

Chapter 2

Distribution of Individuals

2.1 Introduction

The distribution of individuals is a field mainly studied by behavioural sciences. It is largely concerned with animals, although some models can be applied to plants. Behavioural ecologists study decision rules that follow non-sessile individuals on when to start a movement; speed and direction of a movement; sites at which to stop, forage, be vigilant, or rest; and time spent for each activity. The result of these behaviours is an individual pattern of habitat use. Measured along the life of an animal, this pattern demarcates a home range. This chapter begins with a description of movement strategies in animals as mechanisms that result in an individual pattern of distribution. It is followed by two sections that discuss two types of descriptive models of individual habitat use: home-range estimations and site suitability models. The analytical approach is presented in the following two sections, and it is based on foraging theory, which developed models to predict residence times in foraging areas and to resolve the trade-off between forage and defence against predators. The chapter concludes with an analysis of the expected distributions at equilibrium.

2.2 Movements

Movement is a change in the spatial location of a whole organism in time (Nathan et al. 2010). Most living creatures move to a greater or lesser degree. Sessile species such as plants have a stage of development where they can move. The movement may be passive or active. Most species without a nervous system passively move due to the direct effect of external factors such as wind or pollinators for pollen and seeds, or a single active response to environmental conditions, as is the case with micro-organisms.

The study of movement has a long tradition in the field of animal behaviour research. It was studied in the first half of the twentieth century, when it was argued that animals moved based on simple orientation mechanisms triggered in response to environmental stimuli: tropisms, taxes, and kinesis (Gould 1982). During the second half of the twentieth century, the study of movement followed three well-defined lines: (1) neuro-ethology, especially of invertebrates, focused on the underlying sensory and neural mechanisms; (2) cognitive psychology focused on the information-processing mechanisms that underlie navigation; and (3) behavioural ecology focused on the adaptive importance of different movement strategies.

At the beginning of the twenty-first century the study of movement was revolutionised, and three simultaneous phenomena were promoted: the new emphasis on spatial dimension as a global concern of ecology, the development of new technologies to track animals accurately anywhere on the planet, and the progress of new methods of statistical analysis and new computational tools for processing movement patterns. This new approach defines itself as *movement ecology* and has a clear emphasis on the statistical description of the movement, the relationship between external conditions and the spatial response, and the effects on distribution patterns (Getz and Saltz 2008; Holyoak et al. 2008; Nathan 2008; Nathan et al. 2008; Giuggioli and Bartumeus 2010). The capacity to collect high-resolution spatio-temporal movement data was due to recent technological advances encompassing numerous techniques, such as miniaturised radio transmitters, global positioning systems, cellular and satellite networks, acoustic transmitters, global positioning systems, and light-level geo-locators (Viswanathan et al. 1999; Bartumeus et al. 2005; Bartumeus and Levin 2008; Smouse et al. 2010; Urbano et al. 2010).

In summary, there are four paradigms in the study of movement. Some have shown a successful integration, as is the case of studies of information processing in food searching (Stephens et al. 2007; Dukas and Ratcliffe 2009). Others have been developed in relative isolation. For example, movement ecology has little connection with previous studies in other disciplines, despite the call for greater integration, probably due to its recent development (Nathan et al. 2008; Giuggioli and Bartumeus 2010).

2.2.1 Ethology of Movement

Insects show adaptations to follow cues that are specific for a type of patch or prey. Olfactory and visual cues are common mechanisms. A well-known example is that of male moths, which search for suitable female mates by sensing sex pheromones in the air. The species-specific odour is blown downwind, and males search for these trails by casting back and forth across the wind. When they detect the olfactory sign stimulus, the males fly upwind to the source (Gould 1982). Classical experiments of Nobel Prize winner Niko Tinbergen showed how a digger wasp finds its tunnel home.

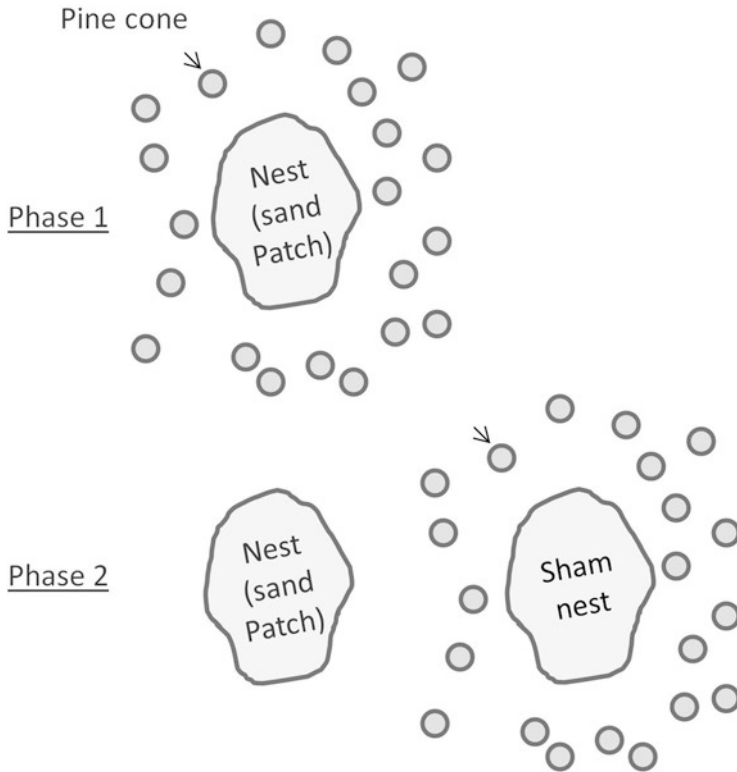


Fig. 2.1 Classical Tinbergen's experiment on insect cognition (modified from Tinbergen 1963)

He hypothesised that once back in the vicinity, wasps used local landmarks to guide them to their nests. To test this idea, he placed rings of pine cones around the nests, waited until each wasp flew out on a hunting trip, and then moved the circles a metre or so away (Fig. 2.1). Invariably, the wasps would return to the centre of the pine cone ring and search for their nests (Tinbergen 1963).

Searching for distant targets can be made when environmental cues are either available or not. Many terrestrial predators use regular roads when searching for prey patches in their territories. Studies using signs or camera traps, for example, show that felines and canines tend to use trails and roads built by people. The other famous case is flower recognition by bees. Another Nobel Prize winner Karl von Frisch showed experimentally that the navigation system of bees is based on the sun-centred pattern of polarised ultraviolet light in the sky. Adult white butterflies *Pieris rapae* follow natural and man-made topographical structures as they range from one area to another (Baker 1978). These animals follow roads, hedges, and lines of telephone poles, and they orient towards distant objects. The butterflies use different cues depending upon wind conditions and probably other abiotic factors.

Recently, Lohmann et al. (2008) proposed a new hypothesis to explain long-distance natal homing in salmon and sea turtles, called *geomagnetic imprinting*. Several marine vertebrates move across vast distances of ocean before returning as adults to their natal areas to reproduce. Salmon are known to use chemical cues to identify their home rivers at the end of spawning migrations, but this is not a possible explanation of long-distance orientation. Both salmon and sea turtles detect the magnetic field of the Earth and use it as a directional cue. Turtles also derive positional information from two magnetic elements (inclination angle and intensity) that vary predictably across the globe. Lohmann et al. (2008) argued that salmon and sea turtles imprint on the magnetic field of their natal areas and later use this information to direct natal homing. The simplest variant of this hypothesis involves imprinting on a single element of the field (e.g. inclination angle or intensity), and to locate the area later in life; the animal would need only to find the coastline and then swim north or south along it to reach the target region. Even though Lohmann et al. (2008) showed that some field data support their hypothesis, they did not provide a possible proximal (neurophysiological or cognitive) mechanism that might support it.

2.2.2 *Cognitive Aspects of Movement*

Non-sessile animals move within their home ranges and occasionally out of them. Most controlled movements that involve changing position can be defined as *goal orientation*, or movement towards a different place where the animal can find better conditions. Dyer (1998) classified goal orientation movements based on scales, which in turn related to previous experience with the goal, in three types: (1) heading for a nearby object in plain view, (2) heading for an unseen patch of resources within a familiar home range, and (3) heading for home from a distant, unfamiliar location.

