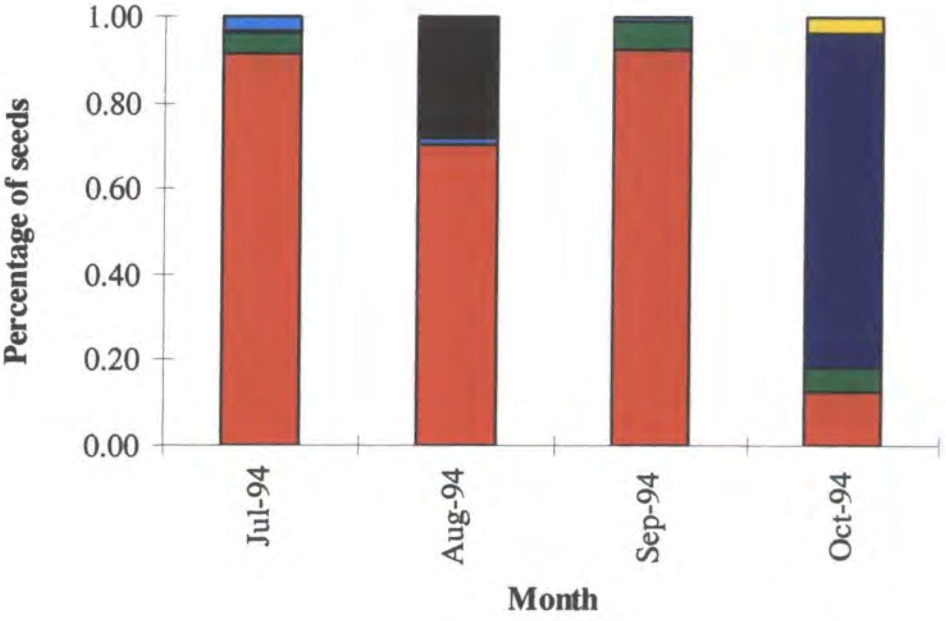


Fig 4.8(b). Proportion of seeds from the fruiting plants in the diet of martens during 1994.

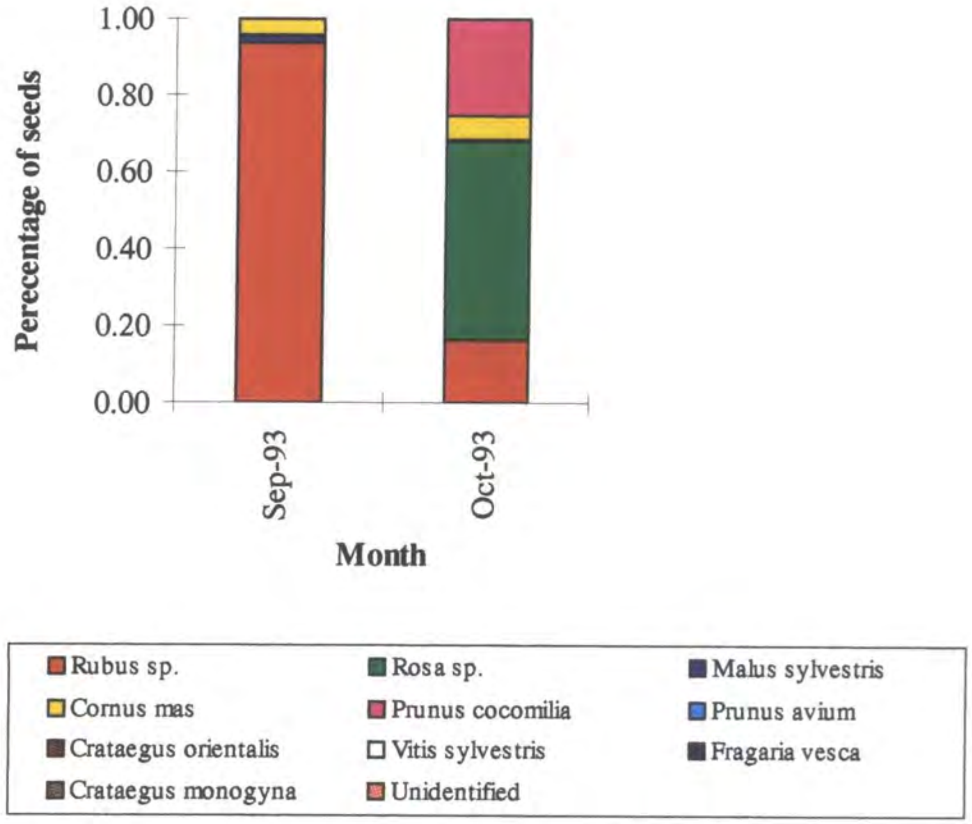


Fig 4.9(a). Proportion of seeds from the fruiting plants in the diet of bears during 1993.

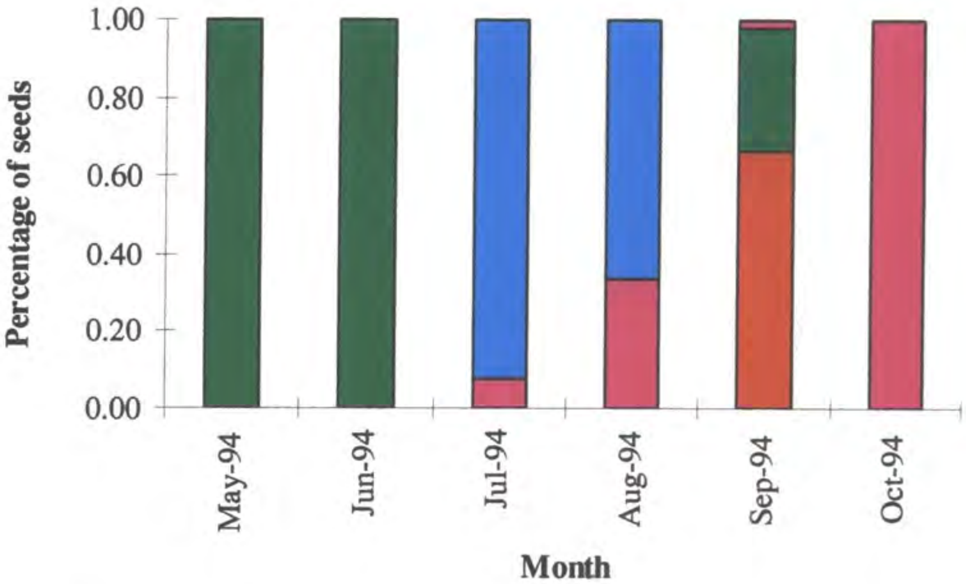


Fig 4.9(b). Proportion of seeds from the fruiting plants in the diet of bears during 1994.

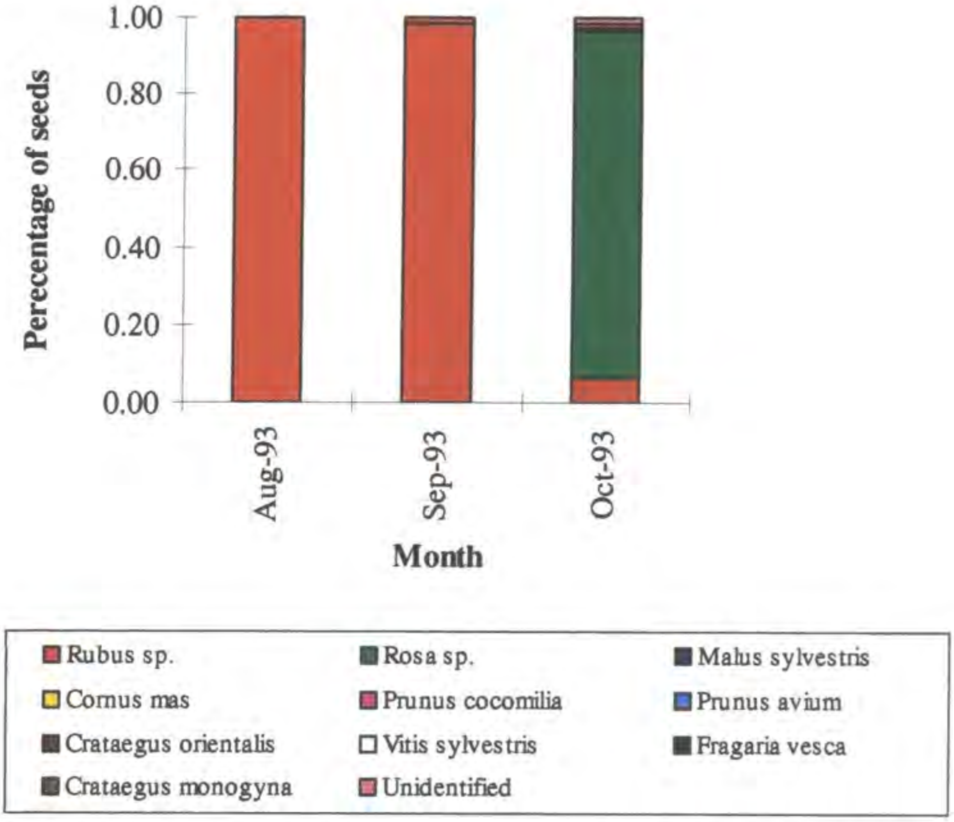


Fig 4.10. Proportion of seeds from the fruiting plants in the diet of wolves during 1993.

4.3.2.2. Factors affecting the numbers of damaged seeds in the faeces

An analysis of variance examined the proportion of seeds found intact out of the total number of seeds found. This revealed that the proportion did not differ between the carnivore species consuming the seeds (Table 4.10., 4.11.). On the other hand, individual plant species differed in the survival of their seeds. During the detailed analysis of damaged seeds that follows, the percentages always indicate lack of physical damage (intact seeds/total number of seeds) after passage through the carnivores' gut.

From Table 4.12. it is apparent that *Malus sylvestris* was the species most often damaged by foxes (11.0%), martens (15.5%) and bears (4.4%). This is a species

Source of Variation	Sum of Squares	DF	Mean Square	F	Significance
Carnivore (Ca)	195.60	3	65.20	0.49	not sig.
Seed species (Ss)	3004.56	8	375.57	2.81	p<0.01
Ca-Ss	1412.02	14	100.86	0.76	not sig.
Residual	42209.55	316	133.58		
Total	54363.20	341	159.42		

Table 4.10. Results of ANOVA analysing the effects of Carnivore and Seed species on the arc-sine transformed proportion of intact seeds out of the total.

Seed species	Fox		Marten		Bear		Wolf	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Rubus sp.	441.72	49.40	154.63	44.10	1778.44	1110.71	226.13	156.90
Rosa sp.	69.44	16.25	25.70	7.18	3474.00	1365.43	47.00	34.72
M. sylvestris	24.55	3.36	10.00	2.37	44.33	24.46	2.00	0.00
Cornus mas	8.00	1.54	3.00	2.00	77.60	35.82	0.00	0.00
P. cocomilia	6.27	1.24	1.00	0.00	78.14	33.66	13.50	11.50
Prunus avium	23.29	4.58	6.62	2.03	92.50	7.50	2.00	0.00
C. orientalis	10.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
V. sylvestris	11.67	6.12	0.00	0.00	0.00	0.00	1.00	0.00
Fragaria vesca	608.00	127.00	575.00	545.00	0.00	0.00	0.00	0.00
C. monogyna	40.00	14.67	0.00	0.00	0.00	0.00	0.00	0.00
unidentified	31.00	25.72	43.00	0.00	0.00	0.00	2.67	1.20

Table 4.11. Means and standard errors of the number of seeds found intact in the carnivores' faeces.

Seed species	Fox	Marten	Bear	Wolf
Rubus sp.	0.32	3.59	0.05	2.24
Rosa sp.	7.98	16.91	4.26	0.35
Malus sylvestris	11.05	15.54	4.40	0.00
Cornus mas	0.00	0.00	0.00	0.00
Prunus cocomilia	0.00	0.00	1.17	-
Prunus avium	0.32	0.52	16.80	-
Crataegus orientalis	0.74	-	-	-
Vitis sylvestris	24.37	-	-	-
Fragaria vesca	0.20	0.00	-	-
Crataegus monogyna	0.00	-	-	-
unidentified	0.80	4.44	-	-

Table 4.12. Percentage of the seeds found damaged in the carnivores' faeces out of the total.

which contains soft seeds that can easily be damaged by chewing. The seeds of *Rosa* sp. were found to be damaged quite frequently (8.0% by foxes and 16.4% by martens). Foxes also damaged *Vitis sylvestris* seeds (24.4%) and they were the only carnivore consuming these fruits. The seeds in this case again are very easy to damage.

Bears were the only carnivore found to inflict any significant damage to the seeds of *Prunus avium* (16.8%), although seeds of this species were only found twice in bear scats and there is a possibility that the sample is not representative of the actual survival rate (Table 4.12.). Wolves (2.24%) and martens (3.59%) were the only carnivores inducing any measurable damage to *Rubus* sp. However, the survival rates were very high and only because the other three carnivores had even higher seed survival rates by comparison it appears that *Rubus* were not doing well.

Cornus mas and *Prunus cocomilia* seeds were almost never damaged by any carnivore and it is not difficult to understand the reason for this since they are among the hardest to break of the seeds studied. Foxes never damaged *Crataegus monogyna* and martens never damaged *Fragaria vesca. Malus sylvestris*, surprisingly, never suffered any damage by wolves but its seeds were only found in one faeces.

From the seeds' point of view, wolves were the carnivores least likely to damage seeds, as the average survival rate for the seeds passing through their gut was 98.8%. Four species of seed were consumed by all the carnivores studied and their survival rates were as follows: I found that for *Rubus* sp. the best survival rate was through the gut of the bears. *Rosa* sp. passed almost intact (99.7%) through the wolves digestive system. *Malus sylvestris* did not suffer any damage when consumed by wolves, and the same happened with *Prunus cocomilia.* The interaction of the effects of carnivore and seed species was not significant as damage was related to the seed species rather than the carnivores. Furthermore, all survival rates were high.

