Note to readers:

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'New Zealand is as close as we will get to the opportunity to study life on another planet.' (Diamond 1990)

Although the physical environment has been described as a habitat template for animals (Southwood 1977), many animal species can also significantly modify their surroundings (Johnston 1995). The New Zealand fauna has numerous examples of both, as well as many ancient taxa that have evolved into unusual forms. In this chapter we examine animal habitat in natural and human-modified environments. We begin by examining the geological origins and biogeographic patterns of New Zealand animal species diversity and community composition. These biogeographic patterns will be explained in terms of general ecological concepts of limiting factors and environmental gradients. Every animal species is adapted to a specific combination of environmental characteristics, referred to as the species' ecological niche. Areas with these specific environmental characteristics define the species' habitat. The transformation of natural landscapes for human land use has significantly fragmented the habitat of many native animal species. We end this chapter by examining the effects of human landscape transformation and animal invaders on the New Zealand environment and native animal species.

Animal diversity and composition

The extent of animal diversity

The importance of animals in the environment can be demonstrated by their sheer abundance. There are approximately 9.8 million animal species on Earth, compared with 3.8 million plants and lower taxa (Heywood 1995). Approximately 28,800 animal species are indigenous to New Zealand, although barely 50% have been identified (Table 21.1) (Halloy 1995; Taylor & Smith 1997). The number of species in an area is known as its species richness, or alpha (α) diversity. This quantitative measure of biodiversity (i.e. biological diversity) is a simple descriptor widely used in ecology
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(Gotelli 1995), biogeography (Brown & Gibson 1983; Cox & Moore 1993), and conservation (Gaston 1996). An extensive literature is devoted to quantification of other biogeographic, ecological, demographic, and genetic aspects of biodiversity. Species diversity can vary significantly between areas representing biomes, ecosystems and communities, and along environmental gradients. The variation or turnover of diversity along an environmental gradient is a measure of beta (δ) diversity. Animal species richness can also vary over time in response to environmental change, seasonal migration, population dynamics, the behaviour and movement of individual animals, and the vagaries of weather. The most obvious biogeographic trend in terrestrial diversity is the increase from high-latitude polar regions to low latitude tropical rainforests. Within a smaller area, species richness also tends to be highest on sites of intermediate disturbance and resource availability, but this generalisation remains the topic of ongoing research.

Origins of New Zealand animal diversity

Geological history is important to explain the diversity and origins of New Zealand fauna because many endemic taxa are relics from when New Zealand was attached to the large Gondwana supercontinent (Cox 1991). The Rangitata orogeny (140-110 million years BP) was the single opportunity for amphibians, reptiles, birds, and other animals to colonise the continental remnant of New Zealand. Many animals from this wave of Cretaceous colonists have survived as 'living fossils'. As a result, New Zealand has a disproportionate number of terrestrial taxa representative of Mesozoic and Palaeozoic lineages that are absent from other biogeographic regions (e.g. archingulid spiders, micropterygid moths, petalurid dragonflies, kiwi, moa, weta, velvet worm (Peripatus), and the tuatara, Sphenodon punctatus) (Bishop 1992; Cooper & Millener 1993). However, more recently evolved taxa such as snakes and mammals (with the exception of three bat species) were unable to colonise New Zealand after the ancestral landmass separated from Gondwana about 80 million years ago. The long geological isolation of New Zealand also allowed for extensive in situ evolution, and a high level of endemic species. Hyperdiverse terrestrial taxa include flatworms (Platyhelminthes, >50 species), earthworms (178), snails and slugs (>1000), moths (>1500), and beetles (>4300) (Daugherty et al. 1993) (Table 21.1). New Zealand has been colonised naturally in more recent early Tertiary geological history by 'sweepstake' dispersals from Australia. Colonists that have accidentally crossed the Tasman Sea on prevailing westerly winds and ocean currents include the waxeye (Zosterops lateralis), spur-winged plover (Vanellus miles), welcome swallow (Hirundo tahitica), Australian coot (Fulica atra), Australasian harrier (Circus approximans), kingfisher (Halcyon sancta), fantail (Rhipidura fuliginosa), and black stilt (Himantopus novaeseelandiae).

