

Uncertainty and predictability: the niches of migrants and nomads

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7.1 Introduction

Environmental conditions vary across space, fluctuate over time, and ultimately define the area that can be inhabited by an organism at a given time. The ecological requirements of individuals may also fluctuate seasonally, for instance with specific requirements for successful reproduction. Movements in response to the environment can be seen as a general strategy for dealing with such variability, but can take on a variety of forms. For instance, birds may undertake local movements at scales up to

a few kilometres over the course of a year to long-distance intercontinental migrations over distances exceeding 10^4 km. We will here contrast two patterns differing in the regularity of movements—*migration*, here defined as seasonally recurring and predictable movements of individuals along a geographic or environmental gradient, and *nomadism*, at seasonal time scales involving less regular movements in response to environmental fluctuations, and typically also characterized by between-year variability in the geographic location of reproductive events.

At a population level, migration and nomadism resemble, respectively, advective and diffusive processes, although both involve directed species- and state-dependent individual movement decisions, some of which are independent of the environment. Nevertheless, we can conceptualize the two patterns as being close to the end points of a continuum of advection–diffusion processes, with the diffusion coefficient being smaller (relative to the advection coefficient) for migrants than for nomads. Understanding the variability between species in movement decisions is therefore important, not only for understanding the diversity of movement patterns, but for predicting the patterns and consequences of population spread.

Understanding movement decisions requires insight into ecological niches and their dynamics. While acknowledging the role of predator avoidance and competition as important for the evolution and maintenance of many migratory systems (Fryxell and Sinclair 1988b), we will follow the Grinnellian/Whittakerian tradition of focusing on environmental requirements and resource variability. We argue that much of the diversity observed in seasonal movement patterns by migrants and nomads in many taxa can be understood and predicted by spatiotemporal variation in the resources needed for survival and reproduction, as modulated (and sometimes driven) by density-dependence within and across species. We do this by discussing spatial and temporal niche dimensions and their functional significance for animal movements, within a context of life history evolution, annual cycle organization and the proximate control of movement decisions. Many of our examples will be for birds, since this class of animals is particularly well-studied and illustrates well the diversity of movement patterns, many of which are intermediate between migration and nomadism, and many of which remain enigmatic after centuries of research interest.

7.2 Seasonality, environments and the evolution of migration and nomadism

The factors governing the evolution of migration are not completely understood (Chapter 2). Early work on the evolution of migration and partial

migration, where only a fraction of a population migrates, emphasized the importance of environmental stochasticity and competition (e.g. Cohen 1967; Alerstam and Enckell 1979). Even though later studies have argued that environmental stochasticity is not necessary in order to generate partial migration (Kaitala *et al.* 1993) and instead emphasized the role of frequency- and density-dependent processes (Lundberg 1987; Kaitala *et al.* 1993; Taylor and Norris 2007), it is generally believed that migration is more likely to evolve in species that are dependent on seasonal, largely predictable, and heavily fluctuating food resources (e.g. Fryxell *et al.* 2004; Boyle and Conway 2007; Chapter 3). For the large-scale bird migration systems of the northern hemisphere, there has been much focus on whether seasonal migration originated in birds breeding in northern habitats (shifting wintering areas southwards due to climatic cooling) or southern habitats (taking advantage of emerging breeding sites further north). However, this debate has largely failed explicitly to incorporate the fossil record and fluctuations in climatic seasonality over geological time scales (Louchart 2008), and the repeated occurrence and loss of migratory behaviour within taxa at the level of modern bird families (e.g. Helbig 2003). For instance, sedentary oceanic species of duck such as the Hawaiian Duck (*Anas wyvilliana*) and Laysan Duck (*Anas laysanensis*) have presumably all derived from widespread migratory Palearctic waterfowl species. More surprisingly, migratory behaviour can re-emerge from sedentary ancestors. The ‘threshold’ model of expression of migratory behaviour in partial migrants (Pulido 2007) suggests that a latent tendency toward migratory behaviour can persist in avian gene pools, which opens the possibility of evolving towards obligate migration patterns if the environment changes or the species disperses into more seasonal habitat (Salewski and Bruderer 2007; Chapter 2).

Resource dynamics vary between environments, and the relationship between organisms and their resources is not consistent across taxa. An exciting hypothesis is that habitat or resource associations might present evolutionary precursors for long-distance migration. Levey and Stiles (1992) showed that Neotropical–Nearctic migration tended to develop within families of frugivorous or

nectarivorous birds of edge, canopy or open habitats—i.e. performing altitudinal or local movements within the tropics—that are therefore predisposed to tracking variable resources across space and time. This was largely confirmed in a phylogenetic comparative analysis of Austral migration in the Neotropics (Chesser and Levey 1998).

The evolutionary origins of nomadism are even less known. Nomadism is characterized by a lack of the regularity in spatiotemporal movements that we normally ascribe to migration, and this has been linked to the characteristics and resource dynamics of ecosystems where it is commonly found. At any given site, nomadic species may appear in large numbers, then not be seen for many years. The typical environment where we find nomads is a low-productivity region where the resources are highly variable and unpredictable in both time and space (Davies 1984; Dean 2004). Deserts and semi-deserts are the most frequently cited examples of such environments. Productivity in these ecosystems is clearly affected by rainfall, but it is much less clear which components of abiotic and biotic environmental variability are most important for promoting a nomadic life-style (Wiens 1991; Dean 2004; Newton 2008). Also, not all species in these environments are nomadic and it has been debated to what extent nomadism is best predicted by diet or other factors (Allen and Saunders 2002; Woinarski 2006; Allen and Saunders 2006).

Nomadism is not restricted to desert areas but is also found in raptors and owls tracking rodent abundance in northern Europe, North America and along the Siberian tundra. Even though the climate is clearly seasonal at these latitudes, the resource environment is unpredictable. Many rodent populations display quasi-cycles but the synchrony levels off with distance, and there is spatiotemporal variation in rodent density that has favoured nomadic behaviour in rodent predators, rather than regular migration or a sedentary lifestyle. Another interesting dynamic resource is tree-fruit crops in boreal forests, whose densities vary greatly from year to year, with peak years practically always followed by years of poor production. These resources are exploited by seed- and/or fruit-eating birds often classified as irruptive migrants. When resources are abundant they can be resident but in

some years they undertake long-distance movement far beyond their normal range. The minimum distance they have to move is set by the spatial correlation in resources (Koenig and Knops 1998). In terms of regularity, irruptive migrants fall somewhere between regular migrants and nomads, but are closer to the latter.

Since nomadism is not as clearly defined as migration, the classification of a species as nomadic or not could simply reflect the amount of knowledge we have on movement patterns. Frequently, a lack of observed regularity for a given species has resulted in movements being classified as nomadic. However, a closer look at the movements of eastern Australian landbird species, using a combination of large-scale survey databases, suggested a number of distinct movement patterns, many of which can be seen as a nomadic movements superimposed on more regular north–south movements (Griffioen and Clarke 2002). Furthermore, partial migration may in fact be quite widespread among Australian landbirds (Chan 2001), resulting in a mixture of migratory and non-migratory populations. Variability in migratory and nomadic movements between individuals in a population, and between years for an individual may further obscure the distinction between migration and nomadism (Mueller and Fagan 2008).

To sum up, neither regular migration nor nomadic movements seem to be strongly evolutionarily constrained, and movement strategies are variably expressed both across and within ecosystems. Many organisms show movement patterns that challenge any attempt to classify species as being strictly either migrants or nomads (Cheke and Tratalos 2007), and there exists a continuum of movement strategies that cannot be easily categorized. A major challenge, therefore, is to understand how variability in contemporary ecological niche characteristics can predict the diversity of large-scale movement patterns, given contrasting life histories.