4.3.2.3. The Relationship between seed weight and seed number.

As was expected the mean weight of each carnivores' faeces was related to the body size of the species (Table 4.13.). The number of seeds contained in each faeces was divided by the faeces' weight in order to produce a standardised measure of seed density (number of seeds per g) that would override the problem of the large variation of the faeces' weight (Table 4.14.). Faeces that contained more than one species of seeds were excluded from this analysis. Additionally there was a large variation on the weight of the seeds of each plant species. In general a relationship existed between the mass of seeds .and their density in faeces. Regression analysis revealed this to be statistically significant for fox and bear but not for marten and wolf (Table 4.15.).

	Fox	**marten**	**bear**	**wolf**
Mean	4.01	1.76	221.44	24.93
Standard error	0.26	0.13	42.73	3.83
Minimum	0.20	0.28	3.76	5.14
Maximum	25.93	5.34	539.28	43.14

Table 4.13. Descriptive statistics on the weight of faeces containing seeds (weight in grams).

Seed species	**Mean seed mass**	**Mean number of seeds per gram of faeces**			
		fox	marten	bear	wolf
Cornus mas	0.4867	1.78	1.40	0.71	-
Crataegus orientalis	0.0421	8.11	-	-	-
Fragaria vesca	0.0004	344.29	645.63	-	-
Malus sylvestris	0.0116	7.95	4.51	0.71	0.10
Prunus avium	0.1767	3.86	3.44	2.65	-
Prunus cocomilia	0.5567	0.77	1.01	0.19	0.38
Rosa sp.	0.0121	21.93	22.88	26.33	4.62
Rubus sp.	0.0023	131.96	83.57	17.73	9.84
Vitis sylvestris	0.0293	2.48	-	-	-

Table 4.14. Mean mass of each seed species and mean seed density found in the faeces of each carnivore.

Equation		R^2	ANOVA					
				df	SS	MS	F	signif.
fox	y= -154.19x+69.097	0.109	Regression	1	164780	164780	25.038	p<0.001
			Residual	204	1342541	6581		
			Total	205	1507321			
marten	y= -205.77x+69.355	0.027	Regression	1	50898	50898	1.994	not sig.
			Residual	73	1863346	25525		
			Total	74	1914244			
bear	y= -29.261x+15.908	0.216	Regression	1	2824	2824	13.510	p<0.001
			Residual	49	10241	209		
			Total	50	13064			
wolf	y= -12.726x+7.471	0.076	Regression	1	76.858	76.858	0.658	not sig.
			Residual	8	934.921	116.865		
			Total	9	1011.779			

Table 4.15. Results of linear regression examining the relationship between seed weight and seed density in each carnivore's faeces.

4.4. DISCUSSION

4.4.1. Frugivory index

During the analysis of the frugivory index (FI) it became apparent that the importance of fruit in the diet of carnivores steadily increases as the year progresses from spring towards September as has been shown in numerous other studies (Cook and Hamilton 1944, Ballenberghe *et al.* 1975, Slobodyan 1976, Servheen 1983, Goszczynski 1986, Papageorgiou 1988, Mattson *et al.* 1991, Clevenger 1993a, b, Sarafini & Lovari 1993). During September I found that frugivory was elevated to its highest values before slightly declining in October. Conclusions drawn during the following discussion are based on the assumption that carnivores eat the flesh of the fruit together with the seeds, without rejecting the latter. I believe that this is a realistic assumption since selective feeding on the flesh of the fruit has not been reported for carnivores. Another assumption that has been made is that all the species of fruit were equally available to all the carnivores in this study.

The above data set further revealed that bears were the most frugivorous carnivores as all their faeces contained seeds. This is hardly surprising when we consider published literature on the diet of brown bears. In most cases there is evidence that brown bears depend heavily on a fruit diet whenever such an option is available (Pearson 1975, Slobodyan 1976, Servheen 1983, Cicnjak 1987, Adamakopoulos 1991, Mattson *et al.* 1991, Clevenger *et al.* 1992d, Frackowiak and Gula 1992). There are cases reporting that brown bears switched to fruit even when high-protein foods (e.g. livestock) were easy to obtain (Pearson 1975, Elgmork & Kaasa 1992). Mattson *et al.* (1991) suggested that this is probably because foods containing a large proportion of digestible carbohydrate are more efficiently converted to fat than protein-rich foods and so would accelerate fat accumulation during hyperphagia. Furthermore, it has been suggested (Pearson 1975, Willson 1993a) that failure of fruit crops may be associated with reduced pre-hibernation fat deposition and, as a result, lowered reproductive success.

Foxes had the second highest FI and the importance of fruit in their diet has also been well documented (Cook & Hamilton 1944, Macdonald 1981, Goszczynski 1986b, Papageorgiou 1988, Hernández 1993). However, it is apparent from the literature that red foxes regularly supplement their diet with rodents and other small mammals (Scott 1943, Patalano & Lovari 1993). In many cases the importance of fruit is limited or even negligible (Errington 1937, Southern & Watson 1941, Goszczynski 1974, Reig & Jedrzejewski 1988). It must also be taken into account that red foxes together with grey wolves, can only reach the lower branches or wait until fruits have fallen to the ground where they face competition with other animals such as wild boars and ground feeding rodents.

Wolves were third most frugivorous as far as the FI is concerned although this is based on very small sample sizes. The general outcome of the literature review is that wolves, although they take fruit, it is usually of secondary importance compared to animal matter (Ballenberghe *et al.* 1975, Salvador & Abad 1987, Okarma 1993, Thurber & Peterson 1993). According to my study also, when the remains of fruit were found in faeces their contribution to the total volume was usually small.

Martens were the least frugivorous carnivores in my study. Many of their faeces were composed solely of mammal hair and bones. Nevertheless, in autumn, the period when most of the shrub species were in fruit, many of the marten faeces were composed entirely of fruit. Published studies on the diet of martens, give a picture of variable importance of the role that fruit plays in the diet. It fluctuates between being very significant (Lockie 1961, Goszczynski 1986, Clevenger 1993a, 1993b, Lucherini & Crema 1993, Serafini & Lovari 1993, Cheylan & Bayle in Clevenger 1994) to secondary importance (Hargis & McCullough 1984, Buskirk & Macdonald 1984, Nargosen & Forsberg 1989). Martin (1994) suggested that in some cases, vegetation might be used as a substitute when the preferred prey could not be obtained. He added that the use of high-density patches of plant foods, such as berries, may provide lower energetic cost/benefit ratios than if they hunted mammalian prey.

There was a significant difference in FI among carnivores overall between the two years of the study with 1994 being the highest. The high FI value of that year can be attributed to the considerable increase in the martens' frugivory. However the fruit production did not differ between the two years of the study (Chapter two). This opportunistic feeder shifted its diet towards a heavier dependence on fruit when the conditions (e.g. reduced numbers of favourable prey) probably became more favourable for this kind of feeding.

There were no significant differences of the FI between transects. Based on the information derived from this data set we can conclude that the seed shadows produced by of the carnivores exhibit considerable temporal but very limited spatial variation. Carnivores have long through the gut passage rates as will be discussed more extensively in Chapter five. Therefore it is possible that local deposition does not imply local consumption.

4.4.2. Presence of seed species in the faeces.

One question that this study set out to answer concerned whether the carnivores were consuming fruits according to their temporal availability. Excluding *Rosa* sp. the mean length of the fruit displays in the area was two months (Table 2.6). This value is similar to that reported by Herrera (1984a) for shrublands (2.2-3.5 months) and temperate forests (0.6-1.3 months) (see Chapter two).

In June, the phenology surveys indicated that the only fruit available that month was *Fragaria vesca* although the analysis of carnivore faeces recorded the reoccurring presence of *Rosa* sp. seeds. Table 2.6. indicates that in fact there were unripe fruits of *Rosa* sp. available. Since the phenology surveys were not carried out during winter, the table does not show the presence of fruits from the previous year that remained on the plant and could still be consumed by frugivores. The consumption of *Rosa* sp. by carnivores is very widely documented (Slobodyan 1976, Meriggi *et al.* 1991, Clevenger *et al.* 1992d, Clevenger 1993b, Lucherini and Crema 1993, Buskirk and Macdonald 1984).

Fragaria vesca seeds actually appeared in faeces in July although they fruit only in June and this is probably because faeces were collected up to a month after they had been deposited due to the experimental design. During this month *Rubus* sp., *Prunus avium, Rosa* sp., *Malus sylvestris* and *Prunus cocomilia* seeds were also found in faeces. The phenology survey found that, with the exception of *Prunus avium,* all the rest of the fruits must have been unripe when eaten. The carnivores were either sufficiently fond of these fruit that they were consuming them before they reached their full nutritious potential or the shortage of other food sources was forcing them to do so. It is well documented in the literature that when *Prunus avium* comes into fruit and in the years that the crop is good, carnivores utilise this resource extensively (Cook and Hamilton 1944, Goszczynski 1986). *Rubus* sp. show a wide distribution and the large size of the crop provides carnivores with a valuable energy source (Cook and Hamilton 1944, Ballenberghe *et al.* 1975, Slobodyan 1976, Macdonald 1981, Berducu *et al.* 1983, Buskirk and MacDonald 1984, Goszczynski 1986, Adamakopoulos 1991, Meriggi *et al.* 1991, Clevenger *et al.* 1992d, Clevenger 1993a, b).

In August *Rubus* sp., *Prunus cocomilia, Prunus avium* and *Fragaria vesca* seeds were consumed by carnivores. The first two species were readily available from the plants. *Prunus avium* however was not. Its presence in the diet can be explained either because faeces were lying on the ground for sometime before collection and/or these fruit were consumed after they had fallen to the ground. *Fragaria vesca* is a small and inconspicuous plant and could be fruiting in areas but not detected during the phenology surveys.

September is the month of abundant fruit availability for the carnivores. *Rubus* sp., *Cornus mas, Prunus cocomilia, Prunus avium, Rosa* sp. and *Malus sylvestris* all appeared in the diet. Apart from the last two species all were ripe during this month. In October *Prunus avium* disappeared but additionally *Crataegus orientalis* and *Vitis sylvestris* became available. These two months coincide with the peak of the fruiting season in the study area. In October the apples of *Malus sylvestris* ripened and soon after that they fall on the ground making them accessible to foxes and wolves, carnivores which do not possess arboreal feeding abilities and as a result the consumption of this fruit greatly increased (Cook and Hamilton 1944, Slobodyan

1976, Macdonald 1981, Goszczynski 1986, Cicnjak *et al.* 1987, Papageorgiou *et al.* 1988, Meriggi *et al.* 1991, Clevenger *et al.* 1992d, Clevenger 1993a).

From the above it is obvious that carnivores in many cases consume the fruit even before they were ripe. It is not clear whether this could affect the germination potential of the seeds as this would depend on whether they had the time to fully develop before consumption. This could be an interesting aspect to investigate in future studies.

During the data collection period I often observed that a number of fruit species fall to the ground soon after ripening. The effect was most pronounced with the following species: *Prunus cocomilia, Malus sylvestris, Cornus mas* and *Prunus avium.* This effect is most probably an adaptation in order to increase consumption by ground foraging frugivores (Herrera 1989).

If we compare all the carnivores feeding on fruiting species over summer and autumn we find that they show some differences in their diet and these data come to support The observations of Patalano & Lovari (1993) discovered an absence of food competition between red foxes and grey wolves. In July, all carnivores were feeding on *Prunus avium* but martens also concentrated on *Rubus* sp. and *Rosa* sp. although bears were mainly feeding on *Prunus cocomilia* which was their preferred fruit (Servheen 1983, Cicnjak *et al.* 1987). Bears often focus their feeding activity on one or two trees of the above mentioned species during the same night. They usually climb up the tree and bend or break the branches to the ground where they can feed at their leisure. *Prunus cocomilia* trees stripped of their branches were a common sight in the area during August. During this month foxes and martens fed on the remaining fruit of *Prunus avium* as well as *Rubus* sp. which start ripening their fruit. Wolves also started feeding on this species as soon as it was ripe. For the period June-August, Herrera (1989) found in south-eastern Spain that the dominant fruit species in the carnivores diet were: *Prunus mahaleb* and *Juniperus phoenicea.* In September the diet was still dominated by *Rubus* sp. In this month *Cornus mas* and *Rosa* sp. appeared in the diet which closely resembles the findings by Herrera (1989) who found that during the period September to November *Rubus* sp. and *Rosa canina* occurred most often in the faeces. Serafini & Lovari (1993) reported that red foxes and stone martens were feeding on *Cornus mas* during this period. The availability of fruit increased in quantity and variety. It is the month, with the most species of shrubs being in fruit and the carnivores took advantage of this feeding opportunity. All carnivores consumed several species of fruits in October as *Malus sylvestris* became ripe.

Fruiting species that were not found very often in carnivore scats during this study have however been reported in the literature such as *Crataegus* spp. (Cook and Hamilton 1944, Servheen 1983, Clevenger *et al.* 1992d, Clevenger 1993b), *Fragaria* spp. (Cook and Hamilton 1944, Slobodyan 1976), *Vitis* spp. (Papageorgiou *et al.* 1988, Adamakopoulos 1991, Clevenger 1993a) and *Cornus* spp. (Papageorgiou *et al.* 1988).

Vaccinium species are often reported in the literature as being consumed regularly by carnivores (Cook and Hamilton 1944, Lockie 1961, Ballenberghe *et al.* 1975, Pearson 1975, Slobodyan 1976, Berducu *et al.* 1983, Buskirk and MacDonald 1984, Mattson *et al.* 1991, Elgmork and Kaasa 1992, Clevenger *et al.* 1992d, Frackowiak and Gula 1992). However, in this study they were never found in the scats although they do grow in the area. Two of these blueberry and blaeberry are found in Frakto area. Another fleshy fruit present in the area is *Sorbus aucuparia,* which is also consumed by carnivores studied elsewhere but not in the present study (Lockie 1961, Berducu *et al.* 1983, Clevenger 1993b, Marchesi *et al.* in Clevenger 1994). *Juniperus* spp. seeds have been found in carnivore faeces (Hargis and McCullough 1984, Clevenger 1993a and Cheylan and Bayle in Clevenger 1994) but were never found in this study either.