New Zealand vertebrate diversity is highest among lizards and birds (Table 21.1), even though they have different biogeographic origins (Atkinson & Millener 1991). Avian diversity results from an ongoing trickle of immigration, so no single bird genus shows high species diversity. The seabird fauna is particularly diverse because the New Zealand archipelago spans over 20° latitude of the Southern Ocean from the
Table 21.1 Indigenous and introduced animal species in New Zealand. Most figures are the best approximation of the number of species identified and suspected in each taxonomic group. Totals and subtotals have been rounded.

| Invertebrates | Arthropods | | | |
| | | Estimated number of indigenous species | Number that have been identified | Identified species that are endemic (%) | Number of introduced species in the wild |
| | | c.20000 | c.10000 | 90 | c.1100 |
| | | c.4600 | c.2600 | 90 | c.60 |
| | | c.120 | 53 | ? | ? |
| | | c.2000 | 1517 | ? | ? |
| | | c.600 | c.200 | ? | ? |
| | Molluscs | | | | |
| | | c.1300 | c.500 | 100 | c.33 |
| | | c.3500 | c.2000 | ? | at least 6 |
| | Worms | | | | |
| | | c.11400 | 414 | ? | c.600 |
| | | 220 | 178 | 43 | c.25 |
| | | c.4200 | c.430 | 100 | c.230 |
| | | 430 | 80 | 30-35 | c.75 |
| | | c.1200 | c.400 | 56 | c.50 |
| | | c.2600 | c.2100 | ? | ? |
| | | c.27500 | c.14400 | c.2200 |
| | Vertebrates | | | | |
| | | c.1100 | c.870 | 5 | ? |
| | | c.100 | 94 | 62 | ? |
| | | c.35 | 28 | 90 | 20 |
| | | 4 | 4 | 100 | 3 |
| | | 61 | 61 | 100 | 1 |
| | | 88 | 88 | 57 | 34 |
| | | 61 | 61 | 30 | 0 |
| | | 2 | 2 | 100 | 34 |
| | | 41 | 41 | 5 (2 spp.) | 0 |
| | | c.1500 | c.1250 | c.6000 |
| | | c.28800 | c.15600 | c.8200 |

*Includes 350 sponge species, 400 cnidarians, 400 echinoderms, 900 bryozoans, and c. 50 species from minor taxa.

**Includes 34 cetacean species and 7 pinnipeds, many of which are seasonal migrants.

Taylor and Smith (1997)

Subantarctic to the subtropics. The diversity of reptiles (and many other flightless groups) probably arose from only a few colonising ancestral species that subsequently evolved into many different species by adaptive radiation (Towns et al. 1985).

The absence of mammals and the unique assemblage of other taxa have allowed many New Zealand taxa with spectacular adaptations to exploit ecological niches typically used by mammals elsewhere (Cooper et al. 1993). Many large flightless birds occupied the ecological niches of browsing animals (11 moa species) or grazers (kakapo, Strigops habroptilus, and takahē, Notornis mantelli) that are usually occupied by ungulates in other biogeographic regions. Among the invertebrates, 16 weta species fill the niches of mice and rats, resembling rodents not only in their biomass but also in nocturnal foraging and diet, use of diurnal shelters, and polygamy. The absence of
mammalian predators allowed predatory roles to be filled by many species, including 15 species of giant carnivorous snails, reptiles, and birds. A guild of medium-sized kiwi species evolved in the absence of burrowing carnivorous mammals, feeding by probing the soil for invertebrates. Kiwi are convergent with mammals in their burrowing and nocturnal habits, reliance upon olfaction rather than vision, and aggressive maintenance of year-round rather than seasonal territories. The absence of predatory mammals is commonly associated with morphological and life history traits such as gigantism, longevity, and low reproductive rates. These traits also predisposed New Zealand animal species to rapid declines (extinctions) once mammals arrived (Holdaway 1989).

**Spatial patterns of New Zealand bird diversity and composition**

Studies in many biogeographic regions of the world have identified latitudinal and altitudinal gradients of plant and animal species richness, and the paucity of animal species on peninsulas. Speciation, dispersal, climate, topography, primary productivity, competition, and disturbance are important factors responsible for these geographic patterns (Huggett 1995).

Few systematic surveys of geographic patterns of terrestrial animal diversity have been conducted in New Zealand. The most geographically comprehensive field survey of birds was conducted by 800 volunteers in the Ornithological Society of New Zealand from 1969 to 1979. Maps of the presence or absence of almost 150 bird taxa in 10,000-yard grid square areas were published in *The Atlas of Bird Distribution in New Zealand* (Bull et al. 1985). The spatial pattern of native land and freshwater bird species richness derived from maps in this atlas is shown in Figure 21.1. Richness is high in many coastal grid cell areas, which have habitat for both coastal and interior forest bird species. Hotspots of high bird species richness in Northland, south Westland, and northwest Nelson coincide with regions of high plant diversity (Enting & Molloy 1982). Bird species richness also decreases toward southern latitudes, and from west to east.