7.3 Annual cycles and the control of movement decisions

From the perspective of life history evolution, movement is not an isolated phenomenon, but has evolved in concert with the other biological events

in the annual cycle. Therefore, it is not surprising that we find differences between regular migrants and nomads not only in the mode of large-scale movement, but also in many other respects. For long-distance migration to work, individuals need adaptive linkage of endogenous rhythms to predictable environmental states (Newton 2008). Nomadism, on the other hand, can be seen as an adaptation to variability, and the lack of predictable changes in resource abundance demands more spatial and temporal flexibility in the organization of the annual cycle. Hence, movement decisions also need to be less rigidly controlled by the endogenous mechanisms ultimately controlling the annual cycle. This decoupling increases the responsiveness of nomads to environmental cues, both in terms of movement trajectories (Nathan *et al.* 2008) and the possibility of environmental input triggering transitions between life history stages such as movement and breeding phases (Dawson 2008). Hence, one can also expect larger variability between individuals and populations with respect to the life history stages that are expressed at any time. The less rigid endogenous control of nomads also implies that different states can more easily mature and/or wane simultaneously, and more easily be expressed at the same time (Wingfield 2008). Conversely, migrants may be more time-constrained due to prolonged migratory periods and the need to complete associated life history stages, such as pre-migratory fattening and moult in birds (Chapter 4).

It seems reasonable to argue that the reduced flexibility in annual cycle organization found in migrants compared with nomads might render them more sensitive to temporal resource dynamics, and thereby also more prone to cascading seasonal cycle effects. Understanding the balance between ultimate mechanisms controlling annual cycles and the proximate environmental control of movement decisions might therefore be important for understanding the evolution of large-scale movement patterns such as nomadism and migration.

This balance can sometimes be addressed in terms of trade-offs. All mobile organisms face the trade-off between staying or leaving (Andersson 1980; Dean *et al.* 2009), and the difference between migrants and nomads is mainly in the extent to which annual cycles are influenced by environmental

input. However, even for the 'evolutionarily fixed' annual cycle of many migratory species, movements within the non-breeding area can greatly affect survival. Resident species also face such a trade-off; they may for instance need to disperse in order to escape sudden inhospitable conditions. Post-reproductive and juvenile dispersal is a common feature of many animals, and frequently combines with migratory or nomadic movements, yet the two are rarely considered jointly (see, e.g., Winkler 2005). Nevertheless, interesting new perspectives are likely to arise from considering variability in movement strategies both in terms of factors promoting dispersal on the one hand and factors shaping the dispersal event on the other hand.

7.4 Habitat selection and niche dimensions

Migratory and nomadic movements can be considered in terms of habitat selection across space and time. Much focus has been on habitat preferences *per se* and the link with food resources, such as the need to move in order to track specific food resources or disperse in search of habitat of sufficient quality to ensure survival or reproduction. However, many species are generalists, so the link between habitat and food resources may be rather weak. Furthermore, food resources are only one of several habitat requirements, and movements will be constrained by landscape-specific patterns and individual requirements.

Even for species having a rather specialized diet during the reproductive phase, it is quite common to switch to a more generalist diet during migration. Most passerine birds breeding at northern and temperate latitudes are mainly insectivorous during the breeding season, but rather omnivorous for the rest of the annual cycle. Some species, such as migratory *Sylvia* warblers, switch to a diet consisting mainly of fruits prior to and during migration (Chapter 5). Interestingly, non-migratory *Sylvia* warblers are omnivorous or insectivorous year-round in the Mediterranean region (Jordano 1987). The utilization of fruits is morphologically constrained in these species, but it is also a rather predictable and stable food source in seasonal

environments. Many nomadic or invasive species also rely on widely available food resources, such as seeds or fruit. On the other hand, fluctuating abundances of rodents seem to be the primary driver for the nomadic movements of many specialist predators such as boreal and Arctic owls and raptors. The diversity of alternative food sources may be important for determining movement strategies in these species; for instance, a north–south gradient from nomadism through partial migration to residency was found for European populations of Tengmalm’s Owl (*Aegolius funereus*; Korpimäki 1986).

Hence, while fluctuating food abundance seems important for triggering movement in the first place, diet may or may not constrain the actual migratory or nomadic movements. There are certainly cases where species track food resources closely, such as birds following swarms of army ants in order to feed on flushed insect prey. But, typically, migratory movements and the exploratory or anticipatory movements of nomads force organisms into new kinds of habitat where food resources are likely to be different. An important issue is therefore to what extent animals prefer and search for certain habitat types when they are on the move. In other words, to what extent do migratory and nomadic animals occupy similar niches throughout the year? Much early work on large-scale bird migration systems hypothesized that species were adapted to certain habitat types and kept these habitat associations year-round, although increased competition with residents on wintering grounds might force migrants to shift or broaden their niche, e.g., by utilizing alternative habitats. Empirical results do not, however, clearly support such generalizations; although many species in a broad sense occupy similar niches throughout the year (Salewski and Jones 2006), microhabitat associations may be species-specific or even state-specific. As an example of the latter, American Redstarts (*Setophaga ruticilla*) breed in moist deciduous forests with abundant shrubs, but survival and breeding output is affected by the quality of the wintering habitat. Competition on Jamaican wintering grounds leads to habitat segregation, with dominant individuals (adult males) occupying high-quality mangrove and moist forest and less dominant individuals (females) ending up in drier

scrub habitats of lower quality (Studds and Marra 2005). In general the idea of niche-following versus niche-switching is an unexplored frontier in understanding the diversity of migratory systems (Nakazawa *et al.* 2004).

While there has been some interest in linking the diversity of movement types to variability in habitat characteristics, predictive success has been limited. For instance, while nomadic movements in birds are frequently linked to desert habitats, there is an interesting difference between deserts in the northern and southern hemispheres. In the former, migratory bird species are more common than year-round nomadic species, whereas the opposite pattern is found in the latter (Dean 2004). In Australia almost half of the desert bird species are nomadic and the general explanation is the lower and more erratic primary and secondary production in the Australian deserts compared with, for example, North American deserts, where nomadism is rare (Wiens 1991). Dean (2004) noted a general trend for nomadic species to occur in more open habitats, but in general it remains an open question what aspects of a habitat are important.

Our focus in the remainder of the chapter will therefore be on general niche dimensions common to the diverse habitats and regions where we find migrants and nomads. Habitat structure and resource variability in space and time are such dimensions. A central feature of both migratory and nomadic lifestyles is the movement of individuals across landscapes and the need for integrating information en route in order to determine movement paths, search out suitable locations for foraging or breeding and otherwise allocate time or resources (Chapter 6). Such integration is constrained by the movement modes of organisms; whereas many migratory species follow a comparatively fixed schedule of alternating movement and foraging/resting, nomads typically have a much more flexible schedule. Conversely, the distribution of habitats and resources across a landscape determines the feasibility of various movement modes. In other words, we may need to bring in elements of landscape ecology.

An explicit consideration of landscape heterogeneity brings in complexity, but also interesting new perspectives. Some overarching notions of landscape

ecology are always useful to keep in mind, such as the scale dependency of ecological patterns and processes, and the distinction between the scale of observation and biologically relevant scales. It can for instance be helpful to recognize that the definition of migration is actually scale dependent; even a perfectly regular migrant with strong site fidelity might show random movement patterns at short time scales, and some migratory birds, such as the White Stork (*Ciconia ciconia*) and swifts (Aves:Apodidae), may be largely nomadic on the wintering grounds. More generally, nomadic behaviour is constrained by seasonal fluctuations in home ranges, and these vary across species as well as habitats and food resources. During migration, scale dependent patterns of habitat preferences may be evident. For instance, Deppe and Rotenberry (2008) found species-specific preferences for broad vegetation types at a Yucatan stopover site, as well as a response to vegetation structure within these vegetation types.

Other general issues of relevance for animals searching for resources are the hierarchical nature of patchiness and the tendency for characteristic temporal scales of biotic variability to increase with their spatial scales. Hence, free-ranging predators may search for high-density prey patches in a hierarchical manner—a classical example being pelagic seabirds seeking out highly productive areas such as frontal zones, where large concentrations of forage fish can be found, and within this area using a range of cues, such as the presence of other seabirds, for locating individual fish schools within which they hunt for individual fish. Variability in abiotic structuring variables such as temperature often show such ‘reddened’ spectra (variability increasing with increasing observation scale). On the other hand, when considering their functional significance, spatial and temporal scales may sometimes need to be decoupled. Whereas temperatures typically vary smoothly (and hence somewhat predictably) both over time and space, rainfall is rather unpredictable in arid regions of the world, but may induce spatially predictable patterns in resource abundance. A high spatial correlation may for instance occur if a sudden rainfall moves quickly over a large area, thereby synchronizing the growth conditions. The synchrony may soon break down

depending on local characteristics. Nomads that are moving around in the landscape may either decrease or reinforce the patchiness of resources depending on how easy it is for them to spot the good patches.