At all scales, goal orientation movement necessitates that the animal obtain two general sorts of information about the environment. First, the animal must be able to discriminate between different directions (body orientations) relative to some external reference (a celestial body, a landmark, or a chemical cue). Second, the animal must be able to determine its position in space relative to its goal. The animal can use a simple measure of location or it may be able to measure angular position and distance in relation to some reference (Dyer 1998).

To characterise the specific cognitive challenge faced by an animal that is orienting to a goal, Dyer (1998) identified three parameters that affect in some way the procurement of positional and directional information and therefore the goal: (1) the geometry of the space containing the goal, (2) the distance of the goal from the starting point, and (3) the variability of the environmental cues that provide navigational information.

Cognitive maps are mental representations of space, independent of immediate contingencies (Tolman 1948). An animal with a cognitive map should not need to

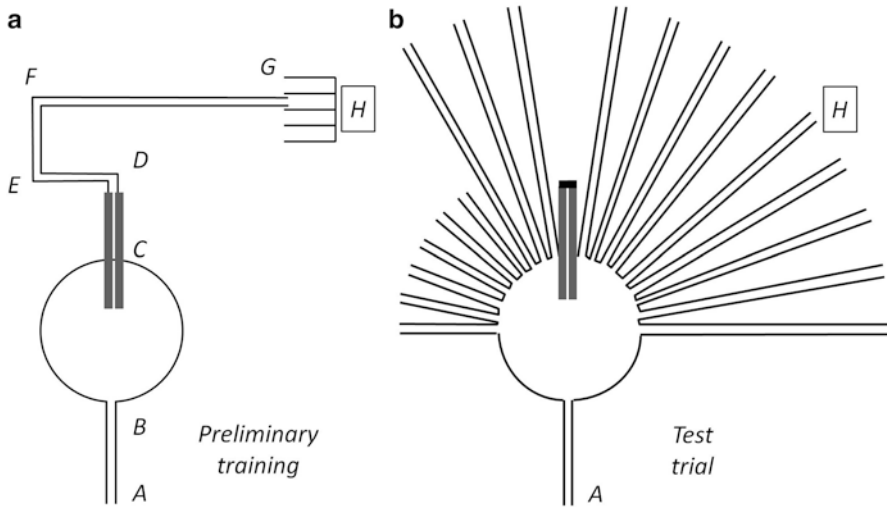


Fig. 2.2 Mazes used in classical Tolman's experiment with rats, testing spatial memory. Meaning of letters in text (modified from Tolman 1948)

follow gradients or landmarks and should take novel routes across unknown terrain. According to Tolman (1948), a feature of a cognitive map is the ability to make novel short-cuts between two points. He conducted an experiment to test this idea. In the first part, he used the maze represented in Fig. 2.2a. The animals ran from A across the open circular table through CD (which had alley walls) and finally to G, the food box. H was a light which shone directly down the path from G to F. After four nights, three trials per night, in which the rats learned to run directly and without hesitation from A to G, the apparatus was changed to the maze shown in Fig. 2.2b. The starting path remained the same but a series of radiating paths was added. The animals again started at A and ran across the circular table into the alley and found themselves blocked. They then returned and began exploring practically all the radiating paths. Rats showed a significant tendency to choose the patch that ran the closest to a point where the entrance to the food box had been.

Some authors are sceptic about the conclusions of this and similar experiments and suggest that no animal has been conclusively shown to have a cognitive map (e.g. Bennett 1996). Recently, Jacobs and Schenk (2003) proposed that a cognitive map is composed of two sub-maps, one derived from directional cues and the other derived from positional cues.

Food hoarding has been one of the preferred behaviours used to investigate the role of memory in animal movements in the last 20 years. Nicky Clayton and her colleagues have been pioneers of this type of study. A research line involved food-storing behaviour of western scrub jays *Aphelocoma californica* in the laboratory. They have investigated several aspects of behaviour that indicated complex mental capabilities of this species. One study demonstrated that scrub jays remember what they have stored and use episodic-like memory to remember when and where they

have stored food (Emery and Clayton 2001). Another experiment was conducted by Clayton and Krebs (1994) using two storer/non-storer pairs of species, marsh tit *Parus palustris*/blue tit *P. caeruleus* and jay *Garrulus glandarius*/jackdaw *Corvus monedula*. These pairs were compared on a one-trial associative memory task with results that suggest food-storing birds respond preferentially to spatial information than non-storers.

2.2.3 *Movement as an Adaptation*

Behavioural ecology defines behaviour as a design that results from natural selection, and foraging theory conceives behaviour as decision rules modelled by this evolutionary process (Stephens and Krebs 1986). The function of movement is varied, the main one being to search for resources. The movement can fulfil other purposes such as escape from predators, patrolling an area, dispersing, or exploring to learn or evaluate changes in the environment. The rules of movement are usually different depending on these motivations.

In most cases movement is an adaptation for resource searching, so its components are expected to be affected by the distribution of resources. Because of the hierarchical nature of spatial distributions of resources, we would expect to find animals initially using gross cues, indicative of certain habitats; then homing in further using patch cues; and finally employing cues from individual resources. Bell (1991) classified searching behaviour based on ecological scales. He firstly analysed mechanisms related to patch location and then how animals restrict search to a patch. He assumed that, when searching for a resource patch, an animal attempts to localise an assemblage of resources, whereas when searching within patches, it avoids leaving the assemblage until it becomes unprofitable to remain. The following terms are used depending on scale. For locomotory movements and scanning within a patch, the term is *local search* (Jander 1975). Immediately after leaving a patch or a resource and seeking others, regardless of its orientation mechanism, it is designated as *ranging* or *travelling*. Ranging refers mainly to the internal constraints, i.e. search using orientation mechanisms until finding external sensory information (Jander 1975), while travelling refers to external constraints, i.e. moving along a matrix without resources (Charnov 1976). Movements between habitats are called *dispersal* or *migration* (see Sect. 1.5).

An example of an adaptive approach to the study of movement is provided. Cassini and Krebs (1994) conducted a field experiment with hedgehogs *Erinaceus europaeus*, in which they recorded movement behaviour in response to food manipulations. Hedgehogs are nocturnal solitary insectivores with overlapping home ranges (Morris 1991a, b). When active, they spend most of the time searching for food (Wroot 1984). The study was conducted in a 4-ha ground in Oxford, United Kingdom. In order to analyse the distribution of hedgehogs, the study area was divided into four sectors—NW, NE, SE, and SW. A ‘prey item’

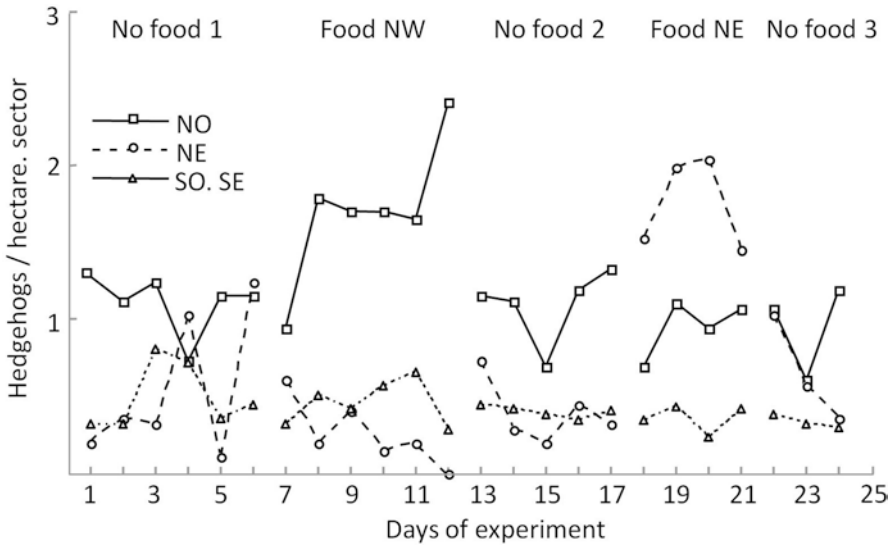


Fig. 2.3 Results of a field experiment on foraging hedgehogs *Erinaceus europaeus*. Explanation of references in the text (modified from Cassini and Krebs 1994)

consisted of two chunks of cat food. A 'patch' consisted of 36 prey located in a sector of the study area. The five experimental phases were (1) 'No food 1'; (2) 'Food NW', with 36 prey distributed in a 10×10 -m grid and flags marking the prey sites; (3) 'No food 2'; (4) 'Food NE', prey randomly distributed in a sector with no flags; and (5) 'No food 3'. On the last day of the 'No food 2' phase, 25 flags without food were located in SW sector in a 10×10 -m grid (the 'Flag' test). During the phases without food addition, hedgehogs expressed a natural preference for NW sector, and they responded to the experimental manipulation by increasing the use of those patches that received additional food (Fig. 2.3). During the experiment, hedgehogs were individually observed, counting the number of times they changed 90° in the direction of their movement (turns/10 min). Hedgehogs responded differently to the two experimental manipulations (Fig. 2.3). When they had information on food location (regular distribution and visual signals), they showed more straight movements, but when they did not have environmental cues (random distribution of no signalled food), they increased the frequency of turns. Ad libitum observations allowed getting a description of the actual behaviour of hedgehogs: in 'Food NW' experimental phase, they moved in a straight line for several metres after they initiated movement following a capture, while in 'Food NE' phase, their movement resembled *area-restricted searching* behaviour. In summary, hedgehogs were able to learn about the properties of the environment and responded efficiently to improve foraging success.