The absence of *Vaccinium* sp., *Sorbus aucuparia* and *Juniperus* sp. from the faeces in the study area is probably a result of the presence of more preferable fruits during their ripening period. The acorn and nut producing species were possibly utilised to certain extent after October when sampling ended as it has been reported for this period for bears (Berducu *et al.* 1983, Cicnjak *et al.* 1987, Adamakopoulos 1991, Clevenger 1992d, Frackoviak & Gula 1992), foxes (Papapgeorgiou *et al.* 1994), wolves (Papageorgiou et al. 1994) and martens (Hargis & McCullough 1984). Therefore, the early winter diet has to be studied for Frakto area in the future to provide a more complete data set.

According to my findings foxes and martens dispersed most of the fruiting species in the study area found to be consumed by carnivores. These data agree with the findings of Debussche and Isenmann (1989) in Montpellier (France) where red foxes and stone martens together accounted for 91% of the mammal-dispersed plant taxa.

4.4.2.1. Number of seed species found

The majority of the scats analysed contained only one species of seed regardless of the carnivore concerned. Foxes however, tended to consume more than one species during the same period compared to wolves and martens. Bears though, were the carnivores that deposited the greatest variety of fruit in their faeces. Brown bears have a lengthened carnivore gut (Herrero 1972, Herrero 1978) which could allow more than one feeding bout to mix and be deposited in one faeces. This is possible, maybe to a lesser extent, for the other carnivores too. Therefore the best interpretation of these results is that the carnivores were feeding on these fruits during the same 1-2 day period and not necessarily during one meal. Another possible explanation is that these fruit species grow close together and so they are eaten at the same time.

4.4.2.2. Combinations of seed species found in faeces

The positive associations between seeds that were found in fox faeces were: *Malus sylvestris-Crataegus monogyna* and *Cornus mas-Crataegus orientalis.* These fruit species ripened more or less in the same period, so it is not surprising to find them together. I believe that the significant χ^2 values were a result of the scarcity of the *Crataegus* sp. seeds found in scats, as *Crataegus monogyna* was only found once and this was with *Malus sylvestris* seeds. *Crataegus orientalis* seeds were found five times and two of these were found together with *Cornus mas* seeds. Again the numbers were very low and therefore finding these two species together could be a coincidence. *Malus sylvestris* and *Crataegus monogyna* were often found growing in the same area (Fig 2.1.b, e). *Cornus mas* and *Crataegus orientalis* were relatively rare plants in the study area and thus their seeds are not found together in faeces very often.

The negative correlations (*Rubus* sp.-*Rosa* sp. and *Malus sylvestris-Rosa* sp.) which mainly reflect the fact that foxes were consuming these fruits at different times of the year. These species have overlapping ripening periods, as *Rosa* fruits remain on the plant for most of the year. Foxes are possibly maximising the exploitation of an important feeding item by not consuming *Rosa* sp. fruits, while other fruits are present and available for shorter periods. Another possibility is that *Rosa* sp. fruits are not highly favourable feeding item and are only utilised when alternative fruit is not available. (Table 2.5., Fig. 4.1, 4.2, 4.3, 4.4)

Prunus cocomilia and *Prunus avium* were found to be significantly associated in martens' faeces. The two fruit species are quite similar in structure and belong to the same genus. Additionally they have an overlapping ripening period at the beginning of August and were found to grow close to each other. The negative correlations for this carnivore were *Malus sylvestris -Rubus* sp. and *Rosa* sp.-*Rubus* sp. This could be for two reasons: a) the animal gets enough energy by feeding on one of the two species and does not need to forage for supplementary food and b) the differential temporal exploitation of the two fruit species.

The pairs of fruit positively associated from bear scats reflected the animals' tendency to consume 2 or 3 species of fruit in each meal or the same period. As a result they had the highest number of positive associations and no negative associations. Bears have much higher energy requirements than the other carnivores of interest because of their much bigger body mass. This probably forces them to consume as many palatable fruit as they encounter during feeding. I found that most of these fruits ripen almost simultaneously, with *Prunus avium* ripening first and *Malus sylvestris* ripening last. Furthermore *Prunus cocomilia* and *Cornus mas* comprised three out of five positive associations, and were eaten by bears far more often than by the other carnivores.

4.4.2.3. Frequency of appearance of the seed species and species diversity in the altitudinal zones

The frequency with which each fruit species appeared in the faeces clearly declined with increasing altitude. The diversity of fruiting trees though did not show a clear relationship with altitude. A comparison with Table 2.5 reveals that carnivores were dispersing some seed species in altitudinal zones where the plant species were not found in the vegetation surveys e.g. in the 1100-1299 m zone *Crataegus orientalis,* and *Cornus mas* were dispersed by the carnivores although they were not found growing there. The same happened in the 1300-1499 m zone with *Vitis sylvestris, Crataegus orientalis, Prunus avium, Prunus cocomilia, Cornus mas,* and *Malus sylvestris* and in the 1500-1700 zone with *Prunus cocomilia, Prunus avium,* and *Malus sylvestris.* Species such as *Sambucus nigra, Sambucus racemosa, Sorbus torminalis, Sorbus aucuparia,* and *Juniperus communis* were never found in carnivore faeces but were growing in good numbers in the altitudinal zones from which faeces were collected, suggesting that these species are probably dispersed by birds or herbivorous mammals.

4.4.3. Numbers of seeds found in faeces

4.4.3.1. The effect of carnivores

Bear faeces contained the highest average number of seeds, a fact that apart from demonstrating the importance of fruit in the animals' diet, was also influenced by the large size of the faeces produced. Foxes had an average of 30.6% more seeds in their faeces than wolves, although the latter produced 622.5% larger faeces. If the size of the faeces was equal foxes would have 8.13 times more seeds in the faeces than wolves did. For equal size foxes would consume 8.2 times more seeds than bears and 1.4 times more than martens. Undoubtedly fruits form a much greater part of the foxes diet. These carnivores produced many more faeces than any other and as a result they dispersed many more seeds throughout the habitat. The bear scats found in the area were just a fraction of the number of fox faeces. However, the high number of seeds contained in each of the faeces brings them to the second position considering the number of seeds dispersed.

4.4.3.2. Number of seeds found

Rubus sp. seeds were found in the highest numbers in the carnivores faeces. It was a fruit eaten by all the carnivores very frequently and for as long as the fruits persist on the plant. Palatability, a high energy reward, and a widespread distribution are probably the reasons that make it highest in consumption by the carnivores. However, it would be an oversight not to mention that seeds of this species were among the smallest produced by fruit-producing shrubs in the area and tens of seeds are contained within each fruit. Consumption by brown bears can be very high, as much as 18 Kg of *Rubus* sp. berries at one meal (Willson 1993a). This author also suggests that bears commonly ingest 16000 *Vaccinium* sp. fruits per day.

Rosa sp. seeds were the second most numerous. This is a fruit which is relatively small and has numerous seeds and is available for much longer than any other fruit. *Fragaria vesca*, a fruit only rarely found in faeces, has minute seeds and the large number contained in each fruit elevated them to the third most numerous in this study. *Crataegus orientalis* and *Vitis sylvestris* were found only in small numbers and this is related to the fact that they are rarely found in the study area.

If we separate the data for each of the two years of the study, some differences in the diets of the carnivores begin to emerge. During the first year, all carnivores focused their feeding on *Rubus* and *Rosa* fruits. These are undoubtedly among the most numerous fruits produced in the area and therefore their consumption is probably proportional to their availability. The next year foxes again were mainly consuming *Rubus* sp. and *Rosa* sp. Martens consumed a very high number of *Fragaria vesca* seeds in addition to *Rubus*. However, this does not mean that martens concentrated their feeding on strawberries as these seeds were found very infrequently in their faeces and it is just an indication that high numbers were consumed in each meal. The most remarkable change of diet was the spectacular increase in the consumption of *Prunus avium* during this year. The fruit production of these trees was much higher this year and clearly carnivores seized the opportunity to exploit a very palatable resource.

4.4.3.3. Factors affecting the numbers of damaged seeds in faeces

The general outcome of this analysis was that, on average, all species of seeds suffered very little damage after passing through the carnivores' digestive tracts only exceeding 20% in one case (*Vitis sylvestris*), with most cases being less than 10%. Herrera (1989) found that only 0.89% of the seeds found in carnivore faeces were damaged. He also found some extreme cases where a high proportion of seeds of particular species were damaged (*Pistacia terebinthus* 98.5%, *Juniperus communis* 37.5%). By comparison, the species that suffered the highest damage in my study (*Vitis* sp.) was never found damaged in Herrera's study.

I suggest that the very high proportion of seeds passing intact through the gut is a result of the dentition adaptations of the carnivores which are not suitable for grinding food items like seeds. Furthermore, their digestive system has not got the adaptations needed to break down the tough cell walls of the seed coats. Therefore they usually digest only the fruit pulp and even that not very efficiently. This is in contrast to ungulates like wild boar which can destroy all ingested seeds e.g. *Crataegus monogyna* (Herrera 1984b). Seeds like *Cornus mas* and *Prunus cocomilia* were almost never damaged after ingestion, mainly because of their hard seed coat. The same was true with *Rubus* sp. which has a minute size, making it very difficult to be ground up by carnivores teeth. The species that suffered the greatest damage were *Malus sylvestris* and *Vitis sylvestris,* both of which have relatively soft seeds and are very susceptible to breaking. *Rosa* sp. seeds were often damaged too. Willson's (1993a) observations in Alaska demonstrated excellent germination for seeds of many species found in brown bear and American marten scats. She also suggested that perhaps the greatest risks of seed damage occur for large seeds that might be masticated before being swallowed or spit out.

4.4.4. Summary

The study on the frugivory of carnivores was initiated by an analysis of the Frugivory Index where bears were found to be the most frugivorous, having seeds present in all their faeces. Foxes and wolves followed, with martens being the least frugivorous. During 1994, the carnivores were significantly more frugivorous than 1993.

The temporal availability of each fruit species coincided with their consumption by the carnivores in most of the cases. However, there were a number of occasions where the fruits seemed to have been consumed before they were ripe. Fruit species such as *Rubus* sp., *Rosa* sp. and *Malus sylvestris* were readily eaten by all the carnivores. Nonetheless, there was evidence that sometimes one carnivore concentrated its feeding on a particular fruit species more than others did.

Bears and foxes had a tendency to deposit more than one species of seed in each faeces. There were a number of positive and negative associations of seed species in the faeces. These were probably influenced by the phenology of these species as well as a result of the proximity of the areas in which they were growing. After a comparison between the altitudinal zones where the fruiting species grow and the zones that their seeds were dispersed by the carnivores, it was found that many species of seed were deposited in altitudes where the plants do not grow.

Foxes dispersed the highest numbers of seeds in the study area and bears were second, as they deposited large-size faeces which contained many seeds. Of the dispersed seeds the ones that were deposited in the highest numbers were *Rubus* sp., *Rosa* sp. and *Fragaria vesca*. The species of the seed determined to a large extent the probability of damage after passage through the carnivores digestive tract. *Cornus mas* and *Prunus cocomilia* were the most damage resistant whilst *Vitis sylvestris* and *Malus sylvestris* were the most vulnerable.

CHAPTER FIVE

5.0. GENERAL DISCUSSION

5.1. Quantity of seed dispersal

The effectiveness of seed dispersal is a result of the combined effect of the quantity and quality of seed dispersal (Schupp 1993, Fleming & Sosa 1994). The quantity is affected by the abundance of the disperser. The number of faeces collected from the carnivores reflect to a certain extent their abundance in the study area. The declining order of the number of faeces found was: fox, marten, bear and wolf. The importance of fruit in the diet also influences the quantity of seeds that will be dispersed. Bears are the most frugivorous dispersers with 100% of their faeces containing seeds. A fact that clearly demonstrates their importance to the fruiting plant ecology in the area. Foxes came second with the majority of their faeces containing seeds followed by wolves and martens.

The territoriality demonstrated by some species might influence the quantity of dispersal. These species very often exclude conspecifics and in many cases other competitor species from their territories. Grey wolves, unlike brown bears which can congregate to feed on extensive fruit production areas (Pearson 1975, Luque & Stokes 1976), are very often hostile to conspecifics (Chapter 3) and sometimes even prey on other carnivores like stone martens (Papageorgiou 1994). In this case, although they defend a large territory because of their energetic requirements, they are poor dispersers because they eat fruit irregularly. Thus they are possibly reducing the number of visits to fruiting plants by other frugivorous carnivores which have the potential of removing fruits that grow in that area. However, this possibly has a minimal effect in the present study because of the low numbers of wolves and the seasonality of their appearance.

The reliability of dispersers is another complicating factor affecting dispersal quantity. Foxes and martens were present in the area during the whole year but bears and wolves only appeared in late summer and early autumn. Furthermore, during the second year of the study, wolves did not appear to consume any fruit. From the plants' point of view, they were unreliable dispersers.

As far as the number of seeds dispersed per visit is concerned, bears were again first among the carnivores. Bear faeces contained on average 21 times more seeds than those of martens which had the lowest number of seeds per scat. In Chapter 4 we find that fox dispersed the greatest number of seeds in the study area. Bears dispersed the second highest number of seeds although the number of faeces collected from them was much lower than from the martens which came third.