Finally, we note that the functional significance of niche dimensions should be considered at the appropriate level of response; while one or a few food resources may be integrating the environment at scales appropriate for understanding the movements of a single species, landscape patterns may in fact be more successful in integrating the environment at scales relevant for explaining community composition in space and time (Pavey and Nano 2009). As a first approximation, we will, however, consider resource dynamics at the level most proximate to animal movement. In the following two sections we will discuss the functional significance of temporal dynamics and spatial heterogeneity of resources for migratory and nomadic animals.

7.5 Temporal dynamics of resources

7.5.1 Seasonality

Most resources are dynamic, with local resource abundance fluctuating over time. These fluctuations occur across different time scales and the magnitude of the fluctuations may vary with time scale. For many organisms, the amount of food available is rather predictable from one day to the next. For others, there can be enormous variation and little predictability even at very small time scales. Such lack of predictability can be due to infrequent pulses of food resources. For instance, the Giant Red Velvet Mite (*Dinothrombium pandorae*) in the Mojave Desert of North America lives in burrows underground without feeding, sometimes for years on end (Tevis and Newell 1962). After very unpredictable heavy rains, swarms of flying ants and termites appear, and the mites emerge, to hurriedly scurry over the desert floor eating their fill during a few hours of frantic activity. During the brief resource pulse the mites mate; once the pulse wanes, they return to their burrow, to wait again for the next chance at feeding and reproduction. In the study cited above, only ten such emergences occurred in a 4-year period.

In many cases, large-scale movements can be found when the resources in a landscape vary on

such a long time scale that animals that cannot simply hunker down locally (like the Giant Red Velvet Mite) need to travel far beyond their home ranges to survive and/or reproduce. Within a year there may be seasonal variation in resource abundance driven by periodic climate forcing, a phenomenon often exemplified by the arctic, boreal and temperate areas of the Northern Hemisphere, where latitude is assumed to reflect differences between summer and winter productivity (Dingle *et al.* 2000). Almost all of the variance in the proportion of migratory birds is explained by latitude in both North America and

Europe (Newton and Dale 1996a,b) and a high proportion (78%) is explained in butterflies along the Australian east coast (Dingle *et al.* 2000). The seasonality in temperate areas is mainly driven by changes in temperature (Fig. 7.1(a),(c)), whereas in Australia, being the driest continent, seasonality (if present) is often, but not exclusively, due to variation in precipitation. In many tropical regions, seasonality is pronounced in precipitation, leading to regular altitudinal and latitudinal migrations, e.g. in frugivorous birds in the Neotropics, and ungulates in the savannas of east Africa (Holdo *et al.* 2009b). The

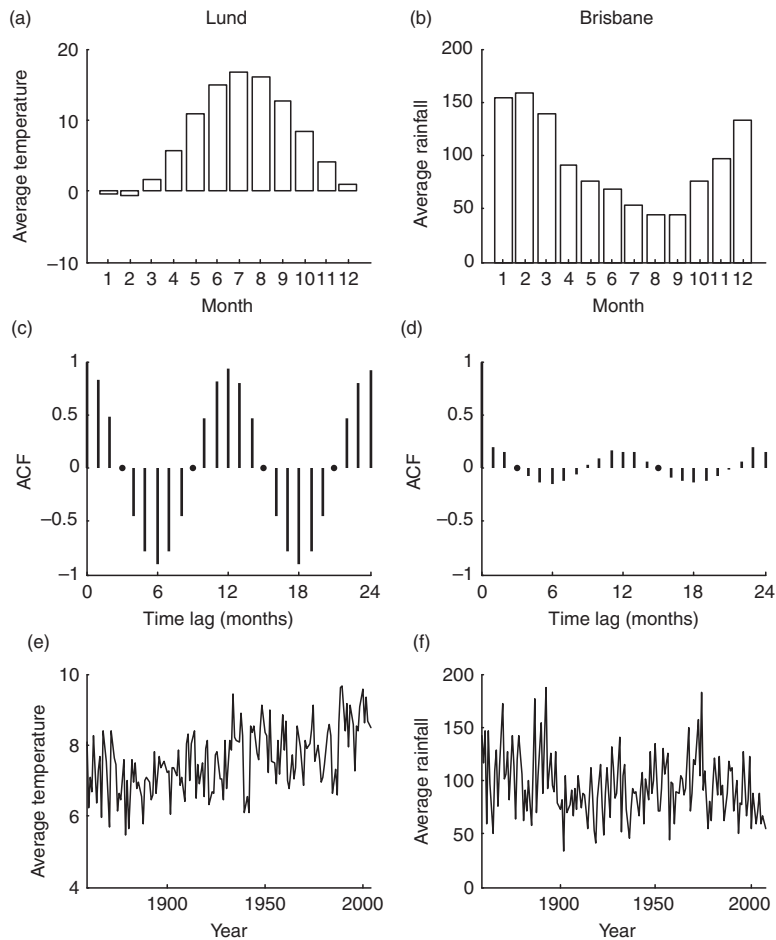


Figure 7.1 Examples of seasonality in temperature (a, c, e) and rainfall (b, d, f). The upper top panels show the average temperature for each month (1 = January, 2 = February...) in Lund (55°43'N, 13°09'E) and the average rainfall in Brisbane (27°29'S, 153°02'E). The mid panels show the autocorrelation function (ACF) and in the bottom panels the time series of average annual temperature and rainfall are plotted. The data from Lund are from 1859 to 2004 (SMHI) and the Brisbane data were collected at the Brisbane Regional Office during 1859–2007 (Rainman software; Clewett *et al.* 2003).

seasonal pattern of rainfall may be obvious in a given year but due to inter-annual variation it is less predictable than are the seasonal shifts in temperature in temperate Europe (Fig. 7.1). The striking seasonality in the temperate areas of the Northern Hemisphere is very predictable, in the sense that winter is always followed by spring. The regularity of such seasonal variation is most probably a necessity for the successful adjustment of morphology, physiology and behaviour needed for an individual to implement a long-distance migratory annual life cycle. However, the exact timing of events, such as the last frost night, bud burst, etc., varies between years, so many details of migration can vary due to behavioural and other modes of plasticity.

In all oceans, vast basin-wide fronts can separate low-productivity sub-tropical gyres and high-productivity temperate gyres (Polovina *et al.* 2001). These fronts can provide transient bands of high resources for mobile predators such as Albacore Tuna (*Thunnus alalunga*) and Loggerhead Turtle (*Caretta caretta*). The positions of these fronts can vary seasonally by up to 1000 km, and also vary more erratically between years due to factors such as El Niño events. Movements of these consumers are thus comparable to nomadic movements in terrestrial environments. Other marine taxa have very regular seasonal migrations; e.g., grey whales (*Eschrichtius robustus*) in the eastern Pacific and high-latitude dolphins (Mammalia:Delphinidae). *En passant*, we note that the term ‘migration’ is sometimes used by aquatic ecologists to refer to diel movements of individuals (e.g., zooplankton in the water column), or to historical dispersal events in biogeography. Although these certainly can represent long-distance movements, their relevance is mainly at either very short or very long time scales, and are different (particularly the latter) from our focus here.

7.5.2 Stochasticity

Environmental stochasticity is random variation that affects the whole or parts of the population in a similar way (Lande *et al.* 2003), and adds a stochastic element to the regularity of seasonal environments (Fig. 7.1(e),(f)). On an inter-annual time scale, resource dynamics are stochastic, for example in the sense that the onset and length of the growing season varies unpredictably between years, as does

productivity and the total amount of resources available. An example of stochastic seasonality is given by the occurrence of insect larvae, vital food resources for many bird nestlings (e.g. Visser *et al.* 2006). There is strong seasonality based on the annually recurrent period every spring, set by the phenology of plants, when resource availability for growth and reproduction is optimal for herbivorous insects. However, since plant phenology varies from year to year depending on environmental conditions, the timing of the optimal period for the herbivore also varies annually (e.g. Asch and Visser 2007). Hence, individual insect predators trying to optimize the timing of migration returning from the wintering grounds have to make this decision in the face of uncertainty. More generally, individuals may have to rely on environmental cues to trigger the transition from one life history stage to another, as well as to adjust to local conditions (Ramenofsky and Wingfield 2007).