2.2.4 Statistical Description of Movement

Traditional studies that investigate the adaptive value of movement were mainly based on experimental tests conducted in small scales. These studies were limited by the lack of statistical tools to describe the movement patterns. Recently, modern methods to interpret behavioural changes in movement trajectories or to identify the role of resource distribution on animal movement patterns have been developed (Giuggioli and Bartumeus 2010). The most important contribution that has been made to movement ecology approach is the use of statistical tools borrowed from physics, such as Lévy statistics and anomalous diffusion, and optimal stochastic search (Giuggioli and Bartumeus 2010). Several studies have suggested that food searching in several species of vertebrates follows what is called a Lévy flight (Mandelbrot 1982). When animals spend time without finding sparsely and randomly distributed resources, they appear to start a random search trajectory, which is composed of jumps with lengths that follow a heavy-tailed distribution, corresponding to a power law (Viswanathan et al. 1999).

In modern movement ecology, individual trajectories are followed with GPS and bio-loggers, which allow recording details of animal movements (Giuggioli and Bartumeus 2010). Trajectories are often analysed by considering the collection of fixes as a series of random events (e.g. displacements, turns), whose spatial and temporal distributions are assumed to produce patterns that can be interpreted statistically. These methodologies have been applied to numerous species, and the number of publications has grown exponentially. A few examples published in a period of 3 years are in bacteria (Jarrell and McBride 2008; Zhang et al. 2010), in plants (Damschen et al. 2008), in insects (Ovaskainen et al. 2008), in fish (Patterson et al. 2009), in reptiles (Godley et al. 2008), in birds (Mandel et al. 2008), and in terrestrial (Dalziel et al. 2008) and marine mammals (Gurarie et al. 2009). Also, there is a large number of reviews on modelling techniques and concepts.

An example of a study in movement ecology is provided. Ramos-Fernández et al. (2004) have determined the distribution of the sojourns made by fruit-eating spider monkeys *Ateles geoffroyi*, who forage in a semievergreen tropical forest in Yucatán, Mexico. The results show power-law behaviour $P(l) \sim l^{-\alpha}$ with an exponent $\alpha=2.2$, which suggests that these foraging movements may be described by Lévy walks. Boyer et al. (2006) suggested that this Lévy foraging behaviour may be the outcome of the distribution of resources. They observed in the field that spider monkeys can follow regular routes, so they hypothesised that their foraging movements rely on processing information on resource distribution. They developed a foraging model in which (1) monkey territory is composed of many foraging patches with varying sizes and in which the spatial structure can be varied and (2) foragers know the location and size of the targets and follow a simple foraging strategy of maximising food intake in a minimum travel distance. They used this model to explore the conditions that lead to Lévy foraging patterns. They found agreement between the field exponents (for step length, tree size, and waiting time distributions) and their theoretical values at a special parameter $\beta_c=3$, suggesting that the model

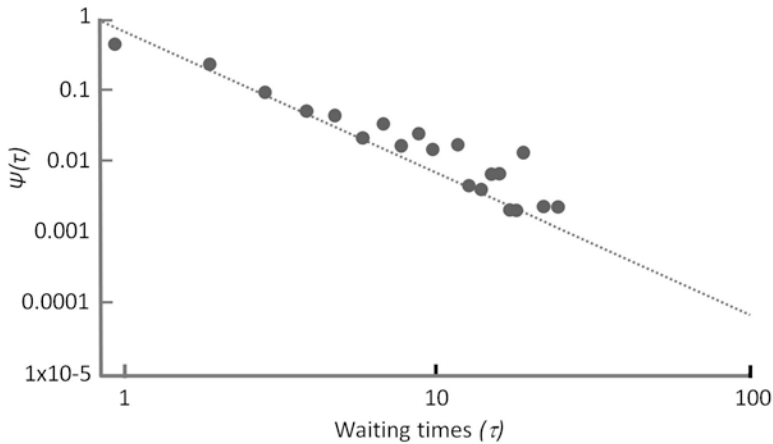


Fig. 2.4 Movement ecology of primates, based on a study by Boyer et al. (2006). Once a monkey has stopped at a tree, it stays for a time τ before moving to another site. This waiting time is plotted against its fit by an inverse power law $\Psi(\tau) \sim \tau^{-w}$, with $w \approx 2.0$ (one time unit represents a 5-min interval)

correctly captures the interactions between spider monkeys and the environment (Fig. 2.4). This study by Boyer et al. (2006) is an attempt to link the statistical approach of movement ecology to other areas of behavioural research, such as cognitive ecology and foraging theory.

2.3 Home Ranges

The home range is a concept applicable only to mobile animals. There are descriptions of the home ranges of birds, reptiles, amphibians, fish, and some invertebrates. However, it has been studied mainly in terrestrial mammals, carnivores being the favourite taxonomic group. Burt (1943, p. 351) provides the first definition of home range as ‘that area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range’. The study of home ranges followed the inductive direction from data to theory. Its evolution is the consequence of the advent of radiotelemetry in the late 1950s. The animal carries a transmitter implanted or attached to a collar or harness. The transmitter emits a signal that is captured by a receiver from distance. This method was adopted as the main tool for fieldworks by wildlife researchers. Hundreds of studies using radiotelemetry have been published since its release. Satellites have improved enormously the use of radiotelemetry in two directions. On the one hand, the interpretation of satellite images and the development of geographic information systems substantially improve the acquisition of environmental information that can be compared

with home-range locations. On the other hand, some transmitters implanted in the animals can now be used through satellites, which allow the following from almost any researcher location to any animal position in the world. This new technique has been used for oceanic vertebrates, migrant birds, and many other species that live in hard environments or move extensively.

Many reasons have been advocated for estimating home ranges, in both research and management fields. Several studies deduce social organisation and breeding system for the overlapping of home ranges. Knowing home ranges also provides information on foraging and food choices, limiting results, among other important components of habitat. However, it is important to note that the study of home ranges was the result of a technological opportunity. In other words, once the technique was released and the data obtained, then came the scientific questions. Therefore, the study of home ranges is characterised by a strong empiricism, so it is often difficult to use this information to test hypotheses arising from a theoretical framework.

Data used to estimate home ranges are a collection of points on a map for each radio-tracked individual. The boundaries of a home range are difficult to measure because the number of points normally decreases to the centre of the area, so decreasing the precision of the measurements. Several methods exist to transform this set of locations in an area that can be considered an animal's home range. The most common statistical methods to estimate home ranges are grids, minimum convex polygon, circle and ellipse approaches, Fourier series (Anderson 1982), harmonic mean distribution (Dixon and Chapman 1980), fractal estimators (Bascompte and Vilà 1997), and Kernel estimators (Powell 2000). Brief descriptions of these methods follow.

A first method consists of a grid superimposed on the study area and represents a home range as the cells in the grid having an animal's locations (e.g. Doncaster and Macdonald 1991). This simple approach has several advantages. It avoids assuming that data fit some underlying distribution. Occasional sallies are easily identified as cells visited only once. It allows straightforward comparisons between samplings taken at different moments in the same study area. A traditional and spread method is to estimate the minimum convex polygon. It is also easy to implement and consists of a draw that results from joining known or estimated locations that produced the smallest convex polygon (Hayne 1949). Again, the advantage is that it is not necessary to assume any statistical distribution of the spatial distribution of the individual. However, it has several problems, such as high sensitivity to extreme data points, an outline only with large sample sizes, and incorporation of large areas that are never used (Powell 2000). Bivariate normal models use circles or ellipses to estimate home ranges; animals are assumed to move randomly about their home range, with the most probable location being the very centre; then a 95% ellipse is calculated around the mean location. The area of this ellipse is an estimate of the animal's home range (Jennrich and Turner 1969). In recent years, Kernel density estimators are probably the most common method used for individual use of space. This produces an unbiased density estimate directly from data and is not influenced by grid size or placement. Therefore, it is considered the best estimator available (Powell 2000).