5.1.1. Size of the seed bank and fruiting plant density

One of the interesting aspects of the ecology of the study area would be an investigation of the extent with which the number of seeds that land on a transect is proportional to the density of fruiting plants that grows on that particular transect. The Distropi transect was that on which the highest number of seeds were deposited (31,297). Not surprisingly it was also the transect with the highest fruiting plant concentration (Table 2.3.). Second in density of seed deposition was Ahladorema, though the number was almost half of that on Distropi. The plant density on the former transect though, was only the fourth highest considering the plants along the transect, and fifth for those inside the canopy (Table 2.4.). The possible explanation for the fact that very few fruiting trees grow from these seeds is that the conditions on this transect and the layer of gravel that covered the ground were not very suitable for the germination and growth of the fruiting plants. Krusovo was third in the number of seeds it received and was followed by Virgin forest and Connector. For these transects the density of fruiting plants was roughly equivalent to the number of seeds that landed on them.

5.2. Quality of seed dispersal

The quality of seed dispersal by carnivores is influenced by the post-digestion seed viability. Another concern is whether seed germinability is altered after passing through the digestive system of carnivores compared to the germinability of seeds collected directly from the trees. A series of preliminary experiments under controlled and natural conditions were carried out during the present study in order to tackle these questions but unfortunately yielded no results i.e. no seeds germinated (Appendix II). However, while the faeces were kept in storage, the *Prunus avium* seeds from one bear scat germinated, indicating that seeds were viable after passage through the animal's gut. Furthermore, there was no germination from the control seeds that have been collected from the plants indicating that either the storage conditions or the germination trials were not suitable for these seed species. Lieberman & Lieberman (1986) undertook some interesting germination trials testing the effect that the passage though the gut of an animal has on the ingested seeds. They tested a total of 52 animal and seed combinations including birds, bats and monkeys. They compared seeds that were collected directly from the plants and seeds that had passed through the animals' digestive tract. No overall differences were found and germination enhancement was not common. Nevertheless, the effect of some animals on particular seeds was significant varying between positive and negative. Rogers and Applegate (1983) found that germination rates of seeds from black bear faeces were higher than those of seeds in uneaten fruits and the same was reported for culpeo foxes by Bustamante *et al.* (1992). Auger (1994) found that black bears did not have any negative effect on the viability of six out of seven fleshy fruits that she tested and there was only a 14% decrease for one species. It was demonstrated in Chapter 4 that very few seeds suffered any mechanical damage and there were no differences in the damage caused by the various carnivores. However, the species of seed made a difference. Soft coated seeds (*Malus sylvestris, Vitis sylvestris*) were damaged more easily but even in these cases, the overall "survival" was high. Rogers & Applegate (1983) suggested that it is actually to the carnivores advantage not to destroy the seeds during digestion as this may increase processing times for these items and also reduce the chances of poisoning from seed toxins known to exist in some members of the Rosaceae. Thus, in this study as it was the case with most of the other studies of carnivores (Applegate, Rogers, Casteel & Novak 1979; Rogers & Applegate 1983;. Herrera 1989; Chavez-Ramirez & Slack 1993; Auger 1994) the quality of seed dispersal provided by them was high.

The number of seeds of a particular plant species that are dispersed in a habitat is a measure of the dispersal success of the plant. Nonetheless, if a large number of seeds was deposited in one clump this measure of success could be found insufficient. In a theoretical situation where all the seeds land on one spot there is always the possibility that this substrate could be unsuitable for germination. Thus, the whole investment of the plant on the dispersal of its seeds would be jeopardised. There is a possibility that rodents, dung beetles or ants (Byrne & Levey 1993) will scatter some seeds around and spread them over a wider area but there is also a good chance that the rodents will act as seed predators and destroy most of the seeds (Janzen 1982, Chavez-Ramirez & Slack 1993). It has been suggested that a high concentration of seeds might attract more seed predators to the faeces (Stiles 1992, Murray *et al.* 1994). Nonetheless, Murray *et al.* (1994) reported that plants might have evolved yet another mechanism to increase the number of defecations from a given volume of fruit intake. They suggested that fruit laxatives might increase the frequency of defecation and thus seeds from a given fruit might be deposited in a greater number of faecal clumps. They presumed that both predation and competition would be reduced for seeds in smaller clumps (but see Howe 1989).

As it was mentioned in the previous chapter the diminishing order of the numbers of seeds dispersed was: *Rubus* sp., *Rosa* sp., *Fragaria vesca, Prunus cocomilia, Malus sylvestris, Prunus avium, Cornus mas, Crataegus orientalis, Crataegus monogyna* and *Vitis sylvestris*. The immense numbers of *Rubus* sp. seeds were spread across 36.86% of the faeces deposited by all carnivores (Table 4.5.) and hence some of them could well have the possibility of reaching a suitable site for germination. The seeds of *Malus sylvestris* were the second highest and were found in 15.71% of the faeces. *Fragaria vesca* seeds however, although numerous were only found in four faeces, thus not giving the species high probabilities for successful establishment.

5.2.1. Dispersal distances

The distance that zoochorous plant propagules are carried away from the parent plant is directly related with the animal's mobility and its gut passage rates. It was only possible to find information on the passage rates of red foxes and brown bears: Debussche and Isenmann (1989) reported that the intestinal transit time of the red fox is 5-10 h or more and suggested that they perform long distance seed dispersal of several hundred metres to a few kilometres. During feeding trials at Cologne Zoo, captive brown bears were fed with plum and kiwi fruits (Kolter, pers. communication). It was found that passage rates varied according to the size of seeds and even between batches of the same species. Some seeds were defecated in just three hours after consumption but usually it would take up to 24 hours for all the seeds to pass through. For a few small seeds it took up to 72 h. I believe it is reasonable to assume that stone martens and grey wolves have similar retention times to the red foxes.

In order to estimate the distances that seeds are likely to be dispersed by these carnivores we would have to look at their daily movements. Goszczynski (1986) reported that stone martens move an average 6.4 km/day, grey wolves 25.7 km/day and red foxes 9.1 km/day. Blanco (1986) reported a little shorter distances for red foxes between 3.4 and 6.3 km/day. Brown bears have been reported to move 5 km in 1.5 h and between 16-25.6 km in a 12-hour period (Craighead 1976, Berns *et al.* 1980, Knight 1980) during their routine daily activity.

It is apparent from the above that it was possible for the two large carnivores (bear and wolf) to transport the seeds acquired in one meal from one end of the research area to the other (14 km straight line distance) or even move seeds in from outside the research area and vice-versa. It is possible that as far as distances are concerned the ranges of these two carnivores are unparalleled by any of the other animals in the area (see also Rogers & Applegate 1983). Even the two medium sized carnivores (fox, marten) could actually move seeds from one transect to the other with ease. This is particularly possible for the transects that run closely for part of their length like Krusovo-Connector-Distropi and Krusovo-Ahladorema.

5.2.2. Propagation of seeds on the transects

The quality of seed dispersal is also affected by the pattern of deposition. All the faeces analysed for this study were collected from transects that followed forest roads. This might look unsuitable for seedling establishment initially as traffic would crush anything that sets roots on a transect (Chavez-Ramirez & Slack 1993). This is true most of the time. However, in many cases secondary roads that are opened in order to harvest a particular forest stand are often left unmaintained after the work is completed and are soon overtaken by vegetation. They actually become open habitats for colonisation and an opportunity for establishment of species that are not doing very well inside the canopy. The substrate of these transects is soil apart from Ahladorema which is mainly covered with gravel and thus they are suitable for the establishment of plants. Carnivores regularly use these man made openings and deposit seeds of fruiting plants on them.

One of the main interests of a study of seed dispersal by animal vectors is where and for how far the seeds of the consumed fruits are likely to be dispersed, the seed shadow in other words. In the following paragraphs I will make an attempt to highlight the possible impact that carnivores have on the dispersal of the fruiting plant diaspores in my study area. This will be achieved by comparisons of the phytosociological data from Chapter 2 with the contents of the faeces that landed on the transects. As it was mentioned in Chapter 2, there were immature *Prunus avium* and *Prunus cocomilia* trees but no adults on the Ahladorema transect (Table 5.1.). *Sambucus racemosa* and *Sorbus aucuparia* on the other hand did not produce any saplings. *Prunus avium* seeds were mainly transported to this transect by bears and foxes and to a lesser extent by martens. *Prunus cocomilia* was mainly deposited there by bears and also in low numbers by foxes. *Sorbus aucuparia* and *Sambucus* *racemosa* were never found in carnivore faeces and it appears birds were not dispersing their seeds efficiently on this transect.

On the Connector transect the seeds of *Prunus avium* were transported by foxes and in rare cases by martens possibly from elsewhere since no mature plants of this species were found on the transect. No established young trees were found of *Sambucus nigra, Sorbus torminalis* or *Juniperus communis.* These species were not consumed by the carnivores either. On the Virgin forest transect the situation was different. All the fruiting species found were regenerating well. *Sorbus aucuparia* although not consumed by carnivores was probably efficiently dispersed by birds. The carnivores were filling the seed bank with other species such as: *Prunus cocomilia, Malus sylvestris, Rubus* sp., *Fragaria vesca, Prunus avium, Crataegus orientalis*, and *Vitis sylvestris.*

	Di			**Vf**			**Kr**			**Co**			**Ah**		
Fruiting species	**S**	**I**	**A**	**S**	**I**	**A**	**S**	**I**	**A**	**S**	**I**	**A**	**S**	**I**	**A**
Rubus sp.	√	?	√	√	?	√	√	?	√	√	?	√	√	?	√
Rosa sp.	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√
Malus sylvestris	√	×	√	√	×	×	√	×	√	√	×	×	√	×	×
Cornus mas	√	×	×	×	×	×	√	×	×	√	×	×	√	√	√
Prunus cocomilia	√	×	×	√	×	×	√	×	√	√	×	×	√	√	×
Prunus avium	√	×	×	√	×	×	√	√	√	√	√	×	√	√	×
Crataegus orientalis	√	×	×	√	×	×	√	×	×	√	×	×	×	×	×
Vitis sylvestris	√	×	×	√	×	×	×	×	×	×	×	×	×	×	×
Fragaria vesca	√	×	×	√	×	×	×	×	×	×	×	×	×	×	×
Crataegus monogyna	×	×	√	×	×	×	×	√	√	×	×	×	√	×	×
Sambucus nigra	×	×	√	×	×	×	×	√	√	×	×	√	×	√	√
Sambucus racemosa	×	×	×	×	√	√	×	×	×	×	×	×	×	×	√
Sorbus torminalis	×	×	×	×	×	×	×	×	×	×	×	√	×	√	√
Sorbus aucuparia	×	√	×	×	√	×	×	×	×	×	×	×	×	×	√
Juniperus communis	×	×	×	×	√	√	×	√	√	×	×	√	×	×	×

Table 5.1. Comparison between species of seeds that were dispersed by carnivores and the presence of immature plants and adults on the transects. **S** = seeds dispersed by carnivores, **I** = presence of immature plants, **A** = presence of adult plants. √ = recorded on the transect, × = no record, ?= unknown. **Transects**: Ah = Ahladorema, Di = Distropi, Vf = Virgin forest, Co = Connector, Kr = Krusovo.

The Distropi transect barely had any regeneration at all and no young trees of *Cornus mas*, *Malus sylvestris* and *Sambucus nigra* were found although mature plants were present. This was not because seeds did not reach the transect, as all the carnivores were depositing seeds on it. Wolf faeces containing seeds were found only on this transect. There was a diverse mixture of seeds landing on this transect with the aid of carnivores, but for some reasons that cannot be identified, they failed to produce any detectable regeneration. A future study could shed some light on this interesting subject.

The diverse fruiting plant community on the Krusovo transect generally maintained good levels of regeneration. The exceptions were *Prunus cocomilia* and *Malus sylvestris* for which no established young trees were detected although seeds of both were deposited on the transect by bears, foxes and martens. *Crataegus monogyna*, *Sambucus nigra*, and *Juniperus communis* were well established on the transect although they were not dispersed there by carnivores. These species have been reported to be extensively consumed by thrushes (*Turdus* sp.) and warblers (*Sylvia* sp.) (Snow and Snow 1988). Furthermore the above carnivores were consistently depositing seeds of the following species: *Rubus* sp., *Rosa* sp., *Malus sylvestris*, *Cornus mas*, *Prunus cocomilia* and *Prunus avium* on this transect.

As mentioned previously there are several cases where seeds of a fruiting species were deposited on a particular transect although no adult plants were recorded during the vegetation surveys. Although these seeds might have originated from plants that were not detected by the surveys it is possible that they were transported from another transect where the adult plants can be found. It is difficult to make an accurate estimate of possible dispersal distances since the exact distance between the spot that the faeces were collected and the spot were the adult plants grow is not precisely known. *Malus sylvestris* seeds were dispersed on Virgin forest, Connector and Ahladorema although there were no adult plants in the vicinity. One potential source for these seeds is the Krusovo transect, indicating dispersal straight line distances from a few meters up to 4 km (see Map 2.2.). *Cornus mas* seeds were found on

Distropi, Krusovo and Connector but no fruit bearing plants of this species were found on these transects. Again dispersal distances could be between a few metres to 4 km. Another case was that of *Prunus cocomilia* and *Prunus avium* that seeds were deposited on Distropi, Virgin forest, Ahladorema and Connector. The only transect that adults of these species were detected on was Krusovo and that makes possible dispersal distances up to 4.5 km. *Crataegus orientalis*, *Vitis sylvestris* and *Fragaria vesca* were also successfully dispersing their seeds on the transects (Table 5.1.) but no adult plants were found on any transect and therefore I have to assume that the adults were growing further away from the transects where they could not be detected by the vegetation surveys.

According to the parameters of my study, the number of transects that a carnivore would deposit seeds on would affect the quality of dispersal offered by this particular carnivore. It would be an indication of how widespread the deposition is in this particular habitat. Bears, foxes and martens were depositing seeds on all the transects. Nevertheless, there were big differences on the numbers deposited on each transect (Table 4.9.). Wolves were the only carnivore depositing faeces on just one transect.