In contrast to the strongly seasonal environments of temperate areas, many arid regions are characterized by unpredictable and highly variable rainfall with low or no correlation between monthly and even daily rainfall (Box 7.1, Figs 7.2–7.4). All organisms inhabiting this environment have to adapt to the tension between drought and flood, boom and bust. In stochastic and unpredictable environments anticipatory movement is not feasible and organisms benefit from any adaptations that make it possible to respond rapidly to changing conditions, and for mobile organisms, to glean information about long-distance rainfall events (Shine and Brown 2008). Some taxa may be able to detect spatially patchy pulses of production over long distances, for instance by sensing the position of rain clouds. One advantage of group living is that if a few individuals are able to pick up appropriate cues, other individuals can exploit this information. Holdo *et al.* (2009b) have argued that a combination of both effects may underlie observed population fluctuations of migratory wildebeest (*Connochaetes taurinus*) in the Serengeti.

Since a lack of temporal (and spatial, see below) predictability of resources is unlikely to favour the evolution of migration (see Chapter 2) many organisms have instead adopted a nomadic life style in unpredictable and fluctuating environments

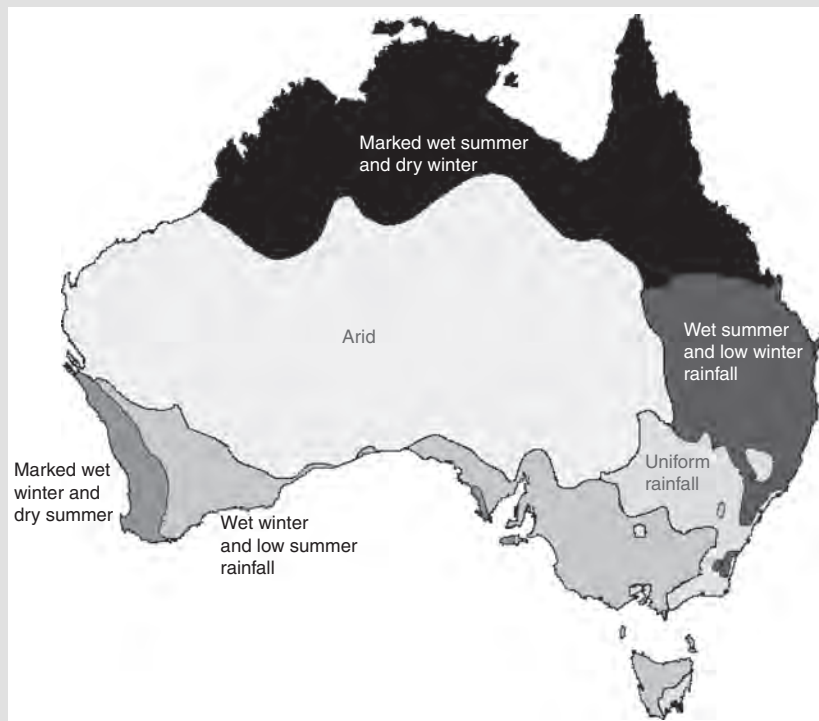
Box 7.1. Exploring resource dynamics: Australian rainfall and bird movements

In order to understand the evolution and maintenance of large-scale movement patterns it can be helpful to explore the spatiotemporal dynamics of the resources making up the niche of a species. In particular, it is important to understand how predictability, variability and other statistical properties vary across space and time. Long time series of data on resource dynamics are rarely available and it is often difficult to find good enough surrogates (see Boyle and Conway 2007), particularly at the large geographic scales required for comparative analyses of movement patterns. However, in arid regions rainfall is a driver of plant growth, which also affects insect density and water availability in general. Therefore we use rainfall as a proxy in an exploratory exposition of temporal dynamics and spatial variability of resources important for understanding the diversity of movement patterns in Australian landbirds.

Australia is the second driest continent on Earth, only surpassed by Antarctica. Most of the interior is extremely arid, with more or less seasonal rainfall along the coasts, most notably along the easternmost (east of the Great Dividing Range) and northernmost parts of the continent (Fig. 7.2). Such seasonal predictability is reflected in positive (although weak) autocorrelation at time scales of a few months and a characteristic sign-switching pattern in the autocorrelation function (Fig. 7.1(d)).

Alternatively, the issue can be explored in terms of variance spectra, quantifying how the variance of the time series varies with observation scale. Wavelet analysis (e.g., Percival and Walden 2000) has become a popular tool for such analyses, not least since it allows a time series to be expressed as a function of both time and scale (Fig. 7.3). The seasonality in rainfall along the eastern and northern coasts of Australia can be seen as

(a)

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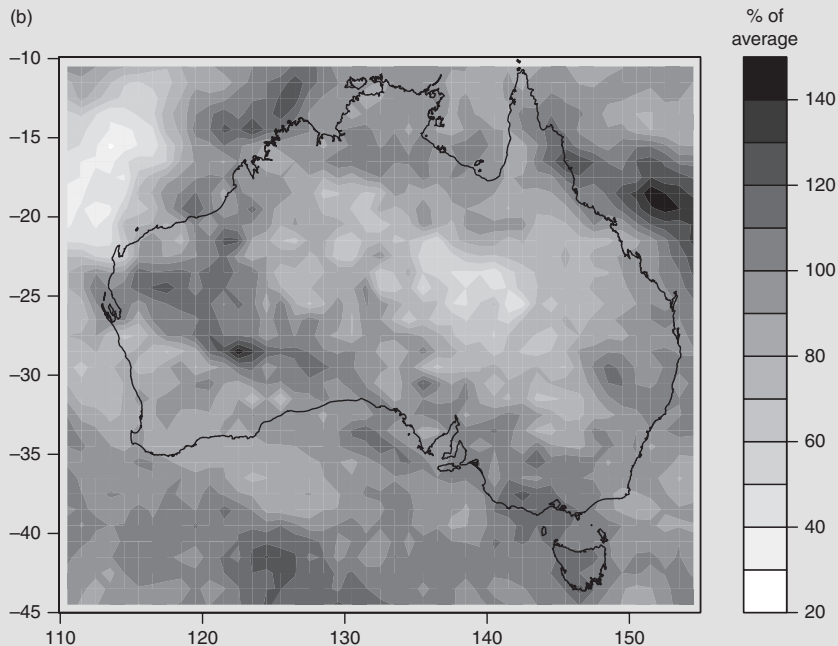
Box 7.1 (continued)

Figure 7.2 (a) Climatic zones of Australia, defined by seasonal rainfall patterns (redrawn from a map from the Bureau of Meteorology, Australian Government; <http://www.bom.gov.au>). (b) Example of spatial heterogeneity in rainfall that is assumed to produce spatial variability in vegetation growth and resource abundance: showing rainfall in February 2004–January 2005, relative to the yearly average (data as in Fig. 7.4), by latitude and longitude.

a peak in the wavelet variance spectra at approximately semi-annual time scales, whereas rainfall in the arid interior appears completely random and unpredictable (Fig. 7.3(a)). A lack of predictability does not, however, mean that there is no structure (Fig. 7.3(b)); clusters of rainfall events are still evident at observation scales ranging from weeks to months. While periods of high rainfall are most clearly distinguishable at temporal scales of months in the more seasonal environments, temporal contrast in conditions in the arid environment is due to sudden rainfall events (Fig. 7.3(c)). Hence, no overall ‘reward’ is expected for a periodic life cycle temporally matching the rainfall pattern, which contrasts with the potential costs of temporal mismatch in seasonal environments.