Species that live together and have similar habitat and resource requirements form a special assemblage of species called a community (MacNally 1995). For example, the threatened New Zealand dotterel (*Charadrius obscurus*) and other shore birds form a community of coastal wading birds. Geographic patterns of species composition are related to patterns of species richness. However, areas with identical numbers of species may have a different assemblage of species if the areas have different habitats or environmental conditions. The distribution of communities of plant species and poikilothermic animal species are often strongly influenced by climatic zones. However, the geographic distribution of homeothermic animal species such as birds is influenced less by environmental temperature than by historical factors such as geological processes, speciation, and evolution (Huggett 1995). This is true for the geographic patterns of New Zealand land and freshwater bird communities, as revealed by a TWINSPLAN classification analysis (Hill 1979) of the bird atlas data (Figure 21.2). Contiguous areas with similar bird species composition form avifaunal regions. These
The geographic distribution and abundance of animal species

The role of the physical environment in determining biogeographic patterns of species diversity and composition rests essentially on the geographic distribution and abundance of each species. All species have a geographic distribution, or range, that encompasses all populations. The range is a fundamental species characteristic (Brown et al. 1996) resulting from evolutionary adaptation to the environment, primarily by the presence or absence of suitable habitat. For example, most native New Zealand land and freshwater bird species occur in a few small areas (restricted distribution), and few regions tend to be separated by barriers to dispersal such as Cook Strait (i.e. separate avifaunal regions on North and South Islands), or they occupy major physiographic regions such as the Southern Alps or the central North Island plateau.
species are found over a large geographic region (widespread) (Figure 21.3). Endemics are species confined to a particular area. Disjunct species have gaps in their distribution that are wider than their normal dispersal distance. These disjunct distributions can result from the formation of natural geographic barriers such as mountain ranges, or widespread habitat fragmentation due to human land use.

Species distributions are also dynamic, always changing in response to conditions of their immediate surroundings (environmental or biological). Each species occupies a finite area over its range, but this area will change, expanding under better conditions, and contracting when environmental conditions are poor. For example, animals may migrate, cross barriers (jump dispersal), colonise new areas (range expansion), and shift ranges gradually through a combination of range expansion, contraction, and differential extinction (range shift). Animal species have a distribution that reflects the spatial extent of suitable habitat as well as behavioural interactions with other animals, and movements to track changes in resource availability over time. Therefore the distribution of an animal species is a function of its resource requirements for growth and reproduction, its ability to exploit available environmental resources, and the spatial distribution of those resources.

All species require certain resources and physical environmental conditions to be able to survive and reproduce. Within the geographic range of a population, individuals will generally live only in suitable habitat. At least four groups of factors determine what is meant by suitable habitat, and influence the distribution and abundance of plants and animals: abiotic, or physical; biotic (excluding humans); anthropogenic (humans); historical, or evolutionary. For physical gradients (e.g. temperature) there is a minimum level below and a maximum level above which an animal's metabolism cannot be sustained. The optimum level for a given gradient is that associated with maximum growth and reproductive capacity (fitness), with their performance attenuating at the extremes.

The tolerance of conditions along a physical gradient varies among species and even among individuals of the same species. A species' tolerance may also be wide for some physical variables but narrow for others. Nonetheless, the relationship between animal abundance and an environmental gradient can be represented by a unimodal, or Gaussian, curve divided into three levels of tolerance (Figure 21.4). Lethal environmental extremes at the tails of the curve disrupt critical biological functions and define zones of intolerance. Within these extremes the environmental conditions will sustain foraging and other activities necessary for individual animals to persist in populations with low abundance. These zones of physiological stress are outside the central range of optimal environmental conditions. The long-term perpetuation of a population is confined to sites with environmental conditions within this optimal range because the conditions must support growth and reproduction in addition to the maintenance of individuals. The biogeographic relevance of this species' response curve is that factors that are closest to limiting by their deficiency or excess will determine an animal's potential geographic distribution (MacNally 1995). More specifically, the range limit of any animal species is determined by that environmental factor for which it has the narrowest range of tolerance at the most vulnerable stage in its life cycle.
The environment as animal habitat

The physical environment in which a population lives and draws resources for survival is its habitat, which provides food and cover essential for population survival. Habitat is most often discussed for animals, but the concept represents a more general interaction between any organism and the physical structure of its living space. It is distinct from a territory, which is an area defended by an individual animal, because it may use only a portion of the total available habitat area. The home range is the area that an individual traverses in its normal activities of food gathering, mating, and caring for young.

The present distribution, activity, and abundance of animals are the result of adaptations to past and present biotic and abiotic conditions, mediated by natural selection. Understanding why an animal population is found in an area requires knowledge of its present ecological relationships with the environment and other animals, and historical factors. Climate change may, for example, explain why a species persists in isolated, scattered relict populations. Also, competitive interactions in the past may explain present distribution and abundance patterns. In sum, understanding animal habitat preferences requires both evolutionary and ecological perspectives.