5.2.3. Post-dispersal seed and seedling survival

Aggregation of seeds in one spot does not seem to affect the germination of some species. Bullock (1981) reported that his experiments with *Prunus ilicifolia* and *Washingtonia filifera* in California showed greatest seedling survival in the most aggregated conditions. He suggested that the results might be attributable to decreased desiccation during the summer, due to mutual shading. The mean above-ground biomass was much greater in the cohorts than in the spaced seedlings. Even massive aggregation did not reduce early survival although it did reduce growth. Nevertheless, high survival rates to maturity are unlikely. Howe (1989) argued that plants that are normally "clump-dispersed" usually produce only one adult plant from a single faecal clump, unless secondary dispersal scatters the seeds.

Janzen (1982) carried out some experiments in Costa Rica to assess the removal of seeds from horse dung by rodents. The author found that in the forest the pile was found by rodents (*Liomys salvini*), within the first two nights after deposition. This was aided by its odour and, if the pile was seed rich, thoroughly mined for seeds. Seeds missed during this time were unlikely to be located by rodents until they germinated or until they were found by random searching in the litter later in the year. Furthermore, more seeds were removed from faeces in forest habitats than from the ones deposited on grassland (also Willson & Whelan 1990). The probability of surviving in a large pile of horse dung was the same as in a small pile. The density of seeds in the dung (seeds/l) though, was important as seeds survival was proportionally less at high densities. Once the density had fallen below a certain level the rodents lost interest. Willson & Whelan (1990) claimed that in their experiments the number of seeds in the large depositions was well within the foraging capacity of the rodents there but they suggested that the number of seeds consumed was limited because feeding was either interrupted or the animal preferred not to spend much time in one place. Therefore, if a similar situation exist in temperate forests, the size of the faeces which is directly related to the species of the frugivore that deposits the seeds might not be as important as originally thought. After the seeds have been scattered from the faeces the size of the seed might be important for escaping predation. Smith (1975) mentioned a comparison which is of relevance to this study: the large *Prunus* seed is rather conspicuous in the litter and soil when compared with that of *Rubus* aggregate, which can be quite small even though it was originally part of a large fruit.

Augspurger & Kelly (1984) investigated the factors affecting pathogen-caused mortality of tree seedlings in Panama and found that both an increase in dispersal distance and a decrease in seedling density reduced the possibility of such attacks (also Augspurger 1983). Pathogens accounted for disproportionately high seedling mortality in the vicinity of parent trees (Augspurger 1984). Their experiments also indicated that light is important for almost all of their 18 seedling species to escape from pathogens.

Howe (1989) claimed that there are two syndromes under which most of the cases of seed dispersal can be categorised. The "scatter syndrome" and the "clump syndrome". In the first case plants should produce relatively unprotected seeds and seedlings that normally recruit as isolated individuals. Low numbers of seeds of these species are usually dispersed by small frugivores. Because recruitment rarely occurs near conspecifics, such species are not likely to invest heavily in structural or chemical defences against herbivores, pathogens, or seed predators that cause density dependent mortality. Plants with the "clump syndrome" should produce seeds and seedlings well defended by chemicals, lignification, or mechanical protection against a variety of density dependent agents of mortality (Howe 1989). The main dispersal agents for these species are frugivores with a large body size that deposit many seeds with each defecation. For these clump-dispersed species high recruitment of offspring near the deposition site is usually the case. A likely result will be a high density of tightly aggregated seedlings, saplings, and adults, resulting in the exclusion of heterospecifics (Howe 1989).

Figure 4.6. and Table 4.6. demonstrate that carnivores quite often deposited more than one species of seed in their faeces. This phenomenon was mainly observed in the faeces of bears and foxes and the former regularly deposited three species of seeds together. Furthermore, there was a considerable number of significant positive associations found in the faeces of the carnivores studied. Loiselle (1990) carried out an investigation in Costa Rica on the importance of seed composition in the droppings of tropical fruit-eating birds. This author found that from a plants perspective, the specific combination of seeds deposited by birds may greatly influence subsequent growth and survival of seedlings. Multi-species mixtures of seeds were common in bird droppings and often interspecific competition was high after germination, as some of species generally outperformed others. The author concluded that selection for seed dispersers may be influenced among other factors by the probability of seed mixture occurrence and composition.

Lieberman & Lieberman (1986) concluded that the only clear advantage of ingestion of seeds may be their movement away from parent plants. It appears as though the potential to colonise new habitats as they become available or changes of conditions (e.g. clearing, landslides, fires etc.) is the only unchallenged advantage of seed dispersal. It is probably good enough even if it stands alone since there are thousands of plants which go to great lengths and invest heavily on fruits in order to attract the important animal vectors that have the potential to disperse its seeds to the ideal habitat and therefore maximise its reproductive success.

5.2.3.1. Factors affecting the regeneration of the fruiting species

An interesting aspect of seedling survival occurring soon after germination, is shade tolerance. Auclair and Cottam (1971) suggested that the average of 12.6% of ambient light found in southern Wisconsin oak forests is above the compensation point of most forest species. Available moisture which is very important in dry environments, together with time and distribution must be added to the usual factors assumed to determine tolerance. Though it is true that tolerance is a function of surviving long enough to experience suitable environmental conditions for gaining maturity, it is also a function of the much more difficult probability to measure, that of being in the right place (distribution), which is largely determined by the type and behaviour of vectors and to a lesser extent by accident (Auclair and Cottam 1971).

Very few plants of the bird-dispersed species studied by Auclair and Cottam (1971) grow vigorously in forests unless they germinate in openings. Frugivore-dispersed tree species may take part in intermediate seral succession by existing in a suppressed form in shade. Suppression, taking the form of annual cycles of shoot growth and death, leads to successful reproduction only when a sheltering tree is removed. Such suppressed survival is the sole technique of *Prunus* seedlings growing in shade. *Vitis* employs one additional technique: it also may die back annually but its regrowth is lateral and it may thereby reach greater illumination. If it grows near a tree, *Vitis* may ascend to reach better growing conditions. The authors also reported that *Cornus* and *Rubus* employ the lateral movement technique, but clone expansion results rather than aerial stem elongation. *Cornus racemosa* and *Rubus allegheniensis* expand underground and *R. occidentalis* above ground. In these ways a repressed colony in the shade may gradually expand into sunlight, where rapid growth and fruiting occur. When many shoots or individuals arise from a single seed, the probability increases that one will reach good growing conditions. According to the above authors this explains the existence of most clones on the edges of openings in which perching sites do not occur. I believe that it is possible that carnivores could have deposited the seeds on these sites. Auclair and Cottam (1971) argued that the presence of dead clones of *Rubus* and *Cornus* attests to the fact that clone expansion may not always result in escape from the shade. In the present study seeds that land on transects where direct sunlight is available experience very favourable conditions for growth. During the vegetation surveys, it was found that the density of *Rubus* sp. inside the canopy was a quarter of what it was along the transects.

The substrate on which the seeds land has a major effect on regeneration. A bare rock would not be suitable for germination and hence no plant would benefit from dispersal to such a substrate. Of the carnivores studied, martens habitually defecated on rocks thereby lowering the quality of the dispersal that they provided.

In many cases a lack of regeneration by particular fruiting species was evident on some transects, although seeds were deposited on these sites (Table 5.1.). This is often the case when more vigorous species outcompete the species of interest depriving them from vital resources. Alternatively the dispersal site may have been unsuitable. Different plant species favour different environmental conditions and below I will attempt to give some information on the subject focusing on the fruit species consumed by carnivores.

During a study in a Swedish beech forest it was found that increasing soil acidity, increasing solubility of toxic elements, and increasing deposition of nitrogen favoured the regeneration of *Rubus* species (Falkengrengrerup & Tyler 1991). Furthermore, extensive thining of the canopy during forest management also created suitable conditions for these species. A complete canopy removal in Hubbard Brook Experimental Forest (USA) had the same effect (Hughes & Fahey 1991) and *Rubus* *idaeus* became one of the most abundant species (also Osawa 1994). All the first year recruitment of the species came from buried seeds. In contrast, first-year recruitment of the other shrub species occurred through survival of pre-existing stems or expansion of pre-existing patches, or both. A study of the effect of temperature during germination revealed that a fluctuation between 10° and 20° C during night and day periods resulted in good rates of germination (Hogenbirk & Wein 1992, Marcuzzi & Demartinez 1993). On the other hand when the temperature increased to between 15° and 30° C no germination occurred. Ricard and Messier (1996) investigated the light requirements of the raspberry (*Rubus idaeus*) in Quebec (Canada) and found that the plant did not grow inside the canopy in places where the level was less than 7% of the ambient light. On the other hand, raspberry was always present where the light was above 25% of the ambient. Additionally, growth height and total first-year biomass were positively related to the percentage of ambient light that reached the ground. It is clear therefore that the particular species is a colonist with a need to be dispersed to open habitats.

Kollman and Reiner (1996) investigated the light demands and establishment within shrublands of *Crataegus monogyna, Sambucus nigra,* dogwood *(Cornus sanguinea)* and *Rosa canina* among other species. It was found that *Cornus* and *Rosa* were slightly more shade tolerant, whereas *Crataegus* and *Sambucus* apparently had higher light demands. However, none of them was particularly adapted to establish in a strongly shaded environment. There are many consistencies between this study and my findings. Inside the canopy where the plants grow in shade I found a complete absence of *Sambucus* species. *Crataegus monogyna* had a lower density inside the canopy than along the transects. *Rosa* sp. was found to be shade-tolerant having a two times higher density inside the canopy than along the transects. Contrary to their findings though, *Cornus mas* was found to have a higher density inside the canopy (7.25 trees/ha) than along the transects (5.4 trees\ha).

Grubb, Lee, Kollman and Wilson (1996) grew the seedlings of ten European tall-shrub species at 0.3, 1.6, 11 and 63% daylight for 110 days on chalk grassland soil, and on a more nutrient-rich soil under *Crataegus monogyna. Rosa canina, Cornus sanguinea, Juniperus communis* and *Crataegus monogyna* suffered high mortality in 0.3% daylight, but only the last two had loses in 1.6% daylight. Overall mortality in deep shade (0.3 and 1.6%) was significantly greater with higher nutrient supply. *Cornus sanguinea, Rosa canina* and blackthorn *(Prunus spinosa)* increased yield strongly under high irradiance on nutrient-poor soil, and responded also markedly to nutrients. *Crataegus* grew more slowly on its 'own' soil than on grassland soil. *Juniperus* differed consistently from the other species, growing slowly, and responding strongly to irradiance.

5.3. Which are the more important dispersers: Birds or mammals

As was mentioned earlier, the study area supports a very rich avifauna and includes a number of frugivorous birds which probably play an important role in the dispersal of seeds of the local fruiting species. Of the birds that the local avifauna comprises (Tsachalidis, pers. communication) I could find information on the frugivory of the following species: wood pigeon, European robin, blackbird *(Turdus merula),* song thrush *(T. philomelos),* mistle thrush *(T. viscivorous),* blackcap *(Sylvia atricapilla),* jay *(Garullus glandarius),* magpie *(Pica pica)* and carrion crow (*Corvus corone).* As it was expected the main frugivores of the area are thrushes and warblers. A secondary role is played by woodpigeons and corvids. These species act as legitimate dispersers, they swallow whole fruits and defecate or regurgitate seeds intact. In order to overcome the costs of internal handling of seed ballast these birds have increased passage rates. In fact the speed of through the gut passage is correlated with the relative importance of fruits in the diet (Jordano 1992).

Apart from the frugivores there are a number of pulp predators such as: sombre tit (*Parus lugubris),* great tit *(P. major),* blue tit *(P. caeruleus),* willow tit *(P. montanus),* coal tit *(P. ater),* crested tit *(P. cristatus)* and seed predators such as: chaffinch (*Fringilla coelebs),* serin *(Serinus serinus),* tree sparrow *(Passer montanus),* sparrow *(P. domesticus),* siskin *(Carduelis spinus),* gold finch *(C.*

carduelis), bullfinch *(Pyrrhula pyrrhula)* and hawfinch (*Cocothraustes cocothraustes)* (Tsachalidis, pers. communication). These species are obviously damaging the dispersal efforts of the fruiting plants since the seed predators may extract seeds from fruits, discard the pulp, crack the seed, and ingest its contents or can swallow whole fruits and digest both pulp and seeds (Jordano 1992). Pulp predators remove the fleshy part of the fruits therefore minimising their chances of dispersal. The only case that pulp predation might be advantageous to the plant is if the bird carries the fruit away from the parent plant in order to remove the pulp on a nearby perch and subsequently drop the seed there, but these cases are unusual (Newton 1972, Snow and Snow 1988).

Debussche and Isenmann (1989) reported that in Montpellier five bird species (blackcap, Sardinian warbler (*Sylvia melanocephala*), European robin, blackbird and song thrush) accounted together for 98% of the bird-dispersed taxa of fruiting plants. Since four out of the five species (apart from the Sardinian warbler) occur in my study area which has similar climatic conditions, I expect these species to be among the major seed dispersers in Rhodope.

The information on frugivorous birds presented during the rest of this section comes from Snow and Snow (1988) unless otherwise stated. The authors made their observations on bird frugivory in England and consequently there might be differences in the frugivory of these birds in my study area. Therefore the information should be considered with caution. However, since information on birds' frugivory in the study area is absent, this is the only way in which I could make some useful comparisons between birds and carnivores (Table 5.2.). Only the fruiting plants that were investigated for this study have been considered.

Blackbirds were reported to consume: *Rosa canina* from November until March and the meal size was 1-4 fruits, *Crataegus monogyna* from August to March eating 3-13 fruits, *Prunus avium* from June to August eating 1-5 fruits, *Rubus fruticosus* from August to November, *Rubus idaeus* in July and August, *Malus sylvestris* from December to March, *Sorbus aucuparia* from July until November eating 3-16 fruits, *Juniperus communis* in January and February and finally *Sambucus nigra* between August and November. As far as dispersal distances are concerned it was reported that while they care for their young they feed them with fruit that can be carried distances of 160 to 300 meters between the fruiting tree and the nest.