Movement patterns of birds within the Australian continent are not well known, but a combined analysis of large-scale survey databases suggested migratory or nomadic movements for up to 36% of 407 eastern Australian landbird species, and a number of distinct movement patterns (Griffioen and Clarke 2002). Close to

40% of these species were classified as performing local or unclear movements. More regular large-scale movement patterns mainly occurred within or between regions of seasonal and relatively abundant rainfall—i.e. between Tasmania and southeast Australia, and along the sub-tropical eastern coast and towards the seasonal northern coastal and inland areas (Fig. 7.2). Only 20% of the non-sedentary species showed movement toward the drier and less seasonal inland areas. In western Australia, migration is observed in a number of species breeding in the south-western parts of the continent, where rainfall is seasonal. Recent changes in the timing of migration appear to be associated with changes in precipitation rather than with changes in temperature (Chambers 2008).

It is interesting to note that the infrequent rainfalls of interior Australia not only contribute to high temporal variability (Fig. 7.4(b)). Apart from some higher-altitude areas, the temporal predictability in rainfall is also lower in the interior than along the east coast and in northern Australia, both at a day-to-day scale (Fig. 7.4(c))

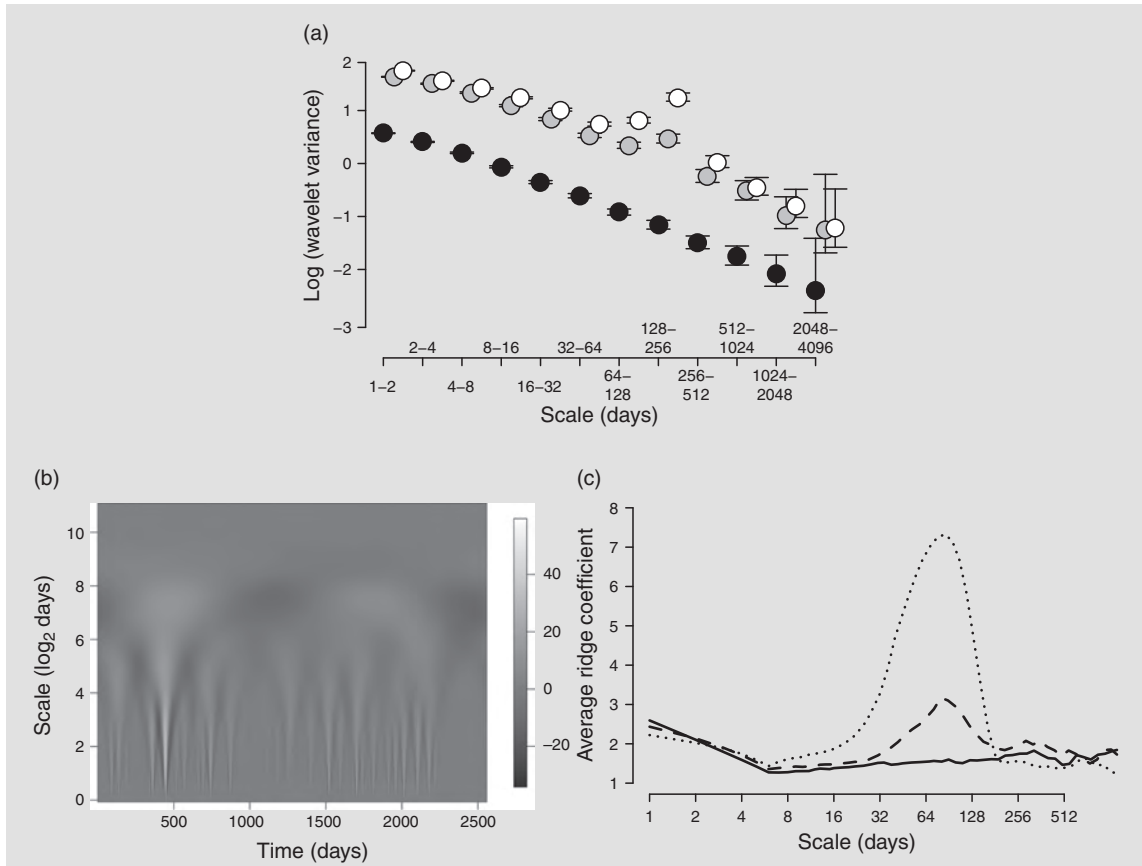


Figure 7.3 Time-scale decomposition of Australian temporal rainfall patterns using wavelet analysis. Data are daily precipitation values from a desert site (Marree; 27°29'S, 138°03'E; 1885–1994; black circles/solid line), a humid sub-tropical site (Brisbane; 27°29'S, 153°02'E; 1887–1994; grey circles/dashed line) and a tropical wet-dry site (Darwin; 12°25'S, 130°52'E; 1872–1996; open circles/dotted line). (a) Estimated wavelet variance based on the maximum overlap discrete wavelet transform, along with 95% C.I. The graphs show how the variance of the time series is partitioned into intervals of observation scale. At all sites, short-term variability dominates, but whereas the linear decrease with increasing scale (on a log–log scale) observed for the desert site indicates a pattern of white noise, the peaks in wavelet variance at semi-annual time scales show a superimposed pattern of seasonality, being stronger for the tropical compared with the sub-tropical site. (b) Time-scale representation of wavelet coefficients from a continuous wavelet transform ('Mexican hat' wavelet) of data from Marree, 1988–94. A lighter colour indicates larger coefficients, i.e. more precipitation. Note how the representation of the time series changes with observation scale; at small scales the detailed day-to-day variability is evident, whereas at large scales we only see coarse fluctuations. (c) Averages of wavelet coefficients along the maximum ridges (lightly coloured in Fig. 7.3(b)), as a function of observation scale. Since the time series here were standardized to zero mean and unit variance before applying the continuous wavelet transform, the three lines indicate how sites differ with respect to the scale dependence of the temporal contrast in rainfall (i.e. the difference between high rainfall events and 'average' conditions).

relevant to en route movement decisions, and at a time scale of weeks (Fig. 7.4(d)), relevant to the timing of life history events such as breeding, migration, staging and wintering. A general north–south gradient in predictability can also be seen for much of the continent, corresponding to the overall north–south axis of

movement observed for many species. On the other hand, there is overall weak positive spatial autocorrelation in rainfall over much of the interior, southern and western parts of the continent (Fig. 7.4(e)). This is in contrast to the situation along the east coast (no overall autocorrelation) and in the north (autocorrelation due to

continues

Box 7.1 (continued)