Environmental determinants of the ecological niche

There are many theories that attempt to explain the selection and use of an area by an animal species (Morrison et al. 1992). These theories share an assumption that animals somehow perceive the correct configuration of habitat characteristics required for their survival (i.e. they select their habitat). Therefore, in order to describe the habitat characteristics of a given animal we need to measure what the animal perceives as important physical characteristics of its living space. The concept of habitat selection developed in tandem with theory on the ecological niche by G. Evelyn...
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Hutchinson. According to the theory, each animal has a species-specific multidimensional fundamental niche that defines its living requirements on the basis of many biotic and abiotic variables. A simple analogy is that habitat is an animal's 'office building' and the niche is the animal's 'profession'. The position and shape of its response (in abundance) to each environmental or resource gradient (see Figure 21.4) define the species' niche. More specifically, the species' fundamental niche is a hypervolume made up of many environmental dimensions within which that species can survive and reproduce. Niche breadth is a measure of the diversity of resources used by an animal species. The species' realised niche is the reduced hypervolume after exclusion from parts of its fundamental niche because of competition or other biotic interactions. Three dimensions of the realised niche for the copper skink (Cyclodina aenea) in Pukerua Bay, Wellington, are represented in Figure 21.5 (Towns & Elliott 1996). Minimum temperature and the abundance of loam and stones are among the most important environmental gradients that affect copper skink abundance. The tolerable range of each gradient defines skink habitat and determines the areas where it can live.

![Figure 21.5](image)

Figure 21.5  Realised niche dimensions for the copper skink (Cyclodina aenea) in Pukerua Bay, Wellington: (a) two environmental gradients, (b) three environmental gradients.

It is difficult to quantify the ecological niche because it is necessary to identify and measure all of these resource dimensions for each animal species and, more importantly, because we can never know exactly what an animal perceives. In general, however, habitat selection can be viewed as a hierarchical decision-making process. At the broadest level, habitat selection is primarily innate; evolutionary forces establish migratory routes, wintering areas, and broad physiological limits to geographic barriers. Within a species' range an individual animal explores alternatives and weighs the costs and benefits of using each habitat type on the basis of resource availability. Within a habitat type an animal will choose specific microhabitats on the basis of abiotic and biotic factors such as mate availability and competition. Many studies have shown that animals (and especially birds) select habitat on the basis of vegetation physiognomy (i.e. size, shape, and spatial patterns of vegetation) more often than floristic composition, but identifying which is more important depends on the spatial scale of analysis (Morrison et al. 1992). Most animals distinguish between gross habitat
types on the basis of vegetation physiognomy, but the flora, or plant taxonomic considerations, determine their abundance within a habitat type.

Each of the many food resources available to an animal has a different nutritional value, a different pattern of spacing and abundance, and a different cost of capture. Because an animal has only limited amounts of time and energy, its choices among different potential foods may critically affect its survival and reproductive success. This summarises the critical role that the acquisition of food plays in the life of an animal, and demonstrates how important it is to consider food requirements in any habitat description. Many studies of animal-habitat selection focus on foraging behaviour because it shows how animals use their habitat (Bell et al. 1991). Species-specific foraging strategies reflect how each animal perceives the spatial pattern of resources in its habitat.

**Land transformation and habitat fragmentation**

Variations in topography, vegetation, soils, and land use within an area create a heterogeneous mosaic of habitat patches that constitutes a local landscape (Wiens 1997). The term 'patch' refers here to an area with more-or-less homogenous environmental conditions. The distribution of breeding habitat patches is especially important for long-term survival of animal populations (Opdam et al. 1993). The main components of habitat spatial pattern that affect population survival are:

- As the amount of habitat decreases, population sizes decrease, increasing the probability of regional population extinction.
- For the same total amount of habitat, increasing habitat patch size increases the probability of population survival, outweighing the negative effect of increasing inter-patch distance.
- Variance in habitat patch size increases the probability of regional population survival because populations in a few large patches can provide colonists for other vacant habitat patches.
- The inter-patch area or matrix determines the 'connectivity' of the landscape, or the ease with which individuals can move around (Lms 1995). If the matrix is inhospitable, rates of habitat-patch recolonisation are reduced.
- The rate of change in habitat patches is more important for population survival than the spatial pattern of habitat in the landscape.

These factors operate at the landscape scale and coincide with human activities that transform natural ecosystems into inhospitable environments that fragment animal habitat and threaten regional population survival (Fahrig & Merriam 1994).