Song thrushes consumed *Rosa canina* between December and February, *Crataegus monogyna* from September to February, *Prunus avium* in June and July, *Rubus fruticosus* in September and October, *Malus sylvestris* in January and February, *Sorbus aucuparia* in August and September, *Sambucus nigra* between August and November with meal sizes ranging between 12-62 fruits. Song thrushes are highly territorial during the breeding season and some males remain so during the whole winter. They drive off intruding conspecifics that come to feed in their territory, often very vigorously and persistently.

The mistle thrush is the largest thrush in the study area and as a consequence it is dominant over the other thrushes. One of their characteristics is the long-term defence of the winter fruit supply. For a period of about three months after breeding has finished mistle thrushes become highly nomadic. They move about in parties between 6 and 30 birds feeding on *Sorbus aucuparia*, yew (*Taxus baccata*) and *Sambucus nigra* among others. In October the nomadic parties break up and individual birds or pairs start defending fruiting trees from all the other frugivorous birds. This usually results into the defended tree maintaining its fruits until spring as only the resident thrush removes them slowly. It is obvious that this is a disadvantage for the dispersal of the seeds of the tree as the resident bird most probably deposits the seeds in the immediate vicinity of the parent tree. This is mainly because the bird, in order to defend its fruit supply, rarely leaves the tree and other birds do not have access to it. Mistle thrushes were recorded to take *Juniperus communis* in January and February, *Rosa canina* between December and February, *Crataegus monogyna* between October and February consuming 2-16 fruits in each meal, *Sorbus aucuparia* between July and October, *Prunus avium* in June and July, *Malus sylvestris* in January and February and elder in July and August.

The robin is one of the small frugivorous birds of the study area and this imposes limits to the size of the fruits that it can consume. For example *Prunus avium* are beyond their gape width and *Crataegus monogyna* are swallowed with difficulty as does any fruit which is a little larger than 8 mm in diameter. When they feed on Rubus fruticosus they usually take a couple of drupelets every time after having dropped the fruit to the ground. They are territorial birds and will only tolerate their mates taking fruit in their territory. The above named authors suggested that robins are very effective seed dispersers as they feed solitarily, moving round their territories. They take fruits in small numbers and deposit seeds thinly but more or less uniformly through their territories which are usually suitable habitats for the development of the seeds. As far as fruit consumption is concerned robins consumed small quantities of *Rosa canina* in December, *Crataegus monogyna* in November and December consuming 1-2 fruits each time, *Rubus fruticosus* from August to October, *Rubus idaeus* in July, *Malus sylvestris* in February, small quantities of *Juniperus communis* in February, *Sorbus aucuparia* in August and *Sambucus nigra* was regularly eaten between August and November.

The blackcap is one more of the small frugivorous birds in the study area. They often feed on *Prunus avium* and *Rosa canina*, two fruits that are too large for them to swallow whole. In the case of *Prunus avium*, blackcaps act as pulp predators, damaging the fruit without dispersing the seed; but they may sometimes disperse the seeds of *Rosa canina*, by ingesting some of them with the pulp. They forage by going to a fruit source, taking a complete feed and then leave, returning for further feeds at regular intervals averaging at around twelve minutes which means that in this time interval seeds have been already evacuated. Because of their small size they are often chased away from fruit sources by most other frugivores, unless their large numbers overwhelm the defending birds (Simms 1985). They have been observed to feed on *Rosa canina* in January and between July and September, *Prunus avium* in June and July, *Rubus fruticosus* in September eating half or a whole fruit each time, *Rubus idaeus* in July and August, *Sorbus aucuparia* occasionally in September and on *Sambucus nigra* regularly between August and October taking three to eleven fruits.

From the Corvidae family, the magpie (*Pica pica*) was reported to take *Prunus avium* in July and August *Rubus idaeus* in July and *Sambucus nigra* regularly between August and November. Jays fed on *Prunus avium* in July, *Sorbus aucuparia* in August and *Sambucus nigra* in September and October. Carrion crows were recorded feeding on fallen apples of *Malus sylvestris* below the tree in January and February. They chose the brown, slightly rotten apples, holding them under the foot and pecking them open to eat the pulp. They were further observed to pick up an apple in the bill and fly off with it for about 150 m, either to eat it or to hide it under the grass. They fed on *Crataegus monogyna* in October and December, *Prunus avium* in July, *Malus sylvestris* in January and February and rarely on *Sambucus nigra* in October.

Wood pigeons have muscular gizzards adapted for grinding food, and long narrow guts unlike the specialised tropical fruit-eating pigeons and were expected to destroy most of the seeds that they consume. However, the authors found from examinations of pigeons' droppings that they are dispersers of several important wild fruits and the seeds are defecated undamaged. It is possible that they achieve this by reducing the grit intake while feeding on fruit to avoid damaging the seeds and releasing the toxins that many of them contain. Digesting periods averaged 1 hour 16 minutes. The fruit species that they fed on were: *Rosa canina* between December and February, *Crataegus monogyna* regularly from September to February, *Prunus avium* in June and July and *Sambucus nigra* between July and October.

Considering the fruit species that both carnivores and birds consume, we discover a temporal difference in the consumption of the *Rosa canina.* All the birds that consume this species do so mainly during the winter. The black cap is the only exception. Carnivores on the other hand, take this fruit from spring until early autumn, a period for which I have evidence for such activity. Although I have no records for the winter period, I cannot see why carnivores should stop feeding on *Rosa* sp. during this period considering that most if not all the other carnivore fruits are not available. Thus, it looks as if carnivores are the most important dispersers of the species, as birds only take it for short periods or as a secondary food.

Rubus idaeus and other *Rubus* sp. are both highly palatable species for birds and carnivores and are readily consumed for as long as they are available. Snow and Snow (1988) refer to the species *Rubus fruticosus* and that found in my study area is *R. canescens*. This should be taken into account when comparisons are made. Their small seed size allows even the smallest frugivores to act as seed dispersers and even pulp predators possibly disperse a number of seeds involuntarily. Jordano (1992) indicated that the maximum number of blackberry (*Rubus ulmifolius*) fruits that can be ingested by birds is five. The *Prunus avium* is another species that is consumed as long as it is available and its fruit production is very rapidly depleted by all frugivores.

Birds mainly consume *Malus sylvestris* in mid-winter when these fruits are rotting on the ground. This is probably a consequence of the size of the fruit that make it impossible for a bird to swallow whole. A rotten fruit is much easier to be cut into smaller pieces that are more manageable. Carrion crows were reported to carry the fruit in their bill and hide it between grasses or under leaves for later consumption. Probably a few of them are forgotten and their seeds later germinate. Carnivores eat the fruit even before it is ripe in my study area and fallen fruits rarely remain on the ground for more than a few days. I agree with Snow & Snow 1988 that this is an indication that apples are probably better adapted for dispersal by mammals.

Crataegus monogyna fruits are very attractive to birds and most of the species feed on them for long periods from autumn until early spring. Sallabanks (1993a) studied American robins feeding on *Crataegus monogyna* shrubs and found that choices made by the birds among shrubs were correlated with three plant traits (decision cues): fruit abundance, fruit size, and fruit pulpiness. The same author (Sallabanks 1993b) found that American robins were defending these shrubs and compared territory owners with conspecifics intruding on defended territories. On average, residents had longer feeding bouts, ingested more fruits per bout and foraged for fruits more slowly than intruders. On the other hand, among carnivores only foxes were found once to consume *Crataegus monogyna* and therefore there is a clear indication that this species is mainly dispersed by birds; a theory which is supported by the fact that the fruits remain on the plant for a few months after ripening.

Snow & Snow (1988) never observed birds consuming *Prunus cocomilia* or any other plum in their long years of observations but Simms (1978) reported that blackbirds, song thrushes and mistle thrushes do consume the fruit. Some of the *Prunus cocomilia* in my study area which are clearly descendants of cultivated varieties with large fruit are well beyond the capacity of thrushes. From this and from the fact that plums start to fall on the ground soon after they are ripe I assume that these fruits are primarily dispersed by mammals.

	MAMMALS				**BIRDS**									
Plant species	Vv	Cl	Ua	Mm	Tm	Tp	Tv	Er	Sa	Pp	Gg	Cc	Cp	**Td**
Rubus sp.	√	√	√	√	√	√	×	√	√	√	×	×	×	9
Rosa sp.	√	√	√	√	√	√	√	√	√	×	×	×	√	10
Malus sylvestris	√	√	√	√	√	√	√	√	×	×	×	√	×	9
Cornus mas	√	√	√	√	×	×	×	×	×	×	×	×	×	4
Prunus cocomilia	√	×	√	√	×	×	×	×	×	×	×	×	×	3
Prunus avium	√	×	√	√	√	√	√	×	√	√	√	√	√	11
Crataegus orientalis	√	×	×	×	?	?	?	?	?	?	?	?	?	1+?
Vitis sylvestris	√	√	×	×	?	?	?	?	?	?	?	?	?	2+?
Fragaria vesca	√	×	×	√	?	?	?	?	?	?	?	?	?	2+?
Crataegus monogyna	√	×	×	×	√	√	√	√	×	×	×	√	√	7
Sorbus aucuparia	×	×	×	×	√	√	√	√	√	×	√	×	×	6
Juniperus communis	×	×	×	×	√	×	√	√	×	×	×	×	×	3
Sambucus nigra	×	×	×	×	√	√	×	√	√	√	√	√	√	8
Total	10	5	6	7	8	7	6	7	5	3	3	4	4	75

Table 5.2. Possible fruit and frugivore combinations in the study area. Information on carnivores comes from the data collected during the present study and information on birds comes from Snow and Snow (1988). ?= There was no report of the particular plant-animal interaction by the authors but the plant species probably do not grow in their study area. The abbreviations for the animal species are as follows: *Vv=Vulpes vulpes, Cl=Canis lupus, Ua=Ursus arctos, Mm=Martes martes, Tm=Turdus merula, Tp=Turdus philomelos, Tv=Turdus viscivorus, Er=Erithacus rubecula, Sa=Sylvia atricapilla, Pp=Pica pica, Cp=Columba palumbus,* **Td**=Total number of dispersers.

No information was found on any bird species consuming *Cornus mas.* I cannot confidently say whether that was a result of the scarcity of the species in England or an indication that birds avoid the fruit. Its close relative the *Cornus sanguinea* fruit was a regular part of the diets of most frugivorous birds. As it was reported earlier, carnivores readily consume the *Cornus mas*.

Juniperus communis, Sambucus nigra and *Sorbus aucuparia* fruits are regularly taken by avian frugivores which seem to be their sole dispersers in my study area. As indicated earlier, there were cases where immature plants of these species were found on the transects in the absence of mature trees. Carnivores were never found to consume their fruits and it is very likely that birds are responsible for the dispersal of these species.

Unfortunately I was not able to find information on the daily ranges of frugivorous birds although data are available on migration distances. It is therefore difficult to estimate the distances that these birds are likely to disperse the seeds of the fruiting plants. One indication is the distances that birds carried fruit to feed their young. For blackbirds this ranged between 160-300 m. Carrion crows carried wild apples for 150 m to hide them for later consumption. These distances together with the rapid passage rates that rarely exceed 30 minutes (Murray *et al.* 1994), suggest that dispersal distances are probably much shorter than these of the carnivores. In those cases where the seeds are regurgitated retention times are even shorter. Frugivorous birds seem not to mechanically damage the consumed seeds and are therefore offering good quality seed dispersal, as do carnivores. Izhaki and Safriel (1990) suggested that the likelihood of a seed germinating in the first rainy season after its ripening, which was the most advantageous period, was definitely enhanced by bird frugivory.

A striking difference was evident in Debussche and Isenmann's (1989) study between birds and carnivores as far as the fruit volume was concerned. The number of bird dispersers decreased and the number of mammal dispersers increased as fruit volume increased (also Herrera 1989). Furthermore, there was a significant correlation between gape size and the eight most important bird dispersers and maximum and mean fruit volume, although not minimum fruit volume. Therefore, larger fruits probably rely more or solely on mammals for their dispersal.

Nests of frugivorous birds, fruiting plants where frugivores defend feeding territories traditional perches for sexual displays are usual sites that create recruitment foci with seed densities much higher than elsewhere in the forest (Jordano 1992) and therefore much more competition among seedlings. Nevertheless, their numbers and fruit preferences probably mean that they disperse the seeds of a more diverse plant assemblage to more spots in the habitat.

A comparison between the number of fruits taken by birds during every feeding bout with the numbers that the carnivore consume during each meal (Chapter 4) shows considerable differences. The number of fruits taken is relative to the body size of the animals and hence birds take considerably fewer fruits (Howe 1989). Even between bird frugivores, the number of fruits ingested per visit has been found to be strongly correlated with body mass (Jordano 1992). The same author stressed that sporadic visits by large frugivores can have far greater effect on crop removal than consistent visitation by small frugivores. The general outcome of this comparison is that birds disperse seeds of more species thinly and over shorter distances than carnivores do. On the other hand they have larger populations and there are more species and individuals of avian frugivores than carnivores in most of the habitats (Willson 1991). As a result carnivores should produce seed shadows differing qualitatively from those produced by avian dispersers. Howe (1989) suggested that frugivores with a small body size such as the birds in the study area should disperse seeds that are adapted for the "scatter syndrome" and large frugivores such as the carnivores should disperse species adapted for the "clump syndrome". If this is the case, then birds and carnivores provide a very different service as dispersers and plants have to opt for the one or the other as their main dispersal agents. However, it seems that the majority of the carnivore dispersed species that were found in the present study have also been reported to be consumed by birds. Which seed shadow benefits these particular fruiting plants the most remains to be investigated in the future.