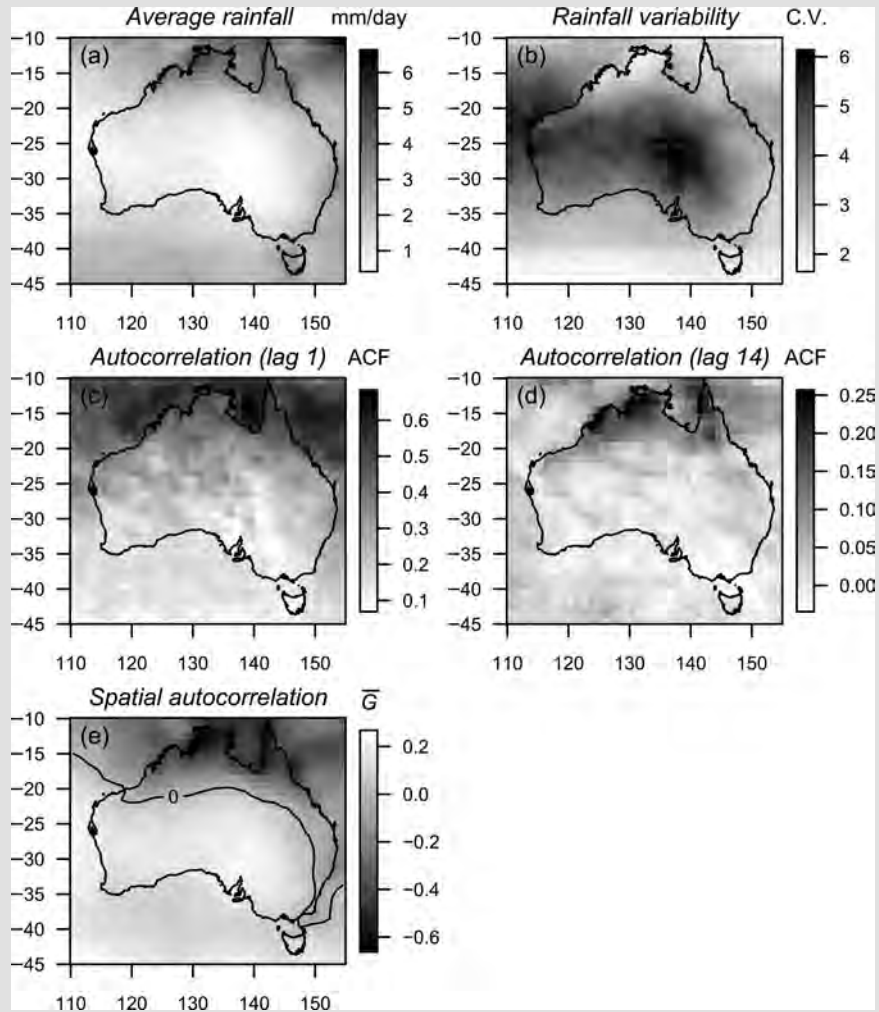


Figure 7.4 Some simple attributes of continental-wide rainfall patterns, potentially useful for understanding niche dynamics, shown by latitude and longitude. (a) Average rainfall, (b) overall temporal variability (coefficient of variation), (c–d) temporal predictability (autocorrelation function at lags 1 and 14 days), (e) time-averaged spatial predictability (local spatial autocorrelation) as estimated by the local G statistic for local rainfall anomalies (deviation from the temporal mean, calculated separately for each cell). The magnitude of the G statistic determines the strength of autocorrelation, and the sign indicates whether autocorrelation is mainly due to spatial clustering of low precipitation values (negative G) or high values (positive G). The analysis was based on GPCP 1-degree gridded daily precipitation data for the period 1997–2007 (<http://www.gewex.org/gpcp.html>).

spatial clustering of droughts), and could facilitate local movements and nomadic lifestyles. Most of interior Australia is grassland and bushland, and rainfall from moving weather systems could synchronize vegetation

productivity at large spatial scales, thereby increasing landscape connectivity and enhancing the detectability and use of high-productive patches for wide-ranging species.

(Newton 2008). A classic example of nomadism is the life history of the Banded Stilt (*Cladorhynchus leucocephalus*), a wader bird that survives along the Australian coast but only breeds when the drought breaks and the rain pours down in the inland desert lakes thousands of kilometres away from the coast (Robinson and Minton 1989). The rain transforms the dry and hostile salt pan lakes into a haven for the banded stilts and large numbers of brine shrimps (*Parartemia* spp.) are produced. The high concentration of brine shrimps provides the resources needed for their energetically demanding breeding, similar to the insect peak crucial for successful reproduction of insectivorous birds in temperate areas (Visser *et al.* 2006). In Australia, nectarivorous birds are also known to undertake regional-scale movements in response to variation in the distribution of flowering plants (e.g. Keast 1968). It has been suggested that, in general, nectar (and probably fruit) is a far more dynamic resource than terrestrial invertebrates and hence demands a more mobile lifestyle for its consumers (Woinarsky 2006). An important challenge is to understand how organisms glean appropriate cues from the environment about the spatial position of patchy and fleeting resources.

7.6 Spatial heterogeneity of resources

Resources are not evenly distributed in space and spatial heterogeneity at the landscape level makes it possible for individuals to compensate for temporal variability by adaptive movement towards transiently rich patches (e.g. Fryxell *et al.* 2005). It is important to make a distinction between spatial variance, i.e. the frequency distribution of resource density, and spatial pattern per se, i.e. the spatial distribution of resources. These are different aspects of a heterogeneous environment, and their temporal dynamics may differ (Klaassen and Nolet 2008). If there is high spatial variance there exists a potential for adaptive movement to take advantage of local food abundance (e.g. Fryxell *et al.* 2004, 2005). The spatial pattern, on the other hand, affects landscape connectivity and the spatial scale of resource heterogeneity, and therefore the possibility to exploit the resources in the first place. If patches are too small or too hard to reach, they may be unusable by a forager of a given body size.

Similar to the temporal dimension of resource dynamics, there are fundamental differences between the spatial properties of environments where we typically find migrants and nomads. In the temperate areas where there is strong seasonal variation in temperature there may also be a strong spatial correlation in some environmental conditions. For instance, a snapshot of the spring temperatures in Europe would give a gradual increase from north to south. As time goes by a wave-like pattern of increasing temperature moves from south to north, which allows, for example, migratory butterflies and birds to track the arrival of spring conditions, like a surfer riding the crest of a wave.

The situation is fundamentally different in, for example, the wet-dry tropics and the arid zone of inland Australia where day-temperatures are less variable but rainfall fluctuates, often greatly (Fig. 7.2(a)). Rainfall is often patchy and one may find areas experiencing drought close to areas having normal conditions (Fig. 7.2(b)). For example, clear spatial patterns in monthly rainfall means only become evident in rainfall data for the Wet Tropics region of north-eastern Australia when very long time scales are considered (Hancock and Hutchinson 2006). In fact, weather stations separated by only 1 km can record very different rainfall patterns (Shine and Brown 2008), while the spatial correlation of annual rainfall may be rather high on a larger scale.

Both undirected movements in response to local conditions and directed movements, possibly in response to previous prospecting or long-range correlations in weather variables, may be of importance in explaining the sometimes remarkable ability of birds to arrive at distant sites close to the timing of rainfall events (e.g., Roshier *et al.* 2008). Organisms can respond to spatial structure across a range of scales, but the question of which spatial scales are relevant when evaluating the abiotic environment in which strategies such as migration and nomadism evolve, is likely to depend on landscape-level constraints as perceived by a given species. For instance, species differ in habitat requirements as well as in perceptual and movement capabilities. In general, there is a smallest spatial scale ('grain') of environmental heterogeneity to which an organism is sensitive, and move-

ment capability, sedentary behaviour or home range behaviour such as territoriality or homing may limit the response to landscape structure at large scales, hence determining a spatial extent of sensitivity. Food or other habitat requirements may be structured by the environment in a way allowing the identification of characteristic scales of resource variability (e.g. Bradshaw and Spies 1992). Such variability and pattern can be translated both into distribution patterns and movement attributes of moving organisms.

Positive spatial correlation in temporally fluctuating resources not only adds an element of predictability for animals making movement decisions, but also affects the area needed for survival of species tracking resources more locally. In the Serengeti National Park Thomson's gazelles (*Gazella thomsoni thomsoni*) have been shown to make adaptive movements on a landscape scale to track rain-driven and spatiotemporally fluctuating resources (Fryxell *et al.* 2004). Modelling work for this system has suggested that the gazelles require unrestricted access to rather large areas to guarantee long-term population persistence, and the area needed increases when resources are positively spatially correlated (Fryxell *et al.* 2005). Hence when resource abundance is low and positively correlated across vast areas, individuals are forced to move long distances, especially if there is temporal autocorrelation as well, for example, in seasonal environments. But when should an individual leave an area, where should it go, and what route should be followed? What are the sources of information available in the environment?

7.7 Spatiotemporal dynamics: information and uncertainty

Both temporal and spatial dimensions are needed to understand the selective pressures for movement. Mueller and Fagan (2008) suggest that resource gradients can vary across four axes: (i) resource abundance, (ii) spatial configuration, (iii) temporal variability of resource locations, and (iv) temporal predictability of resources. These axes are not orthogonal; for example, temporal variability is not independent of abundance, and temporal predictability depends on both temporal and

spatial variability as well as spatial configuration of resource patches. Hence, temporal and spatial attributes of the resource landscape are linked. For instance, high spatial predictability is often accompanied by high temporal predictability. The linkage may be strong, as in the case of temperature gradients experienced by migratory birds at intermediate latitudes during spring migration, or weak, as in the case of patchy and unpredictable rainfall in arid areas. In the former case, spatial and temporal attributes may yield much of the same information to an individual moving in response to a resource gradient, while in the latter case, spatial and temporal attributes to a larger extent yield independent information, and the exact nature of their interaction becomes important. Also, spatial and temporal information can be weighted differently—for instance, temporal dynamics are likely to be more important for sedentary species and decisions regarding the timing of breeding, whereas spatial variability could be regarded as more important for movement decisions in free-ranging organisms.