A typical study on home ranges extracted from wildlife literature is described. The giant anteater *Myrmecophaga tridactyla* is a member of an emblematic group

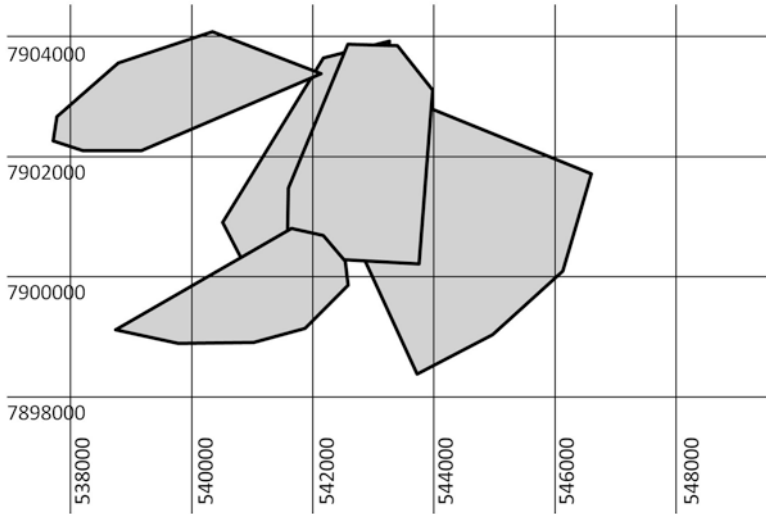


Fig. 2.5 Home ranges of giant anteaters *Myrmecophaga tridactyla* (modified from Medri and Mourão (2005))

of Neotropical mammals. It used to distribute in a wide biogeographical range from Guatemala to Argentina, but now is a locally endangered species due to human persecution and habitat destruction. In spite of its conspicuousness and importance, it is still a poorly known species of Neotropical fauna (Shaw et al. 1987). Medri and Mourão (2005) captured, radio-collared, and monitored seven anteaters of the Pantanal wetland, Brazil. Males covered areas of 4.0–7.5 km² (5.7 ± 1.7 km²), and one of the two females monitored occupied a larger area (11.9 km²) than the males, but none of the curves of cumulative area unequivocally reached the asymptote. The home-range estimates were calculated using the 100% minimum convex polygon and 95% adaptive kernel methods. There was considerable overlap among individual areas used (Fig. 2.5). Giant anteaters rested mainly in forest patches and savanna and frequently used grasslands and scrub savanna for foraging.

2.4 Site Suitability Models

Site suitability models are descriptive models that relate, with the availability of habitat or components of the habitat, normally resources, the probability of utilisation by an individual or set of individuals. *Preference indexes* and *resources selection functions* (Manly et al. 1992) are site suitability models. As it was explained in Sect. 1.4, the term *selection* is not used in this context; instead the general term *site suitability models* is used. Site suitability models have been applied to all levels of organisation, from individuals to species, so I return to them in subsequent chapters. In Sect. 3.2, we will see site suitability models applied to aggregations (at habitat and landscape scales), while in Sect. 7.2, to species distribution (at regional scale).

Site suitability models describe the environment in terms of some attribute of resource categorisation or units. These discrete units of resources (in our case habitats) are often simply a grid cell which divides the home range of an animal. Studies normally involve classifying resource units into qualitative entities or categories or measuring specific variables or properties that are characteristic of those units. Site suitability models have a clear applied approach. The purpose is to use a rapid method for field studies to establish habitat requirements of individuals or populations.

Site suitability models can be used with three types of sampling designs, or three different procedures to estimate *availability*: random, case-control, and use-availability (Keating and Cherry 2004). In a random sampling design, sampling units are selected randomly and the habitat/resource characteristics of units are evaluated according to the presence/abundance or the absence of the target species (at the proper level). In a case-control sampling, two data sets on resource/habitat traits are collected, a pool of sampling units with the species and another pool without it. In the use-availability sampling method, habitat/resource variables are measured in units where the species is present and, then from a pool of all units in which the study area was divided, selected randomly.

Statistical modelling procedures used for site suitability models are of two types: simple sample comparisons and generalised linear models. Indices of selection and simple sample comparisons fit into the first category, while linear regression, logistic regression, log-linear, and proportional hazards models are special cases of the second type of statistical methods. They are applicable to different data sets, but always with the same objective of establishing the statistical relationship between use and availability.

One example of the use of site suitability models to describe habitat distribution of individual organisms is provided. Moose or elk *Alces alces* is a well-known cervid species that inhabits temperate to subarctic regions of the northern hemisphere. Predation, food availability, climate, parasites, and disease are the most important natural factors that can potentially limit moose populations across North America (Van Ballenberghe and Ballard 1994). Hunting is also a major limiting factor of moose populations in areas accessible to humans. Dussault et al. (2005) studied a moose population from a protected area of Québec, Canada. Hunting was prohibited, but there were two potential predators, the wolf *Canis lupus* and the bear *Ursus americanus*, so the prediction was that habitat selection at larger spatial scales should be oriented towards avoiding exposure to predation risk. At a smaller ecological scale, the prediction was that moose habitat selection should be primarily influenced by food availability and secondarily by snow. Forty moose were monitored with GPS telemetry collars. A total of 186 forest stands were surveyed for availability of food, concealment cover, and winter cover. Dussault et al. (2005) expected that, if moose traded off food availability with protection from predation risk, they would be attracted to edge between habitats providing abundant food and sheltering against predation risk. Also, moose that traded off food availability with cost of locomotion in deep snow were expected to be attracted by the edge between habitats providing abundant food and those sheltering from snow. At the landscape scale, the extent of edge density (both edge types) was used as a measure of food

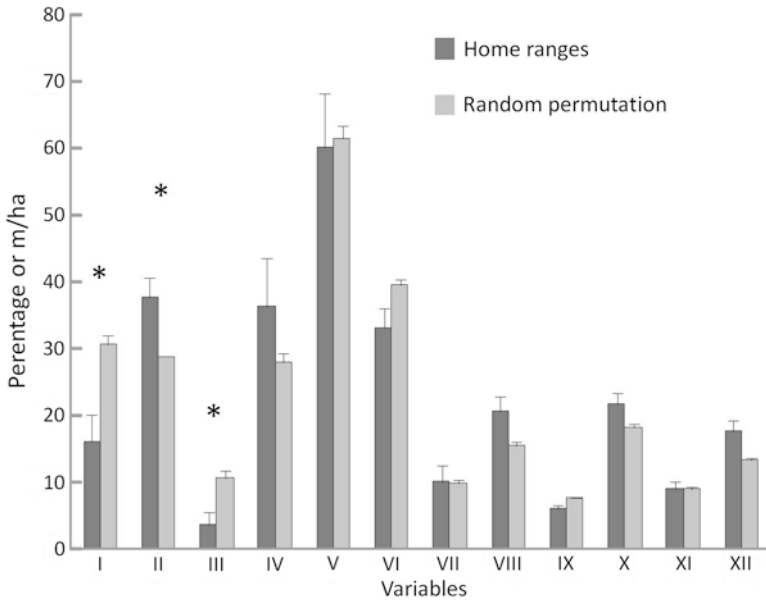


Fig. 2.6 Habitat selection by moose *Alces alces* (modified from Dussault et al. 2005). The comparison between moose home ranges and the random permutations provides an estimation of the variables that are relevant for moose distribution. Variables analysed: (I) overlap with wolf territories (%), (II) density of edge between stands offering high food abundance and stands offering protection against snow (m/ha), (III) area with low snowfall (%), (IV) area with moderate snowfall (%), (V) area with high snowfall (%), (VI) stands offering protection against predation risk (%), (VII and VIII) area offering high food abundance, (IX) stands offering protection against snow, (X) other habitats (non-regenerated and non-forested areas, lakes), (XI) density of habitats providing abundant food and those sheltering against predation risk (m/ha). Asterisk represents statistical differences between bars

and cover interspersed. Habitat selection at the landscape scale was determined by comparing habitat composition and edge density within individual moose home ranges with those available within the study area. At the landscape scale, the authors used a stepwise logistic regression to determine which habitat and edge variables discriminated individual moose home ranges from random permutations. At a home-range scale, habitat use and availability were measured at telemetry locations and within the home range, respectively. Telemetry locations were pooled by individual and period to calculate standardised habitat selection ratios. Selection ratios constituted the resource selection function and were used as the basic unit in all subsequent statistical analyses of habitat preference. The authors used these selection indices to create independent variables by subtracting adjacent pairs of values and then applied a repeated measure MANOVA using individual moose as sampling.