5.3.1. Timing of fruit ripening

A considerable number of studies have suggested that most species of fruit within a temperate forest ripen in late summer and autumn when birds are storing fat for migration (Snow 1971, Thompson & Willson 1979, Thompson 1981, Howe & Smallwood 1982). Shrubs fruiting at that time have energy and nutrient rich pulp to fulfil the needs of birds. There is evidence that many fruiting trees time their fruit displays after selective pressures that were imposed by these foraging avian frugivores together with other factors (e.g. pollination, winter frosts, life history etc.). There is also an immense volume of literature indicating that carnivores increase their frugivory during autumn and that some species rely solely on fruit for subsistence during this time of the year (Cook & Hamilton 1944, Lockie 1961, Ballenberghe *et al.* 1975, Pearson 1975, Slobodyan 1976, Servheen 1983, Pulliainen 1985, Goszczynski 1986b, Cicnjak *et al.* 1987, Papageorgiou *et al.* 1988, Adamakopoulos 1991, Clevenger *et al.* 1992d, Frackowiak & Gula 1992, Goszczynski 1992, Clevenger 1993a, b). It has been reported for brown bears that this increase in fruit consumption is important for the build up of their fat reserves during the pre-dening hyperphagia (Slobodyan 1976, Frackowiak & Gula 1992). Brody & Pelton (1988) report that during late summer and autumn black bears undergo physiological changes in their digestive systems in order to selectively digest and absorb carbohydrates and fats coming from fruits at the expense of protein. At times when the primary fruit species on which brown bears depend failed to produce an adequate crop, the condition of the animals deteriorated (Pearson 1975).

The results of the present study support the evidence of these studies. There was not just an increase in fruit consumption during autumn, but the total number of faeces collected was higher. There could be several causes for this increase: a) The higher fruit production could have attracted far-ranging animals into the area. b) The increased food intake that facilitated the build up of reserves resulted in the increased production of scats. c) The bulk of seeds that accumulated in the guts of frugivores needed to be evacuated more often in order to make room for nutritious food. d) The fruit pulp had a laxative effect on the frugivores (Kolter pers. communication, Murray *et al.* 1994).

5.3.2. Choice of fruit by frugivores

With the exception of primates, colour does not seem to play an important role for choice by the mammals (Debussche and Isenmann 1989). Diurnal mammals can hardly see the coloured fruits among the foliage where the vegetation is dense, and the colour would naturally be of no use to the nocturnal animals, fruit bats etc. Nevertheless conspicuously-coloured fruits are frequently eaten by animals when they come across them. Thus, brightly coloured fruits contrasting with their immediate surroundings (foliage) should be one of the characteristics of the ornithochorous syndrome, whereas dull (e.g. brown and green) colours should be associated with mammalochory. Stiles (1992) too suggested that there is a dominance of yellow and green colour in fruits eaten by animals not having colour vision, a theory that the present study does not support. Most of the seeds found in the scats of carnivores were from red/orange fruits (*Rosa* sp., *Crataegus monogyna, Crataegus orientalis, Rubus idaeus, Prunus avium, Fragaria vesca, Malus sylvestris, Prunus cocomilia*) or black (*Rubus canescens*). Only a few trees of *Prunus cocomilia* bore yellow ripe fruits and *Vitis sylvestris* was the only one with green fruit when ripe. Additionally, no significant divergence in colour between bird-dispersed and mammal-dispersed fruits was found by Debussche and Isenmann (1989). Herrera (1989) found that black fruits were under-represented in the diet of carnivores; brown, white, blue and green were over-represented and finally orange and red were consumed according to their availability.

Herrera (1989) found that the fruit species which fall to the ground after ripening, are significantly heavier, more pulp-rich and containing more seeds than species not eaten by carnivores in southern Spain. Many nocturnal mammals locate fruits by smell (Stiles 1992); some of the fruits in the study area have a sufficiently strong odour that can even be detected by humans (*Fragaria vesca, Prunus cocomilia, Malus sylvestris, Prunus avium, Rosa canina, Rubus* sp.).

Among birds, preferences for one fruit over another is often based on the bird's ability to pluck and swallow the fruits (Snow & Snow 1988). Other factors include the ability to process the fruits internally, the net energy gain from eating each kind of fruit and their nutritive quality. Possible additional factors are the colour and taste of fruits but there is little evidence that they play a significant part in preferences by birds for temperate zone fruits (Snow & Snow 1988). Sorensen (1984) also found that seed passage rates play an important role in determining preferences, particularly if nutritional and other properties of fruit species are similar. Additionally, birds obtain a high rate of energy gain by consuming fruits whose seeds are regurgitated (relatively large seeds) as this results in a rapid elimination of non-nutritional seed ballast and creates space in the gut for more food (Sorensen 1984). It was further indicated that the ease with which the pulp can be separated from the seed in the bird's stomach together with the differences of processing the pulp of different fruit species is probably important.

5.4. Conclusion

During the last ten years, carnivores have attracted the attention of ecologists to their role as seed dispersers. There have been a few studies that describe the seed dispersal of a fruiting plant assemblage by a carnivore (Rogers & Applegate 1983, Bustamante *et al.* 1992, Castro *et al.* 1994, Nogales *et al.* 1996). There were also studies that investigated the seed dispersal by a group of carnivores. (Herrera 1989, Debussche & Isenmann 1989, Chavez-Ramirez & Slack 1993, Willson 1993). The present study however, is unique because a detailed investigation of the interaction between European fruiting plant assemblage and a carnivore assemblage was undertaken in such a way that direct comparisons between the species could be made. Furthermore, it sheds some light on the temporal and spatial aspects of seed dispersal by the four carnivores and it studied the quantity as well as the quality of this dispersal. Botanical data that were gathered from vegetation surveys were compared for the first time with zoological data from the faeces in order to reveal the dispersal syndromes that were operating in the study area. It was possible to estimate what was actually dispersed from the fruits available in the habitat.

Unfortunately among the carnivores studied there is one whose survival in Greece is uncertain in the immediate future: the brown bear. The destruction of habitats and poaching has reduced their populations to critical levels. As it was revealed by this thesis, the bears' function as seed dispersers is unique among the carnivores. So would a possible extinction, apart from the great loss for the animal kingdom, also result in the impoverishment of the plant community of the area?

As it was mentioned earlier Dinnertein and Wemmer (1988) proposed that the extinct Neotropical megafauna once played a major role in the dispersal of the woody flora. They also argued that coexistence between plants and large frugivores shaped the evolution of fruit and seed traits of some plants for consumption and dispersal by large mammals. I believe that it is plausible to make the same hypothesis for temperate ecosystems. Zeuner (in Herrera 1989) reported that during Pleistocene, there were many more species of medium-sized, ground-dwelling mammals in southern European habitats than at present, and most of these became extinct by the end of that period. Even contemporary large mammalian frugivores have been extirpated from the majority of European woodlands, decades or even centuries ago. As a result, Mediterranean habitats nowadays represent an impoverished version of the plant-mammalian interactions that took place when the diversity of mammals was higher than at present (Herrera 1989). Thus, it is possible that a number of large seeded or/and large fruited plants (*Prunus cocomilia, Prunus persica, Pyrus communis*), that previously depended on these frugivores for their dispersal, significantly declined from their previous ranges. Fruit-trees bearing large seeds are mainly found in their cultivated forms nowadays. But what about the wild varieties? Have they vanished from the ecosystems because of the extinction of their dispersers? At present the relative literature on the subject is limited. There is no doubt that we still have a lot to learn about the seed dispersal of most of the plant species on the planet.

APPENDIX I

Common and Latin names of the species that are mentioned in the thesis according to Gruson & Forster (1976), Corbet & Ovenden (1980), Arabatzis (1986) and Aas & Riedmiller (1994):

1. ANIMALS

Common name	**Latin name**
badger	*Meles meles*
bear, black	*Ursus americanus*
bear, brown	*Ursus arctos*
bear, grizzly	*Ursus arctos horribilis*
bear, polar	*Thalarctos maritimus*
beaver	*Castor canadensis*
beetle, violet ground	*Carabus violaceus*
blackbird	*Turdus merula*
blackcap	*Sylvia atricapilla*
boar, wild	*Sus scrofa*
bullfinch	*Pyrrhula pyrrhula*
buzzard, honey	*Pernis apivorous*
capercaillie	*Tetrao urogallus*
cat, feral	*Felis catus*
cat, wild	*Felis sylvestris*
chaffinch	*Fringilla coelebs*
chamois	*Rupicapra rupicapra*
civet, African	*Civettictis civetta*
coati	*Nasua narica*
coyote	*Canis latrans*
crow, carrion	*Corvus corone*
deer, red	*Cervus elaphus*
deer, roe	*Capreolus capreolus*
dormouse	*Muscardinus avellanarius*
dormouse, fat	*Glis glis*
dormouse, forest	*Dryomys nitedula*
eagle, booted	*Hieraaetus penatus*
eagle, golden	*Aquila chrysaetos*
eagle, lesser spotted	*Aquila pomarina*
eagle, short-toed	*Circaetus gallicus*
elephant, African	*Loxodonta africana*
finch, gold	*Carduelis carduelis*
fox, culpeo	*Pseudalopex culpaeus*
fox, grey	*Urocyon cinereoargenteus*
fox, red	*Vulpes vulpes*
genet	*Genetta genetta*
gopher	family Geomyidae
grouse, hazel	*Tetrastes bonesia*

hare, brown	*Lepus capensis*
hare, mountain	*Lepus timidus*
hare, snowshoe	*Lepus americanus*
hawfinch	*Cocothraustes cocothraustes*
hedgehog	*Erinaceus concolor*
jackal, golden	*Canis aureus*
jay, Eurasian	*Garrulus glandarius*
jay, blue	*Cyanocitta cristata*
kinkajou	*Potos flavus*
lynx	*Felis lynx*
magpie	*Pica pica*
mandrill	*Papio sphinx*
marten, American	*Martes americana*
marten, pine	*Martes martes*
marten, stone (or beech)	*Martes foina*
moose	*Alces alces gigas*
mouse, deer	*Peromyscus maniculatus*
mouse, wood	*Apodemus sylvaticus*
muskrat	*Ondatra* sp.
owl, eagle	*Bubo bubo*
owl, great grey	*Strix nebulosa*
owl, Tengmalm's	*Aegolius funereus*
panda, red	*Ailurus fulgens*
partridge	*Alectoris* sp.
pheasant, ring-necked	*Phasianus colchicus*
pigeon, wood	*Columba palumbus*
pipistrelle	*Pipistrellus pipistrellus*
pipistrelle, Kuhl's	*Pipistrellus kuhli*
pipistrelle, Savi's	*Pipistrellus savii*
pocket gopher	*Geomys* sp.
polecat, western	*Mustela putorius*
porcupine, brush-tailed	*Atherurus* sp.
rabbit	*Oryctolagus cuninculus*
rabbit, cottontail	*Sylvilagus* sp.
rabbits, jack	*Lepus townsendii*
racoon	*Procyon* sp.
racoon dog	*Nyctereutes procyonoides*
rhinoceros	*Rhinoceros unicornis*
ringtail	*Bassariscus astutus*
robin, European	*Erithacus rubecula*
robin, American	*Turdus migratorius*
serin	*Serinus serinus*
sheep	*Ovis aries*
shrew	*Sorex* sp.
shrike, lesser grey	*Lanius minor*
shrike, red-backed	*Lanius collurio*
siskin	*Garduelis spinus*
skunk	*Spilogale* sp., *Mephitis* sp.,

	Conepatus sp.
snake, grass	*Natrix natrix*
sparrow, house	*Passer domesticus*
sparrow, tree	*Passer montanus*
solitair, black-faced	*Myadestes melanops*
squirrel, ground	*Spermophilus undulatus,*
squirrel, Columbian ground	*S. columbianus*
squirrel, red	*Sciurus vulgaris*
stoat	*Mustela erminea*
tayra	*Eira barbara*
thrasher, brown	*Toxostoma rufum*
thrush, mistle	*Turdus viscivorus*
thrush, song	*Turdus philomelos*
tit, blue	*Parus caeruleus*
tit, coal	*Parus ater*
tit, crested	*Parus cristatus*
tit, great	*Parus major*
tit, sombre	*Parus lugubris*
tit, willow	*Parus montanus*
turaco	*Tauraco* sp.
vole, bank	*Clethrionomys glareolus*
vole, common	*Microtus arvalis*
vole, northern water	*Arvicola terrestris*
vole, snow	*Microtus nivalis*
weasel	*Mustela nivalis*
whitethroat, common	*Sylvia communis*
wolf, grey	*Canis lupus*
wolf, maned	*Chrysocyon brachyurus*
woodpecker, black	*Dryocopus martius*
woodpecker, green	*Picus viridis*
woodpecker, grey-headed	*Picus canus*
woodpecker, middle spotted	*Dendrocopus medius*
woodpecker, three-toed	*Picoides tridactylus*
woodpecker, white-backed	*Dendrocopus leucotos*