As a simplification, we will in the following paragraphs consider how individuals and their movement strategies are challenged by the temporal predictability of the conditions at the current site, conditions en route, and the conditions at the destination. The environmental conditions and their predictability will affect when to move, what route to follow, and when to stop. This analysis takes a deeper look at the predictability components of the decisions that are more generally reviewed in Chapter 6, and also considers the decisions made by nomads.

7.7.1 When to move?

The timing of movement is an important aspect of a survival strategy in spatiotemporally fluctuating environments. The role of resource dynamics in initiating movement has been studied in detail from a foraging perspective (e.g., Stephens and Krebs 1986), but the importance of resource abundance, its variability, and its predictability for the initiation of migration have received much less attention. It has been suggested that an important component is pre-emption, i.e. to leave an area before habitat quality has declined too much (Dingle and Drake

2007). Pre-emption is typical of seasonal breeders inhabiting and adapted to strongly seasonal and predictable environments; such species are often obligate migrants. These organisms are adapted to escape in time before it gets rough and/or to arrive in time elsewhere when conditions there are benign. For such species the timing of migration is often 'hard-wired', under endogenous control. This contrasts with facultative migrants that respond more directly to prevailing conditions rather than showing anticipatory movements (Newton 2008). In this group, we find aseasonal breeders that often have a nomadic life style.

For migratory birds, it has been argued that pre-emption cannot rely on proximate cues, and that selection ought to act on the migrant's responses to endogenous rhythms or cues that reliably predict habitat deterioration (Newton 2008). An example of the latter is photoperiod, but one could also think of abiotic factors such as rainfall. However, in practice rainfall is likely to vary too much from year to year to be reliable as a cue for anticipatory movements. Nevertheless, environmental variation is likely to modulate the timing and speed of migration. For instance, the earlier spring arrival of migratory birds at their breeding grounds is often interpreted as a response to climate changes (Jonzén *et al.* 2007b).

Environmental processes can either affect the migration process through their effects on food abundance and hence the scheduling of movement and stopover, or they may act primarily as cues. In a thought-provoking paper, Saino and Ambrosini (2008) show that meteorological conditions in Europe during the breeding seasons of many birds covary with those in the winter quarters south of the Sahara desert. They further suggested that migrants may therefore be able to predict meteorological conditions at the beginning of the breeding season and adjust migration schedules accordingly. Saino and Ambrosini do however note that the ability to use this climatic information as a cue depends on the balance between the fitness benefits it provides and the potentially dramatic costs experienced by early arriving individuals in the years when the cue fails to provide reliable information. In more general terms we can ask the following:

7.7.2 When should information be used?

A key aspect to consider is the reliability of information, i.e. the probability that the information is correct. Whether or not a given cue should be used when the true state of nature is uncertain is a decision theoretical problem and the best tactic is to make a decision that maximizes the expected payoff. When individuals do not control the reliability of information they should be more discriminating as the benefit of correct information declines, as the cost of misinformation increases and when acquisition costs are greater (Koops 2004). In the face of uncertainty, collective decision-making strategies regarding the timing and directionality of movement can be adopted, because taking the average of individual strategies within a group or aggregation may lead to lower error than that inherent in each individual's strategy (Simons 2004; Hancock and Milner-Gulland 2006).

For nomads (and nomadic movements of migrants outside the breeding season), the timing of movements is much more flexible and likely to be more directly related to deterioration of resources for breeding or foraging. Movements can either reflect local resource tracking or simply a choice to disperse. In either case, there are trade-offs between staying with or leaving a resource (Dean *et al.* 2009), so in the typical environment of unpredictable and scarce resource pulses, movements are likely to be strongly influenced by local resource dynamics and patch-leaving criteria, combined with the gleaning of information in order to detect resources from a distance.

7.7.3 What route to follow?

By having an inherent time–distance–direction programme synchronized with photoperiod and combined with external cues, for example magnetic conditions, migrants can, in principle, successfully travel across the globe even in their first year (Chapter 6). This is an example of memory-based movement *sensu* Mueller and Fagan (2008), who suggest that all active animal movements can be assigned to one of three different classes; non-oriented mechanisms, oriented mechanisms, and memory-based mechanisms. In their definition,

memory mechanisms include genetic inheritance, individual experience, and information from communication between conspecifics. Non-oriented movement refers to movement where sensory stimuli at the current location affect the movement parameters, whereas oriented movement relies on perceptual cues in areas other than the current position. In practice, long-distance migrants may use a combination of mechanisms, including compasses that may be cross-calibrated or integrated for direction finding (Åkesson and Hedenström 2007). There are clearly some systems that rely heavily upon endogenous control, such as the famous migration of the Monarch butterfly (*Danaus plexippus*), where there is reproduction and mortality en route, so that several generations elapse within each annual migratory cycle.

It is, however, important to be aware that strong endogenous control of migration does not mean a lack of variability between individuals, seasons and years. Even in regular long-distance migrants such as Eleonora's Falcon (*Falco eleonora*), individuals of the same population can follow different routes in a given year (Gschweng *et al.* 2008). Environmental factors such as wind assistance vary between years, and global wind patterns are generally regarded as an important driver of the loop migrations seen in many seabirds and passerine birds migrating between North and South America (Newton 2008; Chapter 4). We need to study the statistical properties of the resource environment to appreciate fully the processes shaping migration patterns and strategies. For instance, inexperienced individuals may have to include external spatial cues to make the preparation for crossing ecological barriers, as shown for the Garden Warbler (*Sylvia borin*) before crossing the Sahara desert (Fransson *et al.* 2008). The statistical properties of the environment may also be influential on the outcome of migration since spatial correlation of environmental conditions en route allows migrants to fine-tune their migration schedule. Hence, it also becomes important to understand how migration is constrained by movement modes, time constraints and their interactions within the annual cycle. For example, climate change effects on the timing of migration for birds are generally more consistent for the more time-constrained spring

migration (when there is strong selection to arrive in time), compared with the more 'relaxed' autumn migration (Lehikoinen *et al.* 2004). Theoretical considerations suggest that ways of integrating environmental change when adjusting to climate change may be rather different for species migrating quickly and with few stopovers, compared with species progressing more slowly and gradually across the flyway (Hedenström *et al.* 2007).

Compared with the overwhelming literature on migration ecology, less is known about the life of nomads (but see Dean 2004). Little is known about the detailed movements of nomadic birds and their proximate control, since they typically inhabit the most sparsely populated regions of the world. Owing to the lack of predictable changes in resource abundance, fixed orientation mechanisms are not useful, and the organisms may suffer from low information availability. The ability to track resources varies across species; highly mobile organisms (e.g., swifts; Aves:Apodidae) can potentially track ephemeral local resource pulses by sensing rainfall events from great distances. However, all nomads can improve their chances of finding resources by adapting their movement to the statistical properties of their environment (Sims *et al.* 2008). Given the energetic costs of large-scale searching, behavioural features favouring an intermittent locomotion that promotes efficient search patterns may represent a real adaptive advantage (Bartumeus and Levin 2008). To our knowledge it is not known if, for example, nomadic desert birds are using 'Lévy-like' movements (where movement lengths are drawn from a distribution characterized by many short movements and fewer longer movements) similar to those found in foraging movements of many organisms. However, the strength of the empirical evidence for biological Lévy flights has been questioned (e.g. Edwards *et al.* 2007).

7.7.4 When to stop?

Birds often switch from an obligate mode to a facultative mode and start responding to local conditions by the end of the migration (Helms 1963). This makes perfect sense, because as the migrants approach benign areas by the end of the trip they should start searching for suitable habitat. Alter-

natively, conditions at high-latitude or high-altitude breeding grounds may still not be suitable, and birds may need to rely on nearby or distant staging sites for survival or build-up of energy resources for breeding (Chapter 5). It has been speculated that migrants have an endogenous response to the expected external cues that would indicate that they have arrived in the winter quarters (Newton 2008). Such a mechanism seems to trigger fat deposition and directional changes, as suggested by results from experiments on Pied Flycatchers (*Ficedula hypoleuca*) held in captivity (Wiltschko and Wiltschko 2003).