At the landscape scale, three variables discriminated the composition of moose home ranges from random permutations (Fig. 2.6). The overlap between moose home ranges and wolf territories was much lower than expected. Moose selected

areas where habitats providing high food abundance were interspersed with habitats providing shelter against snow. Additionally, moose home ranges contained fewer areas with low snowfall compared with random permutations. At a home-range scale, patterns of habitat selection varied between time periods but the tendencies were usually the same. Neither predation risk nor food abundance alone determined habitat preference of moose since stands offering the highest food abundance and those offering the best concealment cover were not the most preferred by moose. In summary, at both scales, moose traded off food availability with exposure to deep snow and predation risk, as expected by the authors.

2.5 Patch Models of Foraging Theory

2.5.1 *Introduction: Foraging Theory and Foraging Behaviour*

Foraging theory was born in 1966 from two studies published by John Emlen and by Robert MacArthur and Eric Pianka. They were interested in foraging behaviour as a mechanism to explain the processes in populations and communities. The principles of their work were adopted by behavioural researchers, and the theory went on to have a huge influence in the next two decades, dominating the field of behavioural ecology. Dave Stephens and John Krebs published their book *Foraging Theory* in 1986, at a time when—paradoxically—the influence of this theory began to decline. However, several of its principles remained central in behavioural ecology: the need to refine the hypothesis so as to generate accurate quantitative predictions, the value of experimental work combined with field observations, and the concept of behaviour as a decision-making process. Foraging behaviour studies expanded in two directions: looking at the neurophysiological and cognitive mechanisms involved in foraging decisions and analysing the ecological consequences at the level of populations and communities. The book ‘Foraging: Behavior and Ecology’, written by David W. Stephens, Joel S. Brown, and Ronald C. Ydenberg in 2007, shows how foraging theory went from being a body of simple but robust models to a rich and diverse field, extending into diverse disciplines such as neuro-ethology, animal psychology, ecology, population biology, and conservation.

The classic theory of foraging emphasises the use of optimisation models as a tool for studying behaviour. Optimisation models are applied to the interactions of the animals with the environment and have the following characteristics:

- They treat the behaviour as a decision-making process. Decisions are not ‘conscious’ in the human sense, but are behavioural alternatives that are subject to natural selection and, therefore, can be analysed with cost–benefit models.
- They analyse the adaptation as a balance between costs and benefits. This balance is achieved through natural selection operating on biological traits.

- They generate hypotheses about the adaptive value and the ecological consequences of foraging, anti-predatory behaviour, and habitat selection.
- Habitat selection is divided in a hierarchy of behaviours that are analysed separately (Fig. 1.4).

2.5.2 *Types of Patches*

The ‘classic’ habitat for foraging theory is a set of patches where the resource, normally food, is concentrated and a matrix through which an individual ‘travels’ without using resources. A patch defines in terms of the availability of one type of resource, mainly food. A patch has the dimensions for the exploitation of one individual. It is affected by the foraging activity so that the resource becomes scarcer as the individual remains in the patch. Foraging patches have two basic properties: the initial density of food and the so-called *gain curve*, i.e. how the resource is depleted as an animal stays. There are three main types of gain curves (Fig. 2.7): without depletion, gradual depletion, and sudden depletion (Sutherland 1996). These gain curves depend on the rate of replenishment of the resource and searching behaviour of the organism. In gain curves without depletion, resources do not diminish their density in the animal’s foraging period. This occurs, for example, in the case of prey that is super-abundant, but has a high anti-predatory response. This behaviour of the prey determines resource availability decreases in the short term, but the abundance stays approximately constant. In sudden-depleted patches, the probability of obtaining resource is constant until all the resource is consumed. This occurs when animals search systematically within a site so that the encounter rate with resource items remains constant until the patch is depleted. The progressive depletion can occur for two main reasons: because the animals search randomly and every time it is harder to find food or because the food must be transported to a central location. Examples of this are birds feeding their chicks or social insects (bees) carrying the food to a central place. In this case there is a cost associated with transportation of the food that determines a gradual decrease of the gain with increasing load to be transported.

2.5.3 *Marginal Value Theorem*

In the case of gradual depletion, the classic model called the *theorem of the marginal value of capture* is applied. This model was published in its first version in 1976 by Erich Charnov. The model predicts an optimum time of departure that occurs when the instantaneous rate of acquisition of resources on the site equals the overall rate environment. In this case, the prediction changes depending on the average travel time between sites or the quality of the patches (Fig. 2.8). The characteristics of the model are:

Fig. 2.7 Type of patches in relation to resource gain functions

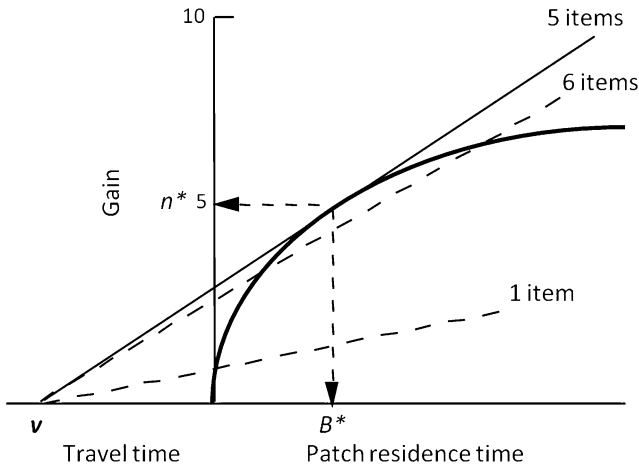
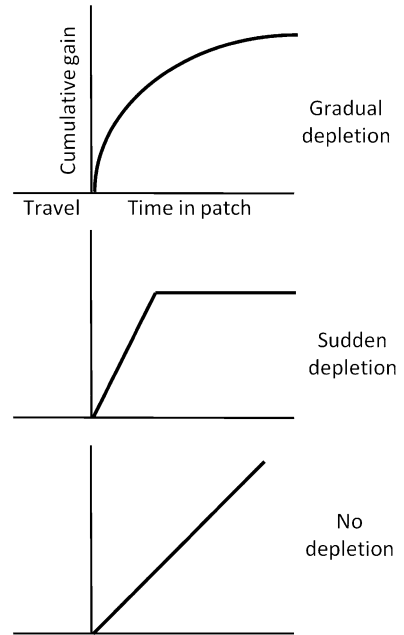


Fig. 2.8 Graphical representation of the marginal value theorem of capture. The maximal slope of the function relating gain to time (travel between patches + patch residence) is reached when $n^* = 5$

Decision: How long to stay in a patch.

Context: Patches separated by areas without resources, slow recovery of the offer, and random search.

Variables involved: n_i = resources obtained at site i , b_i = searching time within patch i , and v = travel time between patches.