**Ecology of spatially fragmented populations**

Most ecosystems are subject to one or more forms of anthropogenic disturbance that causes the loss of total animal habitat area. Short-term human impacts such as changes in land use, and longer-term impacts such as climate change can also affect the spatial pattern of habitats (Bissonette 1997). The term habitat fragmentation is commonly used to describe an overall decrease of habitat area or the partitioning of
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Habitat into small, isolated patches (Harris & Silva-Lopez 1992). Land-use activities that contribute to habitat fragmentation are complex and diverse, but usually involve road building, the clearing of native vegetation for agriculture, and urban growth. Excessive fragmentation of environments (including aquatic, estuarine, grassland, and forest) is also one of the leading causes of animal species extinction. In New Zealand, the use of fire by Maori and the clearing of native forests for agriculture by early European settlers contributed greatly to the extinction of many native bird species (Table 21.2). Most of the New Zealand landscape is now uninhabitable for many native animal species because 63% of the area is domesticated and 73% is significantly disturbed (Taylor & Smith 1997). As a result, threatened native species have continued to dwindle to a small number of relatively isolated populations that may only occasionally exchange individuals. Habitat heterogeneity and the spatial dispersion of habitats affect the viability of these metapopulations (Hanski 1997; McCullough 1996).

Table 21.2  Status of New Zealand's indigenous land, freshwater, and coastal bird species.

<table>
<thead>
<tr>
<th></th>
<th>Endemic</th>
<th>Non-endemic</th>
<th>All</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of 'original' species (living or subfossil remains)</td>
<td>93</td>
<td>38</td>
<td>131</td>
</tr>
<tr>
<td>Number of pre-European extinctions</td>
<td>34</td>
<td>0</td>
<td>34</td>
</tr>
<tr>
<td>Number of species remaining when Europeans settled in New Zealand</td>
<td>59</td>
<td>38</td>
<td>97</td>
</tr>
<tr>
<td>Number of extinctions after European settlement</td>
<td>9</td>
<td>0</td>
<td>9</td>
</tr>
<tr>
<td>Total number of land bird extinctions</td>
<td>43</td>
<td>0</td>
<td>43</td>
</tr>
<tr>
<td>Percentage of 'original' land bird species now extinct</td>
<td>46</td>
<td>0</td>
<td>46</td>
</tr>
<tr>
<td>Number of species surviving in 1994</td>
<td>50</td>
<td>38</td>
<td>88</td>
</tr>
<tr>
<td>Number of species threatened with extinction*</td>
<td>37</td>
<td>0</td>
<td>37</td>
</tr>
<tr>
<td>Percentage of remaining land bird species threatened with extinction</td>
<td>74</td>
<td>0</td>
<td>74</td>
</tr>
</tbody>
</table>

*Categories A, B, and C in Department of Conservation (1994)
Taylor and Smith (1997)

The transformation of natural landscapes into human land-use mosaics converts species with a formerly continuous spatial distribution into these fragmented metapopulations. This environmental fragmentation proceeds in several stages:

1. With an increasing loss and disintegration of habitat, the area of remaining fragments diminishes and the distance between habitat patches grows. This change in habitat spatial pattern has two main effects: local populations become smaller, and inter-patch dispersal gradually decreases. Both of these effects lower the probability of an average habitat patch being occupied by an animal population.
2. Populations in some habitat patches become extinct, by a combination of environmental disturbance and stochastic demographic processes. However, so long as animal dispersal between patches is frequent, immigrants from distant habitat patches may prevent local population extinctions.
3. The duration of habitat patch vacancy will increase as the distance between patches grows and the probability of dispersal between habitat patches decreases.
4. Some of the habitat patches become empty for a long period, but eventually are recolonised, whereas other patches remain empty.
If habitat fragmentation continues, the whole metapopulation may become extinct because inter-patch distances are too great to allow dispersal and reoccupation of empty patches.

If fragmentation stops, the animal metapopulation may reach a regional equilibrium in the number of occupied habitat patches, even though local population extinctions may continue at the scale of an individual patch.

Conservation biology and environmental management increasingly rely upon biogeography to determine how best to retain sufficient wildlife habitat while allowing sustainable use of natural resources (Bookhout 1994; Lidicker 1996). This is often based upon a quantitative spatial analysis of species’ habitat and human land use that draws upon principles from landscape ecology, a new science based on the patch-corridor-matrix paradigm (Forman 1995). Every habitat mosaic element is defined as a patch, corridor, or matrix that can be quantified by attributes such as area, shape, width, and connectivity (Turner 1989). The ability to quantify the spatial pattern of these landscape elements using air photos, satellite imagery, and geographic information systems is prerequisite to assessing the long-term viability of animal habitat and metapopulations. The merits of linking indigenous forest with habitat corridors to allow for interaction of native New Zealand forest birds was reviewed by Thomas (1991).