The weaker endogenous control of nomadic movements enables flexibility in breeding locations and presumably a quicker transition from movement to breeding phases. Still, there may be a need to fine-tune both movements and breeding locations. This is seen in the Red-Billed Quelea (*Quelea quelea*), being intermediate between migratory and nomadic, since it deposits fats and performs directional long-range movements, but shows great variability in breeding locations. Rainfall drives their movement patterns, but since these granivorous birds might starve if they wait until rainfall germinates the seeds, they move ahead of the rains, and when the rain comes they fly back to areas where the previous rainfall has already resulted in new seeds (Cheke and Tratalos 2007). In this way they can manage three yearly breeding events.

Finally, it should be noted that environmental information is not always used. Cultural imprinting may sometimes be strong and result in surprising migration patterns. For instance, a moose (*Alces alces*) population in central Norway migrates from low-lying summer areas through large favourable areas, to end up in poor winter areas situated at higher altitudes (Andersen 1991). According to archaeological records this is a traditional migration route that still persists even though habitat quality has deteriorated.

7.8 Intrinsic control of mass movements

We have in this chapter discussed resource dynamics as an extrinsic driver of movement patterns, but the role of intrinsic factors for modifying and driving movement patterns should also be mentioned.

Some of these may themselves be sufficient for explaining dramatic mass movement patterns resembling those of migrants and nomads. Density-dependent feedback may lead to self-reinforcing spatial flows; for example, travelling waves have been suggested for a range of phenomena, such as the propagation of feeding fronts of sea urchins (Abraham 2007).

A clear class of such intrinsically generated movements can be found in insects in arid and semi-arid environments. For instance, mass migration has arisen independently multiple times in grasshoppers (Orthoptera:Acrididae). There are typically dramatic shifts between two phenotypes in locusts, one that is solitary, and the other that is gregarious. The transition between these phases is believed to be driven by local interactions, such as the 'dilution effect' of grouping behaviour on mortality from predators. Once local groups are sufficiently abundant, they can engage in intense exploitation and interference competition, which leads to movement over large distances. This modality of nomadism is thus at least in part driven by the density-dependent impacts of locusts on their own environment (Simpson and Sword 2008). Climatic variation may trigger the migration, but it develops its own momentum due to the locusts being able to escape limitation by predation, overexploit local resources, and in the course of so doing, gather enough resources to keep moving as a band of destruction across vast landscapes. Abstractly, this example seems to involve an Allee effect (Courchamp *et al.* 2008), in that locally, locusts can escape predation, i.e. reduce mortality, by aggregation. It is not clear if this is a necessary ingredient of such intrinsically driven migration syndromes.

7.9 Conclusions and perspective

Whereas migration can be seen as an adaptation to avoiding severe conditions and exploiting predictable spatiotemporal variation in resource abundance, nomadism can be seen as an adaptation to variability rather than severity. These two strategies can be seen as the end points of a continuum of movement strategies, and in a given species regular migration and nomadism may occur in different seasons or in different areas of the range. In order to

understand this diversity, we may need to advance our understanding of niche dimensions for migrants and nomads beyond a focus on seasonality, habitat and resource associations per se. Landscape attributes and statistical properties of the resource environment are general features that provide a key to understanding and predicting the relative merits of large-scale movement strategies in different environments. These may need to be considered in a context of life history evolution; a pattern of obligate, regular migration is likely to be largely controlled by endogenous processes and characterized by rigidity, whereas nomadism is more under external control and can be seen as flexible rather than rigid (Newton 2008).

Explicitly linking the statistical properties of movement patterns to specific internal traits and/or behaviours has been identified as a major challenge in movement research (Nathan *et al.* 2008). In this chapter we have focused on the statistical properties of resource dynamics motivating movement in the first place, and how they may link to individual movement decisions such as when, how and where to move—i.e., important components of the emerging paradigm of movement ecology (Nathan *et al.* 2008). Spatial and temporal variability and predictability of resources are poorly explored dimensions of the niches for migrants and nomads, and empirical analyses of space–time data of resource abundance (or any index thereof; Box 7.1) may be helpful for linking resource dynamics to the spatial distribution of movement strategies. Simulation studies based on mechanistic movement models coupled with dynamic resource maps would be an alternative approach (see Chapter 8 for a discussion of these alternatives). Climate change offers an opportunity to study variation and adaptation of migration patterns in time and space, including the timing of migration (e.g. Jonzén *et al.* 2007a). A key challenge is to move from purely theoretical, exploratory or correlative studies to making quantitative predictions that can be tested using available data. This may require further efforts to identify the functional importance of various components of resource variability.

Habitat and resource requirements do, however, vary over the course of annual and life cycles, and cannot always be considered separately from an animal's life history stage. Phenotypic differentiation between life history stages is a central issue

here; when annual environmental variability is low, few and relatively undifferentiated stages are needed, whereas high variability may favour more and differentiated life history stages, including switching between mobile and sedentary phases (Wingfield 2008). On the other hand, migration or nomadism may permit species to track conditions to which they are already well-adapted, hence weakening evolutionary pressures to shift, for instance in tolerance of climatic extremes or in the utilization of alternative resources. Also, switching between multiple movement modes such as free-ranging and home-ranging behaviour, searching and resource tracking, may in fact be a general feature of animal movement not requiring special adaptations (e.g., Fryxell *et al.* 2008).

Conversely, the ability to utilize resources may be constrained by the movement modes and perceptual capabilities of organisms. Here lie some of the most intriguing and fascinating questions. For instance: How do nomadic species know when and where to go? How can nomads find suitable localities in vast desert areas? From how far away can they detect suitable conditions? The explicit treatment of the basic mechanistic components of animal movement emphasized by the movement ecology paradigm (Nathan *et al.* 2008) is likely to facilitate our understanding of the interaction between spatiotemporally fluctuating environments and adaptive behaviour, including the large-scale movements of organisms. This may in fact require bringing together elements from diverse fields, such as sensory ecology, communication networks, animal signalling and the use of cues. In a broad sense this is also a question of extending our notion of niche dimensions and resource utilization; different species will have different perceptual constraints, and sensory capabilities will be physically constrained by the environment (Dusenberry 2001). Factors affecting movement and sensory capabilities might in fact covary with resource abundance and variability; for example one could expect low productivity and variable environments also to be open and structurally simple.

In a wider context, a deeper understanding of the niches of migrants and nomads will increase our understanding of the factors structuring animal

communities and assemblages. Most of our understanding of, for instance, the structure of bird communities (Wiens 1989), builds on theory developed in a static framework emphasizing species interactions. However, long-distance animal movements render such interactions weaker and more variable, and the ability to escape predation or competition may in fact be a driving force for migration (Fryxell and Sinclair 1988b).

Both migration and nomadism can have ecosystem-level effects (Chapter 9): directly by, for example, migrants' exploitation of resources, or indirectly by their mere spatiotemporal distribution that can act as a cue for other species tracking seasonal changes. The seasonality of environments where we typically find migrants becomes reinforced by the seasonal movement of organisms. In temporally less predictable environments, nomads that are moving around in the landscape may either decrease or reinforce the patchiness of resources, depending on how easy it is to spot the good patches.

Finally, because mistakes in movement do occur, at the level of the species, migration and nomadism

may permit exposure of individuals to novel conditions that would simply not be encountered by more sedentary lifestyles, and so more broadly contribute to species diversification. The avifauna of the Lesser Antilles, for instance, tends to be dominated by clades comprising migratory and nomadic taxa characteristic of North America (warblers, flycatchers, finches, mimids, doves, and pigeons), and are devoid of sedentary, non-migratory taxa from South America (e.g., antbirds, ovenbirds, woodcreepers). Some of these taxa (e.g., the Brown and the Grey Tumbler; *Cincoerthia ruficaudia* and *C. gutturalis*) have evolved to become quite specialized on the islands they occupy.

In this chapter we have explored the extremes of the continuum of movement patterns exemplified by migrants and nomads, and considered the importance of spatial and temporal heterogeneity and uncertainty, and the scale at which these operate, in shaping movement strategies. In so doing we have demonstrated the strength of the niche concept in framing questions surrounding the mechanisms underlying migration.