2. PLANTS

Common name	**Latin name**
almendro	*Dipteryx panamensis*
amelanchier	*Amelanchier ovalis*
anemone, wood	*Anemone nemeorosa*
apple, crab	*Malus sylvestris*
apple, domestic	*Malus domestica*
ash, common	*Fraxinus excelsior*
ash, manna	*Fraxinus ornus*
aspen	*Populus tremula*
bearberry	*Arctostaphylos uva-ursi*

beech, European	*Fagus sylvatica*
beech, hybrid	*Fagus moesiaca*
birch, silver	*Betula pendula*
blackberry	*Rubus canescens, R. fruticosus, R. ulmifolius*
blackthorn	*Prunus spinosa*
blaeberry	*Vaccinium vitis-idaea*
blueberry	*Vaccinium myrtilus*
buckthorn, alpine	*Rhamnus alpinus*
buckthorn, rock	*Rhamnus saxatilis*
carob tree	*Ceratonia siliqua*
cherry, Cornelian	*Cornus mas*
cherry, wild	*Prunus avium*
cherry, Virginia	*Prunus virginiana*
cotoneaster	*Cotoneaster integerrimus*
crocus	*Crocus sativus*
crowberry	*Empetrum nigrum*
dandelian	*Taraxacum sp.*
danewort	*Sambucus ebulus*
daphne	*Daphne oleoides*
dogwood	*Cornus sanguinea*
elder	*Sambucus nigra*
elder, alpine	*Sambucus racemosa*
fig	*Ficus carica*
fir, hybrid	*Abies borisii regis*
fir, silver	*Abies alba*
grape	*Vitis vinifera*
grape, wild	*Vitis sylvestris*
grass, wavey hair	*Deschampsia flexuosa*
greenweed, Dyer's	*Genista tinctoria*
hawthorn, common	*Crataegus monogyna*
hawthorn, eastern	*Crataegus orientalis*
hazel	*Corylus avellana*
heartsease	*Viola tricolor*
hogweed	*Heracleum lanatum*
holly	*Ilex aquifolium*
honeysuckle, fly	*Lonicera xylosteum*
hornbeam	*Carpinus betulus*
hornbeam, eastern	*Carpinus orientalis*
hornbeam, hop	*Ostrya carpinifolia*
huckleberry	*Vaccinium globulare*
juniper, common	*Juniperus communis*
juniper, Mediterranean	*Juniperus oxycedrus*
juniper, phoenecian	*Juniperus phoenicea*
laureotinus	*Viburnum tinus*
leopardsbane, Austrian	*Doronicum austriacum*
lime, large-leaved	*Tilia platyphyllos*
lilac	*Syringa vulgaris*

lilly, Rhodope	*Lilium rhodopeum*
lords and ladies	*Arum maculatum*
maple, Norway	*Acer platanoides*
mastic tree	*Pistacia lentiscus*
mulberry, white	*Morus alba*
oak	*Quercus dalechampii*
oak, downy	*Quercus pubescens*
olive tree	*Olea europea*
orchid, burnt	*Orchis ustulata*
pear	*Pyrus amygdaliformis*
pear, common	*Pyrus communis*
pear, wild	*Pyrus pyraster*
pine, black	*Pinus nigra*
pine, Scots	*Pinus sylvestris*
plum, cherry	*Prunus cocomilia*
ragwort, wood	*Senecio nemorensis*
raspberry	*Rubus idaeus*
rose, wild	*Rosa* sp.
rose, dog	*Rosa canina*
rowan	*Sorbus aucuparia*
sainfoin, alpine	*Hedysarum alpinum*
soapberries	*Sepherdia canadensis*
spindle tree, alpine	*Euonymus verrucosus*
spruce, Norway	*Picea excelsa*
strawberry tree	*Arbutus unedo*
strawberry, wild	*Fragaria vesca*
sycamore	*Acer pseudoplatanus*
turpentine tree	*Pistacia terebinthus*
violet, dog's tooth	*Erythronium dens-canis,*
violet, Rhodope	*Viola rhodopea*
walnut	*Juglans regia*
whitebeam, common	*Sorbus aria*
whortleberry	*Vaccinium scoparium*
whortleberry, boy	*Vaccinium uliginosum*
wild service tree	*Sorbus torminalis*
willow	*Salix sp.*
yew	*Taxus baccata*

APPENDIX II

GERMINATION TRIALS

II.1. INTRODUCTION

In Chapters 4 and 5 reference is made to germination trials undertaken to investigate the viability of the seeds after their passage through the carnivores' gut. The published literature on germination of the seeds of particular species is very thorough. This is particularly true for cultivated plants. It is well documented that storage conditions can affect to a great extent the subsequent germination of seeds (the introduction to this appendix is based on Mayer & Poljakoff-Mayber 1989 unless other reference is given). Generally seeds remain viable for longer periods when they are dry. Longevity is affected by a combination of the storage temperature and the moisture content of the seed. High temperatures combined with high moisture content and enzymes which originate in an animals digestive tract may reduce the longevity of the seeds. It must be stressed that seed viability is not only a function of the conditions during seed storage. A variety of factors to which the parent plant is exposed during seed formation and ripening can affect subsequent viability of seeds. Such factors include water supply, temperature, mineral nutrition and light.

Even when storage conditions have been optimal many seeds may fail to germinate even when they are placed in conditions which are normally regarded as favourable, such as an adequate water supply, a suitable temperature and an atmosphere of normal composition. However, these seeds are still alive as they can be induced to germinate by various special artificial treatments. Such seeds are in a state of dormancy. As it was mentioned earlier on, the fact that under natural conditions the germination of seeds is delayed, until suitable conditions for establishment prevail, maybe advantageous for the survival of the species. Dormancy is also genetically controlled and is often due to immaturity of the embryos when the seeds are shed.

The first process which occurs during germination is the uptake of water by the seed. This uptake is due to imbibition. The extent to which imbibition occurs is determined by the composition of the seed, the permeability of the seed coat to water and the availability of water in the environment. Different seed species have different temperature requirements for germination. At very low and very high temperatures the germination of all seeds is prevented. A rise in temperature does not necessarily cause an increase in either the rate of germination or in its percentage. Germination is therefore not characterised by a simple temperature coefficient but its effect can only by evaluated in relation to the other factors affecting germination.

Among wild plants much variability in the behaviour towards light has been observed. Seed species can be divided into those which germinate only in the dark, those which germinate only in continuous light and those which are indifferent to the presence or absence of light during germination. Daily illumination has been shown to affect germination with similar effects as photoperiodism in flowering. Light sensitivity is probably related to their germination in their natural habitat. There they may land on the soil, or enter the soil, or be covered by leaf litter, thus exposed to different conditions of light during germination.

For some of the species involved in the germination trials, information on their germination requirements can be found. *Prunus* sp. fruits should be collected when fully mature to assist germination. For *Prunus* sp. excessive drying is detrimental (Grisez 1974). What is excessive actually depends on the species. *Prunus* seeds have embryo dormancy and require a period of after ripening in the presence of moisture and oxygen to overcome it. During stratification periods very good results could be obtained from a regularly alternating temperature range of 36° to 40°F. However, germination was much higher following warm plus cold stratification than cold stratification only (Grisez 1974).

The hips of *Rosa* sp. should be hand-picked soon after the dark-green colour fades into a redish colour or at any time thereafter (Gill & Pogge 1974). Fruits collected shortly after ripening germinate more readily than those allowed to dry in the hip. The seeds of most *Rosa* species exhibit dormancy which is primarily due to conditions in the seedcoats rather than in the embryo. Warm stratification preceding the cold treatment is recommended for *Rosa canina.* Seeds may need to be held in stratification for up to 1½ year before they start to germinate. However, germination test standards have not been set for the species (Gill & Pogge 1974).

The berries or *Rubus* sp. should be picked form the plants soon after ripening (Brinkman 1974). The seeds of many *Rubus* sp. are slow to germinate because they have a hard, impermeable endocarp combined with a dormant embryo. *Rubus idaeus* will germinate after cold treatment for 120 days or longer. Germination of seeds of both blackberries and raspberries was improved when they were scarified with either sulphuric acid for 20 to 60 minutes or a 1% solution of sodium hyperchlorite for 7 days before they were subjected to warm plus cold stratification. Best results are obtained during germination trials for *Rubus idaeus* if a temperature range of 50° to 77° F is applied.

II.2. METHODS AND MATERIALS

Faeces collected during the field seasons were stored in plastic bags. Unfortunately a refrigerator was not available in the study area and as a result some of the faeces were kept for up to two weeks under room conditions before they were refrigerated at +4°C. The faeces were not dried as this can be detrimental for the seeds of some species (Grisez 1974). Some of the faeces were kept for 1 to 3 months under these conditions until enough seeds were found in faeces for the initiation of the germination experiments.

There were two phases of germination trials. The first was carried out in a germination chamber (SANYO MLR-350H) which had the capability of providing several programmed cycles of light, temperature and humidity within a 24-hour period. The seeds were placed in Petri dishes with a layer of sterilised sand at the bottom which was covered with a sheet of water absorbing paper.

It was not possible to find the exact germination requirements of the species involved in the germination trials and as a result a attempt was made to imitate the natural cycle in the study area during spring (Fig. II.1). The conditions in the germination chamber were programmed as follows:

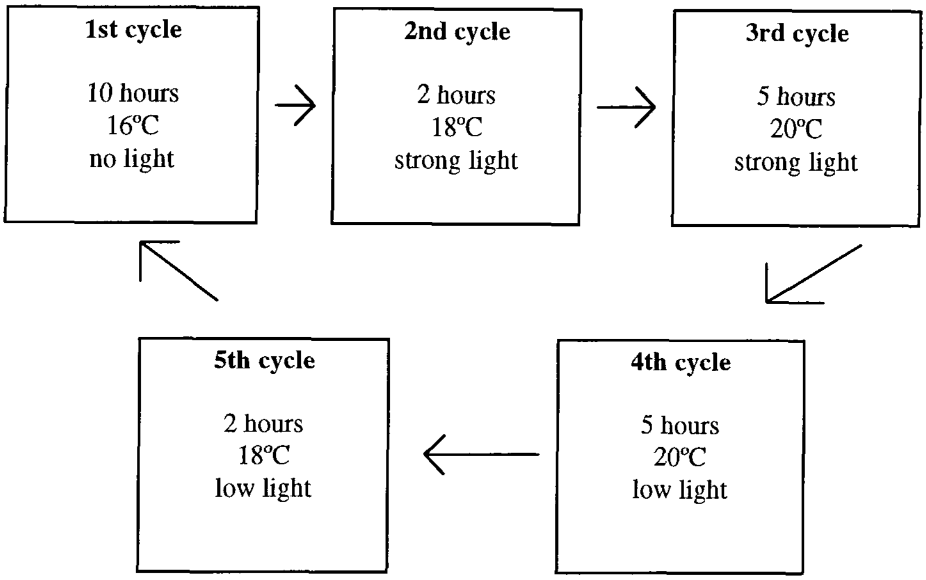


Fig. II.1 The conditions' cycles that were programmed into the germination chamber in an attempt to imitate the natural conditions in the area during spring.

Humidity was not introduced into the chamber as the seeds were watered regularly. The numbers of seeds used in the trial are displayed in Table II.1.

Seed species	**bear**	**fox**	**marten**	**control**	**Total**
Cornus mas	100	30	-	100	230
Rosa canina	100	100	100	100	400
Rubus sp.	100	100	100	100	400
Malus sylvestris	100	30	30	100	260
Prunus cocomilia	30	30	-	30	90
Total	430	290	230	430	1380

Table II.1. Number of seeds that were involved in the germination trials. The control seeds were collected directly from the parent plant after the ripening of the fruit.

The seeds were divided into groups of ten and put into Petri-dishes apart from *Prunus cocomilia* seeds which were divided in groups of five. The numbers of seeds used in the germination trials were limited by the seed availability in the faeces that had been collected by the end of summer of the first field season. The trials were structured in order to give adequate time for slow germinating seeds to germinate by the end of the second field season. This period was constrained when the author had to move back to England and the continuation of the trials would become problematic.

In parallel with the first phase, germination trials were also conducted under natural conditions (Table II.2) in the area of Frakto Forestry Service camp (1400 m altitude). Trials were conducted in a cage constructed of strong iron frame designed to keep large herbivores out. The interior of the frame was further protected by an iron mesh that kept out rodents, birds and large insects. The structure could be penetrated by sufficient rain and light. Inside the cage, whole faeces were placed in plastic plates with holes for drainage.

Carnivore	Transect	Date	Species	No of seeds
fox	Ahladorema	21-10-93	*Malus sylvestris*	23
fox	Distropi	19-10-93	*Rosa* sp.	51
fox	outside transects	10-9-93	*Crataegus monogyna*	11
fox	Distropi	10-9-93	*Prunus cocomilia* & *Rubus* sp.	12 431
fox	Krusovo	28-9-93	*Cornus mas*	14
bear	outside transects	28-9-93	*Rubus* sp.	81,061
bear	outside transects	20-10-93	*Rosa* sp.	1,449
fox	Ahladorema	21-10-93	*Prunus cocomilia* & *Rubus* sp.	360 60
fox	Distropi	10-9-93	*Rubus* sp.	389
control	outside transects	Sep 93	*Rosa* sp.	51
control	outside transects	Sep 93	*Crataegus monogyna*	11
control	outside transects	Sep 93	*Cornus mas*	14

Table II.2. Germination trials under natural conditions. Whole faeces containing seeds were left to germinate. "control": seeds collected directly from the plant after fruit ripening.

II.3. RESULTS AND DISCUSSION

Unfortunately no seeds germinated during either phases. This may be attributed to unfavourable storage conditions that killed the seeds. As it was mentioned earlier the faeces were stored in plastic bags for a varying period of time before drying. As a result high levels of ammonia might have accumulated in the plastic bags, which could be a potential reason for non-germination. Another possibility is that the fruiting species involved in the trials may produce dormant seeds that needed special conditions or treatment to break their dormancy. A long period of stratification in shallow soil under dark, cold and humid conditions is required for some seeds to germinate (Grisez 1974, Gill & Pogge 1974). Some others need treatment with appropriate chemicals or phytohormones to germinate (Brinkman 1974, Mayer & Poljakoff-Mayber 1989). However, any application of these techniques could possibly mask the effects that carnivores would have on the germination of seeds. A detailed investigation of the germination requirements of all the species involved in the germination trials together with multiple treatments were beyond the time schedule of this thesis. I think it unlikely that the lack of germinating seeds was due to the ingestion by the carnivores. The existing literature supports this view (see Chapter 5). Furthermore, a number of *Prunus avium* seeds which were contained in a bear faeces germinated while they were kept in a cold room proving that at least not all seeds were killed by the carnivores. A future study that could focus on this subject could provide a useful insight to the fate of the seeds after they are dispersed. Such information would allow us to have an integrated view on the role that carnivores play in the dispersal of the seeds of the fruiting plants.

Photo. 1. The study area during summer.

Photo. 2. The study area during winter.

Photo 3.

Bear faeces

Photo 4.

Fox faeces

Photo 5.

Marten faeces

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