**Habitat fragmentation in New Zealand**

In New Zealand, more of the indigenous land cover has been converted to farmland than the world average (51% compared with 37%) (Atkinson & Cameron 1993; Taylor & Smith 1997). Indigenous forest habitats once covered 85% of New Zealand but are now largely confined to remote mountainous areas or dispersed in lowland fragments. Kauri and lowland podocarp forests were affected more by deforestation than beech forests. Habitat loss has occurred at three levels: removal (most lowland forests, wetlands, dune lands, and tussock grasslands have been converted to farmland); fragmentation (remnants of native forest are habitat islands surrounded by farmland); and ecological degradation (through pressures from introduced species, industry, pollution, recreation, and tourism).

To demonstrate the importance of this forest fragmentation for terrestrial animals in New Zealand, consider the habitat fragmentation of the North Island brown kiwi (*Apteryx australis mantelli*) in Northland. This region has among the highest number of threatened flora and fauna in New Zealand (Department of Conservation 1994), and a high rate of wildlife habitat loss (1% annually from 1978 to 1983; Anderson et al. 1984). Remnants of the indigenous podocarp/broadleaf forest are surrounded by an agricultural mosaic of pastures, exotic forests, farms, and towns. Some of these forest patches also support populations of North Island brown kiwi, but their long-term future is uncertain (Miller & Pierce 1995). Kiwi are flightless birds that probe the soil for food, so their habitat requirements are determined strongly by characteristics of the soil and vegetation at ground level. Population densities range from one bird per 2.5 ha to one per 55 ha.
Kiwi movements are also strongly affected by human modification of native forest in the landscape mosaic. For example, many North Island brown kiwi (>50%) in the Paerata Reserve, Northland, will travel up to 100 m across open pasture to forage in forest remnants, but few (<10%) will travel 300 m or more (Potter 1990) (Figure 21.6). The land-cover maps in Figure 21.7 illustrate two landscapes 20–30 km north-west of the Paerata Reserve with significantly different spatial patterns of kiwi habitat. These 32 x 32 km subscenes were derived from a 1978 Landsat Multispectral Scanner (MSS) satellite image. The Waipoua landscape is dominated by indigenous vegetation and natural physical processes. However, native vegetation in the Omapere landscape is fragmented into remnant patches widely dispersed in an agricultural mosaic. The diversity of land cover is slightly greater in the Waipoua landscape, which also has more patches with a greater total length of edges (Table 21.3).

Table 21.3  Spatial structure of native forest patches in 32 x 32 km landscapes near Waipoua Forest and Lake Omapere, Northland, calculated with FRAGSTATS v2.0.

<table>
<thead>
<tr>
<th>Landscape statistics</th>
<th>Waipoua</th>
<th>Omapere</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of patches</td>
<td>3733</td>
<td>2641</td>
</tr>
<tr>
<td>Total edge length (m)</td>
<td>4889120</td>
<td>3853120</td>
</tr>
<tr>
<td>Simpson diversity index</td>
<td>0.72</td>
<td>0.61</td>
</tr>
<tr>
<td>Simpson evenness index</td>
<td>0.82</td>
<td>0.71</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Native forest patch statistics</th>
<th>Waipoua</th>
<th>Omapere</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total area (ha)</td>
<td>22771.84</td>
<td>5151.36</td>
</tr>
<tr>
<td>% of the landscape</td>
<td>22.24</td>
<td>5.03</td>
</tr>
<tr>
<td>Number of patches</td>
<td>537</td>
<td>404</td>
</tr>
<tr>
<td>Mean patch size (ha)</td>
<td>42.41</td>
<td>12.75</td>
</tr>
<tr>
<td>Total core area (ha)</td>
<td>10163.2</td>
<td>11084.8</td>
</tr>
<tr>
<td>Number of core areas</td>
<td>178</td>
<td>70</td>
</tr>
<tr>
<td>Mean core area (ha)</td>
<td>18.93</td>
<td>2.74</td>
</tr>
<tr>
<td>Mean nearest-neighbor distance (m)</td>
<td>248.77</td>
<td>366.78</td>
</tr>
<tr>
<td>Edge density (m ha⁻¹)</td>
<td>15.27</td>
<td>6</td>
</tr>
</tbody>
</table>

McGarigal and Marks (1994)

Figure 21.6  Use of forest remnants by North Island brown kiwi in the Paerata Reserve, Northland. (Potter 1990).
The total area and spatial pattern of native forest is significantly different in the Waipoua and Omapere landscapes (black patches in Figure 21.7). These forest patches are high-quality kiwi habitat. Quantitative measures of their patch spatial structure in Table 21.3 assume that the effects of agriculture on kiwi foraging behaviour and breeding penetrate about 160 m into the forest patches, leaving an undisturbed core habitat area. The abundance of larger core forest patches in the Waipoua landscape suggests it has more undisturbed kiwi habitat. The area of a forest patch and its distance to the nearest forest patch will determine whether it will be used by kiwi (Figure 21.8). Kiwi require habitat patches of a sufficient size, but the forest patches must also be within a maximum travelling distance. (Kiwi will not cross large open pastures to search distant forest patches). The Omapere landscape has abundant small forest patches that are dispersed farther apart than those in the Waipoua landscape. Therefore, while agricultural landscapes like Omapere may have a few large forest patches, they are too far apart to support kiwi populations.