Decision criterion: Maximise the rate of acquisition of resources:

$$T = n(v + b) \quad (2.1)$$

Decision rule: Leave a patch when the marginal rate of capture equals the average rate environment:

$$\frac{n_i}{b_i} = \frac{\sum n_i}{(v + \sum b_i)} \quad (2.2)$$

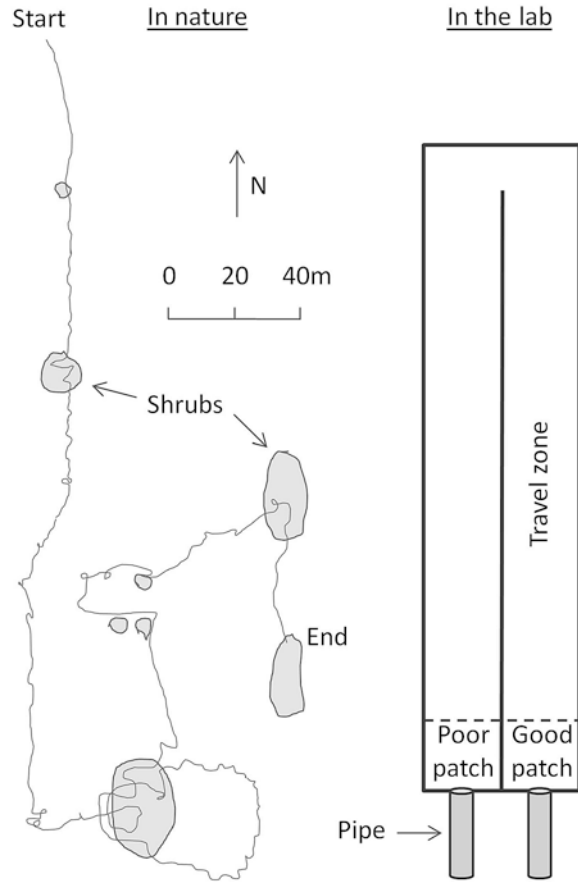
An experiment that was conducted on a South American mammal (Cassini et al. 1990), the screaming hairy armadillo *Chaetophractus vellerosus*, is described as an example of many tests of the marginal value theorem (Nonacs 2001). These animals with a funny name are found in central Argentina and occupy arid and semi-arid environments where the soil is not hard so they can dig its burrows (Abba and Cassini 2008). They are solitary foragers with an omnivorous diet and a preference for insects (Abba and Cassini 2010). One of the few field studies on this species was conducted by Greigor (1985). He used a small roll of thread attached to the animal and was able to describe preliminary animal movements (Fig. 2.9). Armadillos followed a typical pattern with relatively long straight lines interspersed with looping and spiralling movements. This area-restricted pattern was normally observed when armadillos reached a bush. In the semi-desert environment, where these armadillos live, food is concentrated mainly under bushes that are scattered in a matrix of nude soil. This is a typical context of foraging patches and a travelling matrix between them.

Cassini et al. (1990) trained armadillos in a U-shaped alley with each arm being almost 4 m long (Fig. 2.9). The ‘patches’ were the ends of the arms, where two small containers received food items (commercial dog food pellets) through a vertical pipe. Food was delivered in accordance with a patch gain function with a power form, so the feeding schedule simulated a depleting patch. The authors used a discrete version of the marginal value theorem applied to an environment with two equally common patch types, a ‘poor’ and a ‘good’ type, which were encountered in alternation and differed in the rate at which resource depression occurred. The model predicts the number of prey per visit to take from each patch type (p^* and g^*) that maximises capture rate (R) in the cycle of two successive patch visits. Rate of gain in such a cycle is

$$R_{p,g} = \frac{(p + g)}{(r_p + q_g + 2t)} \quad (2.3)$$

where p and g are numbers of prey items per visit to poor and good patches, respectively; r and q are poor and good patch residence times; and t is the travel time between patches. Using (2.3), they calculated by iteration the pair (p^* , g^*) that yields the maximum profitability (R^*). The marginal value theorem predicts that optimal exploitation of each patch type should depend on the average rate of gain in

Fig. 2.9 Foraging by individual armadillos *Chaetophractus vellerosus*. In nature: example of searching trajectory of one night of foraging activity by an armadillo in the Argentinean step (modified from Greigor 1985). It travelled from shrub to shrub, where most insect prey were available. In the lab: Apparatus used in a laboratory experiment with the same species of armadillos (modified from Cassini et al. 1990). Armadillos 'travelled' from one dispenser to the other, when they entered the 'patch'; food item was provided through a pipe



the environment, and thus changing this average should affect the number of prey collected from both patch types. Cassini et al. (1990) manipulated the average rate of gain for the environment by differing s_p . There were two treatments or 'environments', which differed only in the gain curve in the poor patch ($s_g = 0.5$, $s_p = 0.2$ in treatment A and $s_p = 0.4$ in treatment B).

Qualitative trends observed in the experiment were as predicted by the marginal value theorem. Within treatments more prey were taken from good than from poor patches. Between treatments exploitation of good patches decreased and of poor patches increased when the quality of the poor patches was increased. Prey per visit consumed by armadillos in poor and good patches of both treatments closely agreed with the expectation of the patch use model (Fig. 2.10).

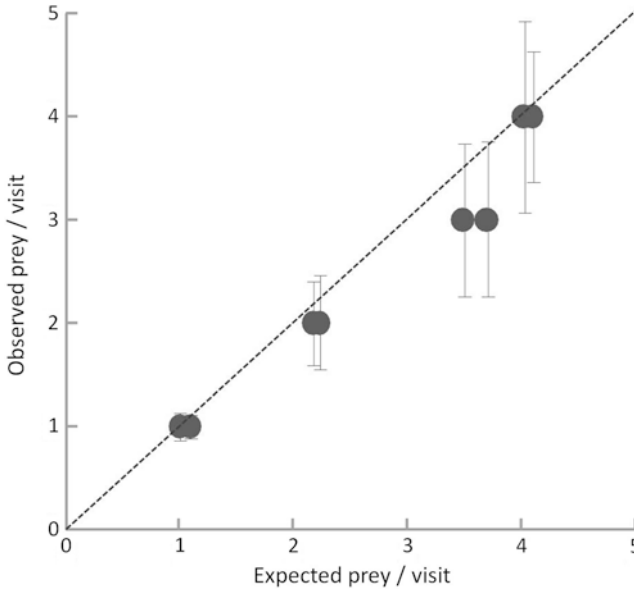


Fig. 2.10 Observed versus predicted consumptions in the experiment with armadillos *Ch. vellerosus* (modified from Cassini et al. 1990, experimental set described in Fig. 2.9)

2.5.4 Patch Selection

An experiment with armadillos was just described in which predictions of a discrete version of the marginal value theorem were tested. Another experiment in a similar set-up was conducted, which differed in the way that armadillos got food in patches (Cassini 1993). The ‘environment’ consisted of a V-shaped runway. Each ‘patch’ was made up of a square plastic grid divided into 400 square compartments of 1.3-cm side. Ten or 40 dog food pellets were randomly distributed, representing ‘poor’ and ‘good’ patches. There were two treatments, ‘long travel’ and ‘short travel’, located at the distal and proximal ends of the runway arms, respectively.

In this experiment, armadillos were free to move within patches and decided a searching strategy. The predictions on patch use of two searching strategies were tested. A *random forager* is an individual that has a certain probability of exploring an already visited section of the patch (Fig. 2.11). Its mean probability of finding food is a decreasing function of time in the patch, and the functions of patch gain are negatively accelerated (Fig. 2.7). Under these conditions, the marginal value theorem predicts that patch residence time and prey consumed per visit increase as travel time increases (Fig. 2.11). A *systematic forager* is an individual that does not visit a section of the patch already visited. Its mean probability of finding food is constant within each patch time and, therefore, the functions of patch gain are linear. Because systematic foragers are always expected to deplete patches fully, no changes are predicted in prey per visit and residence time for each patch type (Fig. 2.11).

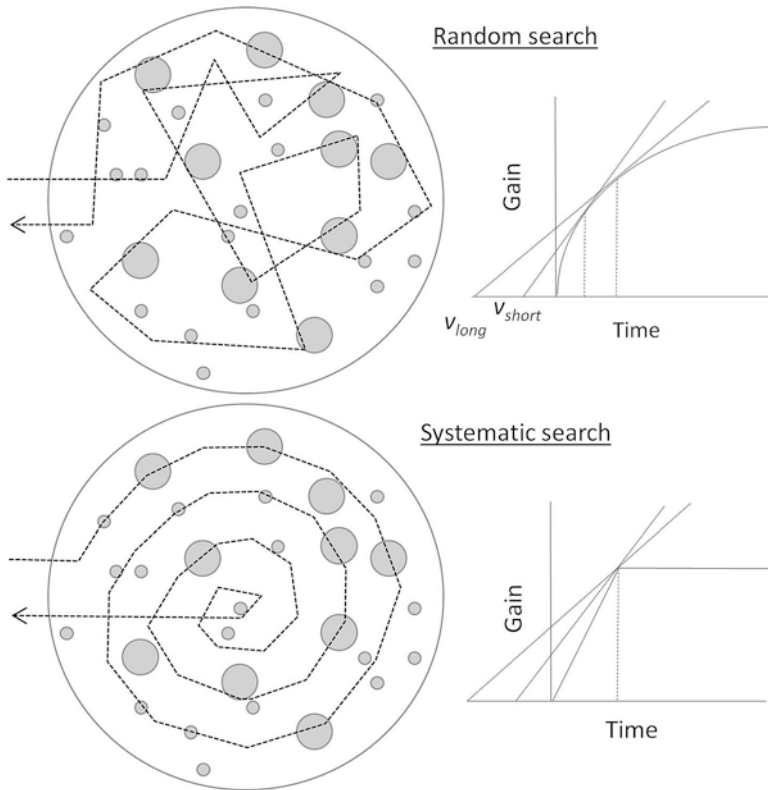


Fig. 2.11 Schematic representation of the searching paths of systematic and random foragers in a circular patch, food randomly distributed prey of two types, and shape of gain functions under both foraging strategies. Foraging theory predicts that random foragers will stay longer in patches when environments have long travel times, while systematic foragers will use the same departure time with long and short travel times (modified from Cassini 1993)

Figure 2.12 illustrates the results of this experiment. Armadillos tended to depleted patches in all conditions, as was expected for a systematic forager. The actual behaviour of the armadillos observed during the training sessions also invalidates random searching. The path pattern commonly observed in the animals while they visited a patch had a spiral configuration: individuals often began foraging at the periphery of the patch and then moved progressively towards the interior, leaving when they reached the centre. This spiral route clearly minimised the probability of revisiting the same compartments.

This example shows how a systematic type of movement within a patch with randomly distributed food produced a linear gain function with sudden depletion. Each patch type may be characterised by the slope of the gain function. Under these conditions, a gain-maximising strategy will predict that a set of poor patches will be abandoned without exploitation because gain is under the marginal value. This is a

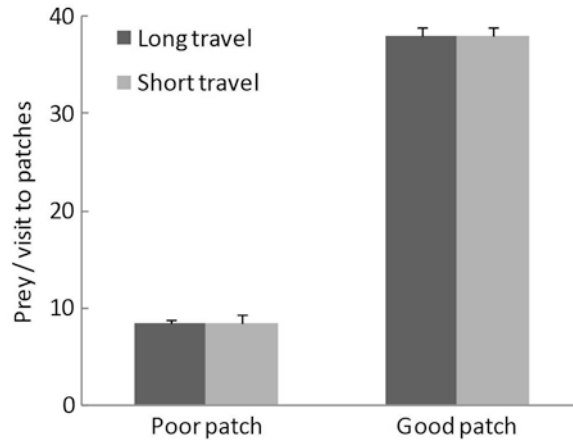


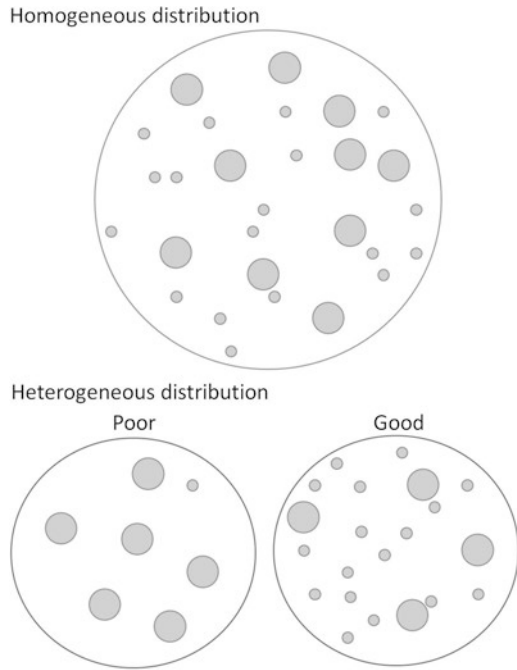
Fig. 2.12 Results of the second experiment with armadillos *Ch. vellerosus*. In this experiment, armadillos developed a systematic search (Fig. 2.11). Under these conditions, the optimal strategy of a rate maximiser is to stay until patches are depleted, independently of patch quality and travel time. Maximal food items were 10 and 40 in poor and good patches, respectively (modified from Cassini 1993)

prediction analogous to the one produced by another famous foraging theory product: the prey choice model (Stephens and Krebs 1986). Foragers are expected to rank patches in terms of their gain function slopes as if they were prey profitabilities in the prey choice case. In summary, systematic searching allows animals not only to use patches more efficiently but to select patches in a way that poor patches are never visited.

2.5.5 Patch and Prey Selection

The classical prey choice model is applied to a homogeneous environment where prey types differ in profitability, while the classical patch use model is applied to patchy environment where patches contain the same type of prey. In nature, resource types frequently concentrate in different areas of the habitat, so resource patches differ in the relative abundances of prey types. Figure 2.13 represents an example of two prey types with two types of distribution. There are 10 highly profitable prey and 18 low profitable prey in both cases. In the homogeneous habitat, the rate of encounter with large prey is high enough and the prediction is that the forager will specialise in this type of prey. In the heterogeneous condition, patch type B has large proportion of large prey, but the overall prey density is low. The opposite occurs for patch type A. In this environment, the expected behaviour depends on the distance between patches. When travel time is large enough between patches, a systematic forager will select patch A exclusively, because prey density in B is low, and will be prey opportunistic when in patch A, because the density of high profitable prey in there is low.

Fig. 2.13 Schematic representation of two environments with same amount of highly (X) and low (x) profitable prey, one with food distributed homogeneously and the other with distribution in patches. Foraging theory predicts prey selectivity in the homogeneous but not in the heterogeneous habitat. See text for details



2.6 Foraging in Heterogeneous Habitats by Plants

The growth pattern of stoloniferous and rhizomatous plants may be considered analogous to the search path of a foraging animal (Bell 1984). Hutchings and de Kroon (1994) defined foraging behaviour in plants as the plastic physiological and morphological alterations that directly or indirectly enhance the capture of essential resources. Aboveground, such responses include the shade-induced elongation of stems and petioles by which laminae are projected upwards, along gradients of increasing photon flux density, into locations with higher light availability and the light-fleck-induced activation of the photosynthetic apparatus that increases the capture of ephemeral light pulses (de Kroon et al. 2009). Belowground foraging responses include the initiation and activation of lateral root primordia and the subsequent growth of lateral roots in patches of substrate with high nutrient concentration, as well as the activation of nitrate transporters in response to high nitrate availability (de Kroon et al. 2009).

Plants often grow in patchy environments and modifications of the growth pattern in response to patch quality may alter the distribution of ramets. Plasticity of some clonal species allows them to change their growth form so that they become more compact in favourable habitat. In a patchy environment, this could enhance the placement of ramets in relatively resource-rich microhabitats. Accordingly, morphological plasticity has been viewed as a behavioural phenomenon, which allows

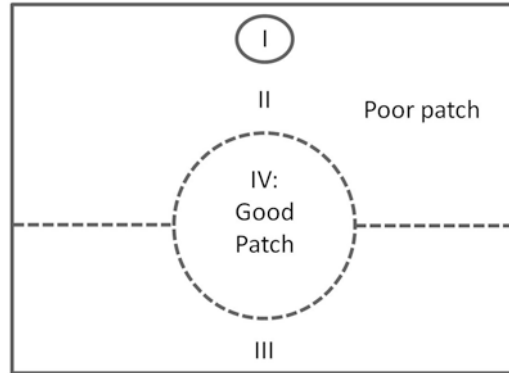


Fig. 2.14 Individual foraging in plants. Experiment conducted with the herb *Glechoma hederacea*, bred in different types of environments. The figure represents the ‘patchy’ environment, with the ‘good patch’ located at IV (the central circle contained half of the potting compost). Roosts were harvested in four fractions of soil: I the small pot containing the original parent ramet; II outside the central circle in the proximal half of the box; III outside the central circle in the distal half; IV inside the central circle (modified from Birch and Hutchings 1994)

clonal plants to arrange their ramets within their environment in a selective manner. This capability has been regarded as a manifestation of foraging behaviour (Grime 1979). Many experiments have been conducted with clonal herbs that showed this plant’s ability to select the best patch where to concentrate growth (Slade and Hutchings 1987; Birch and Hutchings 1994; Cain 1994; De Kroons et al. 2009).