Figure 21.7  Land cover of 32 x 32 km landscapes near the Waipoua Forest and Lake Omapere, Northland classified from a 1978 Landsat MSS image.

Figure 21.8  Distance/area relationships of native forest patches in Waipoua (a) and Lake Omapere (b) landscapes.
In addition to diminishing native animal habitat, fragmentation of native vegetation also encourages the spread of exotic plants and animals. These species have been spread out of their natural range accidentally or intentionally by humans. Exotic species that successfully colonise indigenous ecosystems and cause significant environmental damage are considered biological invaders.

**Effects of animal invaders on the environment**

**Homogenisation of the biosphere**

Humans are the only species in the Earth's history to spread throughout every continent. In the process, our mobile society has also redistributed species at a pace that disrupts ecosystems, threatens human health, and strains economies. These biological invasions are now so widespread that they constitute a significant component of global environmental change (Drake et al. 1989; Lever 1994). Although biological invasions have always existed, the rate at which organisms are being introduced to areas outside their natural distribution is much greater than during any previous era. The phenomenon of alien invasion is both quantitatively and qualitatively different from any natural biogeographic process. Introduced species can affect both biotic and abiotic aspects of the environment. Evidence of these effects has been documented in ecosystem functioning, native species and genetic diversity, hydrology, geomorphology, and soil chemistry (Kirkpatrick 1994).

From a biogeographic perspective, a biological invader is a species that expands its range by exploiting humans as dispersal vectors. Successful invader species accomplish three successive steps: they become established; grow (i.e. find necessary resources, and survive competition and predation); and spread (i.e. reproduce). Despite the thousands of case studies of invaders, few general rules are available to predict whether a recently introduced species will successfully invade a natural environment. Vertebrates tend to be successful invaders because their resource requirements are flexible, and invasions are common in human-disturbed environments. Apart from these generalisations, accurate predictions about a specific animal invasion may not be possible because of the many stochastic variables (Williamson 1996). The present state of biological invasion theory is a probabilistic science, and predictions are akin to weather reports.

**Animal invaders in New Zealand**

The history of animal invasions in New Zealand began about 1000 years ago when Polynesians brought the kiore (Pacific rat) and a now-extinct race of dog, both predators of birds (Druett 1983). The second wave of animal invaders began about 230 years ago when European settlers introduced ship rats, Norway rats, house mice (*Mus musculus*), domestic cats, ferrets, stoats, and weasels. Europeans also successfully introduced more than 30 bird species, carrying with them foreign viruses and parasites that infected New Zealand birds. Introduced diseases were implicated in sudden population...
declines in the bellbird (Anthornis melanura) and the now-extinct laughing owl (Scoeloglauca albifacies) and piopio (Tymagra capensis). In total, at least 54 mammal species, 138 birds and approximately 2000 invertebrate species have been introduced to New Zealand, but 34 mammals (Table 21.4) and 43 bird species dominate the environment (Taylor & Smith 1997). Most of the land in New Zealand (63%) has been intentionally deforested or drained to accommodate humans, sheep, and cattle. The ecology of most remaining natural ecosystems has been disturbed or transformed by introduced browsers, grazers and predators that have defoliated or preyed upon the native flora and fauna (Parkes 1993; Parliamentary Commission for the Environment 1994). Introduced browsers (mainly possums) affect 1.3 million ha of New Zealand native forests (Taylor and Smith 1997).

Table 21.4 Mammal invaders that have significantly reduced New Zealand's biodiversity.