Birch and Hutchings (1994) conducted an experiment to test whether plants may exploit patches of resources following optimal foraging rules. They grew the herb *Glechoma hederacea* in three artificial soil environments: ‘uniform’, ‘patchy’, and ‘poor’. In the uniform condition, potting compost was evenly mixed with sand (Fig. 2.14). The ‘patchy’ treatment contained the same quantity of potting compost, but half was concentrated in a central resource-rich circle. The poor environment had half of the compost of the other two treatments. This experiment showed that *G. hederacea* was able to produce over two and a half times biomass in the patchy environment. This improvement was achieved by concentrated 80% of root biomass within the resource-rich central circle.

2.7 Balancing Demands and Use of Refuges

There is abundant evidence regarding insects, fish, birds, and mammals that prey are able to respond spatially to the abundance or presence of predators. When the environment with more abundant food resources is also the most risky, individuals that are prey use patches less than expected on the basis of the food supply. A patch in

which food has a homogeneous distribution can be used in heterogeneous form by the effect of predation risk. This is typically the case when the patch is associated with a shelter, such as a den or a border with plant cover for mammals, woodland for birds, or rocks for fish. Prey typically uses with greater intensity portions of a foraging site that are closer to the shelter. However, plant-covered environments are not always a source of refuge, since some predators use them to hide and stalk their prey. Therefore, in some species such as ungulates, the spatial response to the presence of coverage is the opposite, i.e. avoid feeding in areas close to high and dense vegetation.

Brown (1988) extended the marginal value theorem to include the effects of predation risk and alternative activities on patch use. A fitness-maximising forager should cease harvesting a resource patch when the value of its harvest rate (H) no longer exceeds the sum of its energetic cost of foraging (C), predation risk (P), and the missed opportunity cost (MOC):

$$H = C + P + MOC \quad (2.4)$$

This type of modelling the trade-off between foraging and danger avoidance remained elusive during the first developments of foraging theory because the costs and benefits were in different units. More recent developments used a life history perspective that allowed translating both foraging gain and danger into a common measure of fitness (Stephens et al. 2007). These models have proved to be useful in predicting theoretically the response of organisms to changes in predation risk at different scales. However, quantitative tests of these predictions can be difficult, especially when state-dependent costs are incorporated.

Brown (1988) developed a simple method to measure risk while foraging, by means of measuring *giving-up densities*. Foragers at depletable patches do not consume all of the contents. Brown called the amount of food that a forager leaves behind the giving-up density. It is a surrogate of the quitting harvest rate predicted by the marginal value theorem. This model predicts, for example, that a forager should have a higher giving-up density as travel time among patches declines. Giving-up densities have been used to estimate the predation cost of foraging of several species, e.g. rodents (Jacob and Brown 2000), fish (Petty and Grossman 2010), and birds (Oyugi and Brown 2003).

A study conducted by Oyugi and Brown (2003) is described. Giving-up densities of robins *Turdus migratorius* and starlings *Sturnus vulgaris* were estimated to test for (1) the role of cover as safety in microhabitat preferences, (2) temporal habitat preferences, and (3) the habitat quality of mowed grass. The habitat comprised clumps of shrubs and tall trees within open mowed lawn. Experimental patches consisted of trays filled with vermiculate and 30 mealworms *Tenebrio molitor* buried in this substrate. The birds had to search within the patch, and the longer a forager spent in the patch, the lower was the rate at which it found new worms. The number of mealworms left in the resource patch after the birds have quit the exploited patch is the giving-up density. The location of patches was lumped into three distances categories of 0–4, 4–8, and 8–12 m from the cover. Giving-up

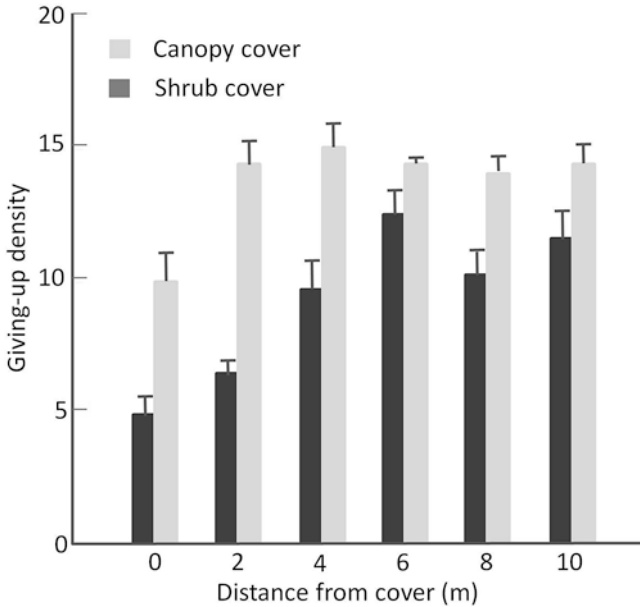


Fig. 2.15 Giving-up densities of birds. Mean $\pm$ SE giving-up densities of American robins *Turdus migratorius* and European starlings *Sturnus vulgaris* foraging on mealworms increased with distance from cover. The type of cover also influenced patch use, with lower giving-up densities near dense shrubs than near tree-canopy cover. Giving-up density was measured as the number of mealworms remaining per tray at the end of each day of observation (modified from Oyugi and Brown 2003)

densities were lowest near cover (independent of cover type) and increased steadily with distance from cover (Fig. 2.15). By using the giving-up densities as a measure of quitting harvest rate and foraging efficiencies (Brown 1988), robins and starlings revealed that microhabitats near cover provide safer feeding areas than those away from cover. Giving-up densities increased with distance from the edge of shrub or tree canopy. Association of risk with closed versus open habitats, or with distance from cover, varies among bird species (Lima and Dill 1990). Other species of birds perceived cover as a source of attacks and stay foraging for shorter periods.

2.8 Distribution at Equilibrium: The Matching Rule

The pattern of distribution of an individual in its home range depends on a decision process. The individuals select between alternative behaviours such as stay, move, forage, escape, or rest. Foraging theory is based on the fundamental principle that this decision process is modulated by natural selection. Optimisation models are

applied, not because animals are expected to behave as perfect machines but as an instrument to organise hypothesis around this principle.

Marginal value theorem is an optimisation model that describes behavioural decisions while foraging in a patchy environment. It predicts the amount of time that the animal should invest in each patch depending on resource availability. But which is the expected distribution in the equilibrium? Staddon (1983) conducted a simple deduction to obtain the overall or molar expectation of patch rules that maximise fitness. He supposed that the environment is composed of two types of depleting patches—‘good’ and ‘poor’—as illustrated in Fig. 2.8, with a power function form:

$$C_t = Ar^s \quad (2.5)$$

where A and s are constants and $0 < s < 1$. Taking the first derivative to find the marginal value gives

$$\frac{dC}{dt} = Astr^{s-1} = \frac{sC_t}{t} \quad (2.6)$$

i.e. the derivative of the cumulative food intake function; C_t can be written as a function of the ratio C/t . From the marginal value theorem, dC/dt should be the same for all patches; thus, for two patches g and p , $dC_g/dt_g = dC_p/dt_p$. If s is the same in both patches, equating the marginal value yields $C_g(t_g)/t_g = C_p(t_p)/t_p$, or

$$\frac{C_g(t_g)}{C_p(t_p)} = \frac{t_g}{t_p} \quad (2.7)$$

Equation (2.7) states that the ratio of the times the animal spends in both types of patches is equal to the ratio of the amounts of food obtained. This is termed the *matching rule*. If it is not the same for both patches, then choice proportions should be proportional (not equal) to payoff proportions, the so-called *biased matching*.

Matching law was firstly described by animal psychologists who have a long tradition of studying behaviour experimentally. They have been observed matching in many experiments where subjects choose between alternatives that reinforce probabilistically (Herrnstein 1961). The ‘psychological’ matching law is applicable in a type of experimental set-up called *concurrent schedules*, in which subjects can distribute their behaviour between two or more simultaneously available schedules of reinforcement. More specifically, individuals of a diverse range of species distribute their responses or time between in proportion to alternative qualities, in experiments with concurrent variable-interval schedules (Baum 1981). In these experiments, reinforcement is based on the passage of time and the requirements for reinforcement change randomly around a mean. Therefore, the animal can learn that the delay in an alternative is greater on average than in the other, but cannot exactly determine the exact moment when the device is ready for delivery of the reinforcement.

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