<table>
<thead>
<tr>
<th>Mammal species</th>
<th>Population estimate</th>
<th>Status</th>
</tr>
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<tbody>
<tr>
<td>Humans (Homo sapiens)</td>
<td>3.6 million (1996)</td>
<td>Population growth rate</td>
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<tr>
<td></td>
<td></td>
<td>1.5% per year (1990–95)</td>
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<tr>
<td>Sheep (Ovis aries)</td>
<td>48.8 million (1995)</td>
<td>Declining; maximum</td>
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<tr>
<td></td>
<td></td>
<td>70.3 million (1982)</td>
</tr>
<tr>
<td>Cattle (Bos taurus, B. indicus)</td>
<td>9.3 million (1995)</td>
<td>At record level</td>
</tr>
<tr>
<td></td>
<td>Feral: c. 2300</td>
<td>(1921)</td>
</tr>
<tr>
<td>Rabbits (Oryctolagus cuniculus)</td>
<td>Tens of millions (1995)</td>
<td>Occupied 56% (15 million ha) of land area</td>
</tr>
<tr>
<td></td>
<td>Feral: 300000–1 million</td>
<td>Feral occupy 3 million ha</td>
</tr>
<tr>
<td>Tahr (Hemitragus jemlahicus)</td>
<td>10000–14000 (1994)</td>
<td>Maximum 60000 (1970s)</td>
</tr>
<tr>
<td>Deer (Cervus spp. and Dama dama)</td>
<td>Domestic: 1.8 million (1995)</td>
<td>Domestic increasing</td>
</tr>
<tr>
<td></td>
<td>Feral: 250000 (1993)</td>
<td></td>
</tr>
<tr>
<td>Pigs (Sus scrofa)</td>
<td>Domestic: 431000 (1995)</td>
<td>Domestic maximum 771000 (1964)</td>
</tr>
<tr>
<td></td>
<td>Feral: &gt;300 000</td>
<td></td>
</tr>
<tr>
<td>Australian brush-tailed possum</td>
<td>70 million (1993)</td>
<td>Occupy &gt;90% of land area; increasing</td>
</tr>
<tr>
<td>(Trichosurus vulpecula)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mustelids</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stoats (Mustela erminea)</td>
<td>Possibly millions</td>
<td></td>
</tr>
<tr>
<td>Ferrets (M. putorius)</td>
<td>Possibly millions</td>
<td></td>
</tr>
<tr>
<td>Weasels (M. nivalis)</td>
<td>Possibly thousands</td>
<td></td>
</tr>
<tr>
<td>Rats</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ship rats (Rattus rattus)</td>
<td>Tens of millions</td>
<td></td>
</tr>
<tr>
<td>Norway rats (R. norvegicus)</td>
<td>Tens of millions</td>
<td></td>
</tr>
<tr>
<td>Pacific rats, kiore (R. exulans)</td>
<td>Tens of thousands</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Feral: insignificant</td>
<td></td>
</tr>
</tbody>
</table>

Taylor and Smith (1997)
Animal invaders have transformed the New Zealand environment in several fundamental ways.

- **Predation**—Native flora and fauna (especially birds, reptiles, frogs, and large invertebrates) have been driven to extinction by introduced mammalian predators (King 1984). Introduced wasps (*Vespula germanica* and *V. vulgaris*) prey upon native moths, butterflies, and native birds. Many native freshwater invertebrate and vertebrate species fall prey to introduced brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*).

- **Competition**—Aggressive introduced animal species like Australian magpies (*Gymnorhina tibicen*) and mynas (*Acridotheres tristis*) out-compete native species for resources. Introduced mallard ducks (*Anas platyrhynchos*) compete and occasionally breed with native grey ducks (*Anas superciliosa*).

- **Ecosystem functioning**—Introduced browsers (possums, deer, and goats) and grazers alter the plant species composition, ecosystem functioning, and ecological integrity of native forests. For example, digging by feral pigs (*Sus scrofa*) accelerates the leaching of calcium, phosphorous, zinc, copper and manganese, increases the concentration of nitrogen in the soil and surface runoff, and reduces surface invertebrates, plants, and organic litter. Pig densities in New Zealand are as high as 43 pigs km$^{-2}$ near Murchison, South Island.

Oceanic islands throughout the world are especially susceptible to animal invaders—the large number of extinct and threatened native New Zealand species is proof of their environmental impact.

**Summary**

This chapter examined animal habitat in natural and human-modified environments. An overview of animal diversity and composition was given before a discussion of the origins of New Zealand animal diversity. The spatial patterns of New Zealand bird diversity and composition were then outlined, followed by a general consideration of the geographic distribution and abundance of animal species. The chapter continued by discussing the environment as animal habitat, and emphasised that understanding animal habitat preferences requires both evolutionary and ecological perspectives. Ecological concepts such as niche, land transformation, and habitat fragmentation were then discussed, together with the importance of biogeographical approaches for conservation biology and environmental management. The issue of habitat fragmentation in New Zealand was discussed in some detail, since the loss of indigenous land cover is high by world standards and has had profound effects on the indigenous fauna. Not only has native animal habitat diminished, but the fragmentation of native vegetation has encouraged the spread of exotic plants and animals. These exotic species may cause significant environmental damage, and the final section of the chapter discussed the effects of animal invaders on the environment.
Further reading
Kuschel, G. (ed.) 1975, Biogeography and Ecology in New Zealand, Dr. W. Junk, the Hague.